

## RESEARCH/REVIEW ARTICLE

# Colonization and demographic structure of *Deschampsia antarctica* and *Colobanthus quitensis* along an altitudinal gradient on Livingston Island, South Shetland Islands, Antarctica

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**Keywords**

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**Abstract**

The colonization capacity and demographic structure of populations of *Deschampsia antarctica* and *Colobanthus quitensis* were studied in different microhabitats between 10 and 147 m a.s.l. on Livingston Island, South Shetland Islands, near the Spanish Antarctic base Juan Carlos I, in February 2002. At the highest site (147 m a.s.l.), mean temperatures were about 1°C lower than at sea level. Both species are less common in inland areas and at the highest altitudes only occur at restricted sites that are frequently snow-free in the early austral summer. The diameters of the largest plants (*C. quitensis* cushions 7–8 cm; *D. antarctica* tufts 10–11 cm) in the populations growing at the highest altitudes (110 and 147 m a.s.l.) suggest that these populations were established about 24–28 years ago. The largest diameter plants (*Deschampsia* 20 cm; *Colobanthus* 18 cm) were found at the lowest altitudes on deep soil. The presence of numerous seedlings and young individuals on the periphery of populations established several years ago or at recently colonized sites suggests an active process of expansion. There were more emerged seedlings of *C. quitensis* than of *D. antarctica*, but the density of established individuals was higher for *D. antarctica*, suggesting these species have different demographic strategies.

*Deschampsia antarctica* E. Desv. (Poaceae), which forms small tussocks and spreads laterally by the production of tillers, and *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae), which forms aggregations of shoots in dense cushions, are the only native vascular plants living in Antarctica. Both species are widespread in the Maritime Antarctic (Holtom & Greene 1967; Corner 1971; Greene & Holtom 1971; Convey 1996; Lewis Smith 2003), where an increase of more than 1°C in mean summer air temperatures over the last five decades (Turner et al. 2005; temperature data available at [www.antarctica.ac.uk/met/gjma/main.html](http://www.antarctica.ac.uk/met/gjma/main.html)) and a concurrent lengthening of the growing season has led to a rapid expansion of these plants (Fowbert & Lewis Smith 1994; Lewis Smith 1994; Grobe et al. 1997; Day et al. 1999; Walther et al. 2002; Gerighausen et al. 2003; Robinson et al. 2003). However, few studies of the reproductive capacity or

growth of these plants have been carried out in Antarctica during a single growing season along an altitudinal gradient and in different habitats.

Livingston Island, with its varied topography and altitudinal gradients, represents a remarkable place to study the influence of temperature and other factors on colonization processes and the potential effects of global warming in the Antarctic Peninsula area, with particular regard to population changes in *D. antarctica* and *C. quitensis*.

The present study was undertaken to determine the distribution of both vascular plants on Livingston Island in order to provide a baseline for future monitoring of their distribution, to determine the demographic structure of the populations and to assess their capacity to occupy new sites. This paper is part of a more general study of the reproductive performances of both species.

## Material and methods

### Study area

The study was carried out in February 2002 near the Spanish Antarctic base Juan Carlos I on Livingston Island, South Shetland Islands (62° 39' 46" S, 60° 23' 20" W) (Fig. 1). The highest point in this area is Mount Reina Sofía (276 m a.s.l.). The area investigated consists of turbiditic deposits composed mainly of shales, sandstones and conglomerates (Arche et al. 1992; Pallás et al. 1992), which are in part covered by pyroclastic material. The studied sites included raised beaches, morainic deposits, ridges, cliffs and erosive platforms (López-Martínez et al. 1992).

Habitat, community composition, colonization and the demographic structure of populations of *D. antarctica* and *C. quitensis* were investigated at eight different locations at 10, 20, 40, 97, 110 and 147 m a.s.l., in the middle and eastern part of the study area, where the vascular plants are more abundant and they reach the highest altitude at which they co-occur (Fig. 1). The populations at the highest sites (110 and 147 m a.s.l.) are surrounded by a considerable amount of bare ground. Two types of habitat were analysed at each location (Table 1): (1) the flattened tops of morainic deposits, ridges or erosion platforms, which have extensive vegetation cover (no, or little, bare ground) and deep soil (hereafter called flat sites); (2) running down from flat sites are slopes with limited vegetation cover (a large proportion of bare ground) and shallower, stonier soil than flat sites (hereafter called peripheral sites). A large bare area at 10 m a.s.l. with only a few small individuals, probably a recently colonized site, was also included in the study.

