ORIGINAL PAPER

Antarctic moss carpets facilitate growth of *Deschampsia antarctica* but not its survival

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Abstract The vegetation of the Antarctic tundra is dominated by mosses and lichens. *Deschampsia antarctica,* the Antarctic hairgrass, is one of two vascular plant species which grow along the west coast of the Antarctic Peninsula. However, little is known about its recruitment and interaction with non-vascular tundra plants. Although several authors propose that tolerance and/or competition should be the main forms of interaction between moss carpets and *D. antarctica*, no relevant studies exist so far. We investigated whether positive interactions are predominant at the Shetland Islands and the west coast of the Antarctic Peninsula and focussed on the role that moss carpets play in the recruitment of *D. antarctica*. Across the studied zone, *D. antarctica* showed a significant association with moss carpets, with higher frequencies as well as more and larger individuals than on bare ground. At one site, we conducted moss removal and seedlings transplant experiments to assess the relevance of the moss carpets for different life stages of hairgrass. All experimental individuals survived until the following summer whether the moss carpet was removed or not, but growth rate was significantly lower in tussocks with moss carpets removed. Likewise, tiller size was higher in plants growing in moss carpets than on bare ground. The detected positive interactions with mosses seem to be important for the expansion of *D. antarctica*, raising the question about their importance under future climate change scenarios.

Keywords Plant–plant interactions · Facilitation · Antarctic tundra · Plant–moss interaction

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Introduction

The Antarctic tundra is among the harshest environments on earth, where only mosses, lichens and two vascular plant species, viz. the Antarctic hairgrass *Deschampsia antarctica* Desv. (Poaceae) and the pearlwort *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae), have been able to establish permanent populations, mainly growing along the west coast of the Antarctic Peninsula (Lindsay 1971; Komárková et al. 1985, 1990, Smith 2003). Although the mentioned authors indicate that *D. antarctica* is a pioneer species that colonizes recently deglaciated terrains, little is known about its regeneration ecology, particularly about the processes relevant for its successful recruitment. This information is important to understand the reported trends of increases in population size and colonization of new areas of *D. antarctica* along the Antarctic Peninsula during the past years (Gebauer et al. 1987; Smith 1990, 1994; Fowbert and Smith 1994; Gerighausen et al. 2003; Parnikoza et al. 2009; Torres-Mellado et al. 2011), interpreted as an effect of the warming trends observed during the last decades (Turner et al. 2005; Turner and Overland 2009). However, experimental studies have shown that warmer conditions per se do neither increase growth of *D. antarctica* in the field nor under laboratory conditions (Day et al. 1999, 2008, 2009).

In extremely harsh habitats, such as the Antarctic, the adverse environmental conditions restrict the plants' capacity to acquire resources; hence, biotic or abiotic amelioration of these conditions or the provision of favourable microsites are supposed to be beneficial for growth and reproduction (Brooker and Callaghan 1998; Callaway 2007). Mosses constitute the most conspicuous component of vegetation in polar tundra ecosystems and influence both microclimate and soil processes to such an extent that they can be considered engineers of these plant communities (Gornall et al. 2007). In several sites of the Arctic tundra, it has been observed that mosses modify their surrounding environments by increasing soil moisture (Gold and Bliss 1995; Parker et al. 1997; Rixen and Mulder 2005; Groeneveld et al. 2007), soil nutrients content (Longton 1974; Gold and Bliss 1995; Roberts et al. 2009) and buffering temperature compared to bare areas (Longton 1974; Groeneveld et al. 2007). These microclimatic modifications create microenvironments that facilitate the establishment of other plant species (Sohlberg and Bliss 1987; Carlsson and Callaghan 1991; Groeneveld et al. 2007). Nevertheless, there is also evidence that mosses negatively interact with vascular plants in the Arctic tundra (e.g. Fetcher 1985; Hobbie et al. 1999; Bret-Harte et al. 2004). Several authors indicate that tolerance and/or competition with the moss is the principal plant interaction in Antarctic fellfields (Komárková et al. 1985; Wasley et al. 2006; Block et al. 2009; Krna et al. 2009), although only the study of Krna et al. (2009) is based on a manipulative experiment, reporting 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 was a moss (Krna et al. 2009). It is well known that sign, intensity and importance of plant–plant (Bertness and Callaway 1994; Brooker and Callaghan 1998; Brooker et al. 2008) or plant–moss (Gornall et al. 2011) interactions vary across wider geographical scales. In addition, as the sign of the interactions can change with ontogeny (Miriti 2007; Soliveres et al. 2010), manipulative experiments with adult individuals could underestimate the importance of facilitative interactions on early stages of the recruitment phase. Furthermore, the facilitative effect most commonly observed among plants is on the survival of individuals but not on their growth (Brooker et al. 2008). Thus, a more exhaustive evaluation of the relevance of facilitative interactions with mosses for the recruitment and survival of *D. antarctica* across its distributional range in the Antarctic seems timely to understand its recent advance and the possible consequences of further warming trends in the Antarctica.

