

Reproduction of Antarctic flowering plants

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Abstract: Reproductive allocation (reproductive biomass relative to vegetative biomass) and seed production were measured for samples of the two native phanerogams occurring in Antarctica. Material collected on South Georgia (subantarctic), Signy Island (northern maritime Antarctic) and Léonie Island (southern maritime Antarctic) allowed an initial comparison of reproduction over a wide latitudinal range. Sizes of vegetative and reproductive structures of *Colobanthus quitensis* were smaller in Signy Island samples than those from South Georgia or Léonie Island. This pattern was reflected in the pattern of seed production. Vegetative and reproductive structures of *Deschampsia antarctica* were generally similar in size at both maritime Antarctic sites, but larger at subantarctic South Georgia. Seed production was similar in each season assessed and at all three sites. In most samples of both species there were close relationships between reproductive and vegetative biomass, and seed output and reproductive biomass. Subantarctic *C. quitensis* showed greater allocation to seed production than material from maritime Antarctic sites. *D. antarctica* showed the reverse pattern, with greater allocation to reproductive biomass and seed production in most samples of maritime Antarctic material, particularly those from Signy Island. Reproductive strategies do not form any specific adaptation to the Antarctic environment for these species. Reasons for the failure of other higher plants to become established in the maritime Antarctic are discussed, and it is concluded that geographical isolation is the main factor. The most important proximate factors influencing propagules which reach potential colonization sites are likely to be the short length and low temperature of the summer season in relation to the time required for establishment.

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Introduction

Antarctic pearlwort *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) and Antarctic hairgrass *Deschampsia antarctica* Desv. (Gramineae) are the only two higher plants whose distributions include Antarctica, where both are limited to the maritime Antarctic biological zone (*sensu* Smith 1984). The wider distribution of *C. quitensis* includes South Georgia (subantarctic), the Falkland Islands, and sporadic sites along the length of the Andean mountain chain, reaching c. 10°N in Mexico; closely related species are known from South Georgia and the Falkland Islands (*C. subulatus*), Kerguelen and neighbouring islands (*C. kerguelensis*) and New Zealand, Tasmania and the subantarctic islands of the Australian sector (*C. muscoides*) (Holtom & Greene 1967, Moore 1970). *C. quitensis* is limited to progressively higher altitudes at more northerly latitudes. *D. antarctica* is also found in South America (Tierra del Fuego and Andean sites to c. 34°S), as well as having a wide distribution on all the subantarctic islands (Holtom & Greene 1967, Moore 1970). Both species are widely, if sporadically, distributed in the maritime Antarctic, including the west coast of the Antarctic Peninsula, the South Shetland, South Orkney and South Sandwich (*D. antarctica* only) islands, and are common on subantarctic South Georgia (Holtom & Greene 1967). There is evidence of recent rapid population expansion at some

maritime Antarctic sites (Fowbert & Smith 1994, Smith 1994) which may be associated with climatic amelioration being experienced in the region (Smith 1990, King 1994). The known southern limit to the distribution of both species (Terra Firma Islands, southern Marguerite Bay, 68°43'S, 67°31'W) appears to be the availability of suitable ice-free habitat with adequate moisture (Smith 1982, Smith & Poncet 1987).

The species' taxonomy, distribution, ecological amplitude and mode and frequency of reproduction were described in several papers resulting from a series of studies in the maritime Antarctic (Holtom & Greene 1967, Greene 1970, Moore 1970, Greene & Holtom 1971, Corner 1971, Edwards 1972, 1974, 1975), in addition to separate reports (*e.g.* Corte 1961a, Komárková, Poncet & Poncet 1985, 1990, Gebauer, Peter & Kaiser 1987). Some of these studies indicated that growth and reproductive activity of both phanerogams at sites on the west coast of the Antarctic Peninsula (maritime Antarctic) were of a similar magnitude to that achieved on subantarctic South Georgia. However, studies carried out in the South Orkney Islands, in the northern maritime Antarctic, indicated that although both species flower as frequently as at South Georgia, the production of mature seed did not occur regularly (*D. antarctica* four years between 1944 and 1974, *C. quitensis* approximately every three years over the same