At the highest site (147 m a.s.l.), mean temperature was about 1°C lower than at 20 m a.s.l. The temperature was measured every hour at the bare ground surface at 20 m a.s.l. and at 147 m a.s.l. from 27 January to 21 February 2002, using Optic StowAway temperature loggers (Onset Computer Corporation, Bourne, MA, USA). Temperatures fluctuated widely, with a mean of 3.96°C at 20 m a.s.l. and 2.99°C at 147 m a.s.l. At 12 m a.s.l., between 1988 and 2002, the mean summer (December–February) air temperature was 2.1°C, the mean annual total precipitation was 109 mm and the average relative air humidity was 80% (Bañón 2004).

### Spatial distribution map

Spatial distribution and cover percentages of *D. antarctica* and *C. quitensis* were determined in January and February 2002. A map at a scale of 1:5000 (Servicio Geográfico del Ejército 1991) was used as a topographic base. The

coordinates of each location were determined using an eTrex summit global positioning system device (Garmin, Olathe, KS, USA). From these data the distribution map was drawn. Plant cover was estimated in plots of 20 × 20 m. The survey was carried out over the entire area, except on the steep cliff between the Argentina and Española coves (caletas). In the inland localities, especially in the western part, where the presence of both species is rare, there are extensive areas without either species. In the survey, points where there is an absence of the species (none present) have been separated for clarity.

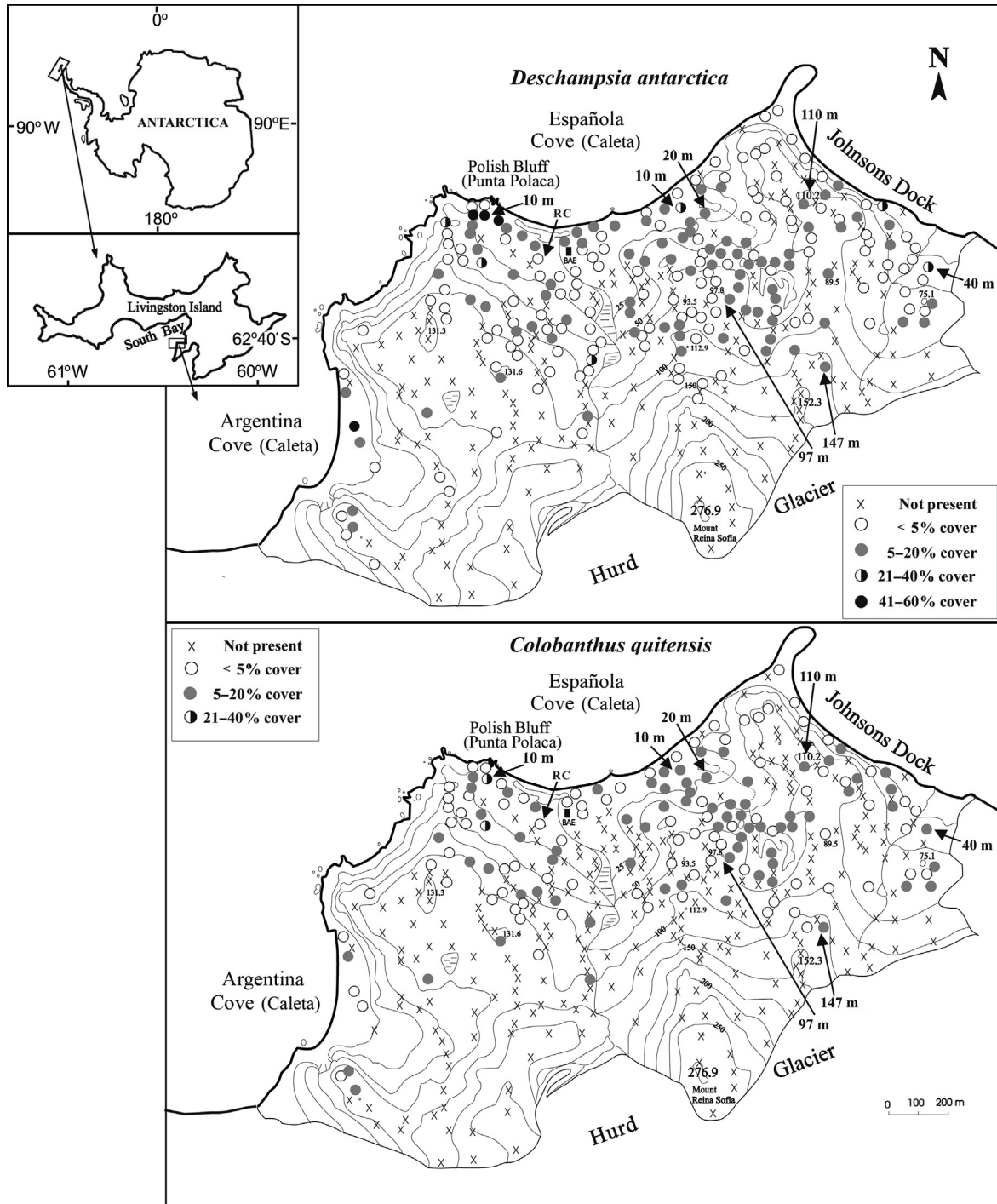
### Vegetation composition

Community composition for each site was determined in six plots of 20 × 20 cm. The cover of both vascular plants, mosses and lichens was estimated using a point quadrat of 100 points at 2 cm intervals. All hits for *D. antarctica*, *C. quitensis*, mosses, lichens and bare ground were recorded. The results are expressed as percentages.

