STUDIES ON *Acaena* (ROSACEAE):
III. FLOWERING AND HYBRIDIZATION ON SOUTH GEORGIA

By D. W. H. WALTON

ABSTRACT. Morphological abnormalities of flowering parts in *A. magellanica* are described. The floral cycle was examined in all three South Georgian taxa. Indirect evidence suggested that floral initiation occurred in long days with a critical day length of about 13 hr. Development of flowers in the capitulum appeared to follow a similar sequence in all three taxa, although site aspect could have a retarding effect. No difference was observed in the rates of development of hermaphrodite and female heads in *A. magellanica*. Scape growth patterns differed between the taxa with maximal growth occurring before pollen liberation in *A. magellanica* and after in *A. tenera*. The hypothesis that F_1 hybridization was normally by *A. magellanica* pollen was supported by the raising of hybrid plants only from *A. tenera* seed.

IN the Arctic flora many of the species pre-form the next year's flowering buds at the end of the current flowering season (Sørensen, 1941). This adaptation is also common in alpine floras, where growing seasons are often restricted by snow lie. Pre-formation of flowers had been reported for two species on South Georgia (Smith and Walton, 1975) but not for the species of *Acaena*. Observations on South Georgia (Walton, 1976) have shown that the production and size of capitula are related both to ecological conditions and to the position of the scape in the growth pattern of the species. Earlier taxonomic studies also indicated that both hermaphrodite and female flowers were found in *A. magellanica* (Lam.) Vahl, whilst the hybrid taxon was characterized by its numerous subsidiary capitula. *A. magellanica*, a very variable species (Walton and Greene, 1971), is known to show a wide range of morphological abnormalities in both its floral and vegetative parts. Accordingly, field investigations were made into floral induction, morphological development of flowers in capitula, scape growth, the effect of habitat on floral development and pollen viability. Observations were also made on the morphological abnormalities found. It was hoped that this intensive investigation might also throw some light on the origin of the hybrid taxon.

MATERIAL AND METHODS

Floral development

The sites of all the populations used have been fully described by Walton (1977). Each capitulum was scored for floral development by using the following categories:

I. Capitulum evident but no flowers open.
II. Flowers opening.
III. All flowers open, stigmas exserted.
IV. Anthers exserted and dehisced.
V. Anthesis finished, spines evident, capitulum in fruit.

Stages II, III and IV were scored in thirds of the capitulum to increase the accuracy of recording in these stages. It only proved possible to apply this detailed scheme to the capitula of *A. magellanica* and the hybrid, the capitula of *A. tenera* Alboff being both too small and too enclosed by leaf bases for accurate scoring.

Floral development of *A. magellanica* was examined at three sites (Point, Dwarf Shrub and Shackleton) both by the repeated scoring of individual marked capitula and by measurements on the whole communities. The hybrid was examined at the Hope site and *A. tenera* at the Dam site. The data were transformed to a floral index (FI) so that the mean development stage at each scoring could be plotted. Each development stage was given an FI number as follows:

Stage I $= 1$
Stage II $\frac{1}{3} = 2$
Stage II $\frac{2}{3} = 3$ to
Stage V $= 11$.

In studies of community development the same FI stages were used. Ten random quadrats were thrown and all the capitula falling within them were scored. The percentage of heads in each development stage at each site was then calculated.

To investigate the possible effect of aspect on floral development, a survey was carried out on sites of different aspects. Two sites were used for each of the cardinal points. All scoring was done on the same day using 20 random quadrats per site. A mean FI value for each stage was found for sites of the same aspect.

Scape growth

Twenty marked scapes were used for each *A. magellanica* and *A. tenera* population, whilst 25 were used at the hybrid site. Scape length in *A. magellanica* and the hybrid was measured from the base of the flowering head to the base of the stipules of the second leaf down the stem, disregarding any bracts. In *A. tenera*, measurements were made to the base of the scape. All measurements (to the nearest millimetre) were taken at intervals of approximately 1 week over periods which differ for the three taxa, because of the difficulty in finding a suitable site for the hybrid and the late onset of elongation at the *A. tenera* site. Curvilinear regressions were fitted to the data both against time and against floral index values by a stepwise procedure which tested the significance (F value) of the reduction in total variance due to the fitting of progressively higher value equations (programme described by Callaghan (1974)).

