FLORAL PHENOLOGY IN THE SOUTH GEORGIAN VASCULAR FLORA

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ABSTRACT. Flowering is described for 16 native taxa and three introduced species on South Georgia. Information is given on these species from other sub-Antarctic islands and the Falkland Islands. At least three species (*Poa flabellata, Festuca contracta* and *Deschampsia antarctica*) pre-form their inflorescences the previous season. Indirect evidence suggests that overwintering of inflorescences may occur in other species. Reproductive specializations include cleistogamy, self-fertilization and a preponderance of anemophilous flowers.

ALTHOUGH numerous phenological studies have taken place on the species of temperate latitudes, work on plants of polar and alpine areas has been much more limited. However, a considerable amount of information does exist on species of the European Alps, together with a steadily increasing amount on plants of the alpine areas of the United States of America (Billings and Mooney, 1968) and New Zealand (Mark, 1970). The relative neglect of the Arctic flora until fairly recently has served to highlight the quality of the work which has been published. Chief amongst these studies is Sørensen's (1941) monograph on the phenology of the plants of north-east Greenland. His detailed work demonstrated the adaptations necessary for species to persist in high-latitude areas and others workers have since found similar adaptations in alpine floras.

Amongst these adaptations, one of the most important is the initiation and partial development of the inflorescence in the summer prior to flowering. Sørensen (1941) found two types of development: periodic, where development was halted at a particular stage even under favourable conditions, and aperiodic, where development proceeded until halted by unfavourable conditions. The role of site aspect, soil and air temperatures, bracts and shoot development were also examined by Sørensen, who was able to show correlations between life forms, distributions and adaptations. In terms of leaf development, he distinguished "winter-green" species, having leaves which function for more than one growing season, from "evergreen" species which have leaves which function for more than two summers.

The climate of the sub-Antarctic islands is less severe than that of north-east Greenland. Despite its temperate latitude (lat. 54°–55°S), South Georgia, with 6 or more months of snow-cover and cool summers, has one of the most rigorous climates amongst the sub-Antarctic islands. Under these climatic conditions it seemed likely that the native sub-Antarctic species might well possess at least some of the adaptations shown by plants from the Arctic. There had been little systematic investigation into floral phenology of any of the islands, except for studies by Werth (1911) on Iles Kerguelen and Huntley (1970) on Marion Island. The flora of South Georgia (Greene, 1964) gives no information on flowering for any species. Accordingly, field notes were made on flowering periods, and these, together with preserved and herbarium specimens, have allowed a preliminary assessment to be made of floral phenology for most of the South Georgian native flora and three introduced species.

METHODS

Field notes were made of the flowering behaviour of almost all of the native vascular species and some of the alien species on South Georgia during the summers of 1969–70, 1970–71 and 1973–74, mainly in the King Edward Cove area, Cumberland East Bay. Herbarium material was collected of many species, and specimens were preserved in formalin-acetic-alcohol to enable the early stages of floral development to be studied. Material of many species was collected immediately after snow melt at the end of winter in 1970 to determine the presence and stage of development of any overwintering inflorescences.

The literature relating to the sub-Antarctic islands and the Falkland Islands was consulted and references to the performance of individual species in other parts of their ranges are included. Nomenclature follows Walton (1975) and detailed morphological descriptions of the species will be found in Greene (1964).

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RESULTS

Native species

Acaena magellanica (Lam.) Vahl

Walton (1977*b*) has described the morphology of floral development in this gynodioecious species. In brief, it is as follows: floral initiation occurs shortly before or after snow melt if day length exceeds 13 h. Inflorescences are terminal but floral shoots also carry about six leaves. Three of these overwinter on an apparently vegetative shoot whilst the other three are initiated before the inflorescence in the following season. The capitulum develops as the scape elongates, the flowers finally opening when it has reached almost maximum length. The hermaphrodite flowers are markedly protogynous. After pollination, fruit may ripen rapidly, reaching maturity within 8 weeks. In the maturation of female flowering heads, anther development is arrested at an early stage, the stamens growing to about only one-third of normal size.

Samplings on 27 September, 8 and 15 October 1970 did not produce any clear evidence of floral initiation. The earliest hermaphrodite inflorescences, which measured up to 10 mm long, including the scape, were found on 22 October 1970 in a site clear of snow for over 3 weeks. In a nearby area which had been snow-free for only 15 days the inflorescences were 4 mm lon[illegible] Floral development and scape elongation continued until 11 November at the former site when the first flowers opened and the stigmas were exserted. Anthesis followed (Fig. 1a) within a few days. The fruits at this site had ripened ready for dispersal by mid-January.