### Demographic structure

The size of all established individuals and the flowering condition for both vascular plants was recorded in February 2002 using six plots of 20 × 20 cm at each site; all plants with their centre inside the plot were recorded. Seedlings that had emerged within the last few months were not considered in further analyses. The size of plants was measured as the largest diameter and on this basis each plant was assigned to a size class (see Fig. 3).

The age of *C. quitensis* cushions was estimated for individuals ca. 5–6 cm in diameter using the number of rosette shoots produced during the current season as the primary criterion. Complementary information including length of branches, branching pattern and distance between shoot bract scars was also determined. The ratio between size diameter and age was considered as an estimate of annual growth rate. Growth rates determined were  $3.7 \pm 0.17 \text{ mm a}^{-1}$  at low altitudes and  $2.9 \pm 0.10 \text{ mm a}^{-1}$  at the higher altitudes. These results fall within the range of the ca. 2–4 mm annual increment in diameter obtained on the South Orkney Islands by Edwards (1975). These values were used as an estimate of the time at which some populations may have become established in certain localities of the Maritime Antarctic (Fowbert & Lewis Smith 1994; Grobe et al. 1997). The estimated growth rates for the different altitudes were used to calculate the age of the measured *C. quitensis* plants (Table 2).



**Fig. 1** Distribution and abundance of *Deschampsia antarctica* and *Colobanthus quitensis* in the area of the Spanish Antarctic base (BAE) Juan Carlos I on Livingston Island, South Shetland Islands, Antarctica. The locations of the studied samples are shown. The location of a recently colonized (RC) site is indicated near Española Cove (Caleta).

Estimating the age of *D. antarctica* plants was more difficult because of the species' tussock habit. However, based on the distribution and size structure of the

population it can be determined whether *D. antarctica* is behaving as a colonizing species or an established one (Casaretto et al. 1994).

**Table 1** Characteristics of the flat sites (F), peripheral sites (P) and a recently colonized site (RC) along the altitudinal gradient in the study area.

Altitude (m a.s.l.) and site type	Characteristics	Soil depth (cm)	Soil pH of bare ground
10 RC	Pebbles, flat raised beach	0–1	–
10–20 F	Flat top of a morainic deposit	2–10	6.4–6.7
10–20 P	Slope running down from flat top	1–2	–
40 F	Flat top of a ridge	8 to >12	–
40 P	North-east slope of the ridge, stable, with some stony soil	3–10	–
97 F	Flat top of an erosion platform, with stones	2–5	5.4–6.7
97 P	Scarce slopes with different expositions running down from the flat top of the platform, stony, gravely soil	0–2	6.1–6.7
110 F	Flat top of a morainic deposit	1–2	–
110 P	Scarce slopes with different expositions running down from the flat top of the morainic deposit, stony, gravely soil	ca. 1	–
147 F	Flat top of a morainic deposit	1–3.5	6.8–7.1
147 P	Scarce slopes with different expositions running down from the flat top of the morainic deposit	0–1	6.5–7.0

### Emergence of seedlings

The *D. antarctica* and *C. quitensis* seedlings emerging in the current growing season, usually in January and February (Edwards 1974), were recorded in six plots of 20 × 20 cm at each site in February 2002. The seedlings of *C. quitensis* had cotyledons and sometimes produced one or two pairs of leaves (exceptionally three). Those of *D. antarctica* consisted of one or two (exceptionally three) leaves.

The annual seedling survival at peripheral sites was calculated by means of the ratio between the number of one-year-old plants to the total number of seedlings from the previous year. In the absence of data on seedling emergence during the previous year, the number of seedlings emerging in 2002 was used as a crude surrogate measure. The accuracy of this surrogate measure depends on the similarity of the number of seedlings that emerge in different years, about which there are no data. Survival percentages were not estimated at the flat sites with low seedling density.

### Statistical analyses

Analysis of variance was used to examine differences in seedling density and individuals, and size of the plants

**Table 2** Estimation means of ages (years) of *Colobanthus quitensis* cushions with different diameters at two altitudes.

