STUDIES ON *Acaena* (ROSACEAE):
I. SEED GERMINATION, GROWTH AND ESTABLISHMENT
IN *A. magellanica* (Lam.) Vahl AND *A. tenera* Alboff

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ABSTRACT. Germination studies in controlled environments showed that the best results were obtained by an alternating daily temperature regime of 20°/10° C. Delay in the onset of germination appeared to be correlated with the heat total in deg. hr./day of particular treatments, but there was some evidence that this response was related to a threshold value. Establishment of *A. tenera* seedlings in the field was highest on stony mineral soil and was greater than that for *A. magellanica* in all successful treatments. Seedling growth in *A. magellanica* was much faster than in *A. tenera*. A linear relationship between air temperature and leaf production was found in phytotron experiments. These results are discussed in the context of initial colonization of South Georgia by long-distance dispersal of fruits and their ecological significance in present-day communities.

THIS paper is the first in a series dealing with various aspects of the growth and physiology of species of *Acaena*, a Southern Hemisphere genus of the Rosaceae. The papers will be mainly concerned with the three taxa occurring on South Georgia (Walton and Greene, 1971) but reference will be made to other species where appropriate.

Acaena is a successful and important circum-polar genus found mainly in temperate latitudes. In tropical latitudes it is restricted to alpine sites. *A. magellanica* is the most widespread species in the genus and occurs on all the sub-Antarctic islands. It grows in a wide range of plant communities on these islands, often being the dominant species. Autecological studies on this and on the two other South Georgian taxa, *A. tenera* and the hybrid *A. magellanica* × *A. tenera* were begun in 1967. The present paper examines seed germination and growth both on South Georgia and in controlled environment chambers in Birmingham in an attempt to explain both the success of these species in colonizing remote islands and their present-day ecological restrictions on South Georgia. Much relevant background information on the terrestrial ecology of the island has been given by Smith and Walton (1975).

MATERIALS AND METHODS

Experiments in controlled environment chambers

Seed which had overwintered in the field was collected in late 1970, air dried and brought back to Birmingham for germination experiments in summer 1971. Large quantities of seed of all three taxa were collected from sites where the respective species were well established. The seed samples were mixed and aliquots withdrawn for sowing.

To test the effect of temperature on germination, two replicates of 50 seeds each per treatment were sown on filter paper in plastic petri dishes. Seeds were removed as they germinated, the criterion adopted for germination being that the length of the extending radicle was at least twice its basal width. Nine temperature regimes were used. Because of the requirements of other workers using the phytotron, the daily light period was divided into two consecutive periods of 8 hr., followed by a dark period of 8 hr. (Table I).

TABLE I. TEMPERATURE TREATMENTS USED DURING GERMINATION EXPERIMENTS

	Treatment (°C)								
	5/5	5/10	5/20	10/10	10/5	10/20	20/20	20/5	20/10
Light 8 hr.	5	5	5	10	10	10	20	20	20
Light 8 hr.	5	10	20	10	5	20	20	5	10
Dark 8 hr.	5	10	20	10	5	20	20	5	10

To check the effect of light on germination, dishes of 50 seeds were sown at 20° and 10° C, half of each being kept in light-proof containers and half under a 16 hr. light/8 hr. dark regime.

An attempt was made to reduce the delay in onset of germination and increase the germination rate by removing any inhibiting substances in the seed coat by pre-treating seeds with 50 per cent ethanol or 50 per cent sulphuric acid.

Collections of seeds made in February 1971 had not been subjected to winter temperatures in the field. These were used to test the effect of cold pre-treatment on germination. Batches of 50 seeds were kept at −4° and −11° C, samples being removed for sowing at weekly intervals from the −4° C regime and at fortnightly intervals from the −11° C regime. Three control sowings of unvernalized seeds were made during the experimental period and a fourth 6 months later.

