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The Growth and Reproduction of Antarctic Flowering Plants

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The growth and reproduction of Antarctic flowering plants

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Introduction

The presence of flowering plants within the Antarctic botanical zone (as defined by Greene 1964*a*) has been known for nearly 150 years. The first to be discovered was a small, wiry grass of tufted or mat-forming habit, now called *Deschampsia antarctica* Desv., while the second proved to be a small cushion-forming pearlwort—*Colobanthus crassifolius* (D'Urv.) Hook. f. Skottsberg (1954) provided the first maps of their Antarctic distribution and summarized the small amount of information available about their reproduction and behaviour.

As known at present, the two species extend from Neny Island (68° 12′ S, 67° 02′ W) in Marguerite Bay, northwards along the west coast of the Antarctic Peninsula to many islands of the Scotia Ridge (figure 59). Elsewhere *D. antarctica* reaches as far north as *ca.* 34° S in South America and eastwards to some of the Sub-Antarctic islands of the south Indian Ocean. The world distribution of *C. crassifolius* is uncertain owing to taxonomic confusion about the relationship of plants in New Zealand with those in South America, as well as doubts about the homogeneity of the taxon in the latter area. If the species in South America is considered in its widest sense, i.e. as embracing all the 'grassy-leaved pearlworts', then *C. crassifolius sensu lato* extends much farther north than *D. antarctica*, certainly well into Peru (to 12° S), with localities north of the equator in Mexico.

In passing, it may be mentioned that other vascular plants have been reported from the Antarctic botanical zone. Of these *Deschampsia parvula* (Hook. f.) Desv. was the only species claimed as a native (Parodi 1949), but it has now been demonstrated satisfactorily that its only record was based on a mistaken identification (Skottsberg 1954; Greene 1967). Discounting *Stellaria media* L., another species reported in error (Greene 1967), two grasses —*Poa annua* L. and *P. pratensis* L. are the only aliens known to be surviving within the zone (Greene & Greene 1963; Longton 1966).

Apart from the data summarized by Skottsberg (1954), little else was known about *D. antarctica* and *C. crassifolius* in Antarctica when the present work began. Rudmose Brown (1928) had claimed that both were normally vegetative due to the shortness and severity of the Antarctic summer, but Skottsberg considered that each produced seed along the Antarctic Peninsula, a fact first clearly demonstrated by Corte (1961). More recently Holdgate (1964) noted that on Signy Island, although growth was vigorous and inflorescences were formed, it was unlikely that seed was often set.

The results presented here, which refer to the distribution and performance of both species southwards from South Georgia, are the first available from a long-term genecological study initiated by the senior author to investigate the performance of both species throughout their world distribution.

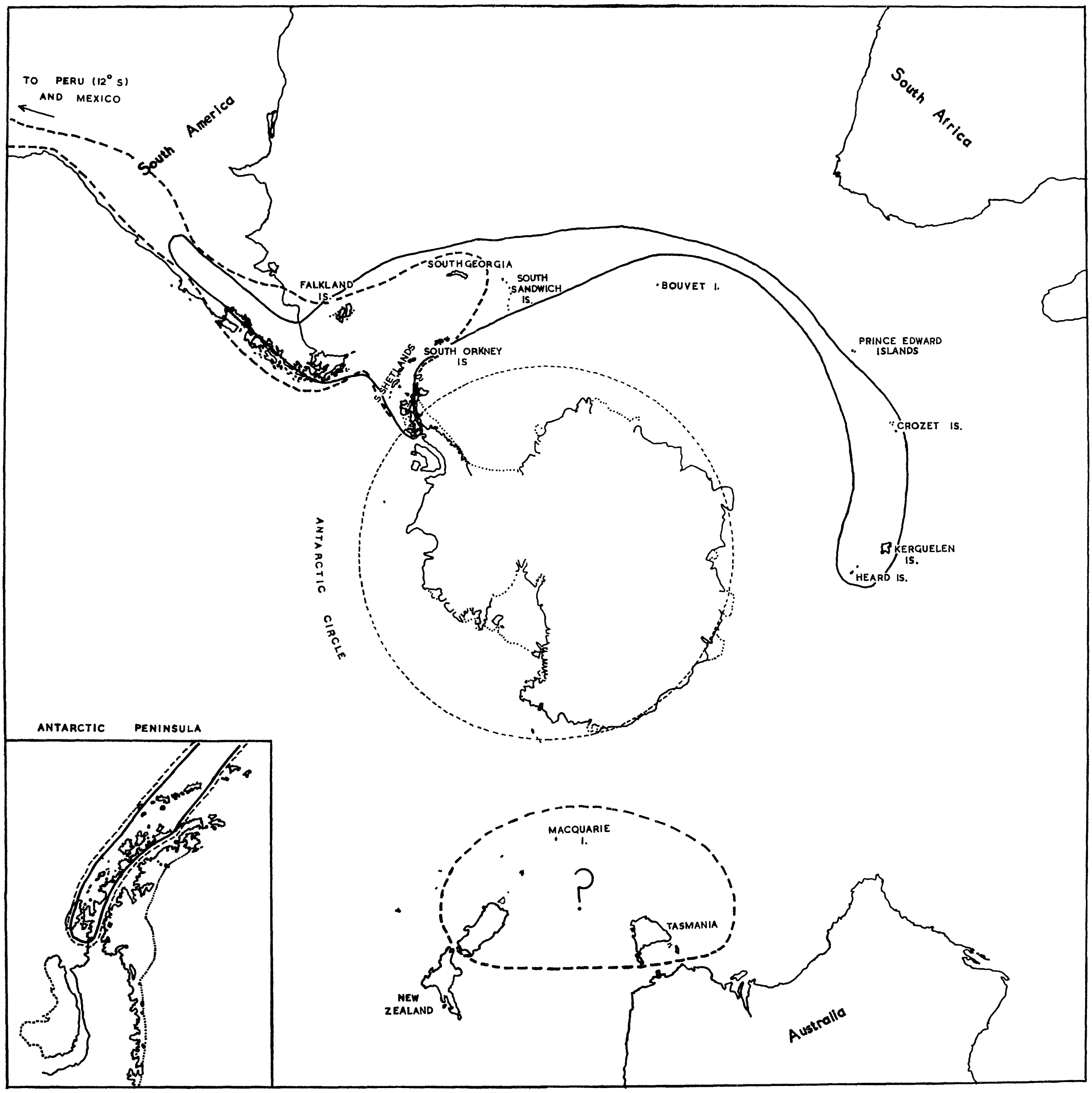

FIGURE 59. World distribution of *Deschampsia antarctica* Desv. (—) and *Colobanthus crassifolius* (D'Urv.) Hook. f. *s.l.* (- - -).