Diameters (cm)	20 m a.s.l.	147 m a.s.l.
1	2.7	3.4
3	8.1	10.34
5	13.5	17.24
7	18.9	24.13
9	24.3	–
11	29.7	–
13	35.1	–
15	40.5	–
17	45.9	–

between altitudes (using altitude as a co-variable) and habitats (flat and peripheral sites) for both vascular plants. To facilitate the analysis, sites at 10 and 20 m a.s.l. were combined. The results were also analysed using analysis of variance (ANOVA) for the different habitats between 10 and 40 m a.s.l.

## Results

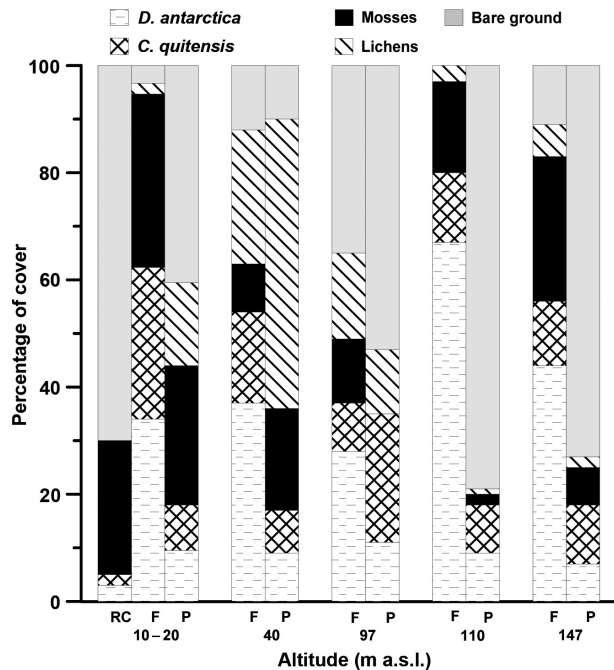
### Distribution and habitats

The two native vascular plants are widely distributed in the studied area, but their abundance decreased with altitude and towards inland localities, especially in the less wind protected western part of the investigated area (Fig. 1). *D. antarctica* was more widespread and usually more abundant than *C. quitensis*. At 71% of the sampled sites both species were found together. At 28% of sites *D. antarctica* was found growing alone, while at only about 1% of sites was *C. quitensis* found alone. At the highest altitudes both species occur in restricted places, in small patches (the largest at 147 m a.s.l. was ca. 25 m<sup>2</sup>) and frequently at sites lacking snow in the early austral summer. These sites are also favoured by nesting skuas (*Catharacta* spp.).

The relative abundance of vascular plants, mosses, lichens and bare ground varied more with the type of habitat than with altitude (Fig. 2). *D. antarctica* was more abundant at flat sites than at peripheral sites. The cover of *C. quitensis* was usually lower than that of *D. antarctica*. At recently colonized sites *C. quitensis* was usually as abundant as, or more abundant than, *D. antarctica*.

Mosses were abundant in the habitats studied, except in the peripheral higher habitats with low moisture





**Fig. 2** Percentage cover of Antarctic native vascular plants, mosses, lichens and bare ground at flat sites (F), peripheral sites (P) and a recently colonized site (RC) along the altitudinal gradient in the study area.

content in the soil. The partly moribund mosses play an important role in facilitating colonization by the vascular plants. The lichens *Cladonia* spp., *Ochrolechia frigida* (Sw.) Lynge and *Psoroma hypnorum* (Vahl.) Gray are common species in the habitats studied, although their abundance varied between sites. In some cases, the vascular plants became established on or amongst these lichens.

**Population size classes**

The largest plants of both species were found at flat sites (Tables 3, 4, Fig. 3). The average diameter of *D. antarctica* was larger than that of *C. quitensis* (Tables 3, 4).

At the peripheral sites, the diameter of both plants varied significantly with altitude, becoming greater at higher altitudes (Table 3), where there was a lower proportion of small individuals (Fig. 3). At flat sites, the mean plant size in both species was independent of altitude, although larger plants were found at the lower-altitude sites (Table 3) where there was a greater proportion of old plants (Fig. 3). At flat sites, the percentage of *C. quitensis* individuals of large diameter was very low at higher altitudes (Fig. 3).

The largest diameters of the studied plants (*Deschampsia*: 20 cm and *Colobanthus*: 18 cm) were found at the lowest altitudes. At the higher altitudes of 110 and 147 m

**Table 3** Mean ( $\pm$ SE) and diameter ranges (in brackets) of *Deschampsia antarctica* and *Colobanthus quitensis* diameters (current season seedlings were not considered) at flat and peripheral sites at each altitude.