period (Edwards 1974)). The South Orkney Islands experience a harsher climate (less sunshine, increased precipitation, lower microhabitat temperatures) than many sites at more southerly latitudes on the Antarctic Peninsula. Physiological studies have shown little or no specialization of the photosynthetic or respiratory apparatus of either species to low mean environmental temperatures (Edwards & Smith 1988), although Jellings, Usher & Leech (1983) found that the chloroplast to cell area index of *D. antarctica* showed an inverse relationship with temperature along a latitudinal gradient, implying a compensatory response to decreasing mean temperatures. The contents of polar lipids and degree of unsaturation of fatty acids in phospholipids and galactolipids in *D. antarctica* show little difference to other Gramineae (Zúñiga *et al.* 1994).

The present study utilized fruiting material of both species collected from two sites in the maritime Antarctic (Signy Island, South Orkney Islands and Léonie Island, northern Marguerite Bay) and one on subantarctic South Georgia, covering a latitudinal transect of c. 14°. Life history strategy models (*e.g.* Grime 1979, Greenslade 1983) predict that species occupying chronically stressful or adverse environments (under the influence of S- or A-selection) will show reduced investment in reproductive activities as a result of the costs associated with survival. In the context of this study, a lower investment in reproductive biomass or seed production for a given vegetative biomass would be expected at the climatically more extreme maritime than subantarctic sites. The primary aims of the study were, therefore:

- 1) to describe patterns of reproductive investment and seed production at each site and
- 2) to identify any systematic variations in patterns observed which may be related to local environmental conditions at each site and/or its position on the transect.

Both species show significant ecological amplitude, especially in more northerly sites, and it is recognized that the present comparisons do not take the fullest range of habitat performance into account. The results of this study are discussed further in the context of previously published reports of aspects of the species' ecology, physiology and genetics (many of which are relatively inaccessible), to identify factors influencing their success in the maritime

Antarctic, and those limiting colonization by other higher plants.

Materials and methods

Sites and collection

These two species fruit only sporadically at all southerly locations. It is thus difficult to optimize the timing of collections, and these difficulties are further compounded by the problems of organizing logistic support to visit three remote localities. Many plants of both species produced mature seed on Signy Island (60°43'S, 45°38'W), in the South Orkney Islands, during the 1989/90 austral summer. Further material approaching maturity of *D. antarctica* was collected on Signy Island during the 1992/93 and 1994/95 austral summers, but *C. quitensis* failed to produce mature seed in these or the intervening years. Material of both species was also collected during the 1992/93 austral summer from sites at Husvik, Stromness Bay, on the north-east coast of South Georgia (c. 54°11'S, 36°43'W) and during the 1994/95 summer from Léonie Island in northern Marguerite Bay (67°36'S, 68°21'W). Although collecting the specimens during different seasons at each site makes comparisons more difficult, it is considered that these collections do allow initial comparisons of patterns of reproductive activity to be made between the three sites.

At all three sites, small numbers of cushions of *C. quitensis* bearing mature seed were collected around coastal rocks or damp crevices (below 30 m a.s.l.). *D. antarctica* was collected from similar sites on Signy and Léonie Islands, and from open stony ground within the abandoned whaling station at Husvik, South Georgia. South Georgia and Léonie Island material was dissected immediately after collection, but that from Signy Island was frozen at -20°C and stored before subsequent dissection.

Monthly mean air temperatures for the summer months (November to March) for Signy Island, Husvik and Rothera Point (c. 10 km north-east of Léonie Island) during the years of study are given in Table I. No climatological data are available for Léonie Island, but the island lies in a radiation "window" close to the Hurley and Turner Glaciers on Adelaide Island and the study site is on the sheltered N side of the

Table I. Mean monthly air temperatures recorded at Signy Island, Husvik (South Georgia) and Rothera Point, during the study summers.