Female capitula (Fig. 1b) were found with flowers just opening on 20 December at a site which had been snow-free for almost 2 months. This is considerably later than for the earliest hermaphrodite heads, and Walton (1974) noted that female flowers did not usually open until well into the period of maximum pollen release. Although the species may be self-compatible on South Georgia, the presence of female capitula and abundant freely dispersed pollen must ensure a high degree of cross-fertilization.

Moore (1968) gave the flowering period of *A. magellanica* on the Falkland Islands as November–December and he stated that the species is self-compatible. On South Georgia, the general flowering period is longer (November–January) with capitula in late snow-bed sites not reaching anthesis until mid-March. Werth (1911) also believed that the flowers were generally

Fig. 1. *Acaena magellanica* flowering heads. a. Female head. b. Hermaphrodite head at anthesis.

self-pollinated on Iles Kerguelen but noted that he had seen an insect crawling over a flowering capitulum and that this might have caused cross-pollination. He said that the flowers smelt of the Indian scent patschouli, and noted that no nectar was produced. Huntley (1970) has suggested from observations on Marion Island that this species is day-length-sensitive rather than temperature-sensitive as far as the onset of vegetative growth is concerned. He recorded the opening of flower buds by mid-September and pollination in early October. The dates given in Huntley's (1970) paper are all earlier than those in Huntley (1971), also for Marion Island, where flower buds are described for October and pollination by early December.

Acaena magellanica × *tenera*

This hybrid is endemic to South Georgia and forms an important constituent in several community types (Walton, 1976). Young inflorescences, up to 1 mm long, were found on 22 October 1970 in an area which had been free of snow for about 1 week. By early November the capitula were visible on scapes *c.* 20 mm long and the first flowers began to open about the middle of the month. Stigma elongation preceded another exsertion (23 November) by several days. The fruit ripened during December and January and the earliest appeared ready for [illegible]spersal by February. New capitula were produced throughout the summer, the peak flowering period being mid-December to the end of January, although a few heads were produced as late as March.

Walton (1979) described the rate of development of the capitula and the elongation of the scape in this taxon. Germination studies (Walton, 1977*a*) have shown exceptionally low viability for the fruits of this taxon, whilst the percentage of viable pollen is also generally less than in either of the parent species (Walton, 1974). It has a normal diploid chromosome complement (Moore and Walton, 1970), which might be expected to allow crossing with either parent, but it appears that back-crossing to *A. magellanica* is the usual route for gene transfer (Walton, 1979). Since both parents are apparently self-compatible, it seems likely that this is also the case in the hybrid.

Acaena tenera Alboff

The earliest inflorescences, found on 15 October 1970 at a site snow-free for about 5 days, were barely 1.5 mm long. On 22 October at another site (snow-free for 12 days), the inflorescences were 3.5 mm long and many plants had two per shoot. At this stage the new leaves were only just expanding and it was not until early November that the first leaf was fully grown. In exposed sites the first leaves produced were often bright red, turning slowly to dark green. The capitula are produced in the leaf axils and are well protected both by the new leaves and by the old leaf bases that clothe the stem. Since it is known that alpine and Arctic species [illegible]hich show dark pigmentation normally maintain higher leaf temperatures than species with green leaves, it is possible that the pigmentation in these early leaves produces above-average plant temperatures which could hasten inflorescence development.

Capitula develop virtually enclosed by the leaf bases and the first flowers were not seen open until just after mid-November. Pollen release began about 25 November and was complete in the earliest heads by early December. Scape elongation was minimal until after anthesis but continued throughout the fruit-ripening period. The first fruits were ready for dispersal by the beginning of February. In the late snow-bank and fellfield sites, floral development was delayed and anthesis did not begin until the middle of January, the fruits ripening in early March. Although occasional flowering heads were found later in the season, most plants had completed flowering by the end of January.

The pattern of floral development and scape elongation on individual plants has been described by Walton (1977*b*). The species is self-compatible and, although cross-pollination can occur, self-pollination appears to be the rule.

Alopecurus magellanicus Lam.

This species has a very limited distribution on South Georgia and did not occur in the principal study area. No information is available beyond Moore's (1968) report of a flowering period in the Falkland Islands of December and January.

Callitriche antarctica Engelm. ex Hegel.