	10-20 m a.s.l.	40 m a.s.l.	97 m a.s.l.	110 m a.s.l.	147 m a.s.l.	p
<i>Flat sites</i>						
<i>D. antarctica</i> diameters (cm)	5.36 ( $\pm$ 0.42) [0.20-20.0]	6.36 ( $\pm$ 0.54) [1.30-15.0]	3.61 ( $\pm$ 0.36) [0.30-7.0]	5.88 ( $\pm$ 0.60) [2.0-11.0]	4.86 ( $\pm$ 0.43) [1.0-10.0]	n.s.
<i>C. quitensis</i> diameters (cm)	4.31 ( $\pm$ 0.34) [0.20-18.0]	5.02 ( $\pm$ 0.57) [0.3-12.0]	3.15 ( $\pm$ 1.18) [0.2-7.0]	5.26 ( $\pm$ 0.70) [3.0-7.0]	4.81 ( $\pm$ 0.41) [1.0-8.5]	n.s.
<i>Peripheral sites</i>						
<i>D. antarctica</i> diameters (cm)	2.16 ( $\pm$ 0.19) [0.2-0.6]	1.63 ( $\pm$ 0.18) [0.2-5.0]	2.22 ( $\pm$ 0.26) [0.3-6.0]	2.53 ( $\pm$ 0.21) [0.8-5.0]	3.02 ( $\pm$ 0.24) [1.0-7.0]	**
<i>C. quitensis</i> diameters (cm)	0.82 ( $\pm$ 0.07) [0.2-5.0]	0.93 ( $\pm$ 0.11) [0.2-4.0]	1.54 ( $\pm$ 0.25) [0.2-10.0]	1.75 ( $\pm$ 0.22) [0.2-4.50]	1.76 ( $\pm$ 0.26) [0.1-7.0]	***

Note: Asterisks indicate the level of statistical significance between the altitudes: \*\*\*p < 0.001; \*\*p < 0.01; n.s. not significant.

**Table 4** Mean ( $\pm$ SE) of *Deschampsia antarctica* and *Colobanthus quitensis* seedlings and individuals per m<sup>2</sup>, as well as the mean diameters (excluding seedlings) for each type of site (altitude 10–40 m a.s.l.).

Parameters	Flat sites	Peripheral sites	Recently colonized site	<i>p</i>
<i>D. antarctica</i> seedlings	2 ( $\pm$ 2)	21 ( $\pm$ 7)	4 ( $\pm$ 4)	*
<i>C. quitensis</i> seedlings	179 ( $\pm$ 71)	1005 ( $\pm$ 170)	8 ( $\pm$ 8)	***
<i>D. antarctica</i> individuals	120 ( $\pm$ 10)	175 ( $\pm$ 12)	15 ( $\pm$ 8)	***
<i>C. quitensis</i> individuals	112 ( $\pm$ 17)	319 ( $\pm$ 50)	62 ( $\pm$ 16)	***
<i>D. antarctica</i> diameters (cm)	5.67 ( $\pm$ 0.34)	1.95 ( $\pm$ 0.13)	2.61 ( $\pm$ 0.42)	***
<i>C. quitensis</i> diameters (cm)	4.49 ( $\pm$ 0.29)	0.85 ( $\pm$ 0.06)	1.18 ( $\pm$ 0.20)	***

Note: Asterisks indicate the degree of statistical significance between the habitats: \*\*\**p* < 0.001; \**p* < 0.05.

a.s.l., the largest diameter reached by *Colobanthus* was 7 and 8 cm, respectively, while in *Deschampsia* it was 11 and 10 cm. The higher proportion of young individuals of both species was found in the periphery of populations established several years previously (Fig. 3). This proportion decreased slightly at higher altitudes.