	Signy Island, South Orkney Islands						Husvik	Rothera Point
	1989/90	1990/91	1991/92	1992/93	1993/94	1994/95	1992/3	1994/95
November	-0.2	-0.1	-0.8	-0.7	1.3	n.d.	5.1	-0.3
December	0.8	0.1	-0.7	2.2	0.8	-1.1	6.0	0.1
January	2.1	2.8	1.7	1.7	1.9	0.4	4.8	2.1
February	2.3	1.8	0.5	1.4	2.7	0.6	6.3	0.0
March	1.7	-0.4	-2.2	0.2	1.4	-1.0	6.1	-1.6
Mean	1.34	0.84	-0.30	0.96	1.62	-0.27	5.65	0.06

Table II. Measures of vegetative and reproductive biomass, seed output and shoot complexity recorded from individual rosettes of *Colobanthus quitensis* as mean (and standard error) or median values. Analyses of variance were used to compare biomass measures and seed counts, and Kruskal-Wallis analyses of variance to compare the numbers of vegetative and reproductive shoots. (** $p < 0.01$, *** $p < 0.001$).

	Vegetative biomass (mg)	Reproductive biomass (mg)	Total number of seeds	Median N vegetative shoots	Median N productive shoots
Signy Island 1989/90	8.23 ± 0.87	5.80 ± 0.58	35.2 ± 3.5	1	3
South Georgia 1992/93	18.47 ± 1.25	11.03 ± 0.67	133.3 ± 8.3	1	4
Léonie Island 1994/95	16.24 ± 0.98	8.04 ± 0.47	53.2 ¹	2	4
Statistical significance	***	***	***	**	***

¹ Mean number of seeds per capsule (13.3, SE 8.2, $n = 30$ capsules) multiplied by median number of reproductive shoots.

island. It is likely to be significantly warmer than indicated by meteorological data recorded at Rothera Point.

Plants of *C. quitensis* have a cushion growth form, comprising an aggregation of individual rosette shoots. Each cushion was separated into rosettes arising from below ground (root) level, each with branches including one or more purely vegetative or reproductive (bearing seed capsule) side shoots. Each main shoot was considered to be a functional unit, and its above-ground biomass was separated into reproductive (capsule, calyx and stem) and vegetative (remainder) portions, dried and weighed (accuracy 0.2 μg (Signy Island), 10 μg (Husvik), 1 mg (Léonie Island)). In addition, the numbers of seeds per capsule and of reproductive and vegetative side shoots were recorded (Léonie Island seed counts were performed separately on 30 mature capsules, owing to the wide range in maturity of capsules within

individual dissected rosettes — from inflorescence to empty capsule). Signy Island dissections utilised a single large cushion which appeared to have formed from the coalescence of several individual cushions. Husvik and Léonie Island dissections each used material from four smaller plants growing adjacently in a rock crevice. Twenty-five shoots each of Signy and Léonie Island material and 50 of Husvik material were dissected.

Individual plants of *D. antarctica* were separated into tillers and at least 24 with mature inflorescences were dissected at each site. The above-ground portion was again divided into reproductive (above highest stem leaf, cf. Wilson & Thompson 1989) and vegetative (remainder) biomass, dried and weighed as above (accuracy 1 mg). The number of seeds in each inflorescence was recorded.

