STUDIES IN *Colobanthus quitensis* (Kunth) Bartl. AND *Deschampsia antarctica* Desv.: VI. REPRODUCTIVE PERFORMANCE ON SIGNY ISLAND

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ABSTRACT. Investigations into the reproductive cycles of *Colobanthus quitensis* and *Deschampsia antarctica* on Signy Island have shown that in both species floral primordia were first formed in the autumn prior to the spring in which they matured. *C. quitensis* produced a second flush of buds towards the end of summer but these invariably failed to mature. Habitat differences influenced the flowering performance of both species and, although flowers were produced at most sites each season, widespread production of mature seed occurred in only three of the nine seasons assessed.

Seeds, particularly of *D. antarctica*, increased in length by small amounts during winter under snow, and germination of field-produced seed in natural conditions has been observed in several seasons. There remains some doubt as to the importance of reproduction by seed since seedling mortality appears to be high.

THE occurrence of only two native vascular plant species on the Antarctic Peninsula testifies to the strict limitations which the South Polar environment imposes on plant survival. One of the important factors for a species' survival and colonization is its reproductive ability and a detailed consideration of this is essential for a fuller understanding of the ways in which plants adapt to extreme environments. Previous papers in this series (Corner, 1971; Greene and Holtom, 1971) have dealt with the reproductive success of *Colobanthus quitensis* and *Deschampsia antarctica* within the Antarctic botanical zone but more detailed information is available from Signy Island (lat. 60°40′S., long. 45°40′W.), where a long-term study has been in progress since 1961–62.

The present paper outlines the flowering behaviour of both species on Signy Island and describes the variation of each with locality and season. A description of the habitats, preferences and vegetative performance of both in the South Orkney Islands can be found in Edwards (1972) and Smith (1972), while some of the environmental factors influencing the flowering of South Georgian populations of the grass and pearlwort have been discussed by Holtom and Greene (1967). Of the unpublished field notes or reports, referred to later in this paper, which are preserved in the Survey's Botanical Section Library, that by A. D. Bailey for 1962–65 is additional to those which have been cited at the beginning of the Appendix to Edwards (1972).

DISTRIBUTION IN THE SOUTH ORKNEY ISLANDS

Since the last account of the performance of *D. antarctica* and *C. quitensis* on the South Orkney Islands was published (Greene and Holtom, 1971), further distribution and flowering data have been obtained. Fig. 1 shows the present known distribution of grass and pearlwort within the group, excluding Signy Island which has already been brought up to date by Edwards (1972). Their occurrence does not appear so widespread as in the South Shetland Islands (Lindsay, 1971), but low-lying areas free from permanent snow and ice are more extensive on Livingston and King George Islands.

The following records are additional to those given by Greene and Holtom (1971) and Edwards (1972):

Colobanthus quitensis

Coronation Island *Buttress north of Olivine Point:* 12.iii.1972, BAS MISC. 45 (AAS). *Moraine at snout of Laws Glacier:* 9.i¹.1972, Webb (field record).

Deschampsia antarctica

Coronation Island *Buttress north of Olivine Point:* 12.iii.1972, BAS MISC. 46 (AAS). *Moraine at snout of Laws Glacier:* 9.ii.1972, Webb (field record). *Mansfield Point:* 9.ii.1971, McManmon 208 (AAS). *Meier Point:* 9.ii.1971, McManmon 207 (AAS).

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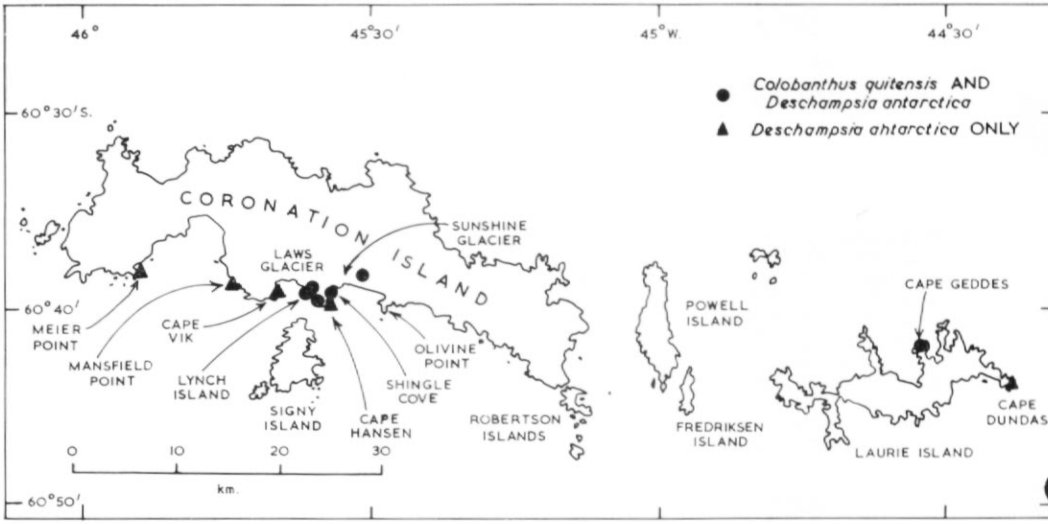

Fig. 1. Distribution of *Colobanthus quitensis* and *Deschampsia antarctica* on the South Orkney Islands, excluding Signy Island.

Flowering Cycles on Observation Bluff during 1968–69

The author recorded the development of the grass and pearlwort populations on Observation Bluff (Fig. 2) at fortnightly intervals during the 1968–69 growing season and intermittently throughout the 1969 winter; some observations were also made in the spring of 1969–70. At

Fig. 2. Community of *Colobanthus quitensis* and *Deschampsia antarctica* at Observation Bluff, Signy Island. The tall stakes are *c.* 1·5 m. high.

each sampling, the mean maturity of 100 grass inflorescences and 25 pearlwort flowers was assessed using the five-point scale described by Holtom and Greene (1967). Samples of *c*. 25 were used for more detailed measurements. Part of the populations were covered by a glass cloche to determine the effects on flower and seed production of shielding the plants from wind.

Deschampsia antarctica

Inflorescence sheaths became visible externally on the grass at the end of December 1968, *c*. 6 weeks after the melt of the final spring snowfalls, and by late January most of the panicles were partly exserted. The emergence of an inflorescence from its sheath was due, initially, to the extension of the panicle (Fig. 3a) but later the elongation of the inflorescence stalk pushed the panicle further out of the sheath. A significant increase in the number of spikelets per panicle was recorded in the latter part of the season, suggesting that the panicles continued to differentiate when partially exserted (Fig. 3b). By the end of March the inflorescences still had not emerged fully or become spreading, and throughout the summer the florets remained closed so that the anthers were never seen exserted from the glumes (Fig. 4a). The average size of seed formed at the end of season was 0·55 mm., less than half the size of mature viable seed.

In samples collected on 19 and 29 March 1969, immature inflorescences 0·2–1·0 mm. in length were detected at the base of several tillers, within one or two rudimentary leaves which were themselves completely hidden by the bases of the mature leaves. It was later confirmed to be these partially differentiated apices and leaves which, together with the youngest mature leaves, survived the winter to continue growth the following season.

Resumption of growth began almost immediately after the winter snow melted and, 10 days later in September 1969 new roots *c*. 5 mm. in length were visible on the old rhizomatous stems. However, for most of the period between September and November the grass was covered by freshly fallen snow, becoming clear for short periods only so that development was slow. In a sample collected on 22 October 1969, the degree of intumescence of certain tillers suggested that they might enclose inflorescences and after dissection 75 per cent were proved to be floral, containing inflorescences at a similar stage of development to those recorded the previous March. On 7 November 1969, each of six slightly swollen tillers dissected contained small inflorescences, the majority of which were feather-like and 0·5–1·0 mm. long, in which the spikelets were faintly discernible, but the most advanced was 3 mm. long with some of the 15 spikelets differentiated into florets with small awns.

Thus it appears that floral primordia in *D. antarctica* are morphologically initiated at the end of summer, physiological induction having previously occurred, and that they become partially differentiated into spikelets before winter. They continue their development the following spring and become recognizable as fertile culms *c*. 2 months after first melt, although frequently covered by snow during this period. The inflorescence sheaths do not become visible until about 6 weeks later when they are distinguishable by the small lengths of blade relative to the basal sheath which, although green, is more prominently veined than in a vegetative culm.