From a theoretical point of view, it has been suggested that facilitative interactions might wane under highly stressful conditions (e.g. Michalet et al. 2006; Holmgren and Scheffer 2010). Nonetheless, other studies suggest no decrease or even increase in the importance of facilitative interactions (e.g. Kawai and Tokeshi 2007; Maestre et al. 2009; le Roux and McGeoch 2010). Hence, the resulting interaction between *D. antarctica* and mosses across the maritime Antarctic could shed light about the prevalence of facilitative interactions under extreme environmental stress.

In this study, we visited several sites with presence of *D. antarctica* on different islands along the west coast of the Antarctic Peninsula and assessed frequency of the hairgrass in association with moss carpets. We compared number and size of the *D. antarctica* stands found in each microhabitat (moss carpets and bare areas) to gain insight into the relevance of facilitative interactions with the moss carpets at the population level. In addition, on one island, we conducted manipulative experiments consisting of the removal of neighbouring moss carpets and planting of seedlings within and outside moss carpets to assess the relevance of the presence of the moss carpets for different life stages of the target plant.

Materials and methods

Study site

Field work was carried out during two summer seasons (2009–2010) during field expeditions of the Chilean Antarctic Institute (INACH). We surveyed the following islands for sampling sites with presence of *D. antarctica*: King George Island (62°00′S, 58°15′W), Robert Island (62°24′S, 59°30′W) and Livingston Island (62°38′S, 60°36′W) of the South Shetland archipelago. On the Antarctic Peninsula, mainland and offshore islands in the vicinity of Paradise Harbour (64°51′S, 62°54′W) were explored (Fig. 1). Detailed site characteristics are given in Torres-Mellado et al. (2011). In brief, on the Fildes (King George Island) and Coppermine Peninsulas (Robert Island), the herb–moss communities were characterized by the presence of *D. antarctica* and dominated by moss species such as *Sanionia georgico-uncinata* (Müll. Hal.) Ochyra & Hedenäs, *Sanionia uncinata* (Hedw.) Loeske, *Syntrichia princeps* (De Not.) Mitt. and *Polytrichastrum alpinum* (Hedw.) G. L. Sm. On Livingston Is., we visited plant stands at Hanna Point (62°38′47S, 60°36′04W) where plants grow near the beach on sandy soils, with *D. antarctica* growing with *S. uncinata* and *P. alpinum*. On the Antarctic Peninsula, we measured plants of *D. antarctica* at the East Coast of Forbes Point (64°52′56S 62°32′15W). Moss species were different from those found on the South Shetland Islands (principally *Bryum pseudotriquetrum*