Pollen counts

Capitula with dehiscing anthers were collected from several populations of each three taxa. Anthers were tapped over a glass slide and mounted preparations made with cotton blue in lactophenol. Ten high-power fields were counted from each slide, viable grains being taken as those which absorbed the cotton blue. The diameters were measured of 25 grains on each slide.

Results

Floral morphology

Although hermaphrodite capitula predominate, female capitula, possibly of multiple origin, are very widespread in *A. magellanica*, the only gynodioecious species known in the genus. Flowers with predominantly male characteristics—large anthers and small stigma—have been found occasionally but are not common. Plants are either hermaphrodite or female, no examples having been found of the two types of flowers on the same plant. Any flowers in the axil of the scape bract are of the same type as the main capitulum. Female plants have been found on all the sub-Antarctic islands, except Macquarie Island and Heard Island, and throughout southern South America (Grondona, 1964; Walton, 1974). Normal hermaphrodite and female capitula from South Georgia are illustrated in Fig. 1.

The aborted anthers of the female flowers were similar in all populations examined, usually being about 25 per cent of the size of normal anthers. Their filaments do not normally elongate, so that the anthers are clustered around the base of the stigma. Stigmas of female flowers are often larger than those of hermaphrodite flowers in the same locality, which in diploid populations are of the X type (Walton and Greene, 1971), as are stigmas in female flowers from areas with tetraploid plants. In South America, hermaphrodite flowers from many apparently tetraploid plants have the XY stigma type. A comparison of stigma and anther proportions for 18 populations is given in Table I. The variation in length/breadth ratios indicates considerable diversity of shape and the difference in size between normal and aborted anthers can be clearly seen. The specimen Holdgate No. 642 from the Falkland Islands is unusual, having almost cleistogamous flowers with small stigmas. Grondona (1964) illustrated a comparable specimen from Chubut, Argentina.

a   b
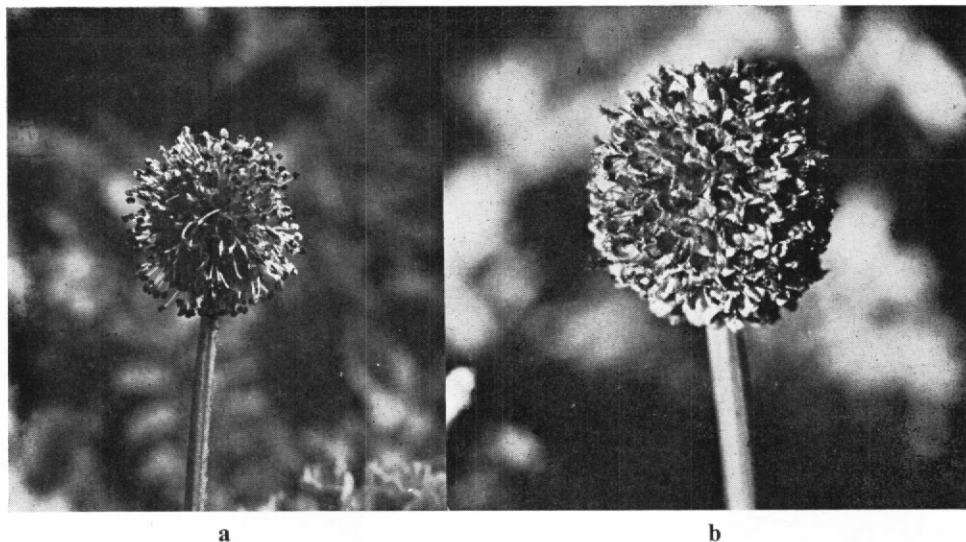
Fig. 1. a. Normal hermaphrodite capitulum of *A. magellanica* on South Georgia. Anthesis with dehisced anthers clearly visible.
b. Female capitulum at the same stage of development with only the stigmas visible.

Inflorescence shape can vary widely in *A. magellanica*. Specimens have been seen from both South Georgia and South America in which the inflorescence appeared in between capitate and racemic, having a small terminal capitulum and a series of individual flowers spiralling down the scape. Plants from the Falkland Islands have been found with markedly ovate terminal capitula and well-developed subsidiary capitula (Fig. 2), whilst a specimen from Punta Arenas had two flowering capitula in which all the flowers were long pedicillate (Fig. 3).