Colobanthus quitensis

Flower buds first appeared on the cushions during December 1968 and the length of the flowers remained relatively constant throughout the season. The ovaries were 0·6 mm. in length at the beginning of January and showed a steady increase in size during the latter half of the summer, the final capsule size being *c*. 1·4 mm. (Fig. 5a). A slight increase in pedicel length was observed in February 1969 (Fig. 5b), but this was not maintained and the flowers remained at the level of the vegetative leaves. Under more favourable conditions the flowers would be raised above the general cushion surface, presumably through a continuation of this elongation. The sepals rarely opened during the summer and the external appearance of the flowers remained unchanged regardless of the maturity of the enclosed stamens and sepals. Dissection of a sample collected in March revealed that the closed sepals had pressed the anthers against the styles of the swelling capsules (Fig. 4b). Abrasion of the anthers had occurred

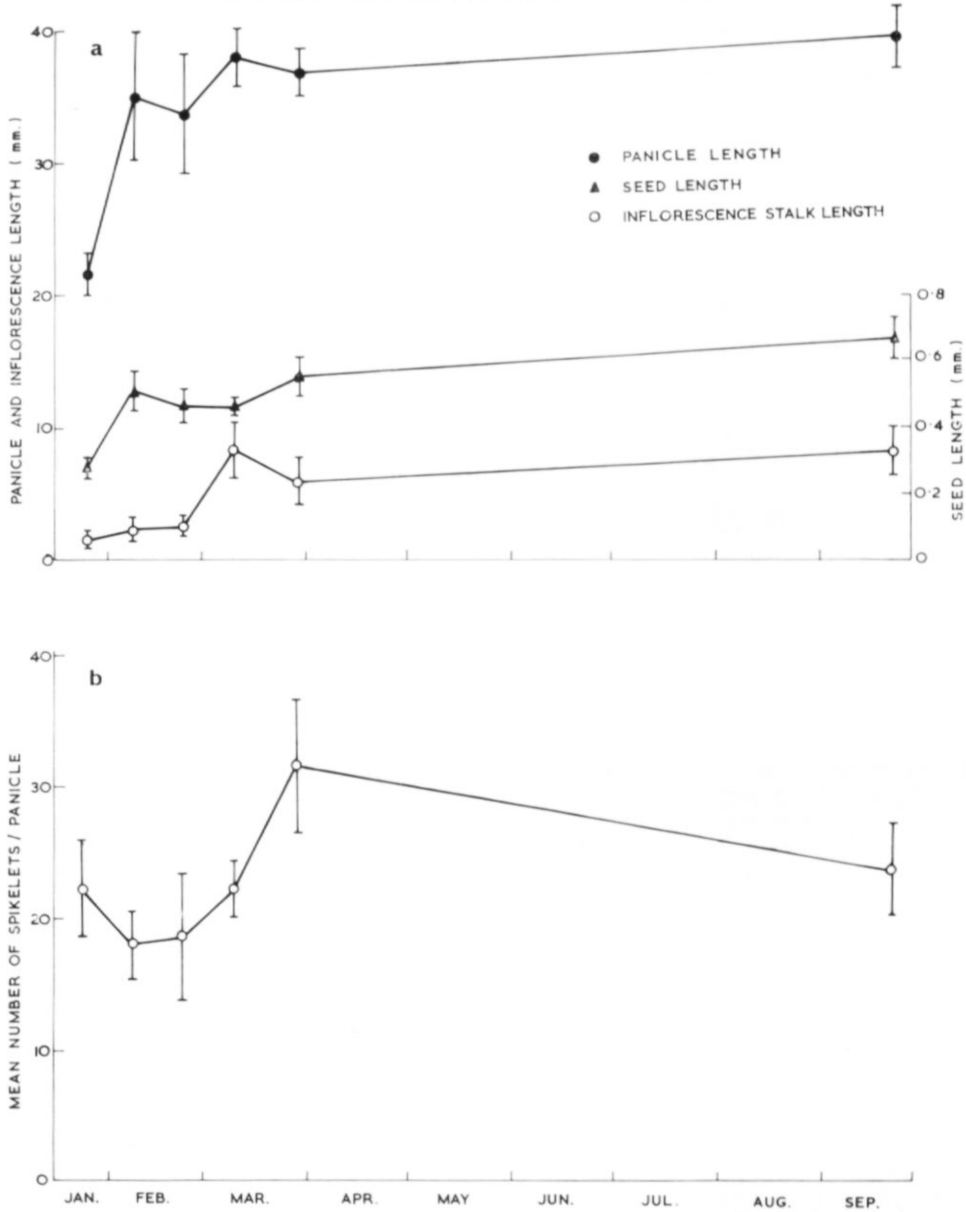

Fig. 3. Mean development of various inflorescence characters and seed of *Deschampsia antarctica* at Observation Bluff, Signy Island, during 1969. The vertical lines indicate 95 per cent confidence limits.

and the contents of the pollen sacs were visible rubbed across the stigmatic surfaces, making cleistogamy highly probable. At the end of season the occurrence of mature seed was found to correlate better with the length of the capsule than with the height of the flowers above the cushion, although none of the capsules had opened, capsules <2 mm. in length rarely containing seed $>0\cdot4$ mm. long. A situation frequently observed in the larger capsules was that, while one or two full-sized seeds might be present in the apex of a capsule, the placenta remained covered with shrivelled brown ovules *c.* 0·2 mm. in length.

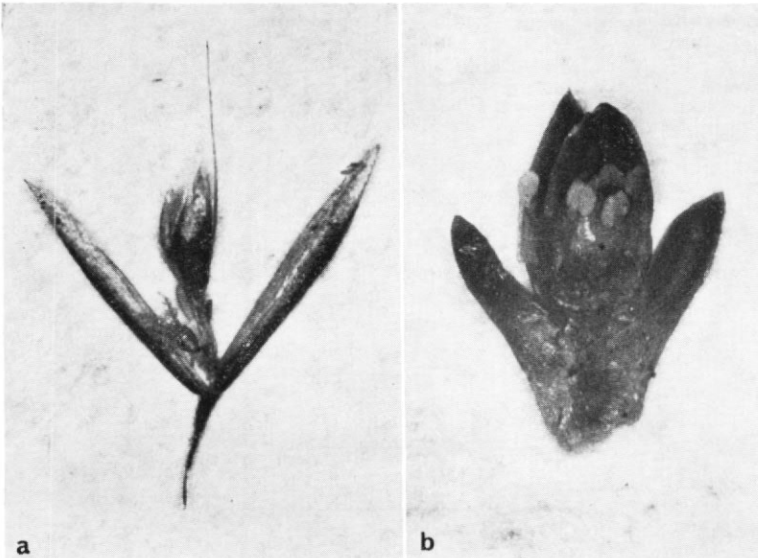

Fig. 4. Floral structure in *Colobanthus quitensis* and *Deschampsia antarctica*.
a. Spikelet of *D. antarctica* showing two florets, one of which has been dissected to show the small ovule. The upper glume is 6 mm. long.
b. Flower of *C. quitensis* showing developing capsule with anthers being pressed against the style and stigma by the sepals. The sepals are 2·5 mm. long.

A large collection of shoots, in March 1969, included flowers at all stages of maturity but buds were noted in some of the leaf axils. Some of the buds were very rudimentary with stamens and ovaries represented by small flaps of tissue and it seemed unlikely that they could have developed much further before winter, while other buds were quite well advanced with green stamens and small ovaries which could probably have developed further if the season had been longer. When these more advanced buds and the developing capsules were measured, the resulting histogram (Fig. 6) showed two distinct peaks suggesting that the buds represented a distinct second set of flowers, such as produced by *C. quitensis* under cultivation in a Birmingham greenhouse (Holtom and Greene, 1967).

Cushions on Observation Bluff still appeared in flower the following October, after the melt of the winter's snow. The old flowers from the previous summer were flaccid and moribund but others, possibly the secondary buds, remained green and turgid for several weeks. Although possessing white fleshy ovules, these flowers failed to develop mature seed and eventually decomposed so that for a short period in November and December the cushions appeared vegetative. A. D. Bailey (unpublished report) also observed green buds at all stages of development in October 1963 and marked four with cotton to study their future development but all decayed without producing seed. Thus it appears that in *C. quitensis* only the main set of flowers is able to develop during winter and that only those capsules near to producing seed at the end of summer actually ripen fully. The disintegration of moribund flowers was rapid and large populations of bacterial-feeding nematodes (*Plectus* spp.; personal communication from V. W. Spaull) were observed amongst their remains in October. Flower buds in early stages of development for the new floral cycle became visible at the end of December.