Fig. 1 Localities sampled on the South Shetland Islands and the Antarctic Peninsula
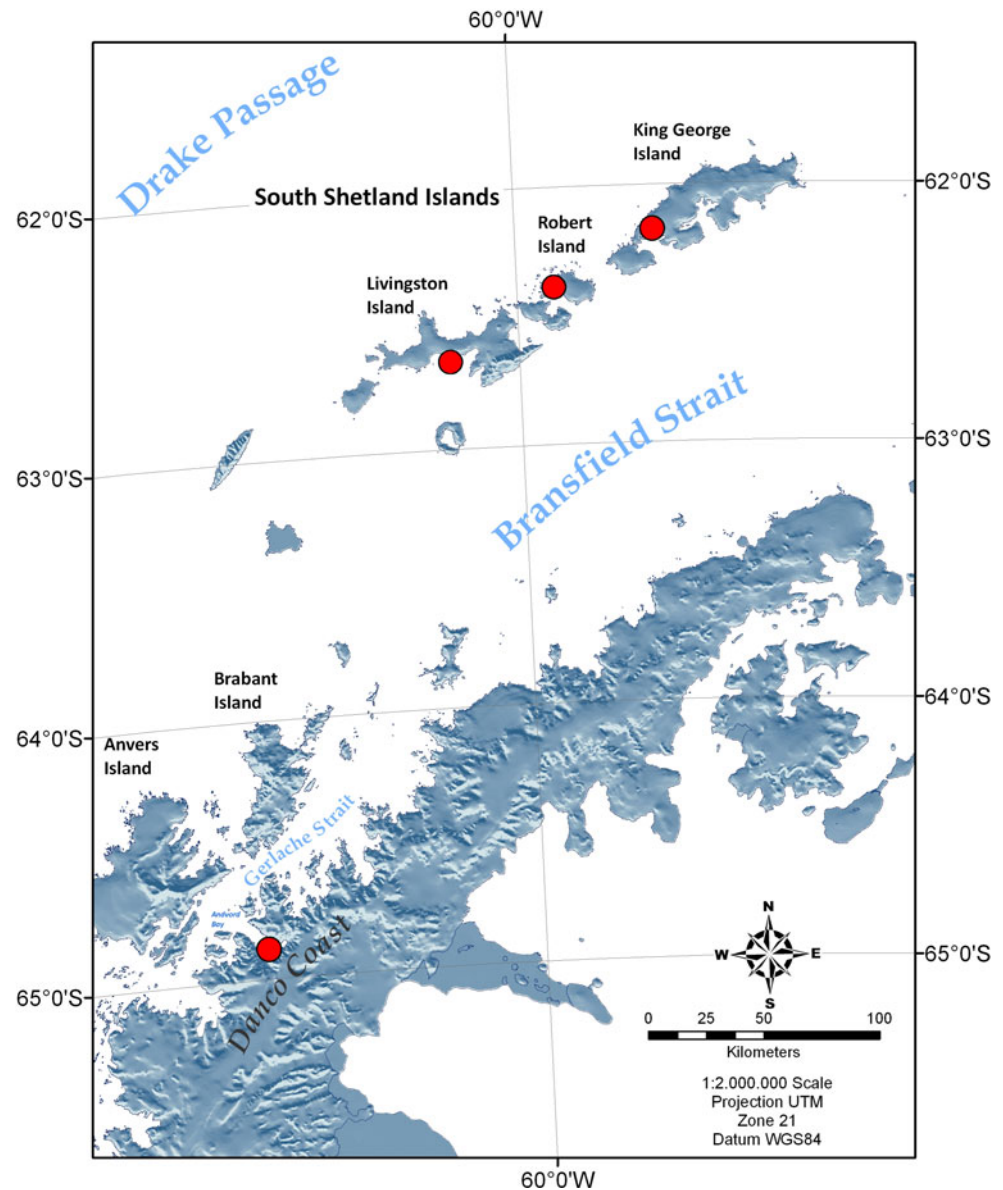
(Hedw.) P. Gaertn., B. Mey. & Scherb., *P. alpinum*, *Polytrichum* sp. and *Brachythecium austrosalebrosum* (Müll. Hal.) Paris).

Climate

The west coast of the Antarctic Peninsula which extends approximately from 63°20′S to 73°25′S, including offshore islands as well as the South Shetland Islands, is characterized by a maritime Antarctic climate (Holdgate 1964). The mean temperature of the western side of the peninsula fluctuates between −3 and –10 °C along a north-south transect (Vaughan and Doake 1996). Temperatures during the warmest months on the Shetland Islands are just above the freezing point (0–2 °C), whilst mean temperatures during winter rarely fall below −10 °C. Rainfall occurs in summer, with estimations between 350 and 750 mm. A warming trend has been observed on the Antarctic Peninsula during the last 50 years. Climatic records indicate that major temperature changes have taken place, with a large increase in the annual mean temperature on the western and northern parts of the Antarctic Peninsula, with Faraday/Vernadksy Station presenting the largest statistically significant (<5 % level) trend, at +0.56 °C per decade from 1951 to 2000 (Turner and Overland 2009). The most marked warming extends from the southern part of the western Antarctic Peninsula north to the South Shetland Islands, and the warming magnitude decreases northwards, away from Faraday/Vernadsky (Turner et al. 2005). The warming trend is more pronounced during winter and spring (Ingolfsson et al. 2003; Steig et al. 2009; Turner and Overland 2009).