On South Georgia, numerous examples have been found of incompletely produced capitula, with the flowers only being formed in the lower two-thirds (Fig. 4). These are especially common in late summer. Incomplete elongation of the scape has also been observed, the capitulum remaining almost surrounded by the uppermost stem leaves. In a few plants much enhanced leaf production has been noted and this, when coupled with inadequate internode expansion, resulted in the production of a leaf rosette at the base of the scape. Fused cupules as illustrated by Grondona (1964) have been found throughout the range of the species.

The hybrid plants on South Georgia show a considerable degree of variability in most characters (Walton and Greene, 1971). All plants examined have been hermaphrodite. Secondary capitula, a characteristic of this taxon, are rare in *A. magellanica* and unknown in *A. tenera*. The scape bracts are often far more leaf-like than those of either parent species, whilst many of the fruits have small subsidiary spines, a feature also found in some populations of *A. magellanica* but never in *A. tenera*. Over 90 per cent of *A. tenera* scapes have a small bract subtending a normal single flower and, although this is also common in many *A. magellanica* plants, the flowers do not always develop normally (Walton and Greene, 1971).

Floral induction

A. magellanica collected in late September on South Georgia showed no evidence of over-wintering flower buds but inflorescences had been initiated on plants clear of snow by the middle of October. The day length at that time of the year was *c.* 13 hr. (Rubin and Weyant, 1965). This is in agreement with the appearance of flower buds on plants grown in Birmingham during late April (day length 13–14 hr.). On South Georgia, although there is a distinct flush

TABLE I. ANTHER AND STIGMA MEASUREMENTS FROM VARIOUS POPULATIONS OF *A. magellanica*

	Anther			Stigma		
	Max. length	Max. breadth	Ratio	Max. length	Max. breadth	Ratio
South Georgia						
(Walton 491; AAS)	1·23	1·02	1·2	5·02	0·94	5·3
(Walton 547; AAS)	0·21	0·34	0·6	3·40	1·11	3·1
Marion Island						
(Moseley s.n.; K)	1·06	0·89	1·2	3·40	0·85	4·0
(Moseley s.n.; K)	0·21	0·30	0·7	3·60	1·06	3·4
Iles Kerguelen						
(Osten 8668; MVM)	0·77	0·77	1·0	3·19	1·06	3·0
(Procter 15; BM)	0·30	0·30	1·0	5·53	1·06	5·2
Macquarie Island						
(Filson 5713; AAS)	0·89	0·85	1·0	3·83	0·81	4·7
(Taylor s.n.; AAS)	0·72	0·77	0·9	1·49	0·26	5·7
Falkland Islands						
(Moore 610a; LTR)	1·23	1·00	1·2	3·60	1·06	3·4
(Holdgate 642; AAS)	0·64	0·64	1·0	0·77	0·26	3·0
Tierra del Fuego						
(Moore 2212; LTR)	0·77	0·60	1·3	2·10	0·64	3·3
(Moore 1689; LTR)	0·38	0·47	0·8	1·91	1·11	1·7
Argentina						
San Juan (Canplin and Ralph 31; K)	1·53	1·06	1·4	2·13	0·43	4·9
Mendoza (Moseley s.n.; K)	0·21	0·26	0·8	3·19	0·85	3·8
Catamarca (Schreiter 6117; MVM)	1·65	0·77	2·1	2·74	0·48	5·7
Santa Cruz (Blake 324; K)	1·50	1·23	1·2	3·40	0·94	3·6
Chile						
(Bridges 1192; K)	0·43	0·38	1·1	3·40	1·60	2·1
(Wederman 598; K)	0·21	0·26	0·8	3·40	0·85	4·0

All measurements in mm. Abbreviations for herbaria follow Holmgren and Keuken (1974).

of flowering in spring, many plants, especially in south-facing sites, produce inflorescences later in the season. Taking these observations together, it would seem that the photoperiod necessary for flower production may simply require to be in excess of 13 hr. for all three taxa.

It appears that plant age may be an important factor in flowering whilst temperature, through its control of growth and leaf production, can obviously exert a considerable secondary effect. In an experiment using cuttings of *A. magellanica* grown in a variety of controlled light and temperature regimes no plants flowered. This may have been because the stem system (and therefore carbohydrate reserve) was not of an adequate size to support flowering. Material grown from seed has shown that, even under favourable conditions, plants must be over 3 years old before they flower.