Plants emerging from snow in early October possessed winter-green leaves, which persisted, but no inflorescences. The earliest flowers were observed in mid-November but, as these were reasonably well developed, it must be assumed that initiation took place at least as early as the beginning of November. Pollen release began in early December with flowering reaching a peak during December and January. Flower production then declined rapidly and few flowers were visible by late March.

Moore (1968), in describing the flowers of this species, has followed Mason (1959), who stated that the flowers are solitary in one or both of a pair of leaf axils with the upper flowers male and the lower female. In fact, for South Georgian material any pair of leaf axils may contain any combination of flowers. Pollination of the female flowers may be anemophilous in populations on drier sites, although in semi-aquatic habitats it is probably hydrophilous. Work by McLaugh[illegible] (1974) on the widely distributed and environmentally tolerant species *C. palustris* L. has shown that viable seed can be set in the absence of male flowers. She suggested that apomixis is common in this species and may be instrumental in preserving its genotypic flexibility. The wide geographical range and undoubted success of *C. antarctica* may be due to a similar system.

The flowering period on Macquarie Island is reported as September–March (Taylor, 1955) and on the Falkland Islands as December–January (Moore, 1968). Werth (1911) noted flowering on Iles Kerguelen from mid-December to February, whilst on Marion Island (Huntley, 1970) flowers were seen before the end of September with fruit ripening by early December.

Colobanthus quitensis (Kunth) Bartl.

In favourable sites with snow melting during October, the plants were found to be fruiting by early January, whilst at exposed sites or those with later snow-lie the flowers did not open until mid-January. Edwards (1974) has described its performance on Signy Island, South Orkney Islands, in detail. Plants there overwinter with their flowering buds in a very early stage of differentiation but despite this fail to develop quickly enough in most years to set viable seed. On South Georgia seed is freely produced. Examination of apices collected in June and September from beneath snow has not revealed any unmistakable evidence of the pre-formation of flowers. Flowering, however, appears to be sporadic and the populations sampled might not have been going to flower the following summer. Holtom and Greene (1967) made various observations on the performance of this species throughout its range. Moore (1968) reported that it flowers fro[illegible] October to December on the Falkland Islands. He stated it to be self-compatible and largely, if not entirely, self-pollinated (Moore, 1970). Pollen release begins at or before anther exsertion, making the flower effectively cleistogamous in many instances. Cross-pollination may occur, since R. Webb (personal communication) has observed large numbers of Collembola (*Cryptopygus antarctica* Willem.) in flowers of this species on Signy Island.

Colobanthus subulatus (D'Urv.) Hook. f.

Flower buds were found in late September, shortly after snow melt, with all floral parts differentiated. The peduncles extended slowly so that the flowers were fully visible by early November. The flowers appear to be normally cleistogamous. The first capsules are ripe in late February. Many capsules do not finish dispersing their seeds until the following summer.

Moore (1970) described this species as self-compatible and usually self-pollinated. On the Falkland Islands it flowers from October to December.

Deschampsia antarctica D'Urv.

Floral apices were found on plants immediately after emergence from snow-cover at the end of September but were in a very early stage of differentiation. By 8 October the largest floral apex found was 1.3 mm long, the flowering shoots usually carrying six green leaves, which had apparently overwintered. Development appeared to be fairly slow with inflorescence length reaching only 2.5 mm by 22 October. Exsertion from the leaf sheath (corresponding to stage 2 of the inflorescence maturity index used by Holtom and Greene (1967)) began in early December and by 20 December many plants had the inflorescences more than half exserted (stage 4). By early January most inflorescences were completely free and expanding rapidly.

Some information and data for South Georgia plants have been given by Edwards (1974) together with considerable data for South Orkney Islands populations. He found that plants on Signy Island always pre-formed their inflorescences which overwintered at a very early stage of development. Holtom and Greene (1967) discussed both field observations and laboratory experiments concerned with floral initiation and seed production in the Antarctic and sub-Antarctic. Using clonal material of South Georgian origin, they found that inflorescence initiation, which took place under long-day conditions, required cold pre-treatment. If the pre-treatment and long-day initiation are essential, the very early inflorescences found on South Georgia in September must have been formed the previous season with the cold pre-treatment having occurred two winters before.

Moore (1968) recorded the species as self-compatible and usually self-pollinated in the Falkland Islands. The exsertion of anthers is uncommon on Signy Island (Edwards, 1974) and rare on South Georgia. On Iles Kerguelen, the flowers are mainly cleistogamous (Werth, 1911) and it appears therefore that this species is normally inbreeding. Parodi (1949) considered this species always cleistogamous in South America.