Studied species

Throughout the Antarctic Peninsula, *D. antarctica* is able to colonize a wide range of soil types, ranging from mineral- and nutrient-poor to highly organic (i.e. ornithogenic soil) (Komárková et al. 1985; Smith 2003). Its morphological adaptations like small leaf area, low stomatal density and a thick cuticle allow to withstand the extremely harsh environmental conditions of the Antarctic (Romero et al. 1999; Gielwanowska and Szczuka 2005). *D. antarctica* occurs mainly in ice-free areas along the Antarctic Peninsula, from the South Shetland archipelago to the Terra Firma Island (Komárková et al. 1985, 1990).

Plant frequency inside and outside moss carpets

We found 10 sites with presence of *D. antarctica* among the different localities visited (Table 1). Plant stands varied in size; the largest was found on King George Island (covering more than 5,000 m^2) whilst the smaller ones were on Robert Island (covering 50 m^2) and Forbes Point (covering 9 m^2), respectively (Torres-Mellado et al. 2011). To assess how frequently *D. antarctica* grows in close spatial association to moss carpets, we blindly threw 1 m^2 quadrants on each site from the centre of the moss carpet, covering various directions and distances. The numbers of quadrants per site fluctuated according to the size of each site, varying between 10 and 35 quadrants (Table 1). The same procedure was repeated on an equal number of

quadrants placed on adjacent bare ground areas. On each quadrant, we recorded the amount of *D. antarctica* individuals and the size of each individual by measuring its longest and shortest diameter (in cm). Size was estimated assuming an elliptical form of the tussock.

Moss carpet manipulation experiments

During January 2009, we selected a site at Juan Carlos Point, Fildes Peninsula, facing the Drake Passage, to perform two experiments: for the first experiment, we selected 20 *D. antarctica* individuals (tussocks) of similar size growing within moss carpets and separated by a minimum distance of 50 cm each. The exact size of each selected individual was recorded as previously described. Ten of these selected individuals were randomly assigned to an experimental removal of their surrounding moss carpet. For this purpose, we carefully removed with a small knife a radius of 10 cm of the surrounding moss carpet around each individual. The other ten individuals were left with no further manipulation as controls. After 1 year, in February 2010, survival and size of all individuals were recorded. The growth rate was considered as the difference in size after 1 year.

For the second experiment, 40 naturally occurring *D. antarctica* seedlings of similar size (one tiller of 15-mm height, with three leaves) were excavated, and root lengths were adjusted to about 15 mm. Twenty of these seedlings were randomly planted within the moss carpet in five plots

Table 1 Localities sampled to assess *D. antarctica* spatial association to moss carpets. Number of quadrants within moss carpets and on bare ground where individuals of *D. antarctica* were present are indicated

Locality	No. of quadrant with *D. antarctica*		Plant size (cm^2)		No. of individuals	
	Moss carpet	Bare ground	Moss carpet	Bare ground	Moss carpet	Bare ground
King George Island						
Nebles point (20)	18	2*	947.3 ± 530.2	29.4 ± 9.8*	47.9 ± 10.1	1.0 ± 0.0*
Collins harbour (25)	24	8*	1,200.4 ± 526.8	47.9 ± 25.9*	18.3 ± 2.3	1.0 ± 0.0*
Robert Island						
A1 (20)	15	3*	61.1 ± 7.1	29.8 ± 1.2*	11.7 ± 1.9	1.0 ± 0.0*
A2 (20)	16	3*	205.4 ± 34.4	119.7 ± 46.5*	9.3 ± 1.3	1.3 ± 0.3*
A3 (20)	17	11	47.5 ± 11.9	71.2 ± 23.5	5.6 ± 1.5	2.6 ± 0.7*
A4 (35)	31	8*	57.1 ± 11.0	78.2 ± 14.6	15.9 ± 2.6	3.3 ± 0.4*
Cop1 (20)	17	8*	85.5 ± 23.6	68.2 ± 30.9	15.2 ± 4.1	2.8 ± 0.9*
Cop2 (20)	17	3*	103.1 ± 28.7	53.6 ± 30.6*	9.3 ± 2.5	1.0 ± 0.0*
Livingston Island						
Hanna point (10)	10	7	19.7 ± 3.9	56.0 ± 35.0*	22.0 ± 2.8	7.1 ± 1.9*
Antarctic Peninsula						
Forbes point (12)	2	0	11.0 ± 0.1	0*	35.0 ± 8.0	0*