METHODS

Information on the field performance of *D. antarctica* and *C. crassifolius* was obtained from direct observations of plants in the field and by a study of an extensive range of herbarium material. The field behaviour on South Georgia was based on the senior author's investigations during 1960–61 (Greene 1964*b*) supplemented by those of R. E. Longton during 1963–65. Farther south, observations, sampling and tests were carried out at the authors' request by British Antarctic Survey personnel. This information was extended by a detailed examination of herbarium material from all areas.

The experimental results from living plants were obtained by studying the responses of cloned material to a range of daylength and temperature regimes in the phytotron at the Research Gardens associated with the Department of Botany, The University of Birmingham. The cloned material was derived from seed collected at Hestesletten (*Colobanthus*, Greene no. 3589) and at Maiviken (*Deschampsia*, Greene no. 3595), Cumberland Bay, South Georgia at the end of the 1960–61 season. The range of conditions available in the phytotron at the time of the experiments is indicated in table 25. Unfortunately the range of regimes used was limited both by the number of chambers and by the requirements of experiments already in progress.

TABLE 25. EXPERIMENTAL CONDITIONS USED IN THE PHYTOTRON

	long days (20 h)		short days (8 h)	
conditions	light	dark	light	dark
continuous 5 °C	20 at 5 °C	4 at 5 °C	8 at 5 °C	16 at 5 °C
fluctuating 5 to 20 °C	12 at 5 °C, 8 at 20 °C	4 at 5 °C	8 at 20 °C	16 at 5 °C
continuous 18 °C	20 at 18 °C	4 at 18 °C	8 at 18 °C	16 at 18 °C
fluctuating 18 to 20 °C	12 at 18 °C, 8 at 20 °C	4 at 18 °C	8 at 20 °C	16 at 18 °C

FIELD PERFORMANCE

The results of this part of the investigation confirmed that *D. antarctica* and *C. crassifolius* are the only two native flowering plants known within the Antarctic botanical zone and that they are confined to the Antarctic Peninsula–Scotia Ridge sector. Although additional sites to those given by Skottsberg (1954) have been discovered, *Deschampsia* is still known from more localities than *Colobanthus*. The latter rarely occurs without the former, and even where they grow together, it appears that *Deschampsia* is usually the more abundant of the two, *D. antarctica* often forming scattered clumps or, locally, small swards in which cushions of *C. crassiofolius* may be sparingly intermingled. Knowledge of their distribution on South Georgia, as given in map 13 (*C. crassifolius*) and map 29 (*D. antarctica*) in Greene (1964*b*), remains unchanged.

The most important results established by the present work may be summarized as follows:

(1) Persistence of a species has only been established for a small number of localities e.g. the survival of both species at Borge Bay, Signy Island, since the 1936/37 season, due mainly to the lack of precise collecting data for many of the older specimens.

(2) A high degree of vegetative uniformity exists in both species, although differences in plant size and vigour were noted. In their southern localities plants of *Colobanthus* form denser cushions, while *Deschampsia* plants assume a more flattened growth form than those farther north.

(3) Inflorescences and flowers are normally present, and it seems clear that they are produced in all localities, almost certainly every year.

(4) A great deal of variation in development of flowers, inflorescences and seeds exists both within and between various localities.

Variation in flower and inflorescence development was assessed by calculating a maturity index for each specimen. A number of developmental stages was recognized for each species (table 26) and by assigning an arbitrary figure to each, with ascending values corresponding to increasing maturity, the stages present on each specimen were scored and the results expressed as a mean figure. The spread of stages within a specimen is usually low and so the resulting index figure may be considered to represent closely the majority state of inflorescences or flowers in an individual gathering.

Table 26. Stages of inflorescence and flower maturity for *Deschampsia antarctica* Desv. and *Colobanthus crassifolius* (D.Urv.) Hook f.

	Deschampsia antarctica		*Colobanthus crassifolius*
0	no inflorescences visible	0	no flowers visible
1	inflorescence sheaths swollen but inflorescences not visible	1	flower buds visible, with sepals closed
2	inflorescence sheaths open, inflorescences beginning to emerge	2	sepals open, capsule closed and < $\frac{1}{2}$ the length of the sepals
3	inflorescences < $\frac{1}{2}$ emerged	3	sepals open, capsule closed and > $\frac{1}{2}$ the length of the sepals
4	inflorescences > $\frac{1}{2}$ emerged, branches erect	4	capsule open, seeds visible
5	inflorescences > $\frac{1}{2}$ emerged, branches spreading		

The results of scoring the maturity of inflorescences for a series of specimens of *Deschampsia antarctica* from South Georgia, the South Orkney Islands, the South Shetland Islands and the Antarctic Peninsula, plotted against the date of collection, are shown in figure 60. It will be noted that development began in all areas in the December–January period and was initially very rapid. Towards the end of the growing season, in the March–April period, most inflorescences on South Georgian plants were fully expanded, whereas those from the South Orkney Islands showed very few inflorescences at this state of maturity although earlier stages were well represented. The situation on the South Shetland Islands is less clear, due to shortage of material, but plants from localities along the Antarctic Peninsula or its off-shore islands clearly developed further than plants on the South Orkney Islands and approached more closely the level of development on South Georgia.