To investigate the dependence of leaf production in seedlings on temperature, germinated seeds of both species were planted in John Innes No. 2 compost and grown in controlled environment chambers at 5, 10 and 20° C. In each leaf number class, seedlings were scored at intervals for numbers of unfolded leaves. The percentage of the total number of seedlings present was then multiplied by the appropriate leaf number to obtain a development index (DI) value. These were added to give a total DI value for each treatment at each scoring. For example, if 10 per cent had no leaves, 80 per cent one leaf and 10 per cent two leaves, the total DI would be $0+80+20 = 100$. Linear regressions were fitted to plots of total DI against time since sowing for the three temperature treatments. The slope of the regression lines provided a mean leaf-production rate for each treatment.

Experiments on South Georgia

Seedlings had been found growing both in moss and on areas of bare ground. Since the ability of seedlings to become established on bare ground is an essential pre-requisite for a colonizing species, it was decided to test germination and establishment of both species in two common soil types at a variety of sites. The soils used were a brown earth (resembling an Arctic brown as described by Tedrow and Hill (1955)) from beneath a *Festuca contracta* T. Kirk grassland, and a mineral soil from a barren area subjected to frost heaving. Details of the six sites used—grassland, heath, fellfield, dwarf shrub, alpine and bog—are given in Table II. All these sites were within 200 m. of each other. A set of six pots (ten seeds per pot) per soil type per species were sunk into the ground at each site. No water or nutrients were provided.

To measure dry-matter production of seedlings and investigate their rates of development with respect to climate only, germinated seeds of both species were grown in fertilized vermiculite at the grassland and fellfield sites. Modified Hoagland's solution (Lewis and Greene, 1970) was watered on to the pots every 3 days. Planting date was 15 November 1970 and four random harvests of 15–19 plants/species/site were taken during the summer. The plants were washed, divided into root, shoot and leaves, oven dried and weighed to the nearest 0·1 mg. The number of leaves and branches was recorded for each plant.

RESULTS

Germination in controlled temperature regimes

The presentation of large amounts of germination data in the form of graphs is costly in terms of space. Various workers have attempted to derive mathematical equations, the constants of which can be used to characterize the germination response (Czabator, 1962; Timson, 1965; Goodchild and Walker, 1971; Janssen, 1973). Janssen (1973) considered that three factors are required to provide a complete description of germination—total germination, mean rate and variation in this rate. In Fig. 1 four factors are used to describe the germination curve. Constant A is the delay between sowing and onset of germination; B is the mean slope of the curve and describes the rate of germination between onset and finish; C is the mean rate of germination calculated from sowing to attainment of maximum germination; D is the maximum percentage germination achieved. No estimate is provided of the variation in rate of germination.