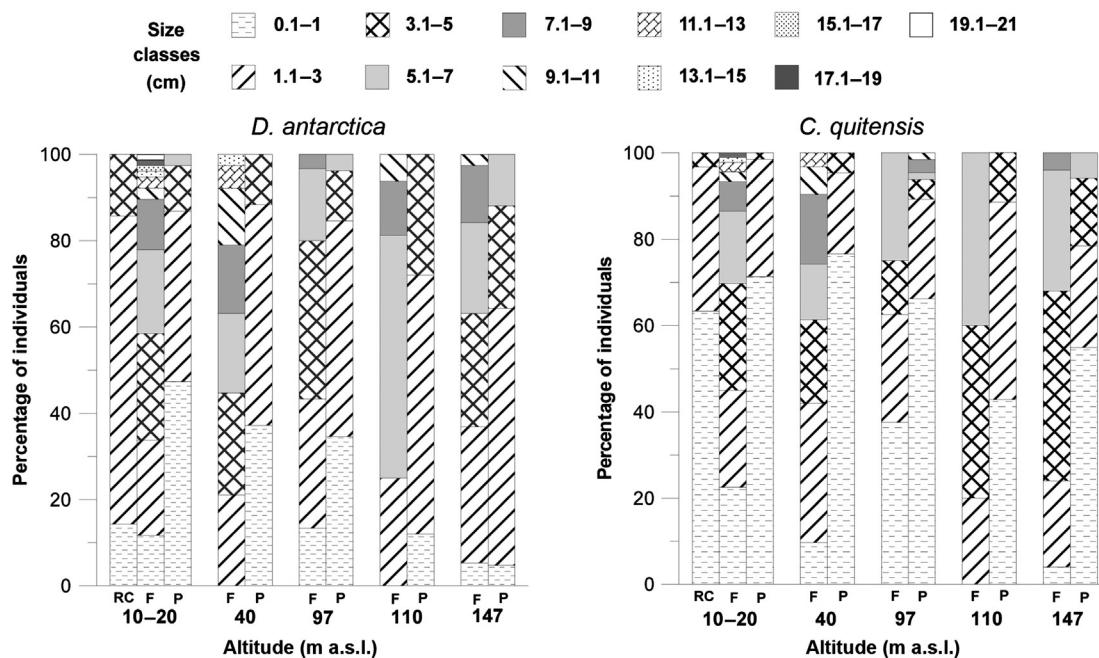
### Density of individuals

The total number of plants (excluding seedlings) of *C. quitensis* was higher (mean  $162 \pm 21.25$  per m<sup>2</sup>) than for *D. antarctica* (mean  $117 \pm 8.68$  per m<sup>2</sup>; *p* = 0.05). However, the density of established individuals at the flat sites was higher for *D. antarctica* (Table 4, Fig. 4). At the different altitudes the density of individuals of *C. quitensis* was lower at the flat sites than at their peripheries (Fig. 4), whereas *D. antarctica* does not show a consistent

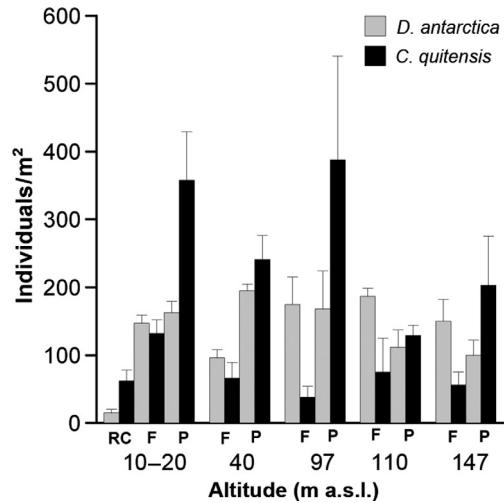
pattern (Fig. 4). The proportion of established individuals with respect to seedling density was higher for *D. antarctica* than for *C. quitensis* (Table 4).

The majority of established individuals were found in a healthy condition and most were flowering or in bud. Moribund or partially dead plants were rare; at the highest altitude some *Colobanthus* individuals with a diameter between 4 and 7 cm were partially dead or moribund.

The percentage of individuals of *C. quitensis* and *D. antarctica* found in bud or flowering was similar: 66 and 64%, respectively. However, *C. quitensis* flowered at a smaller size than *D. antarctica*. Among *C. quitensis* plants, 43% of individuals with a diameter between 0.2 and 1 cm were found either in bud or flowering. The smaller cushions (0.2–0.3 cm) formed by a rosette with several pairs of leaves appear to be in their second growing



**Fig. 3** Proportion of size classes (plant diameter, excluding seedlings) of *Deschampsia antarctica* and *Colobanthus quitensis* in populations at flat sites (F), peripheral sites (P) and a recently colonized site (RC) along the altitudinal gradient in the study area.

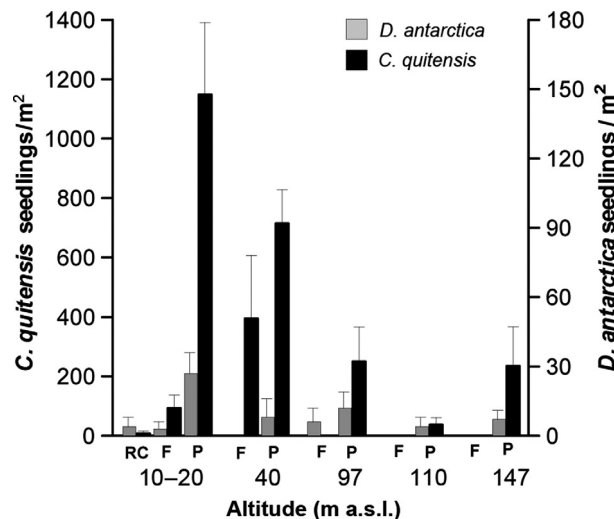


**Fig. 4** Density of individuals of *Deschampsia antarctica* and *Colobanthus quitensis* at flat sites (F), peripheral sites (P) and a recently colonized site (RC) along the altitudinal gradient in the study area (standard error bars shown).

season. Only *D. antarctica* plants with a diameter larger than 0.9 cm were observed with flowers. Few individuals (19%) smaller than 1.5 cm had flowers.