When seed maturity in *Deschampsia antarctica* was assessed by plotting the mean of the five longest seeds per specimen against date of collection it was found (figure 61) that, again, development on the South Orkney Islands was less than on South Georgia. The size of the most mature seeds on plants from the South Shetland Islands was about the same as those formed in the South Orkney Islands, while seeds formed at localities along the Antarctic Peninsula attained the size of South Georgian seed. Germination tests have shown that the South Georgian seed, as well as that formed at localities along the Antarctic Peninsula, is viable. Seed of plants from the South Orkney Islands normally fails to germinate but in one season, 1964/65, when full-sized seed was formed, germination tests showed that this was viable. Taken together these results indicate that the most mature inflorescences are produced regularly only on South Georgia and that farther south the most

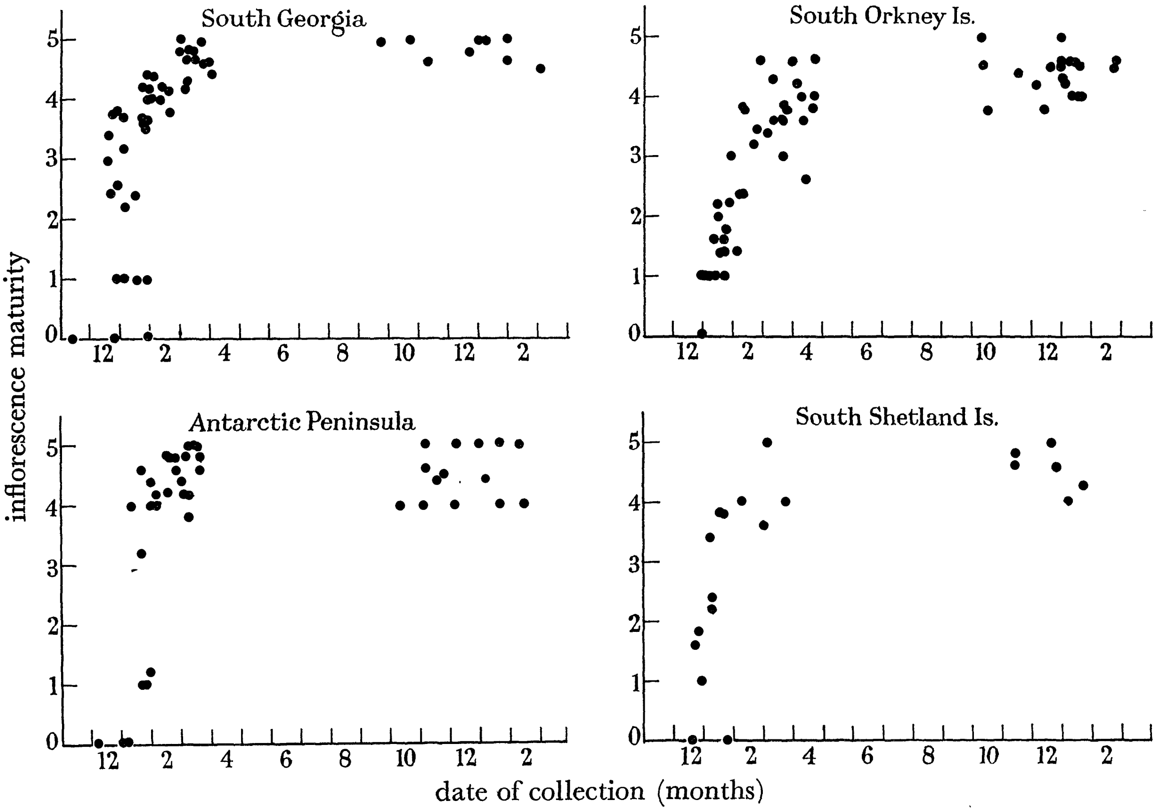

FIGURE 60. Maturity of inflorescences of *Deschampsia antarctica* Desv. according to date of collection.