| Site	Locality	Altitude (m.)	Slope (deg.)	Aspect	Insolation	Wind exposure	Edaphic characteristics	Community type
Grassland	Above south shore of King Edward Cove	50	20–25	N	High	Moderate	Brown earth, good drainage	Closed, tall dense *Festuca contracta* grassland
Heath	Near north-east shore of Gull Lake	80	Level	N	Normal	Moderate–high	Shallow brown earth, medium drainage	Open *Festuca contracta* grassland with many cryptogams
Fellfield	Crest of small hill to south of heath site	90	0–5	Open	High	High	Morainic detritus, good drainage	Very open community of scattered cryptogams and sparse tufts of grass
Dwarf shrub	Above south shore of King Edward Cove	10	15–20	N	High	Low	Peat, very wet	Closed *Acaena magellanica* community with moss
Alpine	Above grassland site	75	5–10	E	Normal	High	Mineral soil, good drainage	Open community of *Acaena tenera, Phleum alpinum* and cryptogams
Bog	Above south shore of King Edward Cove and east of heath site	80	Level	N	Normal	Moderate–high	Peat, waterlogged	*Rostkovia magellanica–Tortula robusta* bog
Shackleton	Side of Mount Duse, King Edward Point	10–15	40	S	Low	Moderate	Scree, good drainage	Closed *Acaena magellanica* community with some moss
Point	King Edward Point	2	Level	Open	Normal	Moderate	Beach gravel, good drainage	Prostrate mat of *Acaena magellanica* with *Poa annua* and *Deschampsia antarctica*
Dam	Beside small dam on side of Mount Duse, King Edward Point	15	30–40	S	Low	Low–moderate	Peaty soil in pockets between rocks	*Acaena tenera* growing in open rocky areas between *Poa flabellata* tussocks
Hope	Below cross at Hope Point, King Edward Point	10	15–20	W	Normal–low	Low	Peat/brown earth transition zone	Hybrid *Acaena* growing between *Poa flabellata* and *Rostkovia magellanica* communities
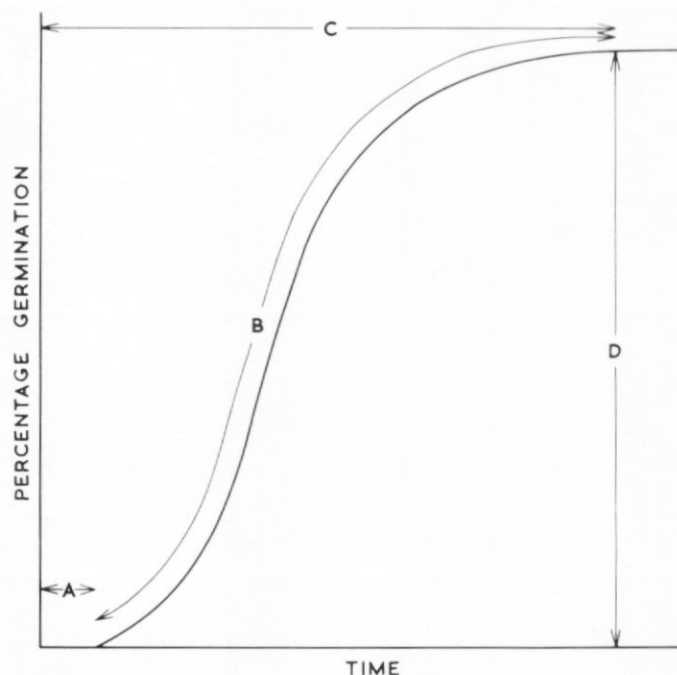
Fig. 1. Idealized germination curve to show derivation of constants used to describe germination.

These four germination characteristics are presented in Table III for the experiments carried out in the nine controlled temperature regimes. Since only one hybrid seed germinated, it is excluded from further discussion. Seeds failed to germinate in three of the *A. magellanica* treatments but in only one of the *A. tenera* treatments. Once germination began there were marked differences in the rate (B) at which the final percentage was achieved. For *A. magellanica* the highest value of B was 7·09, achieved in the 20°/10° C treatment. For *A. tenera* the highest value (9·30) was attained in the 10°/20° C treatment. Overall germination rates (c) were also highest in these two treatments. There was reasonable correlation between rates of germination and total germination. Treatments with similar values of B often had quite different values of c due to different delay periods (A) before onset of germination.

The delay in onset of germination is the period during which the dry seed imbibes water and initiates the metabolic processes necessary for cell division and elongation. It seems likely that the rate of change in a seed from a dormant condition to one of germination is temperature dependent. Fig. 2 shows the delay in the onset of germination in the various treatments plotted against the total daily deg. hr. These latter data are calculated by adding together the mean temperature for all hours of the day, e.g. treatment 20°/10° C has 8 hr. at 20° C and 16 hr. at 10° C, giving a total of 320.