Floral development

Graphs of the total floral index against time for the three *A. magellanica* sites are very similar (Fig. 5). The pattern for the hybrid is only slightly different and this may be due to the test period being slightly later in the summer. Table II gives estimates, derived from Fig. 5, of the time taken to complete each floral stage. At all sites, stigma exsertion (stage III) was short, lasting only 5–7 days, whilst anther exsertion and pollen release (stage IV) was 9–12 days.
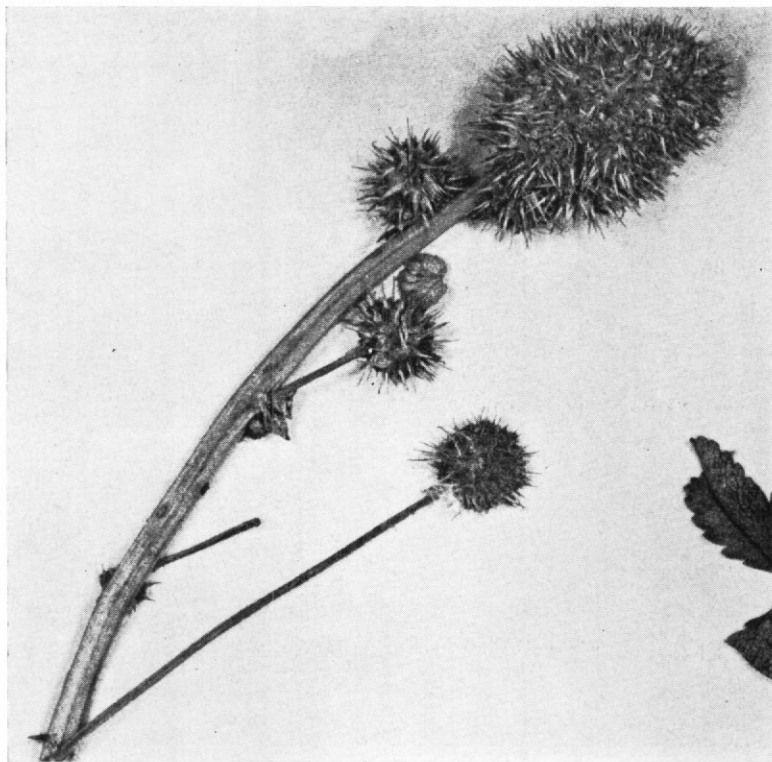
Fig. 2. *A. magellanica* from the Falkland Islands, with ovate terminal capitulum and several secondary capitula. Specimen from K; leg. J. D. Hooker No. 77, Falkland Islands, Antarct. Exped. 1839–1843, as *A. laevigata*.

TABLE II. ESTIMATED LENGTH IN DAYS OF FLORAL DEVELOPMENT STAGES

Site	Species	Floral development stage		
		II	*III*	*IV*
Point site	*A. magellanica*	13	7	12
Dwarf Shrub site	*A. magellanica*	14	5	9
Shackleton site	*A. magellanica*	9	6	12
Hope site	Hybrid	7	6	9·5

In both *A. magellanica* and the hybrid the flowering capitulum developed whilst the scape was elongating, thus carrying it clear of the surrounding leaves by the time the flowers began to open. In *A. tenera* virtually all the floral development took place before any significant scape elongation occurred. The same sequence of stages appeared to occur but the length of each could not be estimated. Since pollen release began when the capitulum was still almost completely enclosed by leaves, it seems certain that the species is normally self-fertilized.

There were differences between the three *A. magellanica* populations in terms of floral development (Fig. 6). The date of onset of flowering was apparently influenced by local topography and aspect. Observations in September and October 1970 showed that there could be

Fig. 3. *A. magellanica* from Punta Arenas, with flowers in the terminal capitulum all long pedicillate. Specimen from SGO, No. 049843; leg. Pablo Ort., s.n., Punta Arenas, as *A. adscendens*.