Festuca contracta T. Kirk

Since clumps of this grass emerging from the snow in late September contained ensheathed spikes up to 13 mm long (Fig. 2), pre-formation of the inflorescences must have occurred the previous summer. Newly exposed flowering tillers usually had two or three green overwintered leaves. By mid-October most flowering tillers had four or five green leaves and at most sites the longest inflorescences had reached 35 mm. At one exceptional north-facing site, inflorescences up to 60 mm long were found as early as 16 October 1970. Examination of flowering tillers suggested there was an inverse correlation in this species between inflorescence length (and therefore stage of development) and the number of green leaves present. Initiation of inflorescences is spread over a considerable period during the previous summer. Exsertion of inflorescences began by early November. Anthesis did not occur, all flowers being apparently cleistogamous.

Tallowin and Smith (1977) suggested that floral induction takes place between early January and late February, with initiation occurring during February and March. Development then continues until the onset of winter when inflorescence initials are usually 10–20 mm in length and spikelet primordia are clearly visible. Resumption of floral development is dependent on long days and warm temperatures. By early October the day length is about 13 h and, although air temperatures may be low, temperatures within the grass tuft where the inflorescence is developing can reach 20°C on a sunny day. Snow melt therefore appears to be the only limiting factor for early spring floral development.

Anther dehiscence in this normally cleistogamous species is thought to occur 1–2 weeks after emergence of the spike in January. Anthesis occurs only in plants in very sheltered habitats. The seeds mature just before the onset of winter. It is clear from the observations of both Tallowin and the author that seed dispersal takes place mainly in winter, the ripe fruits being stripped off the old spike by the abrasive action of wind-driven snow and ice.

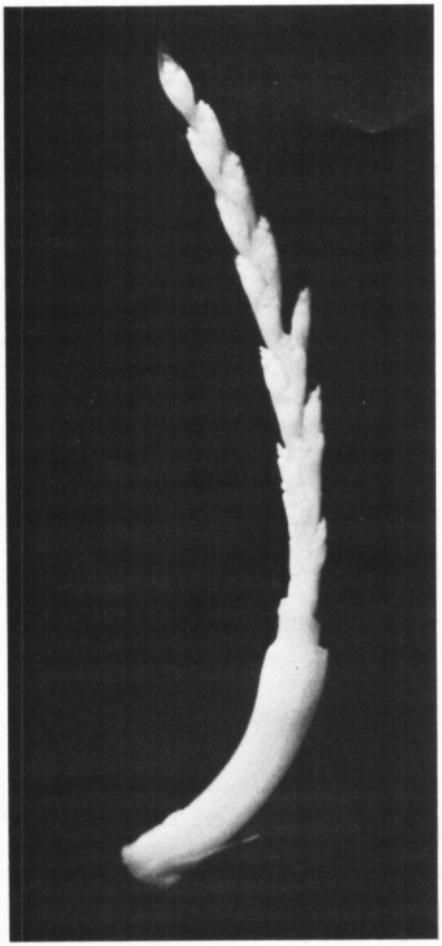

Fig. 2. An overwintered *Festuca contracta* inflorescence. All floral parts are differentiated in this specimen, which was the most advanced example found in early October 1970.

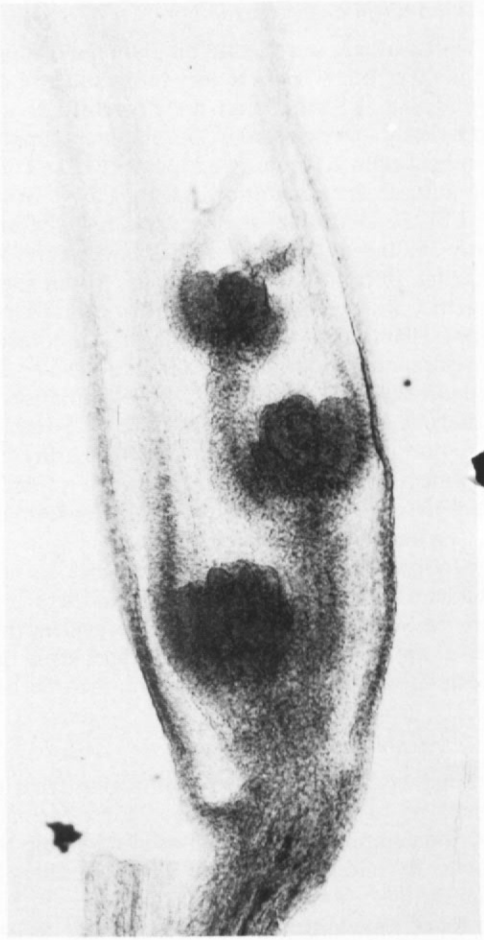

Fig. 3. A spikelet of a *Poa flabellata* inflorescence at the onset of winter. All floral parts are differentiated.