For almost every treatment in which both species germinated *A. magellanica* always germinated before *A. tenera*. There is a clear correlation between the heat total per day and the delay in germination, and it is possible to predict from this the delay that should have occurred before germination of the 5°/10° C and 10°/5° C treatments of *A. magellanica*. These would have been *c.* 16 days (5°/10° C) and *c.* 22 days (10°/5° C). Since neither showed any germination even after 40 days, it is possible that the relationship between temperature and germination is more complex than has been suggested so far. Evidence in Table III suggests that alternating temperatures are more liable to bring about germination than constant temperatures. This is not surprising as seeds experience fluctuating conditions in the field. There may be two critical thresholds operating—one which requires the total daily deg. hr. to be above a certain minimal value to ensure continuity of growth, once stimulated, and another which requires that at

TABLE III. GERMINATION RESPONSE UNDER CONTROLLED TEMPERATURE REGIMES

Species and treatment	Mean delay in onset (days) Constant A	Mean rate (per cent per day) Constants		Mean total germinated (per cent) Constant D
		B	C	
A. magellanica 5/20	6	3·38	2·32	44
5/10	—	—	—	0
5/5	38	2·00	0·05	2
10/20	6	2·24	1·65	38
10/10	—	—	—	0
10/5	—	—	—	0
20/20	4	1·45	1·27	42
20/10	8	7·09	4·11	78
20/5	12	2·55	1·22	28
A. tenera 5/20	8	5·00	3·33	80
5/10	19	4·27	1·88	64
5/5	—	—	—	0
10/20	8	9·30	5·17	93
10/10	18	3·78	1·89	68
10/5	27	1·33	0·41	16
20/20	9	3·17	2·42	92
20/10	6	3·56	2·91	96
20/5	14	4·93	2·55	74

least part of the temperature experienced by the seed during each day should be above a critical level in order to stimulate the change from dormant to germinating. If this is the case, it is possible that *A. magellanica* seeds could be stimulated to germinate if the 160 deg. hr. of 10°/5° C treatment were made up of 4 hr. at 20° C and 20 hr. at 4° C.

In all the treatments in which both species germinated *A. tenera* always achieved a higher final percentage (D) than *A. magellanica*. In terms of population dynamics, this, together with the much greater amplitude in temperature requirements of *A. tenera*, should compensate for the earlier germination of *A. magellanica*.

The results of the cold pre-treatments were not clearly defined (Table IV). There is some evidence that the delay in onset of germination (A) decreased as duration of cold treatment increased. Rates of germination (B and C) varied considerably. *A. tenera* showed slight evidence of an increase in rate of germination (B) with increased time in storage at −4° C. It is concluded that cold pre-treatment cannot be shown to be necessary for germination of seeds of *A. tenera* and *A. magellanica* when these seeds are already more than 6 months old. This qualification is important since it is not possible to determine from the data presented here if newly ripened seed has a cold requirement which diminishes with age. Certainly, on South Georgia most seeds would not experience prolonged winter temperatures of −11° C; −4° C is a much more typical temperature in areas with snow lie.
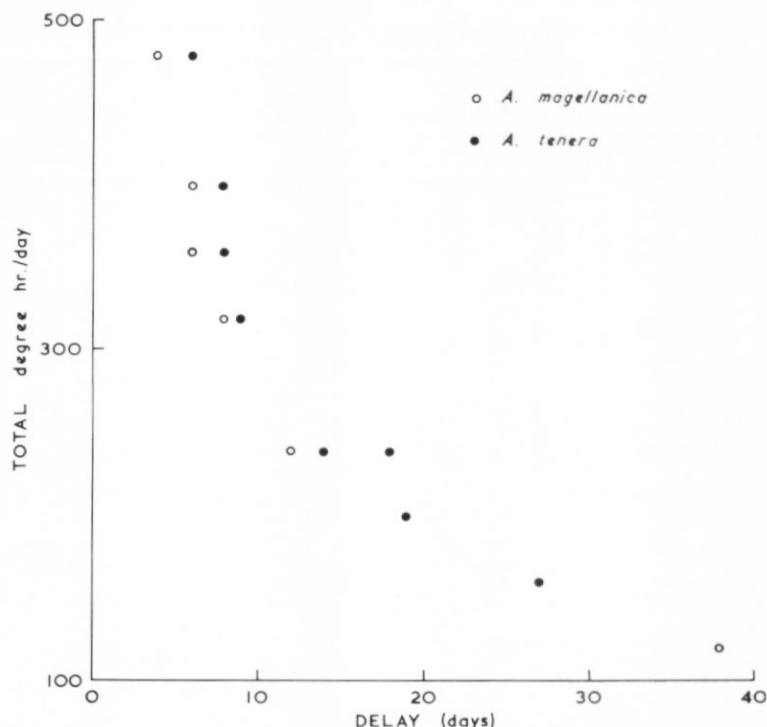
Fig. 2. The delay in the onset of germination in various temperature treatments.