**Seedling distribution and survival**

The number of emerged *C. quitensis* seedlings was greater than for *D. antarctica* (Fig. 5). The recruitment of seedlings was greater at lower than at higher sites (Fig. 5). At all altitudes the number of seedlings was higher at



**Fig. 5** Density of seedlings of *Deschampsia antarctica* and *Colobanthus quitensis* at flat sites (F), peripheral sites (P) and a recently colonized site (RC) along the altitudinal gradient in the study area (standard error bars shown). Note different scales for the two species.

peripheral sites than at flat sites, where the older individuals occurred (Fig. 5). These differences were very significant for *C. quitensis* at the lower altitudes (Table 4, Fig. 5).

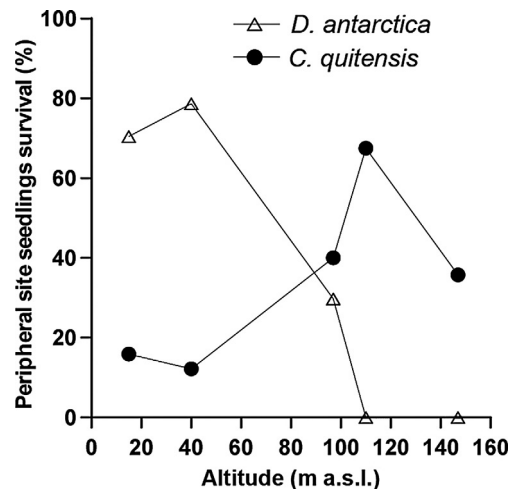
After one year the estimated survival of seedlings varied between species at the peripheral sites (Fig. 6). The survival of *C. quitensis* seedlings was greater at higher altitudes, while for *D. antarctica* there was greater seedling survival at lower altitudes.

**Discussion**

**Distribution**

In the inland areas and at higher altitudes *D. antarctica* and *C. quitensis* grow only in restricted places, commonly at sites that are snow-free early in the austral summer. Such sites favour the development of plants and provide a longer growing season. Global warming is likely to increase the availability of habitats for colonization by new populations and facilitate the expansion of existing populations.

Differences in the behaviour of both species could explain a higher expansion and abundance of *D. antarctica*. The establishment of *Colobanthus* is typically from seed (Edwards 1975), while *D. antarctica* has also the ability to produce ramets (Edwards 1972). The grass *D. antarctica* has a wider ecological amplitude and it is more abundant than *C. quitensis* (Lewis Smith 1994). However, *D. antarctica* and *C. quitensis* plants were of a similar size at the highest sites on the top of promontories, sites that are



**Fig. 6** Seedling survival of *Deschampsia antarctica* and *Colobanthus quitensis* in peripheral sites after one year based on the assumption that the numbers of emerged seedlings during 2001 and 2002 were the same.

also favoured by nesting skuas. The birds play an important role in the dispersion of these species to new areas (Edwards 1972; Parnikoza et al. 2007), which may explain why these plants are sometimes found at sites separated by large uncolonized areas. I concur with Grobe et al. (1997) that *C. quitensis* is occasionally dispersed by birds during nest construction when transported pieces of the grass *D. antarctica* carry along *C. quitensis* shoots and seeds. The *C. quitensis* seeds, which are adhesive when wet, may also be dispersed when they adhere to birds. Wind seems less important for dispersion of seeds over longer distances, except in Antarctic areas with strong winds. The presence of numerous seedlings in the periphery of the studied populations suggests that local dispersion is mainly by wind and also, particularly on the steeper slopes, by water (from meltwater or rain).

### Population establishment and demographic structure

The age structure of populations provides an indication of the colonization process and their maintenance (Silver-town 1987; Casaretto et al. 1994; Hutchings 1997; Watkinson 1997; García et al. 1999). Bigger plants found at the flat sites suggest that they were established earlier than the small plants occurring at their periphery.

The estimated ages of the largest *Colobanthus* cushions (7 cm at 110 m a.s.l. and 8 cm at 147 m a.s.l.) suggest that populations at higher altitudes were established 24–28 years ago. In these locations separated by areas lacking either species (at 110 and 147 m a.s.l.) it is probable that both species may have become established at a similar time by seeds dispersed by skuas from sites where both plants grow together. The sizes of both species were similar in these places (the largest clumps of *D. antarctica* were 11 cm at 110 m a.s.l. and 10 cm at 147 m a.s.l.).

The mean size of both species at each site suggests that the growth rate may be a little higher for *Deschampsia*. Lower mean sizes of these species are found in the habitats with more gaps and shallower soils, frequently at the periphery of populations established several years before (flat sites).