On Macquarie Island, the species flowers from October to January and fruits from February onwards (Taylor, 1955). In the Falkland Islands, both flowers and young fruits were found by Skottsberg on 1 January, whilst Moore (1968) gave the flowering period as November–January. R. I. L. Smith (personal communication) noted that relatively few flowers were cleistogamous on the Falkland Islands, where anthesis is usually well advanced by late December. On Iles Kerguelen, Werth (1911) described the flowers as always cleistogamous, the glumes remaining firmly closed whilst they dehisce directly over the stigma, with a flowering period from the end of December to the end of February.

Galium antarcticum Hook. f.

Plants taken on 14 October 1970 from an area which had been free of snow for about 2 weeks had a few completely developed flower buds. On 25 October, an area at the edge of a snow bank was sampled and again the flowers were found to be completely developed in the buds. Many of the plants had the previous season's fruits still firmly attached. Anthesis was observed at the beginning of December, during which month flowering appeared to reach its peak, continuing at a diminishing intensity until the end of the summer. It cannot be assumed that the overwintered buds provided all or any of the flowers during the summer. It is possible that the fully developed flower buds which overwinter never open, dying during the early spring. If this is not the case, the final stages of development in an overwintered bud and the actual opening of the flower is an exceptionally lengthy process. *G. antarcticum* may be comparable with those Arctic species having an aperiodic development (Sørensen, 1941).

G. antarcticum is one of the few species on South Georgia to produce nectar and the only one to have a strong scent. The species does not appear to be either anemophilous or cleistogamous. The nectar and scent of the flowers must attract some insects which undoubtedly will effect cross-pollination but is seems most likely that self-pollination is the rule. R. I. L. Smith (personal communication) has observed beetles and Diptera on the flowers in South Georgia. Werth (1911) suggested three mechanisms by which self-fertilization might occur:

i. Expansion of the stigma lobes to touch the anthers.
ii. An inward bending of the filaments to allow the anthers to touch the stigma.
iii. The natural fall of pollen on to the stigma from an anther above it in flowers which are not held vertically.

All three mechanisms seem quite feasible as the flowers are protandrous. Werth (1911) recorded this species as flowering on Iles Kerguelen from December to February, whilst Moore (1968) gave November to January for the Falkland Islands.

Juncus scheuchzerioides Gaudich.

Plants sampled immediately after melt showed no signs of floral apices. Flowers developed during November and anthesis and pollen release began in early December. Although many populations were in fruit by mid-January, occasional flowers were seen as late as the end of January.

In the Falkland Islands, Skottsberg (1913) recorded this species in full flower from the end of November onwards with ripe fruits appearing in early February. Moore (1968) gave the flowering period as October to December. On Macquarie Island, Taylor (1955) recorded flowering from December to April and fruiting from February to July. Werth (1911) described flowering and the floral parts in some detail for plants from Iles Kerguelen. He noted that the normal course of pollination resulted in self-fertilization but suggested that insects could cause cross-pollination. Flowering was stated to occur from early January to March. Comparatively little pollen was produced by the protogynous flowers and much of this appeared to cling to the outside of the anthers. On Marion Island, Huntley (1970) recorded plants flowering before the end of October and fruit ripening by late December.

Juncus inconspicuus (D'Urv.) Hook. f.

R. I. L. Smith (personal communication) has observed this species in full flower by early January.

Montia fontana L.

Young flower buds were found as early as 16 October 1970, the flowers at this site opening in early December with pollen release occurring about the middle of the month. The species continued flowering on South Georgia until late March but capsule dehiscence and the release of ripe seeds began in early February. The flowers have no scent and do not appear to produce any nectar. On South Georgia, this species appears to be homogamous (anthers and stigma reaching maturity simultaneously) but not cleistogamous.

On Macquarie Island, Taylor (1955) found this species flowering from November to April with ripe fruits present from December to May. The species is perennial on Macquarie Island as it is on South Georgia and Iles Kerguelen. Moore (1968) noted flowering in the Falkland Islands from November to January and recorded the species as self-compatible and usually self-pollinated. Clapham and others (1962) stated that in Britain *M. fontana* is little visited by insects and normally cleistogamous in dull weather. Whilst stating that self-fertilization was apparently the rule for this species on Iles Kerguelen, Werth (1911) suggested that in some flowers the anthers bend outwards away from the stigma and cross-pollination could be achieved by visiting insects, although cleistogamy was common in this species. On Marion Island, Huntley (1970) found flower buds opening before the end of September, pollination at the beginning of November and fruit ripening by mid-December.