Flowering Cycles on Observation Bluff in Other Seasons

From direct observations of the *D. antarctica* and *C. quitensis* populations at Observation Bluff by various personnel, namely M. W. Holdgate (1961–62), A. D. Bailey (1962–65), C. A. Howie (1964–65), R. I. L. Smith (1964–67) and R. Webb (1970–72), it appears that a similar sequence and timing of floral development to that described for 1968–69 occurred in

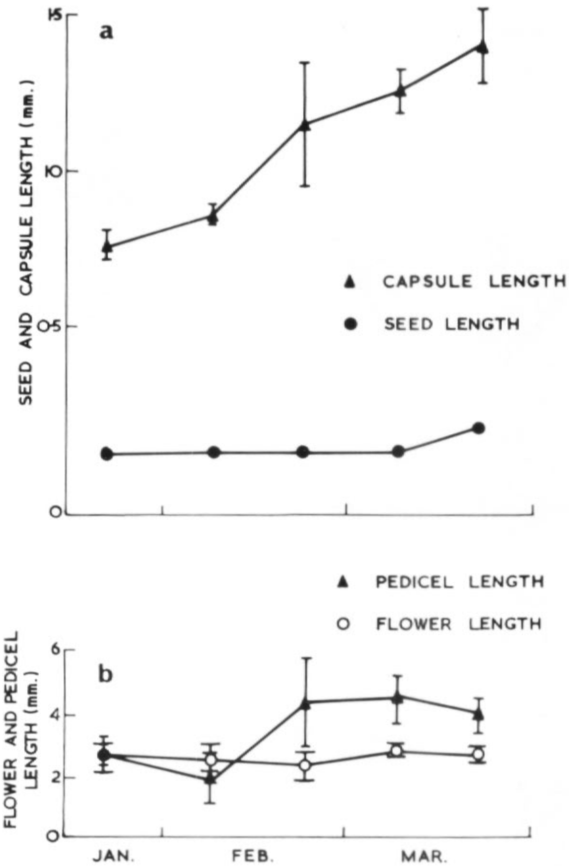

Fig. 5. Mean development of various flower characters and seed of *Colobanthus quitensis* at Observation Bluff, Signy Island, during 1969. The vertical lines indicate 95 per cent confidence limits.

the summers of 1961–62, 1965–66, 1966–67 and 1971–72 (Fig. 7). End of season inflorescences on the grass were usually half exserted but only slightly expanded, while pearlwort flowers remained at the cushion surface with capsules closed. The seeds formed by both species were generally immature in size and not viable, although small amounts of seed approaching full size were produced by some plants, particularly of *C. quitensis*. In the summer following the 1965–66 season, R. I. L. Smith (personal communication) noted that some of the old *C. quitensis* capsules contained "mature brown viable seed" while in December, after the 1966–67 season, the author noted that some full-sized seed had been produced by both species although these were shrivelled and did not prove viable in laboratory tests.

Other summer seasons appear to have been less favourable than 1968–69 for reproductive development, e.g. 1963–64, 1967–68 and 1969–70. One factor in common to these three seasons was the late arrival of snow-free conditions which resulted in the growing season not commencing until the end of November so that the development of flowering structures was retarded throughout the summer. Thus at the beginning of February most inflorescences on *D. antarctica* remained enclosed by their sheaths while sepals of *C. quitensis* flowers had failed to open. At the end of season most grass inflorescences were approximately half emerged with seeds *c.* 0·7 mm. long while the unopened capsules on the pearlwort contained shrivelled brown seeds *c.* 0·3 mm. in length (Fig. 7a). However, the development of some mature-sized *C. quitensis* seed is again a possibility since, at the beginning of October 1964,

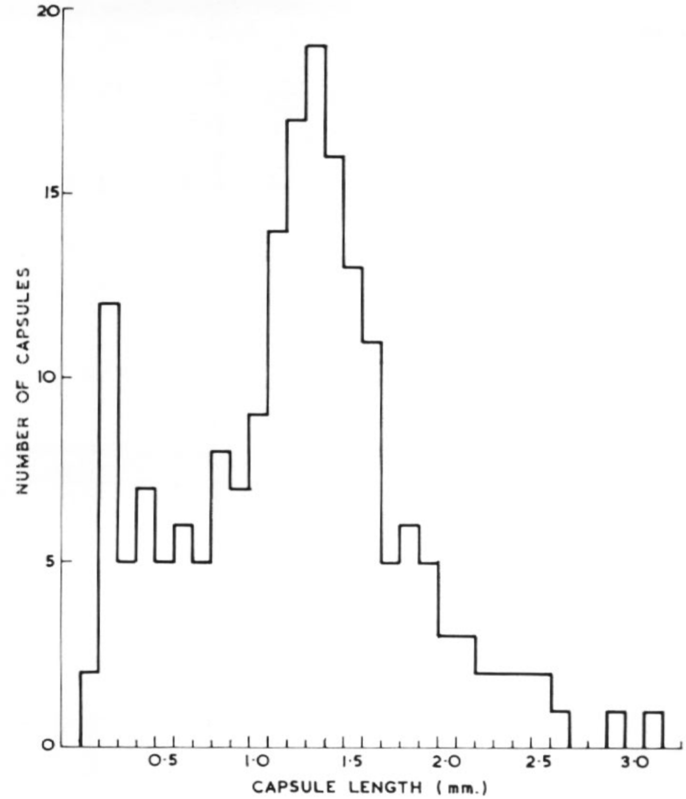

Fig. 6. Frequency distribution of capsule size in *Colobanthus quitensis* on the South Orkney Islands at the end of the 1968–69 summer.

A. D. Bailey (unpublished report) noted that some of the previous season's capsules had opened and contained a small amount of full-sized seed.

The long-term collection of reproductive data from the same site on Observation Bluff has revealed that three of the seasons since 1961–62 have been more favourable for setting seed than the 1968–69 summer. Moreover, a season favourable for one species might not be as favourable to the other as, for example, 1962–63 by the end of which an advanced state of floral development was noticeable with *C. quitensis* but not with *D. antarctica*. The pearlwort flowers were not exserted greatly above the vegetative culms at the end of March 1963 but a large proportion of their capsules had opened exposing buff-coloured seeds 0·6 mm. in length whereas the grass inflorescences, which were partly emerged and spreading, contained seeds which were *c.* 0·8 mm. long, i.e. only half the size of mature viable seed. However, A. D. Bailey (unpublished report) found some large brown seed in the inflorescences of *D. antarctica* after these had overwintered, indicating that 1962–63 had been more favourable for both species.

Development of mature-sized seed of both species within a single growing season was observed in the summer of 1964–65 which was exceptional in that the plants remained largely snow-free for a period of 6 months after the main thaw on 22 September. *D. antarctica* inflorescences had started to emerge as early as the beginning of November and most became fully exserted during January. At the end of March, a large number of panicles was expanded and brown, and olive-green seeds *c.* 1·5 mm. in length had been produced (Fig. 7b). *C. quitensis* flowers also matured fully during this season, new buds first appearing in December and the majority of plants flowering with anthers and capsules exposed at the end of January. A large

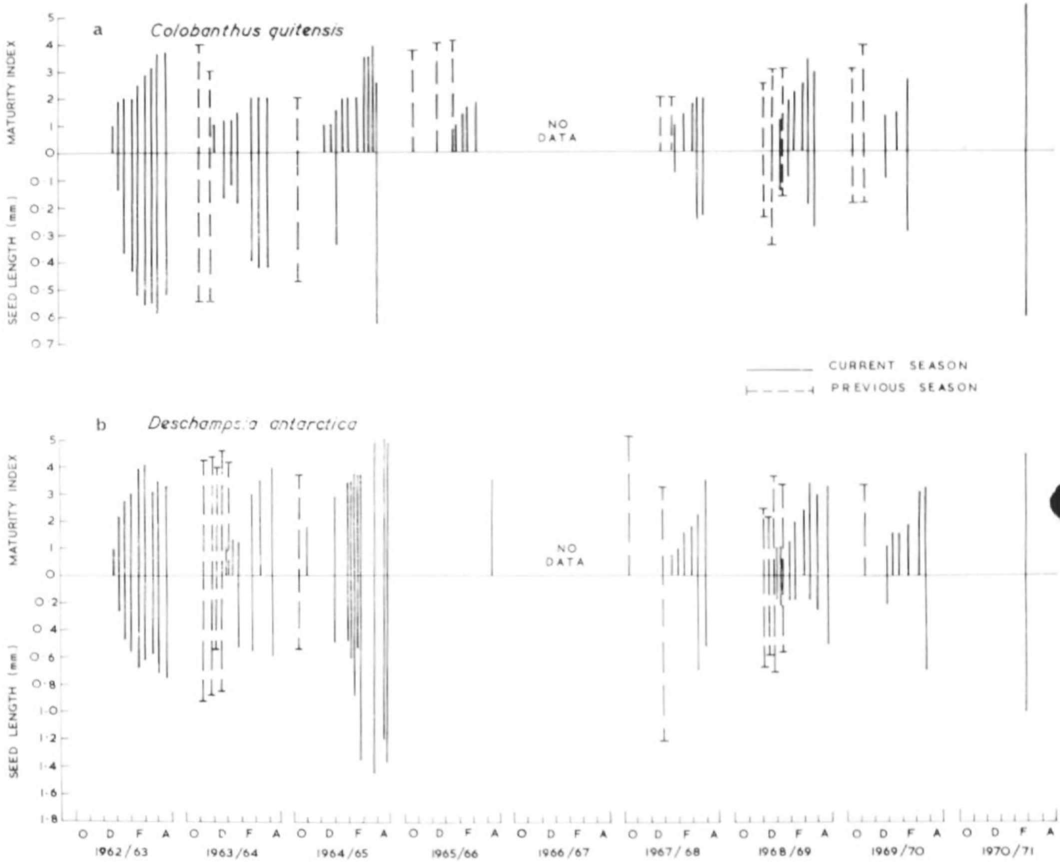

Fig. 7. Variation in reproductive performance of *Colobanthus quitensis* (a) and *Deschampsia antarctica* (b) at Observation Bluff, Signy Island, between 1962 and 1971.

number of capsules opened during March and a mean seed length of 0·64 mm. was recorded. In the latter part of the season young buds were observed on *C. quitensis* cushions when the first set of flowers was well advanced. A number of these buds were marked with cotton by C. A. Howie (personal communication) during March but examination the following October showed there had been 100 per cent mortality over winter.