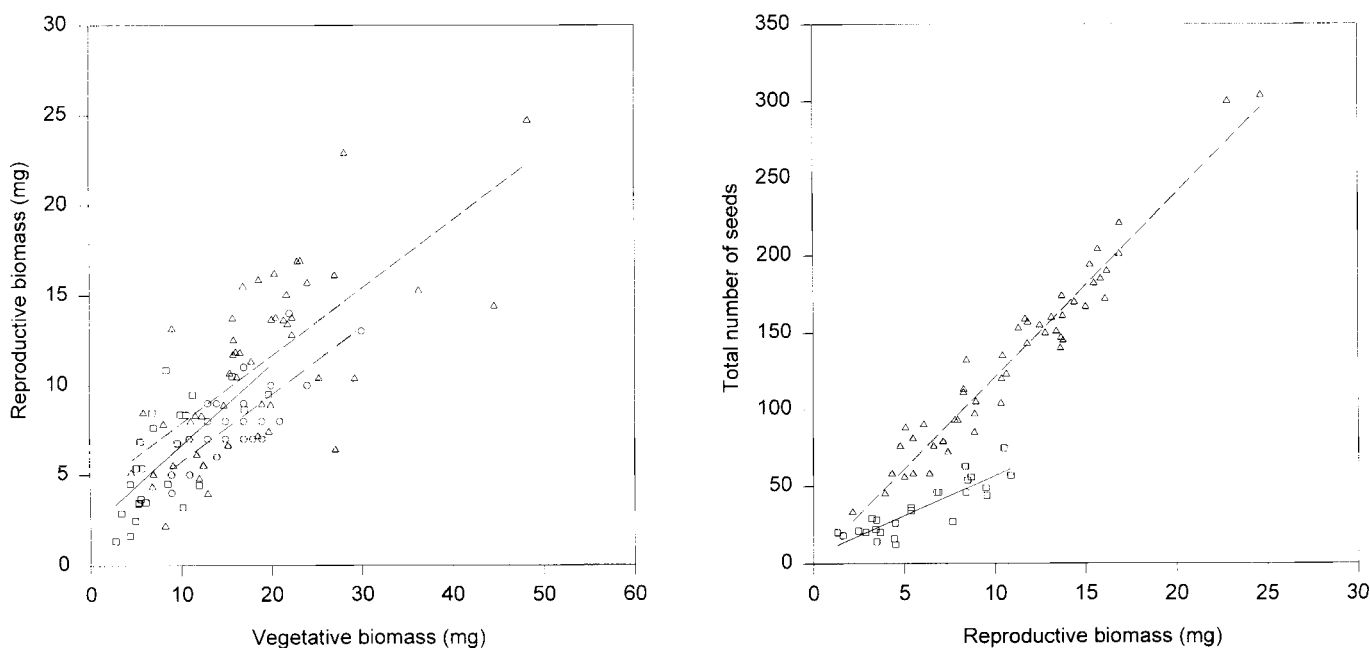


Fig. 1. *Colobanthus quitensis*. **a.** Linear regressions of reproductive on vegetative biomass data from each site. **b.** Linear regressions of seed count on reproductive biomass for material from each site. Key: Léonie Island, \circ - - - - ; Signy Island, \square ———; South Georgia, Δ - - - -.

Table III. Details of linear regression analyses on *Colobanthus quitensis* reproductive data; a) regression of reproductive on vegetative biomass, b) regression of seed count on reproductive biomass (Signy Island and South Georgia data). (NS not significant, * $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Site	Intercept	Gradient	F test	r^2
a)				
Signy Island	2.06*	0.454***	$F_{1,23} = 20.32^{***}$	44.6%
South Georgia	4.11**	0.374***	$F_{1,48} = 45.10^{***}$	47.4%
Léonie Island	1.92*	0.377***	$F_{1,23} = 34.85^{***}$	58.5%
b)				
Signy Island	4.82 ^{NS}	5.23***	$F_{1,23} = 71.39^{***}$	74.6%
South Georgia	1.63 ^{NS}	11.94***	$F_{1,48} = 820.79^{***}$	94.4%

Data analysis

Analyses of variance were used to compare reproductive and vegetative biomass, and seed production, of material from the three sites. Kruskal-Wallis analyses of variance were used to compare the number of reproductive and vegetative side shoots on material of *C. quitensis*. Linear regression was used to describe the relationship between reproductive and vegetative biomass, and between number of seeds and reproductive biomass, for each species and site. Polynomial regression was also used to test for curvilinearity in the data. Regression slopes were compared using the General Linear Model (GLM) of Minitab (1993).

