# STUDIES IN Colobanthus quitensis (Kunth) Bartl. AND Deschampsia antarctica Desv.:

# IV. DISTRIBUTION AND REPRODUCTIVE PERFORMANCE IN THE ARGENTINE ISLANDS

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ABSTRACT. The detailed distribution of *Colobanthus quitensis* and *Deschampsia antarctica* in the Argentine Islands was mapped between 1963 and 1965, and revealed that *D. antarctica* was quite widespread but that *C. quitensis* was confined to three localities. Flowers and inflorescences were produced at most of the sites but mature seed, although set during 1962–63 and 1964–65, was not formed by either species during 1963–64. Germination tests using different temperature regimes showed that seed produced in 1962–63 was viable.

Colobanthus quitensis (Kunth) Bartl. and Deschampsia antarctica Desv. were first discovered in the Argentine Islands during the British Graham Land Expedition, 1934–37 (Bertram, 1938). D. antarctica was seen again by J. Smith in 1957 and by B. J. Taylor in 1960, but apart from these records no other information was available about either species on these islands at the beginning of this investigation.

Observations on the distribution, ecology and reproductive performance of the two species in the Argentine Islands, together with germination tests, were carried out during the period December 1963 to April 1965 while the author was stationed at the British Antarctic Survey station on Galindez Island.

#### DISTRIBUTION OF SPECIES

Fig. 1 shows the distribution and abundance at each site of D. antarctica and C. quitensis in relation to the extent of botanical survey and the amount of ice-free ground. It can be seen that the grass was locally common on the eastern group of islands, extending from Irizar Island in the north to Black Island in the south, whereas C. quitensis was restricted to a single locality on Galindez Island, an island south-west of Irizar Island and Skua Island. The western group of islands was not so thoroughly examined but the vegetation as a whole was poorly developed and the two species were represented by a single tuft (c. 7.5 cm. in diameter) of D. antarctica on the largest island of The Barchans. This difference in vegetation between the eastern and western groups may be a reflection of the nature of the rocks, as the eastern half is composed of Upper Jurassic volcanic rocks (Elliot, 1964) which frost-shatter easily forming mineral detritus, while the western half is mainly composed of Andean granodiorite which is a hard frost-resistant rock smoothed by glacial action.

The Colobanthus quitensis localities were on north- to north-west-facing rocky slopes in close proximity to the sea, at an altitude of 6 m. on the side of Meek Channel, Galindez Island, and on the north-east coast of the island south-west of Irizar Island but reached 15 m. at the south-west corner of Skua Island. The species occupied such habitats as dry cracks and fissures in rocky areas, broad ledges covered by shallow mineral deposits and the sides of drainage channels over rocks, and formed individual cushions 2–5 cm. in diameter. At each locality C. quitensis was associated with D. antarctica but extended over a smaller area, in fact being confined to the most sheltered positions. This is further emphasized by the occurrence of the uncommon male inflorescences of Polytrichum alpinum at the localities on Galindez Island and the island south-west of Irizar Island. The colony on Galindez Island consisted of c. 20 cushions spread over an area 3 m. × 1·5 m. with two cushions isolated about 4·5 m. to the east. The colony on the island south-west of Irizar Island contained two groups of cushions separated from one another by 23 m., the eastern group comprising 20 cushions scattered over an area 3·3 m. × 2·8 m., while the western contained c. 50 cushions spread over an area 9·3 m. × 4·7 m. Detailed plans of the Galindez Island colony (Fig. 2) and the eastern group of the colony on the island south-west of Irizar Island (Fig. 3), showing

<sup>\*</sup> Present address: Hawthorn Hill, 36 Wordsworth Street, Penrith, Cumberland.