Phleum alpinum L.

On 27 September 1970, plants were found shortly after snow melt with floral apices 1–8.5 mm long. In some cases very small floral initials have been found in plants dug out from just beneath the edge of a receding snow bank. Although this suggests pre-formation of flowering apices the previous season, T. V. Callaghan (personal communication) has found no evidence for this. Like *Festuca contracta* and *Poa flabellata,* this species is winter-green.

Samples collected on 8 October 1970 contained flowering tillers with eight or nine green or partly green leaves and floral apices 0.5–2.2 mm long. A sample 8 days later from the north side of the sheltered base of a *Poa flabellata* tussock had inflorescences over 4.5 cm long, completely differentiated although not yet exserted. On Dartmouth Point, on 25 October, the most advanced plants had their inflorescences half exserted and by early November this was common to most north-facing sites. Although anthesis began in early December for the most advanced plants, it was not common until late December–early January at most sites. Seed was ripe by early March on many plants and even at this late stage in the summer a small number of new inflorescences continued to appear and develop until snowfall in early April.

Callaghan and Lewis (1971) and Callaghan (1974) have examined the reproductive cycle of this species on South Georgia in considerable detail. They found that the rate of development of the apparently homogamous flowers appeared to be similar at both sheltered and exposed sites. Although they gave anthesis as February onwards, their sample plants were selected in late January, thus missing the start of general anthesis. Observations on the species in Greenland and Norway indicate that in neither place does pre-formation of the inflorescence or cleistogamy occur (personal communication from T. V. Callaghan). In Greenland, Callaghan has collected floral apices from plants growing in snow tunnels but he believes that this is due to initiation in spring by light penetrating the melting layers of snow. Curl and others (1972) have shown that considerable light penetration can occur, especially through the firn present at the end of winter. On South Georgia, a small number of inflorescences may be initiated very late in the summer and overwinter enclosed in the leaf sheath but it is doubtful if these flower successfully the following season.

Poa flabellata Hook. f.

In early September, flowering spikes were beginning to push clear of the leaf sheaths on plants in favourable sites. By late September, all tussocks, including those just emerged from continuous snow-cover, showed well-developed inflorescences. Scape elongation progressed quickly and by early October many inflorescences were clear of the leaf canopy. Some showed a marked red pigmentation at this stage. Pollen liberation began in mid-October with most inflorescences reaching this stage by early November. Anthesis had finished at most sites by mid-December. Aspect had a considerable effect on the rate of development of the flowers, anthesis having finished in sheltered north-facing sites by 10 November, whilst in south-facing sites it was just beginning. Seeds were ripe by late January and were shed during February and March.

The initiation of the following season's inflorescences occurred during January, an observation corroborated by Gunn (1976) in later years. These developed within the leaf sheaths until the onset of winter, the most advanced reaching over 12 cm long with all floral parts clearly differentiated (Fig. 3). Development was apparently arrested during the winter period but growth began again as the temperature rose in September. This species is always the first to flower on South Georgia, producing very large amounts of pollen. It seems certain to be normally cross-pollinated.

Skottsberg (1913) found that most of the tussock plants on the Falkland Islands had finished flowering by the end of October but that isolated spikes were seen until early January. Moore (1968) amended this flowering period to September–November, although Gunn (1976) observed anthesis in June.

Ranunculus biternatus Sm.

This species is winter-green, allowing photosynthesis to begin immediately after snow melt. The first new leaves produced each season often show deep red pigmentation. Samples taken in midwinter showed no signs of floral apices. About 2 weeks after melt, young inflorescences were found with carpels and perianth just differentiated (14 October 1970). At this site the flowers were fully open by the latter half of December and pollen release began in early January. Small Diptera were observed on the flowers but self-pollination of at least some carpels appeared likely (Fig. 4). Lowland plants were still flowering in early February but by mid-March only a few