Results

Colobanthus quitensis

Biomass measures indicated that Signy Island material of this species was considerably smaller than that from both Léonie Island, c. 900 km farther south in the maritime Antarctic, and subantarctic South Georgia (Table II, Fig. 1). In addition, Signy Island specimens produced fewer reproductive shoots and seeds than the other two sites, with Léonie Island samples being intermediate but still much less productive than those from South Georgia (Table II). It is clear that South Georgian plants in these limited collections were significantly larger and produced considerably more mature seed than their maritime Antarctic counterparts.

Linear regression analyses of the relationship between reproductive and vegetative biomass gave highly significant results (Table IIIa). The regression slopes obtained from the three sites were not significantly different (GLM, $F_{2,94} = 0.17$, $p = 0.847$), and regression intercepts were positive in each case. Linear regression of seed counts on reproductive biomass gave highly significant results (Table IIIb, Fig. 1b). There was a significant difference between the gradients obtained from the two sites (GLM, F test, $F_{1,71} = 49.09$, $p < 0.001$). Inspection of Fig. 1b additionally suggests that plants from Signy Island produced fewer seeds for a given

Table IV. Measures of vegetative and reproductive biomass, and seed output recorded for individual tillers of *Deschampsia antarctica* as mean (and standard error). Analyses of variance were used to test for differences between the data obtained from the three sites. (NS not significant, *** $p < 0.001$).

	Vegetative biomass (mg)	Reproductive biomass (mg)	Number of seeds
Signy Island			
1989/90	6.95 ± 0.40	12.68 ± 0.65	53.4 ± 2.9
1992/93	11.60 ± 1.33	13.32 ± 0.92	50.3 ± 2.9
1994/95	21.28 ± 2.30	10.16 ± 0.60	47.4 ± 3.1
South Georgia			
1992/93	23.96 ± 1.52	21.08 ± 1.80	53.9 ± 3.1
Léonie Island			
1994/95	10.36 ± 0.78	12.79 ± 0.73	45.4 ± 2.0
Statistical significance	***	***	NS

biomass than those from South Georgia. Both intercepts were not significantly different from zero.

Deschampsia antarctica

Vegetative and reproductive parts of plants collected on South Georgia were generally considerably larger than their counterparts both on Signy Island and Léonie Island (Table IV), although Signy Island vegetative biomass measured in the 1994/5 season was close to that attained previously on South Georgia. Seed counts, however, were very similar for material from all sites and seasons. It should be noted that material collected on Signy Island in 1992/93 and 1994/95 was not as mature as that from 1989/90, with the seedheads exerted but not fully expanded.

Linear regressions of reproductive on vegetative biomass were again highly significant, with the exception of Signy Island 1992/93 data (Table Va, Fig. 2a). The regression slopes obtained from the three sites were significantly different (GLM, F test, $F_{3,94} = 15.28$, $p < 0.001$). Linear regression of seed count on reproductive biomass provided the best fit to all Signy Island and South Georgia data, but a quadratic regression gave a better fit to that from Léonie Island ($r^2 = 51.0\%$). The difference between linear regression slopes of material from the three sites was also significant (GLM, F test, $F_{4,117} = 4.03$, $p < 0.01$) (Table Vb, Fig. 2b) and significant positive regression intercepts were obtained. Visual inspection of Fig. 2 again suggests that differences in allocation pattern occur both between years at Signy Island and more generally between sites. In 1989/90 there was greater seed production per unit biomass in Signy Island compared to South Georgia material (the converse pattern to that shown by *C. quitensis*) whereas the reverse effect was seen in 1994/5 (Table V).