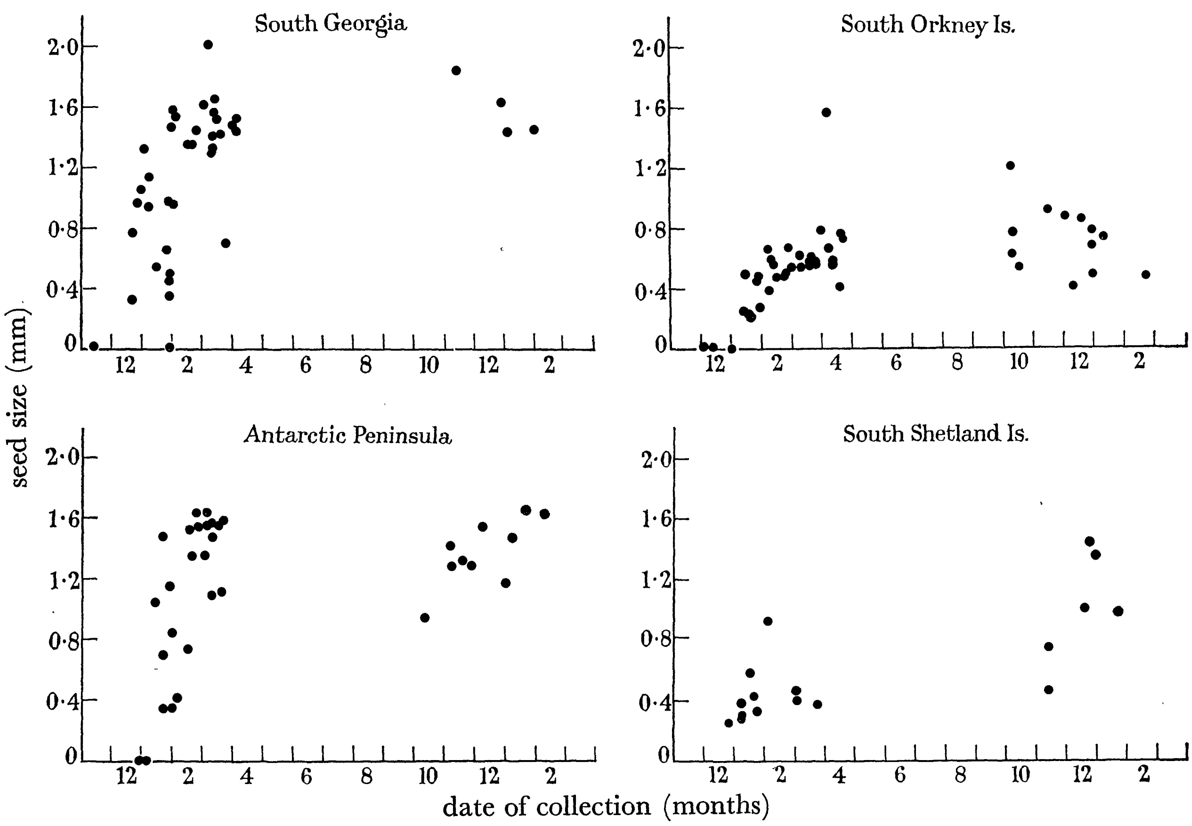

FIGURE 61. Seed size of *Deschampsia antarctica* Desv. according to the date of collection.

mature state is attained by plants along the Antarctic Peninsula with the least development taking place in the South Orkney Islands. Seed size shows the same trend even more dramatically, but it is quite clear that it varies independently of inflorescence maturity, i.e. almost mature inflorescences may have immature seed and vice versa. Comparable results for flower maturity and seed size in *Colobanthus* showed a similar but less marked trend with once more the poorest development being recorded for the South Orkney Islands. However, unlike *Deschampsia*, seed size and age of flower or capsule showed a good positive correlation, maturity increasing in both at more or less the same rate.

The reproductive success of both species was examined over the last 5 years on Signy Island, South Orkney Islands, where detailed observations have been in progress since the 1961/62 season. It was found that although inflorescences and flowers are produced annually, they rarely fully develop. For *D. antarctica* only immature seed was produced in four out of five seasons, the 1964/65 season alone giving full-sized seed. *C. crassifolius* also produced full-sized seed during this season but, in addition, it was found that a little mature seed had been formed in the 1962/63 season. Thus reproductively *C. crassifolius* appears to be slightly more successful than *D. antarctica*, on Signy Island. From a study of marked plants the most interesting results obtained indicate that sometimes the size of the seed sampled at the beginning of one season showed an increase over that of a similar sample at the end of the previous season, i.e. that seed remaining on the plants over winter had increased in size between the two sample dates. These observations need confirmation for other seasons but they suggest an interesting compensating mechanism which could mitigate some of the effects of bad seasons.

Behaviour in controlled environments

Since temperature and daylength are considered to be the two most important environmental factors regulating the growth and reproduction of plants, an assessment was made of the responses of the cloned South Georgian material of *D. antarctica* and *C. crassifolius* to a range of conditions.

Vegetative growth

Growth of plants of *D. antarctica* was recorded by measuring increase in leaf length and the rate of tiller production, while for *C. crassifolius* increase in leaf length and increase in cushion width were recorded. Since the graphs showing increase in leaf length for both species gave results paralleling those showing rate of tiller production and increase in cushion width only the latter will be considered here.

From figure 62, it is clear that for *D. antarctica*, following an initial rapid production of tillers in most treatments, the sustained high temperature conditions, both at 18 °C and 18 to 20 °C, caused the death of the majority of the plants under these regimes. By contrast, there was a large increase in the number of tillers formed at continuous low temperatures (5 °C), but the largest increase was shown by plants under the fluctuating 5 to 20 °C regime. Daylength appeared to have a subordinate effect to temperature, tiller production being only a little better under long days at continuous low temperatures, although the greatest number were formed under short days with fluctuating temperatures. The sustained high temperatures were also lethal to plants of *C. crassifolius* (figure 63), but unlike *D. antarctica*, there was little difference between plants at the continuous low temperatures and the fluctuating 5 to 20 °C regime. Again, daylength appeared of less importance than temperature but plants under long day conditions were marginally larger than those under short days.

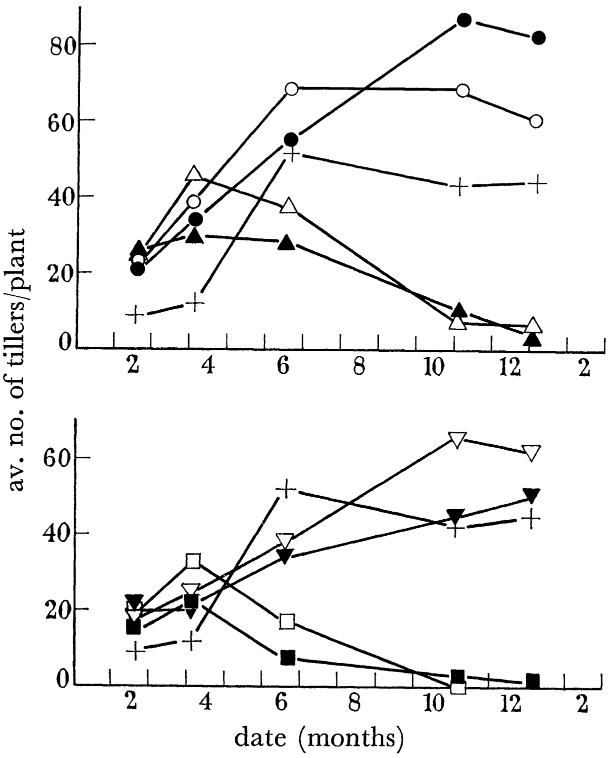

FIGURE 62. The effect of temperature and daylength on tiller production in *Deschampsia antarctica* Desv.