The effect of light on germination is much more obvious (Table V). For both species in all treatments, both rates (B and C) were higher in light than in dark as were the final totals (D). It also appears that lack of light might lengthen the delay in onset of germination. This response to light correlates with assumptions made from ecological observations. The seeds of both species are generally found lying on the ground or on vegetation and it seems unlikely that they normally ever become completely buried before they have had a chance to germinate. Treatments with acid and alcohol to shorten the delay period (A) were uniformly unsuccessful.

Seedling germination and establishment in two soil types on South Georgia

Finding the right ecological niche in which to germinate does not necessarily result in each seed producing a mature plant. If a seed should germinate in an already established community, it will almost certainly suffer from competition effects from its nearest neighbours. If, on the other hand, it falls on bare ground, its chances of establishment will depend principally on the micro-topography of the soil and its interaction with the local micro-climate. The occurrence of large stones offering protection against wind desiccation, and the presence or absence of such periglacial processes as frost heaving and stone sorting, can be crucial factors in providing a suitable climatic niche for germination. The size of the seed or fruit and of its cotyledons can be critical in determining establishment of a germinated seed (Salisbury, 1942), whilst the rate of growth of the seedling during its first summer probably determines whether the species can become permanently established at a particular site from a particular seed.

The germination and development of *A. magellanica* and *A. tenera* seeds in two soil types at six sites 1 year after planting is given in Table VI. The seeds were planted in early February 1970 but no seeds germinated that autumn and overwintered as seedlings. The first seedlings were seen in mineral soil at the dwarf-shrub site at the beginning of December 1970. When the pots were examined in February 1971, frost action, especially in the mineral soil pots, had

TABLE IV. EFFECT OF COLD PRE-TREATMENT ON GERMINATION

Species and temperature treatment	Length of storage (weeks)	Mean delay in onset (days) Constant A	Mean rate (per cent per day) Constants		Mean total germinated (per cent) Constant D
			B	C	
A. magellanica	1	6	0·46	0·32	6
−4° C	2	10	1·33	1·09	60
	3	8	1·14	1·00	66
	4	14	1·28	1·03	74
	5	6	2·67	2·22	80
	6	5	1·59	1·44	78
	7	8	1·30	1·10	56
	8	6	1·89	1·62	68
	9	6	2·60	2·00	52
	10	2	1·18	1·11	40
A. magellanica	2	22	1·15	0·69	38
−11° C	4	14	1·28	0·98	60
	6	5	3·04	2·53	76
	10	2	2·00	1·89	68
A. tenera	1	6	0·54	0·46	18
−4° C	2	10	1·78	1·46	80
	3	12	1·28	1·07	73
	4	14	1·70	1·35	92
	5	11	1·58	1·31	84
	6	5	2·10	1·87	88
	7	8	2·13	1·70	68
	8	9	2·47	1·90	74
	9	6	2·96	2·42	80
	10	2	1·17	1·08	28
A. tenera	2	15	1·10	0·80	44
−11° C	4	14	1·87	1·44	88
	6	5	1·39	1·28	82
	10	2	0·88	0·83	30