The 1970–71 season was another extremely favourable period for the maturation of reproductive structures with the first melt, which occurred at the end of September, being followed by 5 months of record sunshine and above-average temperatures. The floral development of both species followed that described for 1964–65 with *D. antarctica* seed measuring *c.* 1 mm. long by February 1971 on Coronation Island and open capsules with ripe seed being observed on *C. quitensis* at Factory Cove in early March (Fig. 8).

Seed Development and Germination

The possibility of seed of *D. antarctica* and *C. quitensis* continuing development under snow during the winter months was first suggested by A. D. Bailey (unpublished report), who found "a few apparently mature seeds" on 6 November 1963 in grass inflorescences which "were nowhere near producing ripe seed, at the end of the previous summer". He also observed some development of *C. quitensis* capsules as the majority had been closed and approximately half

Fig. 8. *Colobanthus quitensis* at Factory Cove, Signy Island, in February 1971. The occurrence of such exserted open capsules with mature-sized seed is unusual on this island. (Photograph by R. Webb.)

the length of the sepals in April 1964, but by the following October many were open and contained brown seeds.

It was impossible to decide whether Bailey's observations were the result of development during the winter under snow or development during the period between snow melt and the time of sampling, or simply that the end of summer samples were not large enough to include some of the better-developed capsules and inflorescences, and so a detailed investigation was undertaken at Observation Bluff and Factory Cove in 1969. Flower and inflorescence samples for the determination of seed size were collected in April and the plants from which these were obtained were marked and maintained under snow until the melt in September when they were re-sampled and size of seed again recorded. In addition, seeds from detached inflorescences and capsules were measured in April, immediately prior to burial in a deep snow bank, and a further series of measurements taken from them after the snow melted in December. As the same seed sample was being re-measured the errors introduced by variability in the population were greatly reduced and any translocation of reserves to the developing seeds was eliminated.

From the average values presented in Table I it can be seen that there was a significant increase in the size of *D. antarctica* seed during the 1969 winter, even when the plants were continuously covered with snow, but that consistent increases were not detected in *C. quitensis*. Although the significant increase in mean size of *D. antarctica* seed was small, only 0·06 to 0·16 mm., this represents up to 10 per cent of the size of mature seed and might prove significant for the formation of small amounts of ripe seed in seasons when none would otherwise mature.

Information regarding the minimum size that seeds of *C. quitensis* and *D. antarctica* must attain in order to germinate successfully was obtained by the author from tests with seed from South Georgian populations, where a wide range of sizes exists at the end of season. *C. quitensis* seeds 0·5 mm. in length or greater proved viable and no germination was obtained

TABLE I. RANGES OF SEED SIZE IN *Colobanthus quitensis* AND *Deschampsia antarctica* DURING THE 1969 WINTER

	Colobanthus quitensis					*Deschampsia antarctica*							
	Observation Bluff					*Observation Bluff*				*Factory Cove*			
	Lower sward		*Specific site, lower sward*			*Lower sward*		*Upper sward*		*Specific site*			
	1 Apr.	16 Dec.	1 Apr.	22 Sep.	16 Dec.	1 Apr.	16 Dec.	1 Apr.	16 Dec.	1 Apr.	22 Sep.	16 Dec.
Sample size	250	180	100	150	75	150	150	100	100	60	75	50
Seed size (mm.)												
0·2	128	104	89	123	51	–	–	–	–	–	–	–
0·3	100	62	11	22	19	–	1	–	–	–	–	1
0·4	9	5	–	5	2	3	7	23	4	1	4	1
0·5	9	2	–	–	3	33	39	48	18	17	9	2
0·6	4	5	–	–	–	71	47	21	20	29	28	10
0·7	–	2	–	–	–	35	35	7	31	10	13	15
0·8	–	–	–	–	–	8	15	1	16	2	15	15
0·9	–	–	–	–	–	–	2	–	8	1	4	2
1·0	–	–	–	–	–	–	4	–	3	–	2	3
1·1	–	–	–	–	–	–	–	–	–	–	–	1
Mean seed size (mm.)	0·27	0·26	0·21	0·22	0·24	0·61	0·62	0·51	0·67	0·60	0·66	0·72
Significance of difference between means	NS		NS	*		NS		**		**	*	

Figures indicate numbers of seed of each size at each site.
NS Not significant at 5 per cent level. * Significant at 5 per cent level. ** Significant at 1 per cent level.

TABLE II. SUMMARY OF GERMINATION TESTS WITH SEED OF MATURE SIZE PRODUCED IN THE SOUTH ORKNEY ISLANDS

Locality	Date collected	Date tested	Tested by	*Pre-treatment* Overwintered on Signy Island	*Pre-treatment* Plants brought on in greenhouse	*Pre-treatment* Number of days vernalization	*Germinating conditions* Temperature (° C)	*Germinating conditions* Continuous darkness	*Germinating conditions* Laboratory conditions with alternating day and night	Number of seeds tested	Percentage germination
Deschampsia antarctica											
Signy Island											
Observation Bluff	10.v.1963	10.v.1963	A. D. Bailey	—	+	—	25	+	—	"A few"	0
	16.xi.1963	17.xi.1963	A. D. Bailey	—	—	—	25	+	—	20	0
	3.xii.1963	3.xii.1963	A. D. Bailey	—	—	—	25	+	—	"A few"	0
Thulla Point	2.iv.1965	18.iv.1965	C. A. Howie	—	—	—	*c.* 20	—	+	6	0
	16.iv.1965	18.iv.1965	C. A. Howie	—	—	—	*c.* 20	—	+	21	0
	18.iv.1965	18.iv.1965	C. A. Howie	—	+	—	*c.* 20	—	+	7	0
	9.iv.1965	14.i.1966	C. A. Howie	+	—	—	*c.* 20	—	+	7	28·6
Observation Bluff	24.xii.1967	24.xii.1967	Author	—	—	—	*c.* 20	—	+	5	0
Lynch Island	25.iv.1969	1.v.1969	Author	—	—	7*	*c.* 20	—	+	20	0
Colobanthus quitensis											
Signy Island											
Observation Bluff	9.iii.–8.iv.1963	6.vi.1963	A. D. Bailey	—	—	—	25	+	—	400	1·75
			A. D. Bailey	—	—	1	25	+	—	400	2·75
			A. D. Bailey	—	—	2	25	+	—	400	1·75
			A. D. Bailey	—	—	3	25	+	—	400	1·75
		3.x.1963	A. D. Bailey	—	—	—	25	+	—	400	3·50
			A. D. Bailey	—	—	1	25	+	—	400	4·75
			A. D. Bailey	—	—	2	25	+	—	400	1·75
			A. D. Bailey	—	—	3	25	+	—	400	3·75
		12.xi.1963	A. D. Bailey	—	—	—	25	+	—	100	0
		Summer 1965	A. Holtom	—	—	—	*c.* 20	—	+	50†	20†
	12.xi.1963	12.xi.1963	A. D. Bailey	+ (planted immediately collected)	—	—	25	+	—	200	7
			A. D. Bailey	+ (air dried, then planted)	—	—	25	+	—	100	3
			A. D. Bailey	+ (air dried, then soaked for 1 day)	—	—	25	+	—	100	3
		Summer 1965	A. Holtom	—	—	—	*c.* 20	—	+	50†	16†
	16.x.1964	16.x.1964	A. D. Bailey	+	—	—	10	+	—	100	0
			A. D. Bailey	+	—	—	*c.* 20	—	+	100	15
	3.iv.1965	3.iv.1965	A. D. Bailey	—	—	—	*c.* 20	—	+	200	1
		Summer 1965	A. Holtom	—	—	—	*c.* 20	—	+	50†	80†
	23.iii.1965	18.iv.1965	C. A. Howie	—	—	—	30–37	+	—	42	0
			C. A. Howie	—	—	—	*c.* 18	—	+	100	22
			C. A. Howie	—	—	—	*c.* 16	—	+	100	4
	9.iv.1965	14.i.1966	C. A. Howie	+	—	—	*c.* 20	—	+	50	4
			C. A. Howie	+	—	—	*c.* 20	+	—	50	0
	17.iv.1965	14.i.1966	C. A. Howie	+	—	—	*c.* 20	—	+	400	0
	Late 1965	xii.1965	R. I. L. Smith	+	—	—	*c.* 20	—	+	50	25
	7.i.1968	7.i.1968	Author	+	—	—	*c.* 20	—	+	15	0
	22.iii.1969	29.iii.1969	Author	—	—	7*	*c.* 20	—	+	50	0
Lynch Island	25.iv.1969	26.iv.1969	Author	—	—	—	*c.* 20	—	+	100	0

* At 0° C.
† As these seeds were tested in Birmingham, England, they experienced air-dry storage conditions during transport.

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with seed smaller than this. In trials with *D. antarctica*, only seeds longer than *c.* 1·4 mm. proved capable of germination.