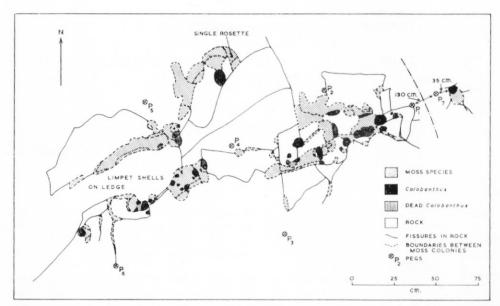


Fig. 2. Plan of *Colobanthus quitensis* colony on the north-east coast of Galindez Island, overlooking Meek Channel, 16 March 1964. The site was sheltered and well drained on a 70° slope.

the positions of individual cushions in relation to topography and associated bryophyte colonies, were prepared and re-examination of these sites in later years should allow changes in density to be followed, thus indicating whether the populations are in equilibrium, expanding or contracting. In contrast to the two colonies just considered, the one at the south-west corner of Skua Island was more diffuse and contained a total of 50 cushions spread over 100 m. of coastline. The cushions were arranged in three groups, those at either end containing c. 20 cushions each with c. ten cushions in the centre.

In all these areas the cushions of *C. quitensis* were compact and green and, although tinged with yellow during winter, they appeared green after the snow had melted. Where a single rosette or a small number of plants was seen, they appeared to be the living remnants of larger cushions rather than young plants developed from seedlings. However, these cushions formed an insignificant proportion of the total number at a site. *C. quitensis* was absent from apparently suitable sites on Skua Island overlooking Skua Creek, the western end of the Corner Islands and the northern ends of Uruguay and Irizar Islands.

D. antarctica occupied north- and west-facing slopes on the northern and western sides of the islands with occasional plants on the ice-free eastern sides, at altitudes ranging from 2.5 m. on Galindez Island to 65 m. on Uruguay Island. At most sites the grass occurred as individual tufts varying from 5 to 12.5 cm. in diameter scattered over a fairly wide area, but on the western end of the Corner Islands, tufts had coalesced to form a small sward covering 0.2-0.4 m.<sup>2</sup>.

Deschampsia antarctica occupied wet and dry habitats. The drier habitats were cracks and hollows filled with mineral material on rocky knolls and on old limpet shell deposits, while the moister habitats were flat ledges flushed by melt water. When the snow receded from the drier areas, the D. antarctica tufts appeared extremely withered and brown with a number of small green shoots just visible in plants which superficially looked dead. These tufts from the drier exposed areas possessed shorter finer and more wiry leaves often with a glaucous appearance compared with the broader greener leaves of the more robust plants from moister habitats.

Birds may have a considerable influence on the distribution of D, antarctica in the Argentine Islands. Deposits of limpet shells, often over 30 cm. deep, were a striking feature of the coastal rocks in many parts of the group. These deposits were found near past and present colonies

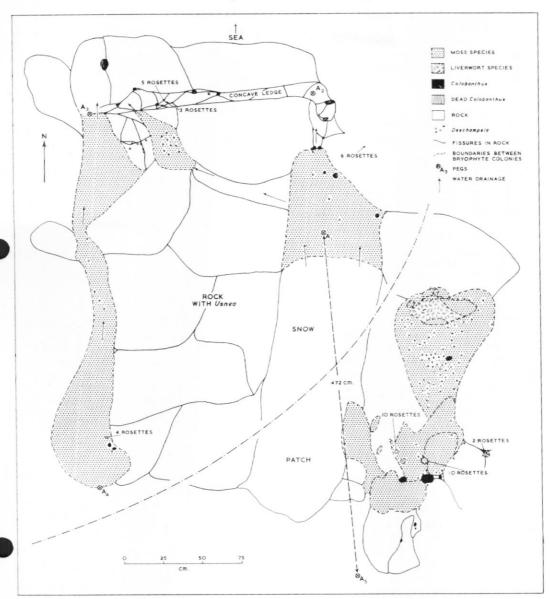


Fig. 3. Plan of eastern group of *Colobanthus quitensis* colony on the north coast of the island south-west of Irizar Island, 21 November 1964. The site was sheltered and well drained on a 25° slope.