Fig. 4. *A. magellanica* with incompletely developed capitula. The top third of the capitulum contains only floral bracts.
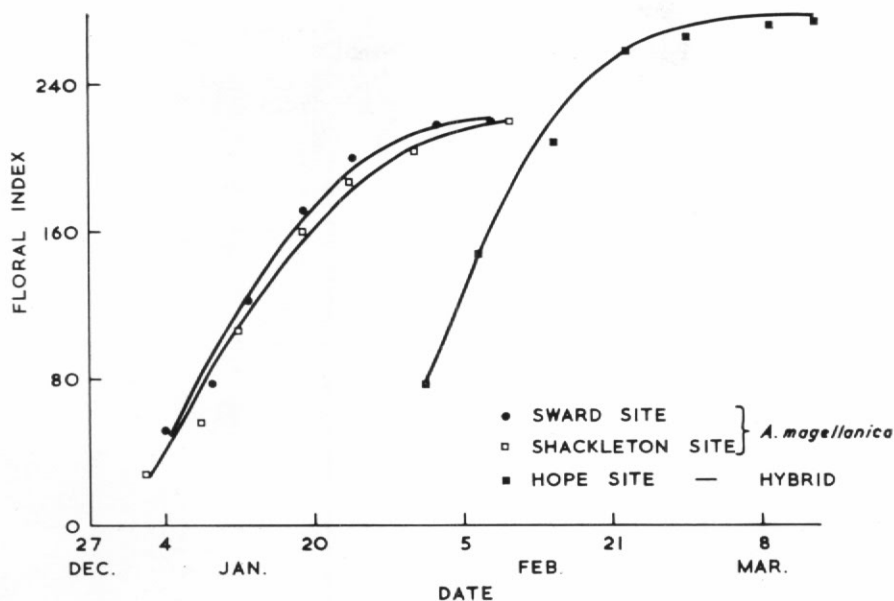
Fig. 5. Fitted regressions of the floral development against time for *A. magellanica* and the hybrid.

2–3 weeks difference in snow melt between north- and south-facing sites of comparable altitude. Plants at the Dwarf Shrub site (north-facing) developed much earlier and much more quickly than those at the Shackleton site (south-facing). The survey of communities of different aspects later in the season showed a continuation of this effect (Walton, 1974), although the time lag between north- and south-facing sites did diminish.

Scape growth

Quartic regressions proved significantly better fits for scape growth data at all sites than any lower-value regressions (Fig. 7). Although the period of elongation at the *A. magellanica* sites was similar, scape length increased more rapidly at both of the sheltered hillside sites (Dwarf Shrub and Shackleton) than at the exposed shore site (Point). *A. magellanica* is the only one of the three taxa to form pure stands with 100 per cent leaf cover. If anthesis occurred whilst the capitulum was below the canopy the chances for effective cross-fertilization would be much reduced. On the other hand, *A. tenera*, which normally occurs as isolated plants in frequently sparse vegetation, apparently completes fertilization before the scape is more than 1 cm. long. Most of the elongation in this species occurs during fruit maturation. The hybrid occupies intermediate habitats and, whilst it can form extensive patches, nowhere does it produce a closed stand. Its long scape-growth period appears to be a compromise between the parental characteristics. Most of the hybrid scapes also bore secondary capitula and it is possible that the use of material for their development contributed to a reduction in the rate of elongation of the main scape.

Since the same marked plants were used for studies of scape elongation and capitulum development, curvilinear regressions were calculated to determine the relationships between scape growth and floral development at the three *A. magellanica* sites and the hybrid site. The curves are shown in Fig. 8. Quartic curves were again better fits than the lower-order curves. The regressions of floral development against scape growth show the same pattern with different rates for all three *A. magellanica* sites but a contrasting pattern for the hybrid in which half of the scape growth appears to have taken place after anthesis.
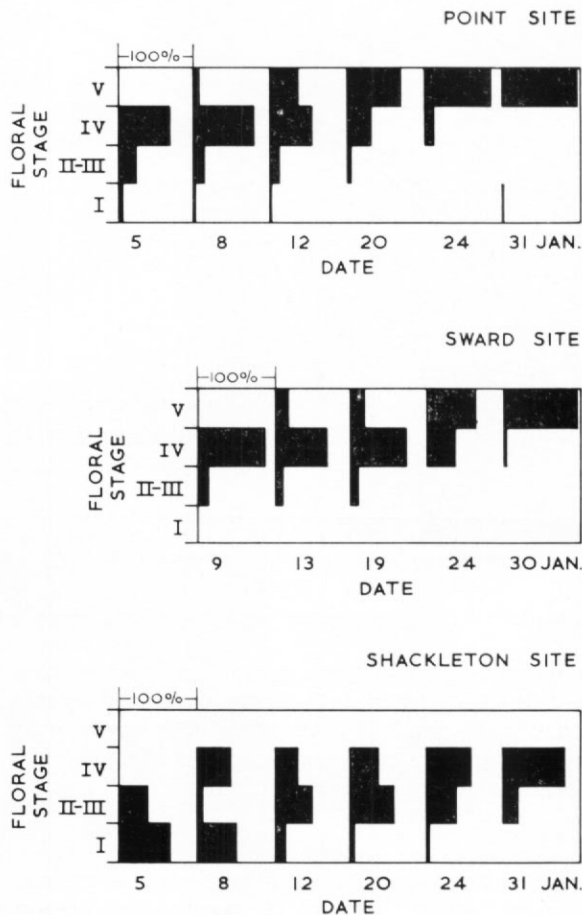
Fig. 6. Histograms of the floral development of *A. magellanica* communities at three sites.