TABLE V. EFFECT OF LIGHT ON GERMINATION

Species and treatment	Mean delay in onset (days) Constant A	Mean rate (per cent per day) Constants		Mean total germinated (per cent) Constant D
		B	C	
A. magellanica 20° C light	4	4·83	3·63	58
dark	5	2·21	1·75	42
A. tenera 20° C light	6	8·50	5·31	85
dark	6	5·45	3·53	60
A. tenera 10° C light	18	6·00	1·85	48
dark	23	4·00	0·18	4

TABLE VI. ESTABLISHMENT AND DEVELOPMENT OF *Acaena* SEEDLINGS AFTER
1 year AT VARIOUS SITES

Site	A. magellanica				A. tenera			
	Brown earth		Mineral		Brown earth		Mineral	
	Mean leaf number	Number of plants	Mean leaf number	Number of plants	Mean leaf number	Number of plants	Mean leaf number	Number of plants
Grassland	0	0	0	0	2·8	4	2·1	15
Dwarf shrub	4·0	2	3·4	9	2·5	4	2·7	25
Alpine	2·0	1	1·1	7	0·8	2	1·0	5
Heath	0·5	1	2·3	11	2·2	5	2·0	15
Bog	0	0	0	0	0	0	0	0
Fellfield	0	0	0	0	0	0	0	0

brought many small stones to the surface and seedlings were gaining considerable advantage from the protection afforded by them. This stone sorting was most evident in the pots at the fellfield and heath sites where the planted seeds were also raised to the surface. No germination occurred at the bog site and it is thought that the permanent flooding of the soil in the pots was the direct cause of this. The high water content ensured low soil temperatures and may also have caused the development of at least partially anaerobic conditions around the seeds.

At the dwarf-shrub site the stand of mature *A. magellanica* plants afforded a high degree of shelter to the pots and had to be cut back to prevent them being overgrown. At the end of the second summer, seedlings of both species at the alpine site had small leaves with reddish tips and functional cotyledons, whilst at the dwarf-shrub site the cotyledons had almost died and only the *A. tenera* seedlings had reddish leaf tips. The leaves of both species were larger at this site than at the alpine site. At all sites the root systems of all seedlings in the brown earth were much shorter and more branched than those in mineral soil.

For both species the highest establishment percentages were achieved in the mineral soil. Of 12 treatments for each species, *A. magellanica* was successful in four and *A. tenera* in seven. In nearly all treatments in which seedlings were established *A. tenera* had a higher percentage than *A. magellanica*. It would appear that the more variable topography offered by the mineral soil might be very important in seedling establishment. *A. tenera*, which grows in more exposed situations than *A. magellanica*, might be expected on ecological grounds to establish better on mineral soil. The protection afforded by the small stones is likely to have played a decisive r... since the slower-growing *A. tenera* seedlings were always much smaller than those of *A. magellanica*. In March 1971, although the majority of established plants were *A. tenera*, their development, measured by mean leaf number, was considerably less than that of the *A. magellanica* seedlings. Not all seedlings managed to become established. All the *A. magellanica* seedlings in brown earth at the fellfield and heath sites, and all the *A. tenera* in the brown earth at the alpine site, had died by the end of March 1971. There was also some seedling mortality in the more favourable grassland and dwarf-shrub sites. Tallowin (in press) noted a similar series of autumn deaths in *Festuca contracta* seedlings growing in bare ground on South Georgia. This may be a common phenomenon caused by desiccation due to the warm dry weather which frequently occurs in late February and early March on South Georgia or to the onset of diurnal freeze–thaw cycles in autumn.

In all but one of the treatments the percentage establishment of *A. tenera* seedlings was very much greater than that of *A. magellanica* seedlings. Since *A. tenera* also had a higher final germination percentage, a greater proportion of its ripe seed is likely to appear as young

plants than is the case with *A. magellanica*. This strategy appears to make maximum use of dry matter, an important consideration in a species with such slow growth.