Key				
○ LD	5–20	▽ LD	5
● SD	5–20	▼ SD	5
△ LD	18–20	□ LD	18
▲ SD	18–20	■ SD	18

\+ cold greenhouse control

Inspection of the plants revealed other differences. Plants of *D. antarctica* under the continuous low temperatures and the fluctuating regimes produced vigorous, upright, tufted growth, with broad, but not very tightly rolled leaves whereas under higher temperature conditions, living plants had a more mat-like growth form with narrower, more tightly rolled leaves. Plants of *C. crassifolius* showed elongation of the internodes and production of lateral branches under all conditions. The internodes were longest and the number of secondary branches least at the sustained low temperatures, but more secondary branches were produced and the internodes were shorter, giving a denser cushion, under the fluctuating regimes. The most compact cushions were formed under the higher temperatures.

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As plants under all conditions were kept well watered, it is unlikely that water deficiency affected the results. However, it is possible that the vegetative differences noted in the plants under the higher temperatures are the result of responses to reduce the transpiration rate. The plants of both species under the warmer conditions showed symptoms of respiratory exhaustion and while no respiration rates (or transpiration rates) were determined, death was probably due to this cause. Throughout the experiments light intensities were high and although the compensation point, at the varying temperatures, was not determined it is thought that photosynthetic rates were not limiting.

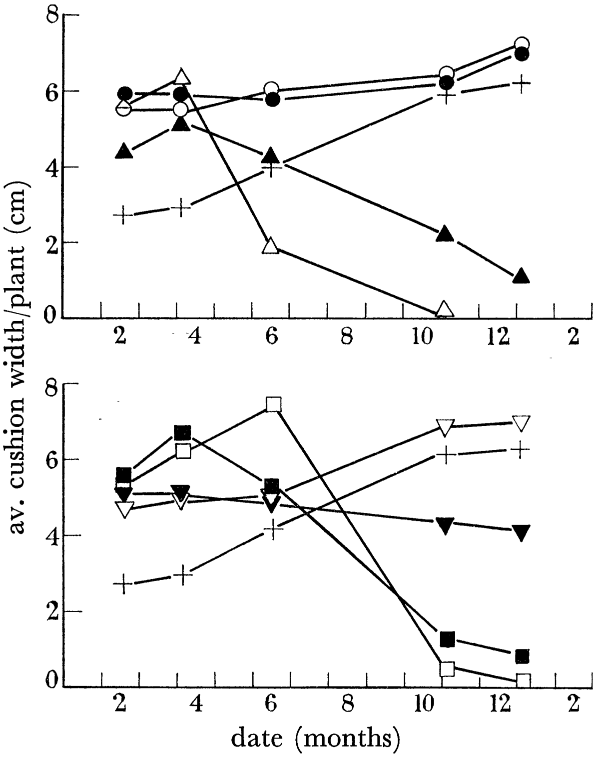

FIGURE 63. The effect of temperature and daylength on cushion width in *Colobanthus crassifolius* (D'Urv.) Hook. f.

Key			
○ LD	5–20	▽ LD	5
● SD	5–20	▼ SD	5
△ LD	18–20	□ LD	18
▲ SD	18–20	■ SD	18
+ cold greenhouse control			

Inflorescence and flower production

It is well known that many plants require a cold pre-treatment in short days before they will flower, and so before investigating the effects of temperature and daylength on the reproductive behaviour of *D. antarctica* and *C. crassifolius*, some of the plants of each species were placed for 4 months under continuous low temperatures (5 °C) with short days (8 h). Subsequently it was found that for *Deschampsia* only plants which had had a cold pre-treatment formed inflorescences, whereas in *Colobanthus* the flowering response was similar in treated and untreated plants. Inflorescence and flower production was studied under the same conditions used for vegetative growth.

From figure 64 it would appear that daylength rather than temperature controls the initial development of flowers in *D. antarctica*, but that the rate of production is more influenced by temperature. Thus, in all treatments, inflorescences appeared first under long day regimes, a marked increase in the period over which inflorescences are produced being noticeable at the lower temperatures. In contrast, flowering in *C. crassifolius* began in most treatments at about the same time, with the exception of plants at the continuous