Pollen fertility

In all except one of the eight populations of *A. magellanica* sampled, pollen viability was apparently very high (Table III). Grain-size varied more between than within populations but was fairly constant overall between 74 and 78 mm. $\times 10^{-2}$. Viability was also very high in two of the three *A. tenera* populations sampled and grain-size was regular. The hybrid populations all showed lowered viability and a wide diversity of grain-size (71–93 mm. $\times 10^{-2}$). The amount of hybrid pollen released is partly limited by two abnormalities. Flowers have been found in which anther dehiscence has not taken place. However, this does not seem to be as common as the non-release of pollen from dehisced anthers. In these the pollen grains remain in the loculi, apparently held together in a solid mass.

HYBRIDIZATION

Chromosome counts for this genus have been provided by Moore (1960, 1964, 1967, 1972), Moore and Walton (1970), Dawson (1960) and Löve (1965). Of the species for which chromosome data are available, all except three are diploid as is the hybrid material on South Georgia. The three species with the higher ploidy levels are *A. saccaticupula* Bitt. in New Zealand,
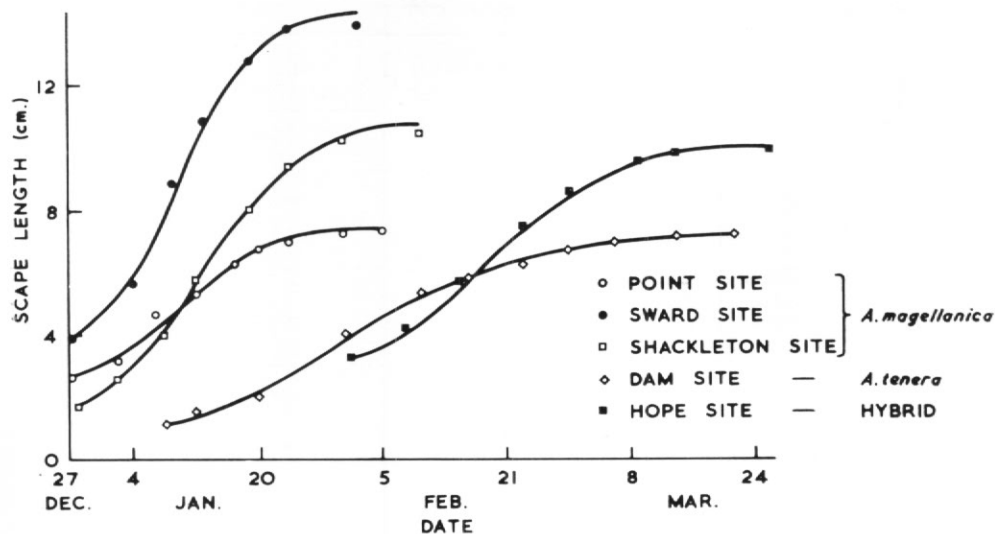
Fig. 7. Fitted regressions of scape growth against time for the three South Georgian taxa.
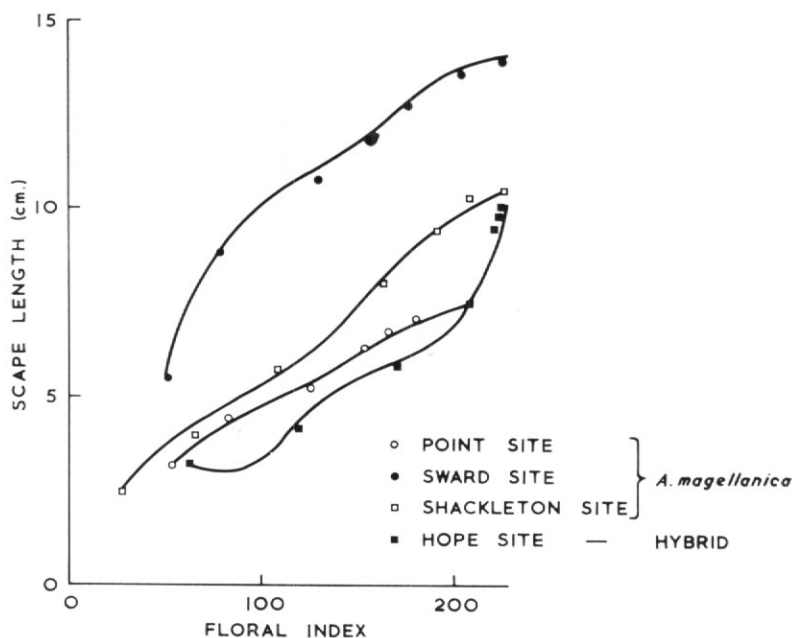