Growth of established seedlings

Considerable differences in rates of growth of seedlings of the two species were noted in casual field observations. In order to quantify the difference, seedlings of both species were grown in a standard medium (vermiculite) at two sites. Under these nutrient-rich conditions, differences in performance between sites were not significant so only data from the most favourable site are presented in Table VII. Two major points are immediately obvious: *A.*

TABLE VII. GROWTH DATA FOR SEEDLINGS GROWN IN NUTRIENT-TREATED VERMICULITE
AT A GRASSLAND SITE ON SOUTH GEORGIA IN 1970–71

	Harvests			
	12 December 1970	16 January 1971	20 February 1971	27 March 1971
A. magellanica				
Mean number of leaves	2·7	8·3	17·2	29·0
Mean number of branches	0	1·1	1·9	2·9
Mean dry weight of leaves (mg.)	2·2	6·2	35·0	109·7
Mean dry weight of shoot (mg.)	0·7	2·5	10·0	45·4
Mean dry weight of root (mg.)	1·8	8·5	39·4	140·6
Mean total dry weight (mg.)	4·7	17·2	84·5	295·6
A. tenera				
Mean number of leaves	1·5	3·7	4·8	4·6
Mean number of branches	0	0	0	0
Mean dry weight of leaves (mg.)	0·9	0·8	2·1	1·7
Mean dry weight of shoot (mg.)	0·5	1·8	2·9	3·8
Mean dry weight of root (mg.)	0·5	1·0	2·5	3·3
Mean total dry weight (mg.)	1·9	2·7	7·5	8·9

magellanica produced more leaves and branches than *A. tenera*, and grew several times more quickly. The production of branches is thought to be highly significant in the context of the life strategy of *A. magellanica* (Walton, 1976), allowing the species a competitive advantage over *A. tenera* which only rarely produces branches.

Dry-matter allocation to organs differs between the species with the root comprising the greatest proportion in *A. magellanica* and the shoot in *A. tenera*. Since the *A. tenera* seedling has to overwinter whilst very small and with few leaves, it appears that the shoot acts as the principal food store. Although *A. magellanica* enters winter as a much larger plant with a substantial shoot, during the summer its rapid growth requires considerable amounts of water and nutrients which necessitates early and substantial root growth.

During the course of the summer the mean number of leaves produced by the *A. magellanica* seedlings was 29·0 and by *A. tenera* seedlings 4·6. To relate this difference in leaf production to temperature was impossible for the field-grown plants. However, in controlled temperature chambers leaf production by the seedlings proved to be almost linear for at least the first six leaves. From the regressions of development index (DI) against time for each temperature

treatment, it was found that at 20°, 10° and 5° C the mean time taken by *A. magellanica* to produce one leaf (leaf-production rate) was 8·5, 16 and 27 days, respectively. For *A. tenera* the equivalent rates were 17, 22 and 36 days. Development indices were calculated for some of the seedling experiments on South Georgia. Leaf-production rate proved to be *c.* 33 days for *A. tenera* for all plantings (equivalent to a constant temperature of *c.* 6° C), whilst that for *A. magellanica* varied from 7 to 18·5 days depending on the planting date. Generally, the later the planting date in December the greater the rate of leaf production.

DISCUSSION

Within any natural environment, the seeds of native species which rely on sexual reproduction for continued survival and dispersal will have evolved physiological responses which suit the local climatic and edaphic factors. With cool summers and winters which normally last over 6 months, South Georgia offers fairly uncongenial conditions for plant growth. The absence of native annual species is not, however, due to a lack of adaptability or suitability in terms of the annual's life cycle, since various introduced annual species have successfully persisted for many years (Walton and Smith, 1973). The preponderance of perennial species is in keeping with the situation in the Northern Hemisphere tundra ecosystems and has resulted in a major emphasis on vegetative reproduction. Many of the native species are also prolific seed producers and colonization by seed can be a significant feature in some habitats.

The germination responses of the three *Acaena* taxa on South Georgia are very different. Since the hybrid seeds had a very low viability under all the test conditions and the taxon, endemic to South Georgia, is believed to spread sexually mainly by F_1 hybrid seed (Walton, in press), it will not be discussed further in this paper.