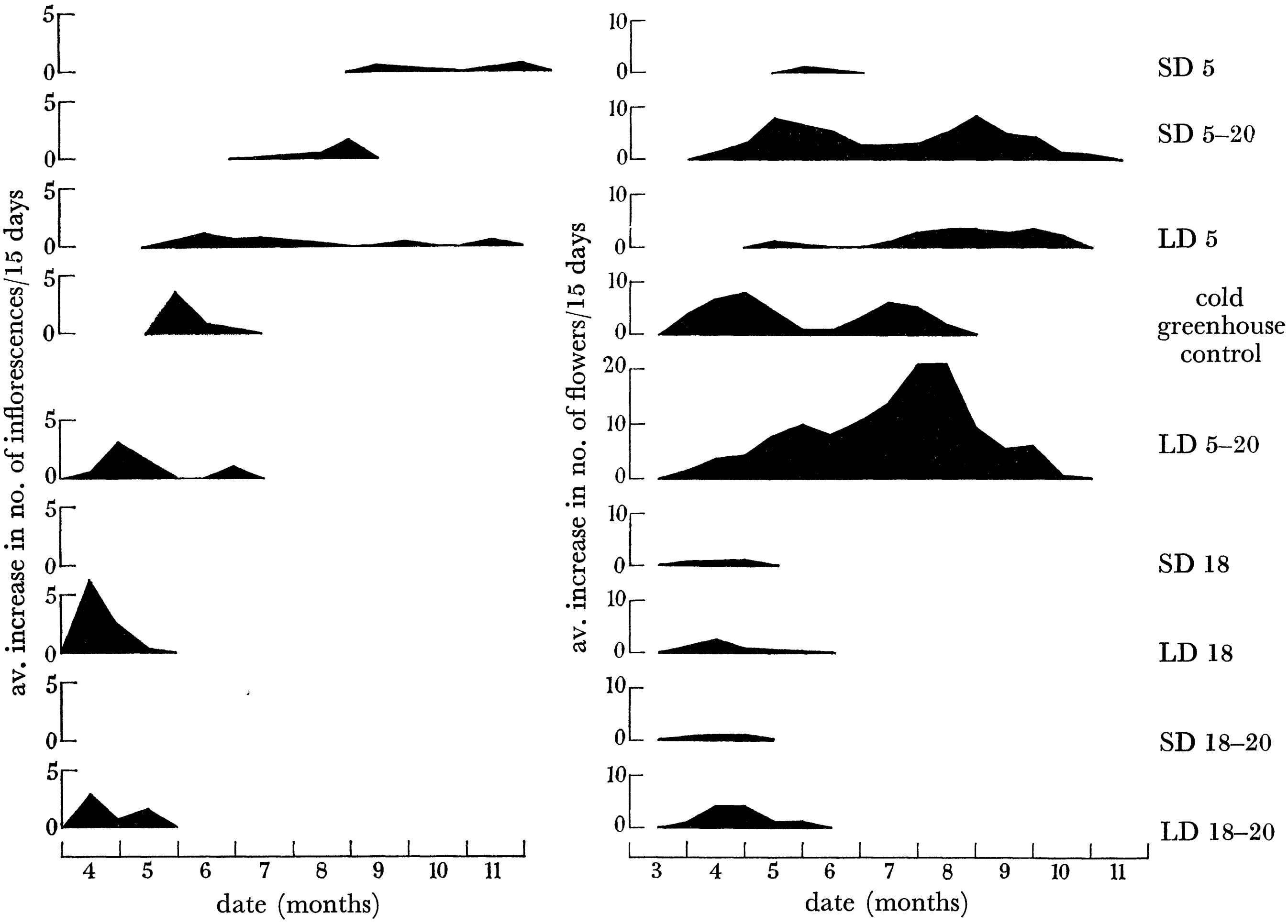

FIGURE 64. The effect of temperature and daylength on the periodicity and duration of inflorescence and flower production for *Deschampsia antarctica* Desv. and *Colobanthus crassifolius* (D'Urv.) Hook. f.

low temperatures, but there is some indication, particularly at the lower temperatures, of an earlier response under long day conditions. Like *D. antarctica*, the duration of flower production appeared to be under temperature control, the period being extended at the lower temperatures, but this time being longest under the fluctuating 5 to 20 °C conditions rather than at continuous 5 °C as in *Deschampsia*. However, as can be seen from the graphs, *Colobanthus*, but not *Deschampsia*, produced an increased number of flowers under the lower temperatures, a point considered further below.

Another striking difference in the response of the two species is evident when their periods of maximum inflorescence and flower production are compared. The graphs for

Colobanthus show distinct double peaks for plants under the fluctuating 5 to 20 °C regime and for the control material, with a less marked response in those under the continuous low temperatures. In *Deschampsia*, on the other hand, there is no evidence of such a response when allowance is made for the difference in the number of inflorescences and flowers produced by both species. This second flowering flush in *Colobanthus* was the result of each plant in the conditions noted producing a second set of flower buds which developed fully and formed viable seeds after the first set of capsules had opened, whereas in *Deschampsia* only a single set of inflorescences was produced per plant. In passing it may be noted that although inflorescence and flower production has only been followed on marked plants on Signy Island, there is no satisfactory evidence so far to suggest that on the South Orkney Islands, or elsewhere, *Colobanthus* produces more than one set of flowers under field conditions.

Data on the average number of inflorescences or flowers per plant are presented in table 27. It will be noticed that for both species, the numbers formed under long days exceeded those produced under short days but the temperature at which they were formed exerted an over-riding influence. This was particularly noticeable for *Colobanthus* where the lower temperatures, especially the fluctuating 5 to 20 °C, resulted in the largest average number of flowers per plant.

TABLE 27. EFFECT OF TEMPERATURE AND DAYLENGTH ON THE REPRODUCTIVE PERFORMANCE OF *DESCHAMPSIA ANTARCTICA* DESV. AND *COLOBANTHUS CRASSIFOLIUS* (D'URV.) HOOK. F.

	Deschampsia			*Colobanthus*		
treatment	av. no. infl.	av. no. seeds	av. seed size (mm)	av. no. flowers	av. no. seeds	av. seed size (mm)
LD 5 °C	4	0·375	1·808	23·38	9·48	0·652
SD 5 °C	1·33	—	—	3·88	—	—
LD 5–20 °C	6	38·91	1·548	145·25	20·55	0·581
SD 5–20 °C	2	—	—	66·63	23·40	0·570
LD 18 °C	8	3·17	1·587	4·63	16·23	0·556
SD 18 °C	—	—	—	3·88	15·84	0·550
LD 18–20 °C	5	7·2	1·600	13·25	22·86	0·580
SD 18–20 °C	—	—	—	1·25	16·33	0·612
cold greenhouse	4·75	15·79	1·644	52·29	36·45	0·571

Finally, it may be noted that inflorescences of *D. antarctica* matured fully under all treatments where they were formed, except at continuous low temperatures. Under the latter conditions the majority of panicles rarely became fully exserted and none expanded fully, while under short days some inflorescences failed to emerge from their sheaths. Similarly in *Colobanthus*, capsule development was normal except at continuous low temperatures where, under short days all remained unswollen, while development was incomplete in some at long days. It was also noted that peduncle length was shortest at the continuous low temperatures.

Seed formation and germination

Data on seed formation are summarized in table 27. It is immediately apparent that in *Deschampsia* seed was only formed under long day conditions, while daylength had little or no effect on seed formation in *Colobanthus*. The effects of temperature on the average number of seeds per inflorescence or per capsule showed no clear trend although once more the highest averages were noted under fluctuating 5 to 20 °C temperatures. When seed size is considered it is interesting to note that in both species the largest seeds were formed under the continuously low temperatures. Germination tests established that seed formed by both species under the various conditions was viable.