Fig. 8. Fitted regressions of scape growth against floral development for *A. magellanica* and the hybrid.

A. californica Bitt. in California and *A. magellanica* in the Falkland Islands and most of South America except the eastern tip of Tierra del Fuego. *A. magellanica* is the only species as yet known with two ploidy levels.

Large-scale hybridization appears to be limited to certain New Zealand species (Cockayne and Allan, 1934; Dawson, 1960; Allan, 1961), where hybrid swarms are common on disturbed

TABLE III. POLLEN COUNTS

Species	Location	Number of heads counted	Total grains counted	Mean percentage viable
A. magellanica	Dwarf Shrub site	3	727	98·4
	Point site	3	1,358	97·5
	Shackleton site	4	1,731	94·8
	Amongst tussock grass	3	1,210	95·0
	Rostkovia bog	3	1,652	97·0
	Sheltered stand	3	1,363	95·9
	Wet gravel area	2	954	95·8
	High-altitude site	3	1,611	50·2
Hybrid	East of Dwarf Shrub site	3	1,096	65·8
	West of Dwarf Shrub site	1	283	49·3
	Hope site	3	1,206	71·0
A. tenera	Beside stream	3	962	95·9
	Dam site	3	865	76·3
	Dry scree run	2	833	93·7

ground and in unstable habitats such as dune areas. An intergeneric hybrid is also known—*Acaena argentea* × *Margyricarpus setosus*—but it is apparently limited to Juan Fernandez (Skottsberg, 1922). Nothing is known about the production of viable seed by *Margyracaena*, but at least some of the New Zealand F_1 hybrids can produce viable seeds (Dawson, 1960). Bitter (1911) described numerous hybrids produced in botanic gardens, almost all of them between New Zealand species, although he did claim a hybrid between the South American *A. myriophylla* Lindl. and *A. anserinifolia* (J. R. et G. Forst.) Druce.

A. magellanica and *A. tenera* are the only South American species known to hybridize. Meiosis has not been studied in the hybrid, which is only found on South Georgia, so that it is not known whether its high infertility is due to chromosomal or genic factors. The lack of hybridization between *A. magellanica* and the other South American species is not particularly surprising, since most of the South American populations of this species are probably tetraploid. Indeed, the area in which *A. magellanica* and *A. tenera* occur together in Tierra del Fuego (Walton, 1974) falls outside the part of the island in which diploid populations of *A. magellanica* are known to occur (personal communication from D. M. Moore). It would therefore seem unlikely that any further examples of the South Georgian hybrid will be found elsewhere.

In the course of germination and seedling productivity studies, three F_1 plants have been produced from *c.* 1,500 seeds of *A. tenera*. A similar number of *A. magellanica* seeds has not produced any hybrid plants. Bearing in mind its distribution (Walton and Greene, 1971), it is highly likely that hybrid populations have originated independently in different parts of South Georgia. The seed collected from hybrid populations on South Georgia shows 0–1 per cent germination (Walton, 1977), so that the establishment of F_2 populations would seem of low probability.

DISCUSSION

The climate of South Georgia, although more rigorous than on most of the other sub-Antarctic islands, is much less demanding than is found in high-latitude northern regions. If the pre-formation of flowers is regarded as an adaptation to short and comparatively hot summers (Billings, 1974), it would be an unexpected adaptation to find on South Georgia with its long cool growing season. Floral initiation in *A. magellanica* appears to be controlled by a critical day-length requirement, which allows production of capitula to occur any time between mid-October and late February, ensuring that plants in sites with unfavourable aspect will still be able to produce flowers even if snow melt is delayed until mid-summer. The late initiated heads must be at a disadvantage and it seems unlikely that flowers produced after mid-January will have much chance of ripening fruit.