Relatively few trials have been attempted using material from the South Orkney Islands due to lack of ripe seed. The production of full-sized seed in the field has not been of common occurrence and the seeds produced by plants growing in the United Kingdom, although apparently mature, have rarely germinated. Most of the germination results available were obtained by A. D. Bailey and C. A. Howie who worked on Signy Island during the favourable seasons of 1962–63 and 1964–65, respectively, and a summary of their results and those of other workers is presented in Table II.

It is difficult to draw definite conclusions from such low germination figures but it would appear that in *C. quitensis* germination is higher with seed which has overwintered and which has remained moist. There are also indications that the ageing of seed over winter could be more important than chilling, since artificial vernalization failed to give a substantial increase in the germination of *C. quitensis* seed, yet high percentage germination figures were obtained by A. Holtom when seed collected in April 1963, 12 November 1963 and 3 April 1965 was later tested at Birmingham, England. She obtained germination percentages of 20, 16 and 80 respectively at room temperature and lighting, whereas the same collections of seed tested previously under similar conditions on Signy Island had shown only 5, 7 and 1 per cent viability.

Seedling Establishment

Although laboratory tests (Table II) suggested that the germination of seeds formed on Signy Island is poor, there are recent records of seedlings of both species arising from germination under natural conditions in a number of places elsewhere in the South Orkney Islands. In February 1966, R. I. L. Smith (personal communication) observed grass seedlings on Lynch Island and he suggested, since these appeared to be of varying ages, that seed might be set every year at this site. Although the author failed to find seedlings in April 1969 when the ground was largely snow covered, R. Webb (personal communication) noted *D. antarctica* seedlings at this locality in February 1971, indicating that the Lynch Island grass population is relatively successful in reproducing from seed.

Seedlings of *D. antarctica* have been recorded on only one occasion on Signy Island. In January 1970, the author observed approximately ten seedlings on Observation Bluff, noticeably amongst areas of moist, dead grass litter. On 6 January each consisted of a single leaf up to 7 mm. in length (Fig. 9a), increase in size to between three and ten leaves being reached by 18 March when only the youngest three or four leaves remained green. At the end of season some of the more advanced seedlings showed signs of tillering but their survival over winter and subsequent establishment is unknown.

Seedlings of *C. quitensis* have been observed on more numerous occasions, the first report being in January 1966 when R. I. L. Smith (personal communication) discovered large numbers amongst the grass swards at Lynch Island and at Observation Bluff on Signy Island. Seedlings were also noted by the author on Lynch Island in January 1968, although these appeared too advanced to have resulted from germination that season. In January 1970, the author again observed pearlwort seedlings at two sites on Signy Island, one at Observation Bluff (Fig. 9b) and the other near North Point, while in January 1971, R. Webb (personal communication) noted seedlings of this species on Lynch Island. In 1969–70 germination probably took place during the first few days of January since several of the seedlings had cotyledons with the testa still attached (Fig. 9c) on 6 January. By 18 March the seedlings had produced one or two pairs of true leaves in addition to the green, leaf-shaped cotyledons. In January 1966, R. I. L. Smith noted that the seedlings of *C. quitensis* on Observation Bluff were particularly abundant on a steep, somewhat unstable, gravelly soil, devoid of cryptogams, below the parent cushions but in 1970, at the same site, the author most frequently observed seedlings amongst the dead sodden remains of old *C. quitensis* cushions.

Although seedlings of *C. quitensis* are apparently not infrequent on the South Orkney Islands, their permanent establishment would appear to be less common. R. I. L. Smith (personal communication) marked out four areas at Observation Bluff which contained a

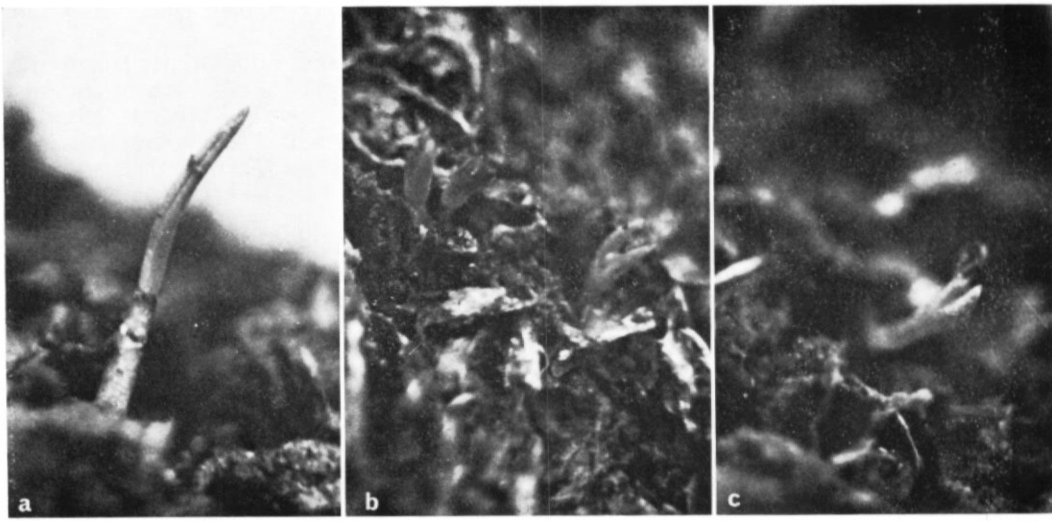

Fig. 9. Newly germinated seedlings of *Deschampsia antarctica* (a) and *Colobanthus quitensis* (b and c) at Observation Bluff, Signy Island, in January 1970. The grass seedling is 7 mm. long and the pearlwort seedlings are 3 mm. in length.

total of 130 seedlings and recorded a 2 per cent loss during their first summer but heavy mortality during the ensuing winter, only 63 seedlings remaining in January 1967. In a similar area on Observation Bluff the author recorded in March 1970 35 seedlings, of which 11 remained alive the following December (personal communication from O. H. S. Darling). A high mortality was also recorded during the seedlings' second summer, when the area became very dry, and on 4 March 1971, R. Webb (personal communication) was able to trace only three seedlings. There is some evidence to suggest that one of the causes of the high mortality during the 1970–71 summer was the high air temperature and the periods of drought associated with this, since the covering of seedlings with a cloche the previous January had also resulted in a high mortality. It has been shown that the temperature of plants inside cloches on Signy Island can rise to high levels (Edwards, 1972) and all 21 pearlwort seedlings enclosed under glass died within 2 months, whereas mortality in the area just outside the cloche was only 3 per cent.

Comparison of Performance between Sites

Moore (1970) gave details of the morphological variability of vegetative and reproductive characters of *Deschampsia antarctica* throughout its geographical range concluding that, in contrast to the range of vegetative size exhibited, the populations showed greater uniformity in their floral measurements. *Colobanthus quitensis*, on the other hand, was an extremely variable species and showed a considerable overlap of vegetative and reproductive characters with the Australian–Neozealandic species, *C. affinis*. From a study of herbarium specimens, Holtom and Greene (1967) concluded that flowers of the grass from the South Orkney and South Shetland Islands developed less fully than those from South Georgia or from sites along the Antarctic Peninsula. Comparable results for *C. quitensis* showed a similar but less marked trend with the poorest development once more being recorded from the South Orkney Islands.

Within Signy Island

W. J. L. Sladen, in the Signy Island station biological register (unpublished), first drew attention to differences in the performance of Signy Island grass populations, commenting that in 1951 plants from Factory Cove "seemed to be doing better than grass from the lawn"

Table III. Mean floral development of *Deschampsia antarctica* from various sites

	Habitat details			Number and maturity of inflorescences		Characteristics of inflorescences						Characteristics of seeds			
	Altitude (m.)	*Exposure*	*Date*	*Number of inflorescences measured*	*Maturity index*	*Inflorescence stalk length* (mm.)	*Panicle length* (mm.)	*Panicle/stalk ratio*	*Total length* (mm.)	*Terminal spikelet length* (mm.)	*Number of spikelets per inflorescence*	*Mean seed length* (mm.)	*Maximum seed length* (mm.)	*Mean number of seeds per spikelet*	*Estimated potential number of seeds per inflorescence*
Ranges given by Moore (1970)	—	—	—	—	—	—	30–130	—	—	4–6·5	—	—	—	2	—
South Georgia															
Bay of Isles, Salisbury Plain	10	High	10.iii.1962	10	4·6	39·6	60·2	1·5	100·8	5·2	55·1	1·2	1·7	2·0	110
Coronation Island															
Buttress east of Sunshine Glacier	175	Low	12.iii.1972	3	3·0	—	—	—	—	—	—	0·6	1·0	—	—
Shingle Cove	20	High	9.iii.1969	8	3·4	12·2	34·8	2·8	47·0	5·2	34·1	0·5	0·8	2·1	68
Cape Hansen, east side	25	Moderate	24.ix.1969	10*	3·2	—	—	—	—	—	—	0·6	0·9	—	—
Cape Hansen, west side	10	Low	24.ix.1969	10*	3·6	—	—	—	—	—	—	0·7	1·1	—	—
Mansfield Point	15	—	9.ii.1971	10	3·4	8·7	31·7	3·6	40·4	4·5	28·8	0·7	1·4	2·3	66
Meier Point	15	—	9.ii.1971	10	3·5	11·4	33·5	2·9	44·9	5·0	24·6	1·1	1·5	2·0	49
Lynch Island															
North coast	10	Moderate	25.iv.1969	25	4·9	25·8	40·8	1·6	66·6	5·8	22·4	1·0	1·7	2·0	45
Signy Island															
Berry Head	15	High	9.iv.1969	25	3·6	4·5	34·1	7·6	38·6	5·2	25·4	0·5	0·9	2·2	57
Starfish Cove	5	High	9.iv.1969	25	3·2	2·6	34·0	13·1	36·6	5·1	27·8	0·5	0·8	2·1	59
Factory Cove, east sward	12	Moderate	10.iii.1969	25	3·0	5·6	40·0	7·1	45·6	5·4	22·4	0·5	0·8	2·3	52
Factory Cove, west sward	5	Moderate	10.iii.1969	25	3·2	6·3	40·3	6·4	46·6	5·4	22·5	0·6	1·2	2·1	48
Berntsen Point	3	High	11.iii.1969	25	2·7	3·0	38·0	12·7	41·0	5·2	29·6	0·5	0·7	2·5	74
Berntsen Point, cloche	3	Low	11.iii.1969	8	4·0	17·1	48·6	2·8	65·7	5·6	22·9	1·1	1·7	2·1	49
Observation Bluff, upper slopes	27	High	10.iii.1969	25	3·4	4·3	35·0	8·1	39·3	5·6	20·7	0·5	0·8	2·1	44
Observation Bluff, lower slopes	23	Moderate	10.iii.1969	25	3·6	8·2	38·0	4·6	46·2	5·6	22·6	0·5	0·7	2·1	48
Port Jebsen	12	Low	28.iii.1969	25	3·7	5·6	47·1	8·4	52·7	5·2	23·6	0·5	0·7	2·2	51