of breeding Dominican gulls. Where the shells were old and disintegrating, they had a typical bryophyte cover but the newer deposits were barren. Plants of *D. antarctica* colonized areas where the bryophyte cover was well-developed, and it is interesting to note that the single tuft on The Barchans was growing on an old shell deposit with the moss *Drepanocladus uncinatus*. Black Island had extensive areas of relatively fresh deposits and *D. antarctica* was absent. The gulls also incorporate dead grass stems into their nests and it is possible that seed from old inflorescences may be transferred from one area to another in this way. On a thin deposit of

old undisturbed guano at the periphery of the blue-eyed shag colony on Uruguay Island, a few small green tufts of *D. antarctica* were seen. Skuas tended to be restricted to the areas of *Polytrichum alpestre* turf, but tufts of *D. antarctica* were only a few metres from some nests on Galindez Island. As there were no penguin or seal colonies in the Argentine Islands, the competition for suitable coastal habitats produced by these animals in other Antarctic areas is absent.

#### RECORDS AND SPECIMENS

The author's field records on which the localities shown in Fig. 1 are based were made between December 1963 and April 1965, and are additional to the following:

# Deschampsia antarctica

Galindez Island: 2.iii.1935, BGLE 1059 (biological register†); 2.i.1957, J. Smith M173A (BIRM\*); 11.ii. 1960, Taylor 60 (BIRM\*); 25.ii.1965, Corner 862 (BIRM\*); 15.iii.1965, Corner 863 (BIRM\*); 20.iii.1965, Corner 864 (BIRM\*).

Skua Island: 27.ii.1966, Northover, Field record 2706.

# Colobanthus quitensis

Galindez Island: 14.xii.1935, BGLE 1308<sup>+</sup> (BM); 29.xii.1935, BGLE 1332 (biological register); 20.iii.1965, Corner 840 (BIRM\*).

Skua Island: 27.ii.1966, Northover, Field record 2707.

### REPRODUCTIVE SUCCESS

Field observations showed that there was much variation in inflorescence production and maturation in *D. antarctica* from different habitats and localities. Plants on the exposed, dry rocky knolls although small with little foliage produced an abundance of inflorescences which appeared to mature earlier than at other more sheltered moister sites. Plants in very moist habitats had well-developed foliage and were usually sterile. It was noticed that flowering culms on plants growing on the dry, exposed rocky knolls were smaller than those from the moister sheltered sites. Table I provides a comparison of culm length between plants from exposed and sheltered sites on Galindez Island along the edge of Stella Creek. In spite of the small size of the samples, the differences are clearly maintained at each stage of maturity.

Table I. Length of flowering culms in *Deschampsia antarctica* at the Stella Creek site on Galindez Island

Date measured	Dry exposed habitat			Moist sheltered habitat			
	Inflorescence stage	Number measured	Mean (cm.)	Inflorescence stage	Number measured	Mean (cm.)	
6.i.1965	2	10	2.6	2	2	6.3	
1.ii.1965	4	10	3.5	4	2	7.5	
28.ii.1965	5	10	6.1	5	2	12.0	

Fig. 4a shows inflorescence maturity for *D. antarctica* at different sites during 1964 and 1965. It is obvious that the site on the side of Meek Channel had inflorescences less advanced in March 1964 than in March 1965 and that this site was also slightly behind the others during 1964–65. The first fully expanded inflorescence of the 1964–65 season was seen at the Meek Channel site on Galindez Island on 1 February 1965, while by the middle of the second week

† Preserved in the Scott Polar Research Institute, Cambridge.

‡ Cited in error as BGLE 1388 by Skottsberg (1954).

<sup>\*</sup> Preserved in the British Antarctic Survey herbarium, at present housed in the Department of Botany, University of Birmingham.