The largest diameters of the studied plants (*Deschampsia*: 20 cm; *Colobanthus*: 18 cm) were found at the lowest altitudes with deep soil. These species reached this largest size at sites fertilized by excrement from penguins at Polish Bluff (Punta Polaca). Tussocks of *D. antarctica* up to 1.5 m in diameter were found in an area with abundant elephant seals on Byers Peninsula, Livingston Islands (pers. obs.), but this may be the result of coalescence of individuals to form an extensive turf. The largest cushions of *Colobanthus* in the studied populations may have become

established about 49 years ago, assuming a growth rate of  $3.7 \text{ mm yr}^{-1}$  estimated from growth measurements of this species at lower altitudes. The population of *D. antarctica* at this site may have become established earlier, since some *Colobanthus* and *Deschampsia* had established among dead *Deschampsia* grass, a strategy previously documented by Edwards (1974).

Lack of vigour in *Colobanthus* cushions greater than 4 to 8 cm, with maximum necrosis in cushions having a diameter greater than 8 cm, has been described by Fowbert and Lewis Smith (1994). In my study area, this pattern was not evident in the lower altitude populations growing in deep soils. At higher altitudes the initiation of necrosis was observed in *C. quitensis* plants with a cushion diameter of 4–7 cm.

### Seedling emergence and survival

The presence of numerous seedlings, mainly of *C. quitensis*, and young individuals at the periphery of populations established several years before or in recently colonized sites, suggests patch expansion and colonization of new areas, although this is less pronounced at the highest altitudes. Temperature has an influence on germination (Corte 1961; Holtom & Greene 1967; Corner 1971; Edwards 1974; Vera, unpubl. data) and seed production (Edwards 1974; Day et al. 1999; Lewis Smith 2003; Vera, unpubl. data). Greater numbers of mature seeds were found at lower altitudes (Vera, unpubl. data). Among *C. quitensis* a high proportion of small plants bore flowers, suggesting that seed production contributes to peripheral expansion.

Seedling survival varied between species in peripheral sites after one year. A higher mortality of *C. quitensis* seedlings at the lowest altitudes may be associated with the extensive cover of mosses and lichens, which may prevent establishment in soil. *D. antarctica* appears to have a competitive advantage in establishing itself among or on mosses and lichens (pers. obs.), organisms that have been shown to provide some buffering from the effects of needle-ice heave on seedling establishment (Heilbronn & Walton 1984; Pérez 1987). Interannual variability in seedling emergence and survival and climatic parameters may also contribute to these differences, particularly as the species may be growing near to their ecophysiological limit (Miller & Cummins 1987; Fowbert & Lewis Smith 1994; Holm 1994; Lewis Smith 1994).

### Demographic strategies

The two species have contrasting demographic strategies, particularly with respect to reproduction by seeds.



*D. antarctica* produces fewer and bigger (length usually more than 1.4 mm) seeds. In the studied area there are on average 4234 seeds/m<sup>2</sup> in the seed bank (Vera, unpubl. data), a figure similar to results obtained from other areas of the Maritime Antarctic (Holtom & Greene 1967; Greene & Holtom 1971; Edwards 1974; Ruhland & Day 2001). Although seedling density was lower for *D. antarctica* than for *C. quitensis*, as has been documented earlier (Edwards 1974; Ruhland & Day 2001), a greater proportion of *D. antarctica* seedlings seem to become established (Figs. 4, 5). Large seeds with plentiful nutritive reserves improve the establishment success of seedlings in harsh environments (Holm 1994). *C. quitensis* produces very abundant but small seeds (Greene & Holtom 1971; Edwards 1974; Ruhland & Day 2001)—an average of 18 402 seeds/m<sup>2</sup> in the seed bank and seeds about 0.6 mm in length in the study area (Vera, unpubl. data). *C. quitensis* populations expand through numerous seedlings but the species suffers a higher seedling mortality than *D. antarctica*, as has been previously observed (Edwards 1974; Fowbert & Lewis Smith 1994) and lower survival success of young individuals (Figs. 3–5). A higher persistence of established *D. antarctica* plants over time may also be inferred from the denser populations at flat sites, in contrast with the dominance of *C. quitensis* at peripheral sites.

The results of this study suggest that the populations of *D. antarctica* and *C. quitensis* on Livingstone Island have the capacity for spreading by seeds at the highest elevations once plants have become established at a site. The population expansion rate does not seem to be very rapid. New populations are becoming established at higher altitudes and *Deschampsia* plants have been recorded in sheltered locations at 165 m a.s.l. The results of this study, as well as other recent work (Gerighausen et al. 2003; Robinson et al. 2003), indicate that as ambient temperatures rise, the growing season lengthens and ice-free areas at higher altitudes expand, new populations will successfully establish themselves over a wider area.

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