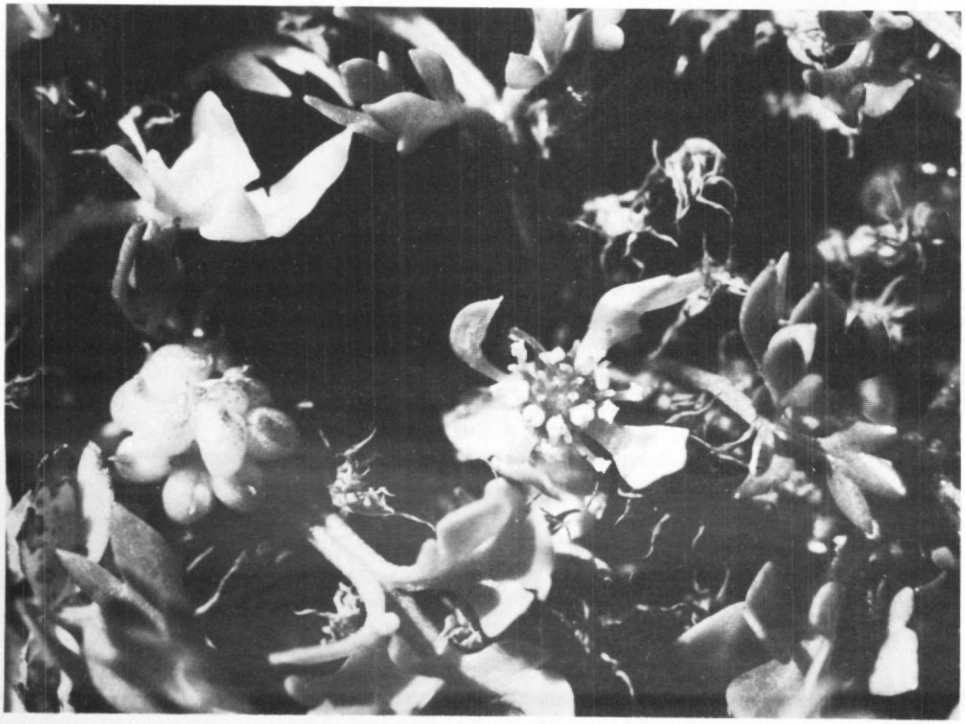

Fig. 4. A flower and fruiting head of *Ranunculus biternatus* in January 1971. The inner stamens can be seen curving over to touch the stigma so effecting self-fertilization.

plants in high flushed sites (probably associated with late snow beds) were still in flower. Fruits began to turn red by early March but were not shed until the following summer.

In the Falkland Islands, flowering is from early November to January with ripe fruits from February onwards (Skottsberg, 1913); it is self-compatible and frequently self-pollinated (Moore, 1968). On Macquarie Island (Taylor, 1955), this species flowers from October to March.

Werth (1911) gave the flowering period on Iles Kerguelen as late December to mid-April with a peak in mid-February. He recognized that self-fertilization was normal, especially for the outermost carpels which are touched by the innermost anthers, but suggested that insects attracted to the small nectaries might cause cross-pollination of the central carpels.

Rostkovia magellanica (Lam.) Hook. f.

Although no inflorescences were found on the plants examined at the end of September, samples collected in mid-October 1970 did show inflorescences with well-developed stigmas and stamens. The flowers were tightly wrapped within the leaf bases. By late October the flowers were just being exserted from the bracts with the perianth still tightly closed. Shortly after this the perianth unfolded slightly and the stigma was exserted. After a few days the perianth opened and the anthers were exposed. Pollen liberation began in early November and by mid-Decemb[illegible] most populations were in fruit. The capsule does not dehisce the same season and often falls from the tiller the following summer before the seeds are released. However, seeds do not need cold pre-treatment for germination and are ripe in the summer in which they are formed. G. J. Lawson (personal communication) noted anthesis occurring below the snow in 1974 due to the late thaw. He observed that, despite his detailed field work on this species, he had never found a seedling of this species.

The protogynous flowers appear to favour cross-pollination, the spatial separation of the stigma arms and the anthers in the fully open flower making it unlikely that self-pollination can occur easily. Despite the apparent lack of floral initials at the initial sampling, the advanced state of development of those found only 2 weeks after snow melt suggests that this species initiates its inflorescences the previous season. Flowering in the Falkland Islands is recorded as October to November (Moore, 1968).

Uncinia meridensis Steyermark

As plants were not collected until early November, by which time the site had been snow-free for over 4 weeks, it is not possible to be certain that this species does overwinter its inflorescences. However, the degree of floral development with the inflorescences just visible between the surrounding leaves (1.4–2.7 cm long, of which the scape accounted for 0.4–0.7 cm) does suggest that pre-formation is necessary. One month later the scape had expanded and was carrying the flowering spike clear of the leaves. The stigmas were all exserted from the low[illegible] female flowers but anthesis had only just begun in the topmost male flowers. Anthesis began shortly after this and by 31 December was finished. Fruits ripened over the next 2 months and began to be dispersed during March (Fig. 5). The marked protogyny of the inflorescences should ensure cross-pollination.