The number of *D. antarctica* plants and its size per quadrant are indicated as means values (±SE). * Indicates significant differences ($p < 0.05$) for randomization analyses in the comparison of frequencies within and outside moss carpets, and *t* tests for plant size and number of individuals. Values within parentheses indicate equal numbers of quadrants for moss carpet and bare ground

of 4 L separated by a distance about 50 cm, whilst the others were planted on adjacent bare ground sites randomly selected similarly as the other group on the moss carpet. Each individual was carefully inserted into a small hole made with a pencil and marked with a metal stick. After 1 year, the survival, size and number of leaf of each planted seedling were recorded.

Statistical analyses

To statistically detect positive associations of *D. antarctica* for a particular microhabitat (i.e., moss carpet or bare ground), we performed randomization tests (Kikvidze et al. 2001) with the software "Resampling Stats" (Resampling Stats, Inc. 1990–1995). First, we calculated for each site the frequency of incidence of *D. antarctica* by summing the incidence on each microhabitat. Then, we randomly redistributed the total number of presence recordings between the within–moss carpet and bare ground habitats. We performed 10,000 runs of random redistributions and then calculated the probability of the observed frequency within moss carpets being generated by chance (see also Cavieres et al. 2002). Further, we pooled all sites and calculated the total frequency of incidence of this species on each microhabitat, and a new randomization analysis was performed. Differences in the number of plants per quadrant and their size between both microhabitats were assessed with an unbalanced *t* test, both for individual sites and by pooling all sites. Likewise, differences in the growth rate between microhabitats in the removal experiment and in the seedling survival experiment were assessed with a *t* test. The survival of seedlings between microhabitats was compared with a proportion test (Zar 1999).

Results

Plant frequency inside and outside moss carpets

Overall, we sampled a total of 404 quadrants of 1 m^2 each, on 10 different sites along the west coast of the Antarctic Peninsula. Of the 202 quadrants sampled within moss carpets, *D. antarctica* was present on 167, (i.e. 83 % of the sampled quadrants) whilst on bare ground areas, this species was present only on 53 out of 202 quadrants (25 %) (Table 1); the randomization analysis for this pooled data set indicate that the frequency of association of *D. antarctica* to the moss carpets is significantly higher to that expected by chance alone ($p < 0.01$); likewise, on the level of individual sites, randomization analyses indicate for 8 of the 10 sampled sites that the frequency of association of *D. antarctica* to the moss carpets is significantly higher to that expected by chance alone ($p < 0.05$; Table 1).

Considering all sites together, a higher number of quadrants with *D. antarctica* was found in the moss carpet areas ($t = 9.11$, $p < 0.01$) than on bare ground (mean ± SD: $17.5 ± 1.4$ vs. $3.5 ± 2.3$, respectively), with the numbers of individual plants being significantly greater on quadrants within the moss carpets at each of the sampled sites (Table 1). Concordantly, the mean size of plants growing inside the moss carpets was significantly greater ($t = 2.5$, $p < 0.05$) than the size of plants growing on bare ground (mean ± SD: $335.7 ± 86.7$ vs. $64.1 ± 153.8$ cm^2, respectively). However, observing each site separately, on sites A3, A4 and Cop1, we did not find significant size differences between individuals growing within the moss carpet and on bare ground, although, on all of these sites, there were significantly more individuals growing within the moss carpet (Table 1).

Moss carpets manipulation experiments

In the moss carpet removal experiment there were no differences in the initial size (tussock diameter) of the individuals assigned to removal of the moss carpet and control (mean ± SE: $2.36 ± 1.38$ vs. $2.42 ± 1.73$ cm, respectively). After 1 year, all experimental individuals survived regardless whether the moss carpet had been removed or not. However, individuals with their moss carpet removed showed a significantly lower growth rate ($4.46 ± 1.02$ vs. $10.6 ± 1.84$ cm/year, respectively) than control individuals ($t = 2.92$; $p < 0.01$, Fig. 2).