Fruit number and fruit weight are apparently correlated with site favourability in *A. magellanica* (Walton, 1976). Considerable differences have been found in the numbers of fruits per capitulum both within *A. magellanica* and between it and *A. tenera* (Walton and Greene, 1971). In sites where the species are successful, i.e. dominant or a major constituent of the community, *A. magellanica* always has a greater number of fruits per head than *A. tenera*, whilst its branching pattern and inflorescence position ensure that it has a competitive advantage over the latter species in terms of potential production of fruiting heads (Walton, 1976).

Although the germination results presented here fall far short of what Thompson (1970) has suggested is necessary for an accurate characterization of germination response, a number of general conclusions are clear. *A. tenera* has a wider amplitude of temperature response than *A. magellanica*, with optimal rates for germination in both species being shown under a fluctuating regime of warm days and cool nights. There does not appear to be a facultative vernalization requirement, although there is some evidence that germination can be enhanced by cold pre-treatment. Since no germination tests were carried out with newly ripened seed on South Georgia, it is not known if there is an after-ripening phase during which the seed is dormant. This appears to occur in *Festuca contracta* and ensures that seed does not germinate in the warm period which often occurs in early autumn of the year of production (Tallowin, in press). Germination of *Acaena* seed has been noted in the field during this autumn period but it was not clear whether old or new seed was involved. Seeds germinating late in the season appear to have a much diminished chance of survival so that the development of a short dormancy period might be expected on the grounds of conservation of resources. Work by Thompson (1975) on the characterization of germination responses in *Silene* has shown that the temperature treatments that favoured germination were often unfavourable to after-ripening. He suggested that there is a distinction between the treatment necessary for ripening or breaking dormancy and that necessary for the mobilization of the seed reserves and the commencement of growth. This may explain the reduced germination percentages achieved in *A. magellanica*, since the ungerminated seeds, if viable, would form a considerable reservoir which could be activated at a later date by a change in climatic conditions. This appears to happen in some of the alien species (Walton, 1975) but does not occur in *A. tenera*.

The ability to colonize bare ground and germinate at low temperatures would be essential for species spreading into new habitats produced by the retreat of ice or snow. The geomorphological evidence for South Georgia (Clapperton, 1971) has suggested that during the

last glacial maximum the island was covered by an ice sheet. The mountainous nature of the terrain undoubtedly ensured the persistence of nunataks throughout the glacial periods but the climate must certainly have been too severe for the survival of broad-leaved plants such as *Acaena*. Transplant experiments have shown that, although *A. magellanica* and *A. tenera* can persist for some time in the more severe climate of Signy Island, South Orkney Islands (personal communication from J. A. Edwards), they do not flourish. Seed germination was also recorded for *Acaena* on Signy Island but none of the seedlings persisted past the one-leaf stage.

Ridley (1930, p. 589) regarded the fruits of *Acaena* as ideally suited to dispersal by birds and animals, the barbed spines catching in feathers and hair. On South Georgia, albatrosses, giant petrels and gulls have all been seen with fruits of *A. magellanica* attached to their feathers. It seems certain that the species was introduced into South Georgia by long-distance dispersal during the post-glacial period (Walton, 1974). Cytological evidence (Moore and Walton, 1970; Moore, 1972) suggests that the introduction was probably direct from the eastern part of Tierra del Fuego or Isla de los Estados. The evidence presented in this paper has shown that, whilst both species are capable of colonizing bare ground, *A. tenera* has an initial advantage in terms of both its temperature response and its high germination percentage. However, the much faster growth of *A. magellanica* coupled with its advantageous branching pattern and high fruit number per capitulum gives this species greater long-term ecological advantages. Walton (1976) has suggested that the high growth rates of *A. magellanica* are certain to result in dominance by this species in any lowland sites favourable for the growth of the two species. The general restriction of *A. tenera* to alpine and exposed sites appears to be due to its lack of competitive ability both at the seedling and adult plant stages.

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