* Inflorescences of the previous season, i.e. 1968–69.
The most mature inflorescences were sampled from each population where possible.

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Table IV. Mean floral development of *Colobanthus quitensis* from various sites

	Habitat details			Number and state of flowers		Characteristics of flowers				Characteristics of seeds			
	Altitude (m.)	*Exposure*	*Date*	*Number of flowers measured*	*Maturity index*	*Pedicel length* (mm.)	*Sepal length* (mm.)	*Capsule length* (mm.)	*Capsule length/ sepal length*	*Mean seed length* (mm.)	*Maximum seed length* (mm.)	*Mean number of seeds per capsule*	*Percentage seeds >0·5 mm.*
Ranges given by Moore (1970)	—	—	—	—	—	>3	1·6–4·0	—	0·9–1·7	*c.* 0·5	—	Numerous	—
South Georgia													
Bay of Isles, Salisbury Plain	10	High	10.iii.1962	10	4·7	5·4	2·6	2·7	1·0	0·7	0·8	23·3	80
Coronation Island													
Buttress east of Sunshine Glacier	200	Low	12.iii.1972	3*	5·0	—	—	—	—	0·5	0·6	—	—
Buttress east of Sunshine Glacier	200	Low	12.iii.1972	5	3·4	2·4	2·3	1·2	0·5	0·2	0·2	30·4	0
Shingle Cove	15	High	9.iii.1969	10 (10)	2·0 (1·0)	5·6 (3·1)	—	1·1 (0·6)	—	0·2	0·3	24·4	0
Cape Hansen, west side	10	Low	24.ix.1969	10	3·1	3·9	2·8	1·5	0·6	0·3	0·6	24·6	8
Lynch Island													
North Coast	10	Moderate	25.iv.1969	25	4·9	7·2	3·1	2·9	0·9	0·7	0·8	23·9	62
Laurie Island													
Cape Geddes	90	—	22.xii.1946	10*	3·6	3·8	2·7	1·7	0·6	0·4	0·6	21·9	17
Signy Island													
Factory Cove, east side	5	Moderate	10.iii.1969	3	2·7	1·3	2·2	0·9	0·4	0·2	0·3	—	0
Factory Cove, east side	12	Moderate	10.iii.1969	1*	4·0	4·0	2·4	1·2	0·5	0·6	0·7	—	—
Factory Cove, west side	12	Moderate	10.iii.1969	25	3·4	6·5	2·7	1·5	0·6	0·3	0·8	23·7	6
South-east of Berntsen Point	15	Moderate	10.iii.1969	6	1·5	1·2	1·0	0·3	0·3	0·1	0·1	—	0
Observation Bluff, upper slopes	27	High	10.iii.1969	3	3·0	2·0	2·1	1·0	0·5	0·2	0·3	—	0
Observation Bluff, lower slopes	23	Moderate	10.iii.1969	25 (10)	3·4 (1·0)	4·4 (2·4)	2·7 (1·6)	1·3 (0·4)	0·5 (0·3)	0·2	0·3	26·7	0
Observation Bluff, lower slopes under cloche	23	Low	12.iii.1969	17	3·9	5·7	3·1	2·1	0·7	0·5	0·7	—	—
Port Jebsen	30	Low	28.iii.1969	25 (5)	3·7 (1·0)	11·4	2·9 (1·7)	1·7 (0·7)	0·6 (0·4)	0·4	0·8	22·0	17
Port Jebsen	30	Low	26.ix.1969	10 (6)	2·0	7·3 (2·7)	—	1·3 (0·3)	—	0·2	0·3	27·1	0
North of Spindrift Rocks	9	Low	27.iii.1969	20 (10)	2·3	8·4 (5·0)	—	1·4 (0·4)	—	0·3	0·6	27·8	2

* Previous years' capsules of uncertain age.
Normally the most mature flowers in each population were sampled but the figures in brackets refer to measurements from secondary buds.

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at Berntsen Point. M. W. Holdgate (unpublished report) also noted that, in general, east- and west-facing swards were less fertile than those which faced north.

Detailed measurements (Table III) showed that shorter panicles tend to be produced at the more exposed sites on Signy Island and that seed size is better correlated with the length of the inflorescence stalk rather than the size of the panicle. It will be noted that the culm length of flowering tillers at Port Jebsen was large relative to the degree of emergence of inflorescences, suggesting that the size of the culms at this site was influenced by some factor other than shelter, possibly soil enrichment, since several cape pigeons (*Daption capensis*) nested slightly up-slope of the grass.

The number of spikelets in an inflorescence was greatest in the more exposed populations and in those most affected by rough seas, namely Berry Head, Berntsen Point and Starfish Cove. It may be that spikelet number is controlled more by salinity than exposure since there was a marked reduction in their number when parts of the Berntsen Point and Starfish Cove swards were sheltered within glass cloches, a reduction not detected in a cloche at Observation Bluff where the site was farther from the sea. The sheltering of swards under glass also had the effect of increasing the maximum maturity of inflorescences to a degree comparable to those on South Georgia (Table III), although it did not appear to stimulate the production of more inflorescences.

From measurements of the floral parts of *D. antarctica*, it can be seen that all panicle lengths fall at the lower end of the range reported by Moore (1970) but that spikelet length does not appear to be depressed (Table III).

Since *C. quitensis* is essentially cleistogamous on Signy Island, considerable variation in reproductive development could be expected. However, the species is more restricted in its range of habitats than the grass and comparatively few differences between populations have been reported. C. A. Howie (unpublished field notes) noted a difference in floral development within individual cushions of *C. quitensis* at Observation Bluff in March 1965 with the flowers on the sides which faced up-hill being more advanced than those with a down-hill aspect and suggested that this was the result of differences in local water content, although the light and temperature levels at the two sides would also have been different. C. H. Gimingham (personal communication) observed that parts of cushions which had flowered prolifically during the 1964–65 season remained exposed when the rest of the sward was covered by a light layer of snow during the following summer and commented that the pearlwort population at Factory Cove was developing more slowly than that on Observation Bluff. Table IV shows that there was little difference between these two populations in 1968–69 and that in none of the Signy Island populations did capsule development approach the range described for the species by Moore (1970), although the sepal length of the plants was not depressed. Moore recorded a capsule content of *c*. 43 seeds from Fuegian and Andean material, and this appears to be reduced to *c*. 25 in Signy Island populations (Table IV).

Mature-sized *C. quitensis* seed was produced at three sites on Signy Island in 1969, apparently associated with greater pedicel and capsule lengths.

On other parts of the South Orkney Islands

Holtom and Greene's suggestion of poor floral development of grass on the South Orkney Islands has been borne out for Signy Island where inflorescence stalk length and seed size were low but populations on Coronation Island seem slightly more successful with smaller panicle/stalk ratios and larger seed. Only on Lynch Island did the grass attain a maturity comparable to that on South Georgia and even at this site the length of inflorescences and their potential seed production were reduced (Table III).