After 1 year of transplantation, seventeen out of the twenty seedlings planted within the moss carpet survived until the following summer (data not shown), compared to only twelve on bare ground. The proportion test indicated that there was no significant statistical difference between both proportions ($z = 3.0$; $p = 0.085$). Nevertheless, the tiller size of the individuals planted within the moss carpet
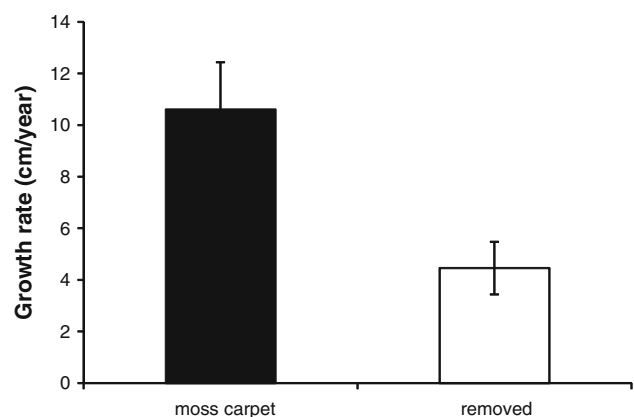

Fig. 2 Growth rate of *D. antarctica* plants with and without moss carpet removal on the Fildes Peninsula, King George Island. Values are means ($n = 10$, ±2 SE)
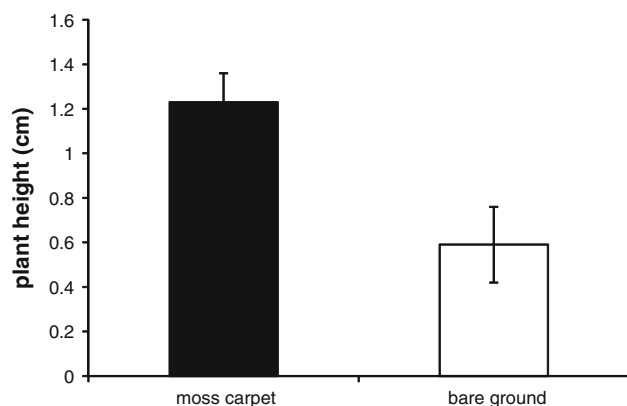
Fig. 3 Growth (height) of *D. antarctica* seedlings transplanted on bare ground areas or on moss carpet on the Fildes Peninsula, King George Island. Values are means ($n = 20$, ± 2 SE)

was significantly higher ($t = 2.3$; $p < 0.05$) than that of the individuals on bare ground (Fig. 3, 1.23 ± 0.13 vs. 0.49 ± 0.17 cm, respectively).

Discussion

Although facilitative interactions have been described in other extremely cold environments such as arctic and alpine tundras (e.g. Carlsson and Callaghan 1991; Callaway et al. 2002; Cavieres et al. 2002; Gornall et al. 2011), this is the first quantitative report on facilitation among plants in the Antarctic tundra across a wider geographical range in the maritime Antarctic. Previously, different authors observed the association between *D. antarctica* and certain mosses (Lindsay 1971; Komárková et al. 1985, 1990; Casaretto et al. 1994; Smith 2003), especially with carpets dominated by *Sanionia* ssp. (syn.: *Drepanocladus uncinatus* Warnst), cushions of *P. alpinum* and *B. pseudotriquetrum* (Ochyra 1998). Nevertheless, only Gerighausen et al. (2003) indicated that colonies of *D. antarctica* are larger when growing within a moss cover on Fildes Peninsula (King George Island). By visiting different sites, we found that *D. antarctica* grew more frequently within moss communities than on bare ground areas, suggesting a facilitative role of the moss carpet. Although, in our experiment, the removal of the moss carpet after 1 year did not affect the survival of *D. antarctica*, it did negatively affect its growth, also suggesting facilitative interactions. Accordingly, growth of seedlings planted inside the moss carpet was higher than that of those individuals planted on bare ground areas, although again the survival of seedlings did not differ between both microhabitats.