Discussion

Both *D. antarctica* and *C. quitensis* have virtually identical distributions in the maritime Antarctic and even on a local

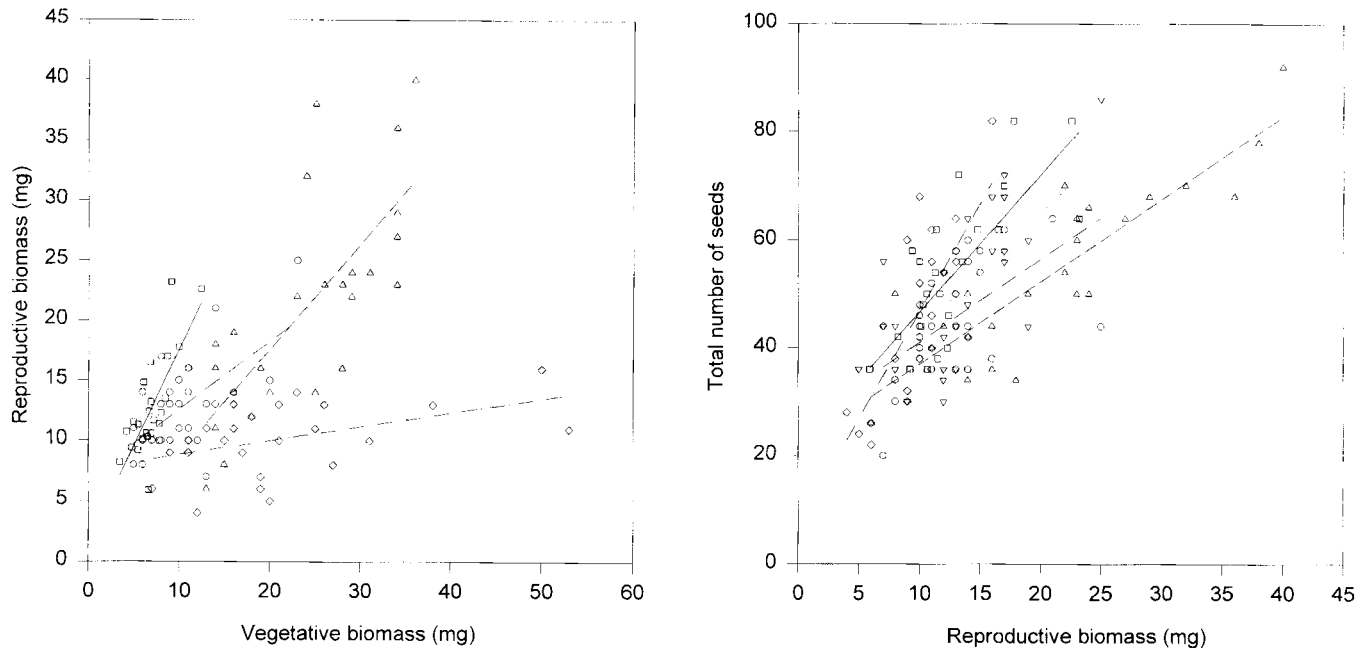


Fig. 2. *Deschampsia antarctica*. **a.** Linear regressions of reproductive on vegetative biomass data from each site and season (Signy Island 1992/3 data are not presented as no significant relationship was found). **b.** Linear regressions of seed count on reproductive biomass for material from each site and season. Key: Léonie Island, ○ - - - - ; Signy Island 1989/90, □ ———; Signy Island 1992/93, ▽ ·····; Signy Island 1994/95, ◇ - · - · - ·; South Georgia, Δ - - - - -.

scale the species are usually found together, although *D. antarctica* is generally more abundant (Holtom & Greene 1967, Fowbert & Smith 1994). Thus it seems reasonable to assume that the environmental influences experienced by both species, and their physiological tolerance of these, are very similar. The data described above provides limited support for the life history predictions of Grime (1979) and Greenslade (1983) in that lower seed production by *C. quitensis* was found at Signy Island and to a lesser extent at Léonie Island than on South Georgia. However, *D. antarctica* showed the reverse pattern in at least some years, and as much variation between years on Signy Island as was observed across the complete latitudinal transect, a pattern more characteristic of a ruderal or *r*-selected species. The two species either show different reproductive responses to stress, or do not experience the same stresses despite their physical proximity.