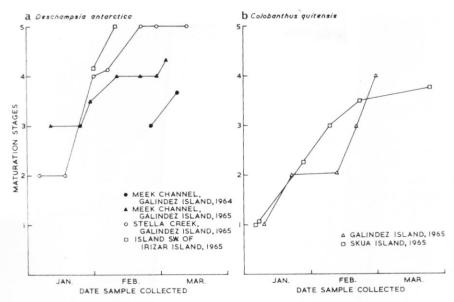


Fig. 4. Inflorescence and capsule maturity, according to the date of observation, for (a) Deschampsia antarctica and (b) Colobanthus quitensis from sites in the Argentine Islands.

of the same month all the inflorescences on the island south-west of Irizar Island were fully expanded, as were those at the Stella Creek site 1 week later. From Table II it can be seen that a specimen from Skua Island collected on 27 February 1966 showed a maturity similar

to plants of D. antarctica at the Meek Channel site at the same date in 1965.

Seed produced by *D. antarctica* during 1962–63 was collected on Galindez Island on 14 March 1964 from a locality *c.* 0.4 km. west of the Meek Channel site and when measured a sample of 100 mature brown seeds gave a mean size of 1.6 mm. No seed from 1963–64 was measured but it was very immature at the end of season and there was no evidence of any maturation taking place during the following winter. During 1964–65 plants from the Meek Channel site had green swollen seeds on 8 February but by 25 February the seed was hard, brown and measured 1.6 mm. (Table II). At the Stella Creek site, mature seed measured 1.6 mm. by 20 March, although on 11 March the seed had been swollen but still green. A sample from Skua Island had hard brown seed by 22 March. The Skua Island observation is of interest as a specimen collected the following season on 27 February 1966 had rather small seed 10.8 mm.).

Occasional seedlings of D. antarctica were observed but they were not common.

During 1962–63 mature open capsules of *C. quitensis* were produced on Galindez Island, and on the island south-west of Irizar Island, but during 1963–64 no buds were seen at the former site, while by the end of March at the site on the island south-west of Irizar Island, flowers were only at the unopened bud stage. No records were made on the Skua Island colony for this season. In 1964–65 mature open capsules were observed in all three colonies, but in the following season Northover collected a plant from Skua Island on 27 February 1966 in which the buds were just opening (Table II). Fig. 4b shows the relative performance for two sites in the 1964–65 season. Buds became visible at the beginning of January and capsules opened from February onwards. However, at the end of March buds were also present but it is thought that they were laggers rather than representatives of a second series. There is no evidence that these late-season buds develop over winter; in fact, the majority became brown and dead during May 1965 after being covered and uncovered a few times by snow and by the beginning of 1965–66 only a few were visible, the rest having presumably decayed (personal communication from I. Sadler).

Table II. Maturity indices and mean size of largest seeds for specimens of *Deschampsia antarctica* and *Colobanthus quitensis* from Galindez and Skua Islands

Locality	Specimen	Date	Old inflorescences or capsules		New inflorescences or capsules	
	number	Duic	Maturity index	Seed size (mm.)	Maturity index	Seed size (mm.)
Deschampsia antarctica						
Galindez Island	J. Smith M173A	2.i.1957	5.0	1.0	_	
	Taylor 60	11.ii.1960	5.0	1.7	_	
	Corner 862	25.ii.1965	_		4.8	1.6
	Corner 863	15.iii.1965	_		5.0	1.6
	Corner 864	20.iii.1965	-	_	4.6	1.6
Skua Island	Northover s.n.	27.ii.1966	_	_	4.0	0.8
Colobanthus quitensis						
Galindez Island	BGLE 1308*	14.xii.1935	3.8	0.6		
	Corner 840	20.iii.1965	_	_	3.0	0.7
Skua Island	Northover s.n.	27.ii.1966	4.0	0.6	2.0	

<sup>\*</sup> Cited in error as BGLE 1388 by Skottsberg (1954).

Seed produced during 1962–63 was collected from the site on the island south-west of Irizar Island on 3 March 1964 when a sample of 75 seeds gave a mean size of 0.7 mm. In the Galindez Island colony, seed measured on 20 March 1965 was 0.7 mm. (Table II), while seed from overwintered capsules at the Skua Island colony had seed 0.6 mm. in size on 27 February 1966.

No seedlings of Colobanthus auitensis were observed in the Argentine Islands.