Few studies have addressed facilitation of vascular plants by bryophytes and the mechanisms involved. Groeneveld et al. (2007) showed that the moss *Polytrichum*

strictum Brid., J. Bot. (Schrader) acts as a nurse plant facilitating the growth of other mosses and higher plants. Parker et al. (1997) demonstrated that *Polytrichum commune* Hedw. increases the survival of white spruce seedlings during drought periods. Similarly, Groeneveld and Rochefort (2005) found that *P. strictum* reduces frost damage in fir seedlings and generates other benefits like enhanced seed germination by providing a more favourable microclimate. Carlsson and Callaghan (1991) showed that in the Arctic tundra, the moss *Racomitrium lanuginosum* (Hedw.) Brid. facilitates the establishment of the vascular plant *Carex* sp. by providing more favourable temperatures compared with other substrates available. Positive effects on seed germination and seedling emergence within moss carpets seem to be related with increased moisture provided by the mosses in water-stressed tundra habitats (Sohlberg and Bliss 1987; Gornall et al. 2011). Although the exact mechanisms behind the facilitative interaction between mosses and *D. antarctica* remain to be explained, some not-mutually exclusive mechanisms, as those commented in studies carried out in the arctic, can be invoked to account for our results based on the scarce references available for Antarctica (see below).

Our results indicate that the moss carpets provide more appropriate conditions for the growth of *D. antarctica* compared to bare ground areas, although this does not imply a higher survival after 1 year. Antarctic mosses occur in different growth forms, but cushion and carpet forms are the most abundant, formed by *P. alpinum, S. uncinata* and *S. georgico-uncinata* (Longton 1988; Ochyra 1998; Victoria et al. 2009). For the Antarctic fellfield, it has been shown that mosses substantially change the microclimatic conditions compared to bare ground (Longton and Holdgate 1967; Walton 1982; Smith 1988; Block et al. 2009). For instance, on Signy Island, the surface temperature of cushions formed by *P. strictum* reached 36 °C during the day (Walton 1982), and even higher temperatures have been recorded for mosses growing on rocks (44 °C, Smith 1988). Temperatures between 8.8° and 10.5 °C have been recorded on carpets of *Bryum argenteum* Hedw. on Ross Island, whereas temperature above bare ground reached only −1.5 °C (Smith 1988). Although *S. uncinata* is one of the most widely distributed carpet-forming mosses in the Antarctic (Ochyra 1998), few temperature data are available. Only Longton and Holdgate (1967) on Galindez Island reported temperatures of 30 °C in a carpet of *S. uncinata* (syn: *D. uncinatus*) which contrasted with the 7.8 °C reported for the bare ground area. Carpet- and cushion-forming mosses reduce convective heat loss, allowing heat conservation, which maintains nocturnal temperatures, a few degrees above the freezing point, and extends the period of metabolic activity and biomass production several days (Smith 1988, 1999).

Water availability is another important abiotic factor in the Antarctic environment which can limit the distribution of plants (Kennedy 1993; Block et al. 2009). Mosses can influence soil moisture in the Antarctic (Gimingham 1967; Gimingham and Smith 1971; Wilson 1990) as it has been shown in the Arctic (Sveinbjornsson and Oechel 1991; Gornall et al. 2007). Differences in water-holding capacity, tolerance to desiccation and to flooding have been reported between moss species in the maritime and continental Antarctic (Gimingham 1967; Gimingham and Smith 1971; Fowbert and Smith 1994; Robinson et al. 2000; Wasley et al. 2006). Species-specific differences have been found in moss water content as percent of dry weight (DW), ranging in five different moss species from 1,600 to 250 % of DW under field conditions (Gimingham 1967). Comparison between different growth forms (cushions, turfs and carpets) demonstrated that carpets and cushions have the highest water-holding capacity (Gimingham and Smith 1971; Robinson et al. 2000; Wasley et al. 2006). Recently, Gornall et al. (2011) reported that moss depth is a key factor determining the sign of the interactions with vascular plants. For several species from an Arctic tundra, they showed that shallow mosses (3 cm depth) had a facilitative effect on plant growth, whilst deep mosses (6 cm depth) had a negative effect. Interestingly, on dry soil areas of Signy Is. in the Antarctica, *S. uncinata* (*D. uncinatus*) forms compact mats of 3- to 4-cm depth, but carpets of 9-to 10-cm depth on water-logged ground (Gimingham 1967). Thus, the presence of mosses would be beneficial for *D. antarctica* to withstand the severe drought conditions generated in the Antarctic due to the strong desiccant winds. Indeed, recent studies demonstrate that soil moisture can be a more relevant factor than temperature in determining the growth of *D. antarctica* (Day et al. 2008, 2009).