A similar trend is apparent in measurements of *C. quitensis* flowers on Lynch Island for 1968–69 when their size equalled that of a typical South Georgian population, whereas production of capsules and seeds on Coronation and Signy Islands during the same season was retarded (Table IV). The greater development of both grass and pearlwort on Lynch Island had been observed in the field, in 1965–66 by C. H. Gimingham and R. I. L. Smith (personal communication), and was confirmed by the author in 1967–68 and 1968–69 and by R. Webb (personal communication) in 1970–71 and 1971–72. It is possible that a large area to the west of Cape Hansen is particularly favourable for vascular plant growth since R. Webb (personal communication) also recorded advanced floral development in the grass and pearlwort populations on the moraine at the snout of Laws Glacier on Coronation Island, opposite Lynch Island, in February 1972 but unfortunately no samples have been available for measurement. Some mature-sized seed was also produced by *C. quitensis* and *D. antarctica* at the west side of Cape Hansen in 1968–69, but not in greater quantity than at several other sites on Signy Island.

It is clear that mature-sized *C. quitensis* seed has been formed by plants at Cape Geddes and at the buttress near Sunshine Glacier in past seasons (Table IV). In *D. antarctica*, seed from previous seasons is not as easy to detect as in *C. quitensis* but swollen seed, approaching full size, was present in the two Coronation Island grass populations measured in 1970–71. Thus it appears that mature-sized seed can be formed by most of the known *D. antarctica* and *C. quitensis* populations on Coronation and Laurie Islands in certain seasons but regular development only seems to occur on Lynch Island.

Possible Causes of Between-site Variation

It is clear that flowers are produced regularly by *D. antarctica* and *C. quitensis* at most sites in the South Orkney Islands which are open to the north (Holtom and Greene, 1967; Greene and Holtom, 1971) but that the two species are strikingly different in their flowering behaviour. Internal genetical control of flowering is primarily important in *C. quitensis* since neither vernalization nor photoperiod appears to affect the onset of flowering in pearlwort cushions, whereas *D. antarctica* is a species more sensitive to environmental conditions, requiring a cold pre-treatment for floral initiation and long days (*c.* 18 hr.) for development of the inflorescence (Holtom and Greene, 1967). Variation in the floral development of both species between and within sites appears to arise from differences in external factors other than light.

Several botanists have commented that water availability is important in determining flowering, particularly of *D. antarctica*, on the South Orkney Islands (unpublished report by A. D. Bailey; Greene and Holtom, 1971; Smith, 1972) and on the Argentine Islands (Corner, 1971). Subjective observations suggested that areas of grass in permanently moist situations on Signy Island remained vegetative but an analysis of soil samples collected in 1966 failed to provide conclusive evidence on this point (personal communication from C. H. Gimingham). However, the changes observed in reciprocal transplants between wet and dry areas on Observation Bluff made by the author in December 1968 confirmed the phenotypic response of the grass to moisture. A vegetative turf produced inflorescences in the season following its transplanting to a drier area while the *D. antarctica* turf transplanted to a waterlogged site showed reduced inflorescence development. The flowering of *C. quitensis* was less affected by soil moisture than *D. antarctica* and transplanted cushions flowered equally in both wet and dry areas but the pearlwort rarely colonizes very moist situations. It is the author's opinion that the reduction of floral development of *D. antarctica* in wet situations on Signy Island occurs largely through a lowering of temperatures amongst the vegetation as shown previously (Edwards, 1972).

Nutritional factors have also been reported to have some effect on the flowering of *D. antarctica* but not, apparently, of *C. quitensis*, Lindsay (1971) observing that grass turves near penguin colonies on the South Shetland Islands were lush but sterile, whereas *C. quitensis* was found flowering freely in nitrogenous and non-nitrogenous habitats. Greene and Holtom (1971) did not record similar effects from flowering plant localities farther south and differences resulting from nitrogenous enrichment on Signy Island were noted mainly as a general increase in the stature and verdure of the vegetation (Edwards, 1972). However, neither grass nor pearlwort is closely associated with penguin-breeding areas in the South Orkney Islands, both more frequently occurring below colonies of ledge-nesting petrels as at Factory Cove, Port Jebsen and to the north of Spindrift Rocks where nitrogenous enrichment is less.

It seems certain that a more important factor controlling the degree of development of *C. quitensis* and *D. antarctica* flowers is the temperature at plant level. By covering small parts of grass and pearlwort communities with glass cloches, thus trapping radiation and decreasing heat loss from the surface of the vegetation (Edwards, 1972), floral performance on Signy Island was improved (Fig. 10). Full-sized seed of both species was induced in this way during 1968–69 when negligible amounts were produced in natural communities on the island, and flowers of both *C. quitensis* and *D. antarctica* emerged further because of increases in pedicel and inflorescence stalk lengths (Tables III and IV). Holtom and Greene (1967) reported that South Georgian populations grown in continuous low temperatures (*c.* 5° C) were slower in producing flowers than plants in fluctuating or warmer temperatures, and that in *D. antarctica* the panicles failed to exsert and expand fully. Peduncle length of *C. quitensis* flowers was also shorter at continuous low temperatures and capsules generally remained unswollen, especially under short days. Thus it appears that plant temperatures on Signy Island may be generally too low for full floral development in *D. antarctica* and *C. quitensis* but that by decreasing the exposure of cushions and turves, the size of seeds, flowers and inflorescences can be increased to levels comparable to those noted at Lynch Island without any other modifications to the micro-environment.

Fig. 10. The glass cloche erected in January 1968 over part of the grass sward at Observation Bluff, Signy Island, on 4 March 1971. The increased development of *D. antarctica* inflorescences and *C. quitensis* flowers, within the shelter of the cloche, is clearly visible. The largest sheet of glass is 30 cm. long. (Photograph by R. Webb.)

The reproductive success of the Lynch Island populations is noteworthy since there is no obvious difference between the vegetative appearance of either the grass or the pearlwort at this site (Fig. 11) and on Signy Island (Fig. 2). It therefore seems unlikely that the increased development of the flowers is due to nutrient enrichment or the greater depth of soil recorded by Greene and Holtom (1971). Greater periods of high temperatures amongst the vegetation on Lynch Island would appear a more likely contributory factor since the island, although not a "radiation trap" in the sense of Holdgate (1964), occupies a sheltered situation with high peaks to the west, north and east on Coronation Island and it might, therefore, experience lower wind speeds. More significantly, several station personnel have observed that the areas at the snouts of Laws and Sunshine Glaciers frequently appear sunlit while the rest of the South Orkney Islands is covered in persistent low cloud. This, and the radiation reflected from

Fig. 11. Part of the large mixed community of *Deschampsia antarctica* and *Colobanthus quitensis* on the northern side of Lynch Island. The slope is *c*. 20 m. high. (Photograph by R. I. L. Smith.)

the surface of the glaciers, could be expected to raise plant temperatures many degrees above ambient (Edwards, 1972). R. I. L. Smith (personal communication) suggested that another factor which might result in Lynch Island experiencing a milder climate than Signy Island was the existence of föhn winds which arise from the high mountains of Coronation Island to the north.

Discussion

Before a species can be regarded as fully adapted to Antarctic conditions, Greene and Longton (1970) considered that it must not only be able to overcome considerable dispersal barriers, but also be able to maintain itself vegetatively and give rise to new generations by sexual reproduction. Greene and Holtom (1971) showed that inflorescences and flowers are produced every year in all regions where *D. antarctica* and *C. quitensis* occur although habitat differences gave rise to local exceptions. The observations of Brown (1912) and Holdgate (1964) suggested that on the South Orkney Islands the two species were less successful in setting seed than at localities farther south or to the north on South Georgia, while Holtom and Greene (1967) showed that plants from the South Shetland Islands appeared to be similarly retarded.

In the ten seasons since 1961–62, during which the detailed performance of the two vascular species has been studied on Signy Island, the widespread production of mature seed in both species occurred in only three seasons, 1962–63, 1964–65 and 1970–71. In addition, *C. quitensis* appears to have been capable of producing some ripe seed in four other seasons, A. D. Bailey (unpublished report) having found such seed in overwintered capsules produced in 1963–64, R. I. L. Smith (personal communication) recording small amounts of swollen seed in 1965–66 and 1966–67 and the author observing field germination of seed which was probably produced in 1968–69.

From a consideration of meteorological data for the summer months of November to March, it appears that the length of season is critical for seed production. In other words, the performance of both species correlates better with mean summer temperatures, which control the length of the snow-free period, rather than with sunshine receipt (Fig. 12). On this basis, one can conclude that since 1947 there appear to have been six seasons with mean temperatures near 0·5° C in which flowers and seeds of both species would probably have developed fully. Although *D. antarctica* produces seed only in long and favourable seasons, small amounts of viable seed may be produced by *C. quitensis* in summers which are not exceptionally long or mild, and the number of seasons in which this species has successfully produced fertile seed may, therefore, be greater.