Throughout their Antarctic range, both *D. antarctica* and *C. quitensis* produce flowers in most years, and viable seed can be set at all sites (Corte 1961a, Greene 1970, Greene & Holtom 1971). Seedlings of both were abundant on Léonie Island, close to their southern distributional limit, in the 1994/5 season. Historically, the proportion of years in which mature seed is produced is low (Corner 1971, Greene & Holtom 1971, Edwards 1974), although likely to increase with current regional climate amelioration. Edwards (1972) considered that *D. antarctica* colonized new sites primarily

by vegetative dispersal, often by the agency of birds. In contrast, studies of Arctic grasses suggest that establishment from seed is the primary form of reproduction (Grulke & Bliss 1988), and Fowbert & Smith (1994) suggest that colonization by *C. quitensis* is likely to be via seeds, as uprooted plants show much lower survival rates than those of *D. antarctica* (Edwards 1972).

Table V. Details of linear regression analyses carried out on *Deschampsia antarctica* reproductive data; a) regression of reproductive on vegetative biomass, b) regression of seed count on reproductive biomass. (NS not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Site	Intercept	Gradient	F test	r^2
a)				
Signy Island				
1989/90	1.43 ^{NS}	1.62 ^{***}	$F_{1,22} = 28.13^{***}$	54.1%
1992/93	14.0 ^{***}	-0.06 ^{NS}	$F_{1,23} = 0.17^{NS}$	n/a
1994/95	7.7 ^{**}	0.12 [*]	$F_{1,23} = 5.83^*$	16.8%
South Georgia	0.02 ^{NS}	0.88 ^{***}	$F_{1,23} = 28.57^{***}$	53.5%
Léonie Island	6.88 ^{***}	0.57 ^{***}	$F_{1,26} = 15.37^{***}$	34.7%
b)				
Signy Island				
1989/90	21.3 ^{**}	2.53 ^{***}	$F_{1,22} = 28.15^{***}$	54.1%
1992/93	21.3 ^{**}	2.18 ^{***}	$F_{1,23} = 21.19^{***}$	45.7%
1994/95	7.0 ^{NS}	3.98 ^{***}	$F_{1,23} = 33.13^{***}$	57.2%
South Georgia	21.7 ^{***}	1.53 ^{***}	$F_{1,23} = 74.61^{***}$	75.4%
Léonie Island	25.6 ^{***}	1.54 ^{***}	$F_{1,26} = 12.12^{**}$	29.2%

For *C. quitensis*, Edwards (1974) found a mean of c. 25 seeds per capsule for sites in the South Orkney Islands and on South Georgia, whilst Moore (1970) reported a mean of 43 seeds per capsule for Fuegian and Andean material. The current study found 34 seeds per capsule for South Georgian plants, but only c. 12–13 per capsule for Signy Island and Léonie Island plants. The smaller size of Signy Island shoots, combined with the low total seed output, supports the contention that environmental conditions in the South Orkney Islands are particularly harsh for the development of reproductive structures by higher plants (e.g. Holtom & Greene 1967, Edwards 1974). Since the 1989/90 austral summer *C. quitensis* is thought not to have produced mature seed on Signy Island, although exhaustive searches were not possible. The 1989/90 summer was one of the warmest in recent years, with a mean air temperature (mean of monthly screen averages, November–March) of 1.34°C. With the exception of the 1993/94 season, subsequent summers have been colder, particularly during November and December, months important for flower and shoot development.

For *D. antarctica*, Edwards (1974) found a mean of 54.6 seeds per inflorescence in South Orkney Island material, virtually identical to that found in the present study, but 110 seeds per inflorescence at a South Georgian site. The species has a wide ecological amplitude and shows a very wide range of plant size on South Georgia, and Edwards' (1974, Table III) data indicate that his material was four- to ten-fold larger (linear dimensions) than most of his South Orkney Islands samples, in contrast to the two- to four-fold mass difference in material obtained in the present study.