#### GERMINATION TESTS

Precisely controlled temperature cabinets were not available but three different rooms were used for the germination experiments. For the higher temperatures (20° to 25° C) an incubator, which consisted of an insulated wooden box heated by a 100 W light bulb controlled by a thermostat, was kept at room temperature inside the station building. For the intermediate temperature (12° C) the incubator was kept in an unheated sonde hut, and for low temperatures (2° to 5° C) the seeds were placed directly in their container in the thermostatically controlled room in the magnetic hut.

For each experiment, two groups of 50 seeds for each species were planted out in separate petri dishes on moist filter paper and placed in a cardboard box to exclude light. The seeds were examined daily for germination and at the same time watered with de-ionized water. A seed was counted as having germinated when the length of the emerging radicle exceeded the breadth. In another set of experiments, seeds were planted in petri dishes as before, but were

placed out of doors in dark conditions on a north-facing ledge.

Seed of *D. antarctica* was collected from the colony *c.* 0.4 km. west of the Meek Channel site on 14 March 1964 from old inflorescences which had been produced in the 1962–63 season. The *C. quitensis* seed was collected from the island south-west of Irizar Island on 3 March 1964 from capsules produced in 1962–63. Seed from both species had therefore over-wintered on the plants under normal field conditions. The mean size of a sample of the seeds for each

species which was used in the experiments has been given above.

Fig. 5a shows the percentage germination obtained at different temperatures with seeds of *D. antarctica*. It is obvious that the temperature affects both the rate and degree of germination with the amount varying from none at 0° C to about 20 per cent at 20° or 25° C. Fig. 6a shows the increase in percentage germination when seed was transferred to a higher temperature. The least effect was obtained with seeds moved from 12° to 20° C. A slightly greater effect was noted with seeds moved from 4° to 12° C but the best results were obtained with those moved from 4° to 20° C. These results suggest that a sharp rise in temperature acts as an effec-

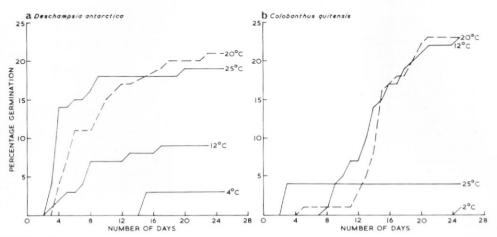


Fig. 5. Daily percentage germination at various temperatures of over-wintered seed of (a) Deschampsia antarctica from the colony 0·4 km. west of the Meek Channel site, Galindez Island, and (b) Colobanthus quitensis from the island south-west of Irizar Island.

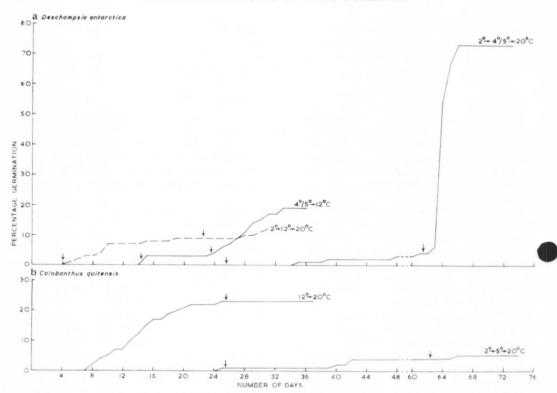


Fig. 6. Effect of temperature increase on daily percentage germination of over-wintered seed of (a) *Deschampsia* antarctica from the colony 0·4 km. west of the Meek Channel site, Galindez Island, and (b) *Colobanthus* quitensis from the island south-west of Irizar Island. The arrows show the date of temperature increase.

tive stimulus and results in a better percentage germination (73 per cent) than continuous high temperatures (19 to 21 per cent).

A sample of 30 seeds which were still green was collected from the *D. antarctica* site at Stella Creek on 11 March 1965 and planted out at room temperature. These seeds had been produced the same season and therefore received no cold pre-treatment as a result of overwintering but, nevertheless, they gave 16 per cent germination after 9 days.