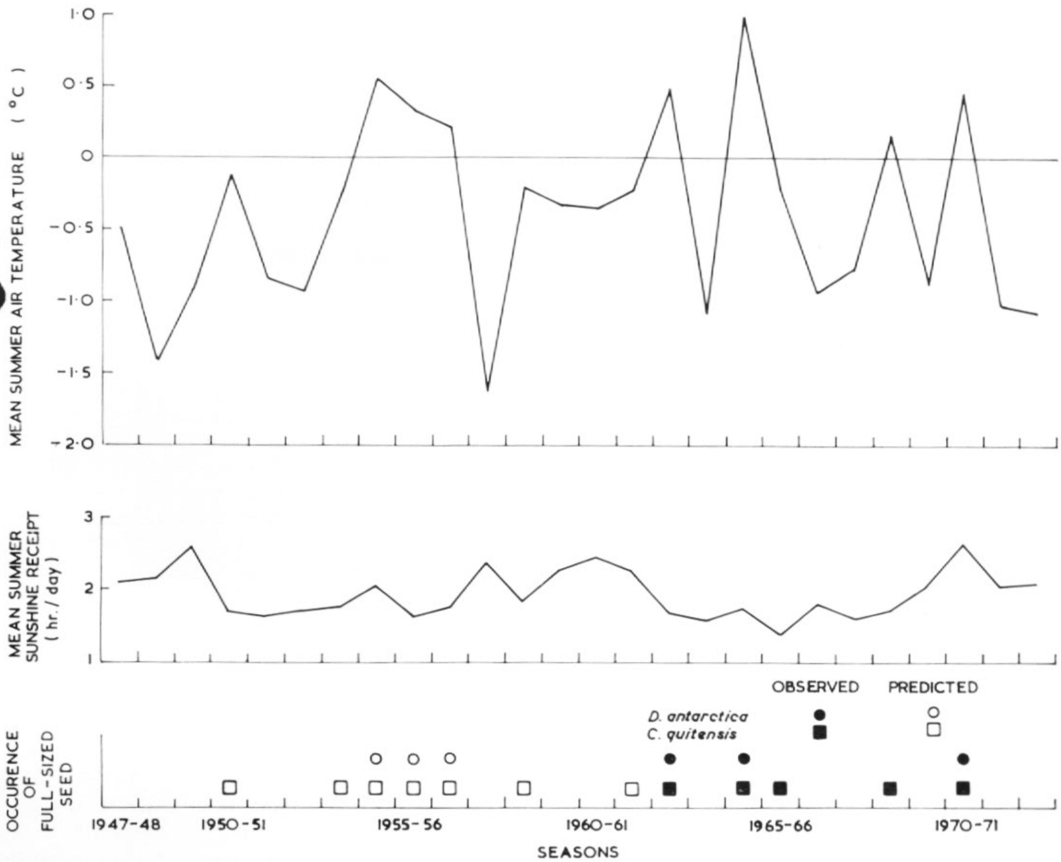

Fig. 12. Correlation of seed production on Signy Island with sunshine and air-temperature data for the periods October to March inclusive since 1947–48.

The discovery that floral initiation takes place in the year preceding flowering is noteworthy since this mechanism appears a common adaptation for seed production during short growing seasons in several species from Greenland (Sørensen, 1941). However, it does not seem so frequent on South Georgia, where Callaghan and Lewis (1971) failed to find evidence for early flower formation in *Phleum alpinum* while D. W. H. Walton (personal communication), in a pilot survey of flowering periods of many species, only recorded the overwintering of rudimentary inflorescences in a single species, *Poa flabellata*.

It has been shown that reproductive variation between sites in the South Orkney Islands is greater than the differences between seasons but the causes of infertility are still incompletely known. The aspect of a sward or cushion affects both plant temperature and the length of snow lie and it was only in the more north-facing situations that the plants flowered vigorously. On Signy Island, excessive soil moisture suppressed flowering, particularly in *D. antarctica*, but in other areas nitrogenous enrichment has been noted to produce similar effects (Lindsay, 1971). It has been known for some time that in many species flowering responds to the balance of nitrogenous substances to carbohydrates within the plant. According to Miller (1931), Kraus and Kraybill demonstrated in 1918 that a good supply of nitrate and high carbohydrate production in tomato led to lush vegetative growth but little floral development, while a moderate supply of nitrate under similar conditions gave less vegetative growth but maximum fruit production, but a poor nitrate supply resulted in both vegetative and floral growth being small. The last combination appears that most commonly found on the South Orkney Islands, whereas the first seems analogous to the situation observed by Lindsay (1971) at some sites in the South Shetland Islands.

Bliss (1956) considered that in the Arctic flowering intensity and seed production decreases with increasing habitat severity and while the results for seed production in *C. quitensis* and *D. antarctica*, in general, agree an increase in the number of spikelets per grass inflorescence was observed at the more exposed sites. If smaller amounts of dry matter are synthesized at the more severe sites, an increase in the partitioning of reproductive effort would certainly prove disadvantageous since fewer florets and seeds could then attain the minimum size and weight needed to be functional.

The reproductive capacity, as understood by Salisbury (1961), of both species is potentially great. From estimates of density and capsule size, *C. quitensis*, on 1 m.^{2} of ground near Spindrift Rocks, produced *c*. 170,800 ovules in 1969 while *D. antarctica* at Observation Bluff averaged *c*. 107,500 florets/m.^{2}. These figures are considerably greater than those reported for another grass, *Phleum alpinum*, on South Georgia (Callaghan and Lewis, 1971) but whereas between 20 and 50 per cent of the *Phleum* ovules actually developed ripe seed, the percentage maturation at the two populations on Signy Island was only 2 and 1 per cent, respectively.

There is obviously a great variability in the number of viable propagules produced per unit area in different populations on the South Orkney Islands; for example, on Lynch Island 62 per cent of *C. quitensis* ovules and 50 per cent of those of *D. antarctica* finally matured. The highest values obtained for Signy Island populations in 1969 were from Port Jebsen, where 17 per cent of pearlwort ovules reached mature size, and from Factory Cove where 6 per cent of grass seeds developed to 1 mm. or more in length. The protection of Signy Island plants within glass cloches resulted in an increase in ovule maturation to percentages comparable to those from Lynch Island, showing that the maturation of seed is environmentally controlled. C. A. Howie (unpublished report) obtained similar results by cultivating the grass and pearlwort indoors for most of the autumn and early winter.

The most noticeable morphological effects of such modifications to the environment were that the inflorescences of the grass became fully exserted and that the flowers of the pearlwort remained open for longer periods. It is suggested that the chance of fertilization is increased under these warmer and drier conditions since the shedding of pollen would be promoted, and the viability of pollen grains is known to be markedly influenced by low temperatures (Fogg, 1963). The presence of mature seed in the apices of *C. quitensis* capsules is consistent with them having developed as a result of successful fertilization, but whether this only results from cross- or self-pollination is unknown. Self-pollination probably predominates on Signy Island since flowers are essentially cleistogamous for much of the time, but some cross-pollination may occur since R. Webb (personal communication) observed Collembola crawling over *C. quitensis* flowers during 1970–71.

The frequency of seedling occurrence on Signy Island shows that it would be erroneous to conclude from the results of the germination tests that seed produced by *D. antarctica* and *C. quitensis* is rarely viable, and it is more likely that the laboratory conditions in which the seeds have been tested have not been ideal. Both Holtom and Greene (1967), using seed from South Georgia, and Corner (1971), using seed from the Argentine Islands, demonstrated that maximum germination in both species was obtained at 20° C, and that a reduction occurred with *C. quitensis* seed at higher temperatures but not with *D. antarctica*. It may be, therefore, that some of the low germination values obtained with seed from the South Orkney Islands were the result of keeping the seed at too high temperatures. Corner (1971) also showed that by subjecting seeds of the grass to a sharp temperature increase from 4° to 20° C, germination increased to three times that at continuous high temperatures. The fact that few tests with

Signy Island seed have been carried out in such alternating temperature regimes might well account for the low germination figures in Table II, since field observations indicated that some of the seed used in the tests was viable under the prevailing climatic conditions. In tests with *C. quitensis* by the author, germination was enhanced by soaking the seed in aerated sea-water for 6 days prior to testing and, moreover, that seed remained viable after 3 weeks in sea-water.

The major uncertainty with regard to the significance of propagation by seed in the South Orkney Islands is the success of seedling establishment. From the meagre information available, it would appear that there is a 50 per cent probability of a seedling surviving its first winter with the theoretical probability increasing each succeeding winter as root and assimilatory systems increase. Mortality can be considerable, even in summer when the seedlings are small, if the ground dries out for long periods. More normally, however, summer mortality is low.

To summarize, a study of the reproductive performance of the two species on Signy Island during the last decade has shown that inflorescences of *D. antarctica* and flowers of *C. quitensis* are produced every summer but that the level of maturity reached by the end of each season varies from year to year. The widespread production of full-sized seed of both species has occurred in three seasons, namely 1962–63, 1964–65 and 1970–71, while *C. quitensis* had the ability to produce smaller quantities of mature seed in several additional seasons. *D. antarctica* does not appear capable of producing full-sized seed on Signy Island in summers of average length.

In conclusion, therefore, it can be said that, while both *D. antarctica* and *C. quitensis* are capable of spreading by seed on the South Orkney Islands, the vulnerability of all stages of reproduction to the vagaries of climate make it likely their reproductive cycles are only completed irregularly. Since the micro-environment of the islands appears more severe than many localities farther south, with lower sunshine (Giles, 1971) and higher precipitation (Pepper, 1954) leading to "wet cold" conditions, it may be that the spread of vascular plants from seed will be more common at sites on or close to the Antarctic Peninsula, and that spread by vegetative means is of greater importance in the South Orkney Islands, particularly on Signy Island.

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