The optimal conditions for maximum seed germination for both species were investigated by a series of experiments which tested the effects of various treatments on seeds of different ages, the results being given in table 28. It will be seen that although seed of both species can be germinated when taken direct from the plant, the amount of germination is increased with age of seed in *Colobanthus* but not in *Deschampsia*. Again it was found that seed of both species would germinate without any pre-treatment but that exposing moist seeds of *Deschampsia* to 5 °C for 1 to 15 days resulted in a steady increase in germination with increase in exposure time. *Colobanthus* seeds showed no increase unless the exposure of moist seeds was sustained for at least 2 to 3 months. Scarification could be used to replace the cold pre-treatment effect in *Deschampsia* but in *Colobanthus* the seeds were too small and easily damaged, so it was rarely successful.

TABLE 28. SUMMARY OF GERMINATION RESULTS FOR *DESCHAMPSIA ANTARCTICA* DESV. AND *COLOBANTHUS CRASSIFOLIUS* (D'URV.) HOOK. F.

	Deschampsia antarctica	*Colobanthus crassifolius*
state of seed		
age	direct from infl. will germinate: older seed gives slightly higher results	direct from flower will germinate: the older the seed, the higher the germination
pre-treatments		
cold	will germinate without pre-treatment	will germinate without pre-treatment
dry at 2 °C	no increase	no information
moist at 5 °C	steady increase in amount with increase in exposure from 1 to 15 days	no effect from 1 to 15 days: increase after 2 to $3\frac{1}{2}$ months
scarification	replaces low-temperature requirement	produces abnormal germination
germination conditions		
light/dark	neither inhibitory	neither inhibitory
temperature	will germinate at 5 °C: rate and amount increases with temperature increase: highest at fluctuating 5 to 18 °C	no germination at 5 °C: rate increases with temperature increase, but amount decreased at high temperature: highest at fluctuating 5 to 18 °C
optimum conditions		
age	immaterial	at least 6 months
pre-treatment	moist at 5 °C for 15 days (or scarify)	moist at 5 °C for at least 3 months
conditions	fluctuating 5 to 18 °C (16/8 h daily)	fluctuating 5 to 18 °C (16/8 h daily)
expectation	80 to 100%	80 to 100%

When the effect of various environmental conditions on germination was investigated, it was found that both species were equally successful in the light and in the dark but the rate and final amount of germination was influenced by temperature. Increasing the temperature increased the rate of germination in both species, but it is interesting to note that while seed of *Deschampsia* will germinate at 5 °C, no seeds of *Colobanthus* germinated at this temperature. Increase in temperature also increased the final amount of germination in *D. antarctica* but in *C. crassifolius* the amount was depressed at the highest temperature (20 °C). Thus, it appears that for successful germination seed of *Colobanthus* has a narrower temperature range than seed of *Deschampsia*, the best results in both cases being obtained at fluctuating 5 to 20 °C temperatures. However, for optimal germination seed should be given the correct amount of pre-treatment, with seed of the appropriate age being selected for *Colobanthus*.

Discussion

It is quite clear from the experimental results that plants of both species have specific, and often contrasting, requirements for growth, inflorescence and flower production, as well as seed formation and germination. However, before an attempt is made to integrate the experimental results with those derived from the field observations, two important questions need to be considered. First, what relationship have the experimental conditions to those experienced by plants in the field? Secondly, since the experimental material came from a single locality on South Georgia, i.e. of Sub-Antarctic rather than Antarctic origin, can it be assumed that plants of both species from the Antarctic zone will have similar responses and requirements?

None of the experimental conditions could be regarded as truly representative of the varied summer climate either on South Georgia or in the vicinity of the Antarctic Peninsula. From the data presented by Longton & Greene (this Discussion, p. 295) it can be said that South Georgian summers at plant level, at least at one site (King Edward Point), close to where the experimental material was collected, are characterized by rapidly fluctuating temperatures, ranging from just below freezing to 20 to 35 °C, i.e. a diurnal range of approximately 20 to 30 degC in high summer. Similar, but lower temperature fluctuations have been reported at plant level on Signy Island (Holdgate 1964) and it is known that fluctuating temperatures are experienced by plants at other sites along the Antarctic Peninsula. Unfortunately virtually no data are yet available as to the extent of the heating effect of solar radiation on plants of *D. antarctica* or *C. crassifolius*. However, it may be presumed that in *C. crassifolius*, with a growth form similar to mosses, comparable heating effects will occur: no doubt they also occur in *D. antarctica* though to a lesser extent. Thus R. E. Longton (personal communication) noted in a gully on Deception Island a temperature increase of 10 degC above air temperature (8 °C) in cushions of *C. crassifolius*, while on Signy Island, M. W. Holdgate (personal communication) found that temperatures in *Deschampsia* plants were usually higher than that of the surrounding air.

The second environmental factor of importance to be considered is daylength. At King Edward Point, South Georgia, December, the month of the southern summer solstice, has a mean daylength of 17·0 h, the figure steadily increasing with latitude, being 18·9 h at Factory Cove, Signy Island, and 20·1 h at Whalers Bay, Deception Island, until the full 24 h is attained at localities south of the Antarctic Circle (Pepper 1954). Thus, of the conditions used in the phytotron, those with long days and fluctuating 5 to 20 degC temperatures approximated most closely to conditions in the field, and were more representative of the vicinity of King Edward Point, South Georgia than sites farther south. However, even at the 5 to 20 degC fluctuation, the time the plants spent at either temperature exceeded the duration of comparable temperatures in the field due to the regularity of changes under the experimental conditions.

No satisfactory answer can yet be given to the second question—can Antarctic plants of both species be expected to show similar responses to the South Georgian experimental material? It is quite clear from the work of Mooney & Billings (1961) on *Oxyria digyna* and the results of many other studies reviewed by Heslop-Harrison (1964) that populations of a single species, taken from different parts of its range, may show distinct morphological and or physiological characteristics of an adaptive nature, i.e. that different responses to the same conditions may be shown by plants, often morphologically indistinguishable, from different parts of a species range.