The results presented in Table IV indicate that *D. antarctica* reproductive biomass represented c. 50% of total tiller biomass in South Georgian material and up to c. 55–66% in Signy Island and Léonie Island material. Whilst at least three inaccuracies are likely to influence the interpretation of these results (ignoring root biomass, loss from dead or decaying vegetative elements, and inter-annual variation in allocation as seen on Signy Island), it is clear that reproductive allocation is high in this species, especially in more extreme habitats in the maritime Antarctic. Wilson & Thompson (1989), in a study of reproductive allocation in above-ground biomass in 40 British grasses, recorded such high biomass proportions only in annual species, with most perennials giving much lower figures (e.g. the congeneric perennials *D. caespitosa* and *D. flexuosa* had values of 5.4% and 18.1% respectively). Maritime Antarctic material of the perennial *D. antarctica* may invest more in reproductive structures due to the harshness or instability of its environment (i.e. the offspring are more likely to survive than the parent plant), although Wilson & Thompson (1989) suggest that stress-tolerant plants (*sensu* Grime 1979) are likely to have low levels of reproductive allocation. Plants in harsher sites may divert resources into reproduction by seed rather than clonal growth, as production of flowering shoots and seeds appears to be less frequent by *D. antarctica* plants forming lush swards on more stable

moist ground than by single plants in drier or unstable areas (Greene & Holtom 1971).

The relationships between reproductive and vegetative biomass, and between seed numbers and reproductive biomass in both species were very strong. The linear regression models provide data that are comparable with wide-ranging reviews of reproductive investment patterns in plants and animals (Rees & Crawley 1989) and herbaceous plants (Aarssen & Taylor 1992).

Reproductive adaptations do not appear to account for the presence of either species in the maritime Antarctic, or for the failure of other species, successful for instance on South Georgia, to become established at higher latitudes. As in Arctic tundra environments, annual life cycles are not practicable (Löve & Löve 1974), since minimum generation time may extend to three years or more (see Bennett, Smith & Smith 1982). A more significant limiting factor may be the rate at which seeds or colonizing fragments can produce roots and leaves to establish new plants. If this is greater than the duration of favourable microclimatic and soil moisture conditions during the short austral summer, then establishment will not occur. Bennett *et al.* (1982) invoke this explanation, in the context of known inverse relationships between the durations of the mitotic cycle, minimum generation time, and nuclear DNA content (Van't Hof & Sparrow 1963, Bennett 1972, Bennett & Smith 1976). Measurement of the DNA content of *D. antarctica* from Galindez Island (Argentine Islands, c. 65°S) and other species from South Georgia gave values at the low end of the range found for temperate species, as would be expected for those with a short establishment time (Bennett *et al.* 1982). Although this may considerably reduce the pool of potential colonists, transplants of several South Georgian and Falkland Islands plant species to Signy Island (Edwards & Greene 1973, Edwards 1980), demonstrated that a number of species could survive the disruption, establish in a probably sub-optimal site and produce viable seed over a period of 2–3 years. In particular, fast-growing grasses (*Poa annua* and *Paradichloa flabellata*) appear to be likely colonists. *P. annua* and the closely related *P. pratensis* were accidentally introduced to the maritime Antarctic (Corte 1961b, Longton 1966) and the latter has survived for over 35 years (Smith 1996). The bipolar grass, *Phleum alpinum* L., has a northern distribution limited by the inability of its depauperized gene pool to produce the adaptations necessary to allow survival in shorter growing seasons, whereas the genecological variation and plasticity seen at its current southern limit on South Georgia suggest that the limit is simply geographical (Callaghan 1974).

Taken together, the results of this and previous studies of *D. antarctica* and *C. quitensis* suggest that their presence throughout much of the maritime Antarctic is more a matter of chance, than due to any exceptional physiological ability or ecological plasticity. Dispersal on a local scale after initial colonization, via biotic agents such as nesting birds (notably

gulls and skuas), appears sufficient to explain their wide distribution within the maritime Antarctic. A number of other species appear to be physiologically capable of making the transition and, particularly in the context of current global and regional warming scenarios, may be expected to succeed eventually, with or without human assistance.

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