The relationship between floral development and scape elongation is strikingly different in *A. magellanica* and *A. tenera*, the hybrid being intermediate between its parents. Whilst there is ample evidence of the intermediacy of many morphological characteristics in natural hybrids (Stace, 1975), there appear to be fewer data concerning their physiological responses. Hybrid vigour is a feature sought after by plant breeders but many hybrids can be less competitive than their parents. In this case the F_1 hybrid plants show some growth characteristics intermediate between the parent species but photosynthetic rates appear to be lower than either (Walton, 1974).

The elongation of the scape before anthesis in one species and after in the other appears to be the principal mechanism controlling the production of F_1 plants. The same developmental mechanism must also influence the direction of any later back-crossing, weighting the chances very heavily in favour of crossing with *A. magellanica*. Application of a hybrid index scoring system (Gay, 1960) to the South Georgian populations (unpublished data) has suggested that F_2 and later generations are not common, although the back-crossing that has occurred has all been towards *A. magellanica*.

The sexual reproductive cycles of the three taxa and their probable interrelationships are summarized in diagrammatic form in Fig. 9. Whilst acknowledging that parts of the diagram are at present only inferred, it is suggested as a possible model on which future investigations
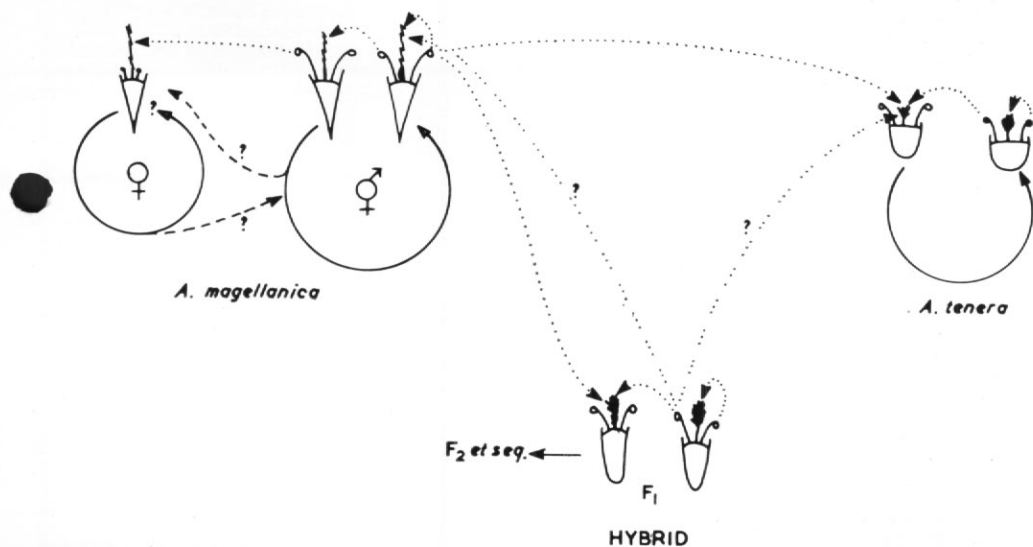

Fig. 9. The probable interrelationships between the reproductive cycles of the three South Georgian taxa.

could be based. Each taxon also has another cycle in which daughter plants are produced vegetatively as parts of the parent system decay.

The superimposition of vegetative cycles on the reproductive ones shown in Fig. 9 would illustrate the difficulties in determining the genomic relationship between two plants or even populations. Clonal establishment is common in many rhizomatous perennials and appears to be particularly important in an understanding of the life cycle of *A. magellanica*. Fertilization of female flowers must always be by pollen from hermaphrodite capitula. No data exist on the inheritance of femaleness but the distribution and morphology of female plants strongly supports multiple origin.

The likelihood of the F_1 cross being generally in one direction is suggested by the data on floral development and the hybrid plants raised from parental seed. The low viability of hybrid pollen together with the lack of normal anther dehiscence in some flowers must decrease the chance of F_2 production by self-fertilization, but the possibility cannot be excluded. This must also be true of the possible fertilization of either parent by hybrid pollen.

The crossing of two quite different groups (Bitter, 1911) within the genus is remarkable when viewed against the lack of hybridization between apparently closely related South American species. It is possible that a similar hybrid existed in South America before the last major glaciation when the diploid *A. magellanica* is presumed to have been more widespread (Moore, 1972) but no evidence has been seen in present collections of its continued existence.

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