The percentage germination at different temperatures obtained with the seed of *C. quitensis* is given in Fig. 5b. It may be noted that a small number of seeds in some of the samples appeared to be infected with a fungus which is believed to have reduced the amount of the final germination. No fungus was seen on seeds of *D. antarctica*. A very small percentage germination (2 per cent) was obtained after 25 days with seeds of *C. quitensis* at 2° C but there was no difference in the final figure (23 per cent) at 12° and 20° C. Unlike *D. antarctica*, the highest temperature (25° C) appeared to suppress development. The transfer of *C. quitensis* seeds from lower to higher temperatures made very little difference to the final percentage (Fig. 6b), in fact, none at all in seeds moved from 12° to 20° C. Seeds moved from 2° to 5° to 20° C showed a small increase in germination, but the final figure (5 per cent) was much lower than that for seed kept continuously at 12° or 20° C (23 per cent). This contrasts with the greatly increased germination obtained with seeds of *D. antarctica* subjected to a sharp temperature increase.

In another experiment, seeds of *Deschampsia antarctica* and *Colobanthus quitensis* were tested under the same culture conditions as before but placed out of doors on a north-facing ledge in a light-proof box. The seeds were maintained in these conditions for 61 days when

the final germination for D. antarctica was 25 per cent and for C. quitensis 10 per cent. During this period, the maximum air temperature recorded was  $8 \cdot 3^{\circ}$  C with a minimum of  $-4 \cdot 6^{\circ}$  C. On 45 days (73·8 per cent) a temperature at or below  $0^{\circ}$  C was recorded, for 15 days (24·6 per cent) the temperature was continuously above  $0^{\circ}$  C, while on 1 day (1·6 per cent) the temperature did not rise above  $0^{\circ}$  C. These temperatures are probably lower than those actually experienced by the seeds and are lower than seeds germinating under natural conditions would experience since mean temperatures at ground level are normally higher than those recorded in the meteorological screen.

# DISCUSSION

In the Argentine Islands, *Deschampsia antarctica* proved to be more widely distributed than *Colobanthus quitensis*. The grass was regularly present on most extensive north-facing ice-free coastal areas with some form of mineral substratum, which were not trampled or fouled by birds. The species mainly occurred as scattered tufts and only at one site was the latter sufficiently dense to form a small sward. *C. quitensis*, on the other hand, was absent from some apparently suitable sites and where it occurred it formed localized colonies always associated with *D. antarctica*. These results support the findings of Greene and Holtom (1971), who reported that, although both species are widespread along the west coast of the Antarctic Peninsula and its offshore islands, at the local level *D. antarctica* is the commoner with *C. auitensis* confined to the more sheltered habitats at lower altitudes.

In the Argentine Islands, both species grew in a range of habitats varying from moist to dry rock outcrops and ledges but it was noticeable that *C. quitensis* was restricted to the more sheltered localities which showed similarities to the radiation traps described from Signy Island by Holdgate (1964). The presence of the uncommon male inflorescences of *Polytrichum alpinum* at two of the three *C. quitensis* sites, as already noted, seems to reflect the more favourable environment of these areas. Deposits of limpet shells were often a striking feature of the *D. antarctica* sites and in view of the low-lying nature of the islands and the prevailing amounts of spray, particularly during storms, both must be able to withstand

considerable levels of salinity in the substratum.

Snow cover is thought to play an important part in insulating the plants from temperature extremes during winter, deep drifts forming over the hollows and ledges and normally persisting without break until the following spring. However, the duration of snow cover depends upon the topography of the locality and the prevailing climatic conditions of the season. At the end of the 1963-64 summer, snow cover was more or less complete over the Argentine Islands by the end of March with virtually all D. antarctica plants being covered from that date until exposed by the spring thaw at the beginning of November 1964. Snow cover was again complete over most plants by the end of March 1965. The C. quitensis colony on Galindez Island, on the other hand, became snow covered on 24 March 1964 but half the colony was re-exposed for a few days 1 month later. The snow did not recede from the colony until 25 November 1964 which was probably about 2 weeks later than at the colony on the island south-west of Irizar Island. Early in the winter of 1965, a similar pattern was followed at the C. quitensis site on Galindez Island, part of which remained covered from the end of March until exposed by the spring melt in mid-December, but individual cushions on the sloping cliffs above the main colony were alternately exposed and covered during April and May until heavy snowfalls during 18-20 May resulted in a complete coverage by 30 May.