A series of clones from material of *D. antarctica* and *C. crassifolius* collected at scattered sites along the Antarctic Peninsula are now being built up for experimental purposes, and it is interesting to note that under uniform conditions, in a cool greenhouse at Birmingham, differences in stature and compactness shown by the original collections are being maintained. Moreover, populations of *Colobanthus crassifolius* from the Falkland Islands and Tierra del Fuego show distinct differences to the South Georgian and Antarctic material in morphological characters, flowering response and in seed germination. Thus ecotypes with different physiological responses are to be expected.

Nevertheless, a comparison between the experimental and the field results seems worthwhile, if only to see what parallels can be drawn between the behaviour of plants in the field, both on South Georgia and farther south, with those under experimental conditions.

It has been established that both species extend northwards from Neny Island (68° 12′ S) along the west coast of the Antarctic Peninsula and on many of its off-shore islands, through the Scotia Ridge, into South America, i.e. the southern part of their austral ranges extend into the mildest and most oceanic part of the Antarctic botanical zone. Although no detailed results are yet available for habitat analyses of factors like water availability, the extreme drought of much of the snow-free areas of Antarctica may be expected to play a prominent role in limiting the southern extension of both species.

Both species are said to occupy comparable situations along the Antarctic Peninsula, many of the localities being north facing. The results of an analysis of twenty-five sites with *Deschampsia antarctica* on Signy Island led Holdgate (1964) to suggest that both species may be limited to what he called 'radiation traps'. However, the most extensive swards of *D. antarctica* and *C. crassifolius*, so far known from the Antarctic zone, occur on an area of Lynch Island, also in the South Orkney Islands, which according to C. A. Howie (personal communication) although north facing can hardly be described as a 'radiation trap'; certainly on South Georgia where both species are widespread and abundant there is no restriction to such sites. It may be, therefore, that restriction to 'radiation traps' only takes place in areas where persistent cloud cover reduces the amount of radiation or where an excess of wind tends to accelerate heat loss from the surface of vegetation.

Although the vegetative uniformity of both taxa suggests that the growth form of the plants are well suited to the range of local conditions at the various localities, *Deschampsia* is not only known from more localities than *Colobanthus*, but it is usually more abundant at each. Indeed the only known extensive area of *C. crassifolius* has developed at one locality from which *D. antarctica* has never been reported. Plants of *Colobanthus* were found to grow much more slowly than those of *Deschampsia* under experimental conditions, both increasing in size at continuous low temperatures, and giving their best responses at fluctuating 5 to 20 °C conditions, but whether growth rates are an important contributory factor to the overall paucity of *Colobanthus* is not known. Information on growth rates and yield in the field combined with a close comparison of local microclimates at a large number of sites are essential before satisfactory progress can be made with this problem.

It is now known that both species regularly produce inflorescences and flowers in all localities in the Antarctic Peninsula–Scotia Ridge sector almost certainly every season. Comparison of the reproductive behaviour between localities, and within localities between seasons, has revealed variability in the maximum state of maturity attained by both species. Their reproductive success on Signy Island and also on the South Shetland Islands is regularly less than on South Georgia or at stations along the Antarctic Peninsula. Inflorescence and flower production under the experimental conditions, while best under long days, was found to be retarded at the lower temperatures, many under continuous 5 °C failing to attain full maturity. Similarly, seed production was adversely affected by the low temperatures, many seeds in *C. crassifolius*, in particular, aborting or failing to develop under the continuous 5 °C regime. If the Antarctic populations show a comparable response it might be expected that the worst reproductive performance would be associated with seasons or areas of least sunshine. In this connexion it is particularly interesting to note that the sunshine figures for Signy Island (table 29) are consistently lower

Table 29. Mean daily hours of sunshine for the months November to February along the Scotia Ridge and the Antarctic Peninsula

		South Orkney Is.	S. Shetland Is.	Antarctic Peninsula	
season	South Georgia	Signy I.	Deception I.	Argentine Is.	Horseshoe I.
1951/52	4·0	1·5	2·5	3·3	—
1952/53	5·9	1·9	4·1	2·7	—
1953/54	5·7	2·1	2·6	3·2	—
1954/55	4·8	2·0	3·1	2·5	—
1955/56	4·7	1·7	4·6	4·9	6·0
1956/57	5·4	1·9	3·3	4·0	5·8
1957/58	4·7	2·3	3·6	4·1	5·2
1958/59	5·3	1·8	3·3	4·3	5·0
1959/60	5·7	2·2	2·7	3·2	—
1960/61	5·6	2·8	3·0	4·0	—
1961/62	5·4	2·2	2·7	3·6	—
1962/63	5·7	1·7	3·1	4·0	—
1963/64	5·5	1·7	1·8	2·5	—
1964/65	3·6	2·0	2·7	4·0	—
average	5·1	2·0	3·1	3·6	5·5

than elsewhere, Deception Island being a little better, while the Argentine Islands and localities further south approach more closely, or exceed the South Georgian figure, a relationship closely matching the reproductive performance of the plants in the field. However, the indication of a possible 'winter development' of seeds on Signy Island suggests a compensating mechanism whereby a little viable seed could be produced even after a 'bad' summer. This mechanism has yet to be investigated under experimental conditions.

If conditions for seed germination of both species in the Antarctic zone parallels that shown by the South Georgian material, no doubt these conditions are regularly satisfied in most localities, probably in most years. No satisfactory experimental results are yet available for defining the conditions and tolerances for the survival of seedlings and the establishment of adult plants, and while seedlings of both species have been noted in a number of localities, their regularity or frequency of occurrence is unknown. However, it is thought that failure in seed production, rather than failure in seed germination may prove to be the more limiting factor.

Taken together, all the available results suggest that along the Antarctic Peninsula–Scotia Ridge the status of *Deschampsia antarctica* and *Colobanthus crassifolius* is that of well established species adequately fitted to survive in their polar environment, both appearing to be well adapted to growing and reproducing under summer conditions of long days with cool but fluctuating temperatures.

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