Moss carpets would also facilitate *D. antarctica* growth through an indirect effect on soil nutrient availability. This might be of particular importance, as it has been shown that *D. antarctica* does not form commonly mycorrhiza in antarctic environments (DeMars and Boerner 1995; Upson et al. 2008). Also, nutrient cycling in the Antarctic is very slow due to the constraints imposed to biological activity by the low temperatures and extreme aridity (Hennion et al. 2006). On Signy Island, Roberts et al. (2009) showed higher values of N, P and K in soil under both a vascular plant cover and moss carpets composed of different moss species than on bare ground. Similarly, Hill et al. (2011) compared the nitrogen content of soils on Signy Is. under moss carpets (*S. uncinata*), *D. antarctica* cover and a mixed stand (moss and grass). They found that the total N content (including organic and inorganic nitrogen) in the soil solution underneath *D. antarctica* was 60 % higher compared to the moss carpet and the mixed stand (both

with similar N content). The authors indicate that *D. antarctica* is able to absorb nitrogen as small peptides as well as soluble organic and inorganic N-forms which would mean faster absorption of nitrogen after breakdown and release from organic sinks (ornithogenic soil or moss-derived peat). This also suggests that *D. antarctica* does not necessarily depend on the nitrogen supply from the nutrient stock of the soil beneath the moss carpet and that probably nutrient absorption is not a limiting factor for the plants in the Antarctic fellfield. Plant communities are frequently found near penguin colonies and bird nests, on nutrient-enriched soils (Smith 2003; Gerighausen et al. 2003). This could be an explanation why no differences were observed in the frequency of *D. antarctica* growing inside and outside the moss carpet at the sites A3 (Robert Is.) and Hanna Point (Livingston Is.): the first was located at the front of Robert Glacier, on enriched ornithogenic soils. Contrastingly, on Hanna Point, plant communities grew on sandy soil, which could be water- and nutrient-limited, but no data are available.

Although our observations indicate that *D. antarctica* and moss species are positively associated due to a facilitative interaction, our results contrast with those reported by Krna et al. (2009) where *D. antarctica* was growth-inhibited when growing with mosses (*S. uncinata* and *B. pseudotriquetrum*). These contrasting results may be explained to some extent by the larger plant size (2.5-cm diameter) and the shorter observation period (only 60 days) during the growing season in the Antarctic summer employed by these authors. Facilitative effects among plants are more common on young individuals than on mature plants (Callaway 2007; Miriti 2007). Additional field observation during our surveys on Fildes Peninsula consistently indicated that colonization of *D. antarctica* starts on the moss carpets and that it is positively associated to *S. georgico-uncinata*, showing no spatial association (i.e. no differences from random distribution) to other moss species in the same carpets (Casanova-Katny pers. obs.). In addition, Fowbert and Smith (1994) reported that colonization of *D. antarctica* in recently deglaciated terrains occurs with the presence of mosses, and recently, two alien vascular plants *Nassauvia magellanica* JF Gmelin and *Gamochaeta nivalis* Cabrera were recorded in association with moss carpets (*B. pseudotriquetrum*, *Ceratodon purpureus*, *S. uncinata* and *Syntrichia* spp.) on Deception Island (Smith and Richardson 2011). Thus, facilitative interactions could occur regularly in the highly stressful conditions of the maritime Antarctic and open the question about the role of moss carpets for plant immigrants in the Antarctic.

The observed increase and expansion of *D. antarctica* populations in the maritime Antarctic in recent years has been interpreted as a response to global warming, with

little or no discussion of the important role that moss carpets may be playing in the current and future colonization of this species. Considering that all new stands of *D. Antarctica* reported by Torres-Mellado et al. (2011) were associated with moss carpets at Robert Island and Forbes Point, our results clearly suggest a pivotal role of the moss carpet in facilitating the growth and colonization of *D. antarctica* across a relatively wide geographical range in the Antarctic. Among the studies addressing the impact of warming on the Antarctic Peninsula, only two have included the moss community. After 2 years, warming reduced the moss cover by 11 % and did not increase the vegetative growth of *D. antarctica* (Day et al. 1999). The same authors also showed that after two growing seasons, water addition had a major impact on plant responses to warming, with mosses and *D. antarctica* strongly improving their performance under warming with water addition (Day et al. 2009). This suggests that mosses would continue playing an important role in the colonization process of *D. antarctica* under the global climatic scenarios predicted for the Antarctic Peninsula because they can influence temperature and water availability, both of which are crucial resources to survive the extremely harsh conditions of the Antarctica.

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