It appears, therefore, that at some *C. quitensis* sites the duration of continuous snow cover may vary for individual plants. While early exposure in spring may be beneficial, it remains to be determined what benefits, if any, result from a delay in establishing snow cover once the winter climatic regime has been established. In more general terms it seems that in most seasons plants of both species are uncovered for 4–5 months during the year, from some time in

November to near the end of March.

Factors in addition to the duration of snow cover must influence reproductive success. During 1963–64 *D. antarctica* inflorescences only developed to stage 3 or 4 by the end of March with no mature seed having been set, while the following year at the same time all inflorescences reached at least stage 4, with many at stage 5, and mature seed was present. Similarly,

C. quitensis had only produced buds (stage 1) by March 1964 but many open capsules (stage 4) with mature seed were present in March 1965. It has also been determined that during 1962–63 both species produced mature seed. When these results are compared with those given by Holtom and Greene (1967) for the same seasons on Signy Island, it is found that both species performed similarly in the two areas over two of the seasons, i.e. only immature seed was produced in both areas during 1963–64, but both species set mature seed in each area during 1964–65; in the third year (1962–63) performance appeared better at the Argentine Islands than on Signy Island. No evidence was found to support the suggestion that seeds increase in size over winter, but this is perhaps hardly surprising in view of the immature state of flowers and spikelets at the end of 1963–64.

In spite of the fact that conditions used in the germination experiments could not be as rigorously controlled as was wished, the results demonstrate the effect of increase in temperature on the amount and rate of germination, higher temperatures clearly improving both in *D. antarctica* but not in *C. quitensis*. When seed kept at low temperatures was transferred to higher temperatures, it was again found that the higher temperatures accelerated and increased germination in *D. antarctica*, particularly if the rise was sharp, but little comparable acceleration was shown by *C. quitensis*. These germination tests have proved that both species are capable of setting viable seed, at least in some seasons, in the Argentine Islands, while the results from the seeds tested out of doors suggest that seed will germinate under field conditions. This conclusion is confirmed for *D. antarctica* by an observation made on 26 February 1964 of young seedlings growing in the colony of the grass on coastal rocks on Galindez Island, *c.* 0·4 km. west of the Meek Channel site.

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#### REFERENCES

Bertram, G. C. L. 1938. Plants and seals. (In Fleming, W. L. S., Stephenson, A., Roberts, B. B. and G. C. L. Bertram. Notes on the scientific work of the British Graham Land Expedition, 1934–37. Geogrl J., 91, No. 6, 523–26.)

ELLIOT, D. H. 1964. The petrology of the Argentine Islands. British Antarctic Survey Scientific Reports, No. 41,

31 pp

GREENE, D. M. and A. HOLTOM. 1971. Studies in Colobanthus quitensis (Kunth) Bartl. and Deschampsia antarctica Desv.: III. Distribution, habits and performance in the Antarctic botanical zone. British Antarctic Survey Bulletin, No. 26, 1–29.
HOLDGATE, M. W. 1964. Terrestrial ecology in the maritime Antarctic. (In CARRICK, R., HOLDGATE, M. and

J. Prévost, ed. Biologie antarctique. Paris, Hermann, 181–94.)

HOLTOM, A. and S. W. GREENE. 1967. The growth and reproduction of Antarctic flowering plants. (In SMITH, J. E., organizer. A discussion on the terrestrial Antarctic ecosystem. Phil. Trans. R. Soc., Ser. B, 252, No. 777, 323–37.)

SKOTTSBERG, C. 1954. Antarctic flowering plants. Bot. Tidsskr., 51, No. 4, 330-38.