Alien species

Poa annua L.

This species is perennial on South Georgia. Plants emerging from snow normally have developing inflorescences up to 8 mm long. Development to anthesis is rapid, usually within 3 weeks of snow melt. Anthesis can be found in early October at favourable sites. Flowering continues throughout the summer until winter snowfall in April. It appears that unexserted inflorescences then overwinter whilst exserted ones die.

Fig. 5. Ripe fruits of *Uncinia meridensis* in March 1974. The hooked rachilla ensures ready dispersal.

Taylor (1955) noted that on Macquarie Island this species is perennial, flowering from September to June.

Poa pratensis L.

Floral development is slower in this species with anthesis generally not occurring until January. Developing inflorescences were not found at snow melt, the earliest floral development being observed about 3 weeks after the site became clear of snow. Flowering is mainly restricted to December–January, although a few new inflorescences may be produced as late as March.

Taraxacum officinale

Although developed inflorescences overwinter in apparently good condition, the flowers fail to open after snow melt and the flowering head dies. Floral initiation is rapid in spring with the first flowers normally open about mid-November and fruit dispersal beginning in late December. Flowering continues throughout the summer.

DISCUSSION

Although South Georgia and other sub-Antarctic islands lie in relatively low latitudes, their proximity to the Antarctic Convergence endows them with unexpectedly rigorous climates, whilst their isolation from major landmasses has resulted in floristic poverty. The vascular flora of South Georgia shows several of the adaptations to cold summer climates listed by Billings (1974):

i. Pre-formation of inflorescences (e.g. *Poa flabellata*).
ii. Cleistogamy (e.g. *Festuca contracta*).

iii. Self-compatibility and self-fertilization (apparently common to most of the species).
iv. A preponderance of anemophilous flowers.
v. Entomophilous flowers small and white or yellow (*Galium antarcticum*).

A summary of these is listed in Table I. Coupled with these floral trends, there is often a high degree of dry-matter investment in vegetative reproduction and all the species are perennial. The retention of winter-green leaves in many species may be an adaptation to a tundra environment (Bell, 1974) and in grasses, which have basal meristems, it could have important advantages at the onset of growth in the spring. In species which do not develop bud scales these leaves may also serve to protect the overwintering meristems. Experimental evidence on the photosynthetic efficiency of the green portions of overwintered leaves of Arctic shrubs (Johnson and Tieszen, 1976) shows that considerable rates of carbon fixation are possible in the second summer, providing immediate support for floral development. Some species may also use these leaves as an overwinter carbohydrate store, especially if rhizome and root systems are not adapted for this.

TABLE I. REPRODUCTIVE FEATURES OF SOUTH GEORGIAN NATIVE PHANEROGAMS

	Pollination mechanism	*Flower characters*	*Self-compatibility*	*Pre-formation of flowers*
Acaena magellanica	A	G ⚥ ♀	*	No
Acaena magellanica × *tenera*	A	G ⚥	*	No
Acaena tenera	A	G ⚥	*	No
Alopecurus magellanicus	A	⚥		
Callitriche antarctica	A (HY ?)	H ♂ ♀	*	No
Colobanthus quitensis	S	C ⚥	*	Yes
Colobanthus subulatus	S	C ⚥	*	Possibly
Deschampsia antarctica	S	C ⚥	*	Yes
Festuca contracta	S	C ⚥	*	Yes
Galium antarcticum	E S	⚥	*	Possibly
Juncus inconspicuus	A	⚥		No
Juncus scheuchzerioides	A (S ?)	G ⚥	*	No
Montia fontana	E (HY ?)	H ⚥	*	Possibly
Phleum alpinum	A	H ⚥	*	No
Poa flabellata	A	⚥	?	Yes
Ranunculus biternatus	E S	⚥	*	Possibly
Rostkovia magellanica	A	G ⚥	*	Possibly
Uncinia meridensis	A	G ⚥ ♀	?	Possibly

A Anemophilous; E Entomophilous; HY Hydrophilous; S Self-fertilization; C Cleistogamous; H Homogamous; G Protogynous.

For several species it has not been possible to confirm that pre-formation of inflorescences does occur. For some species, e.g. *Ranunculus biternatus*, flowering in any individual population appears to be both erratic and limited. Thus the lack of floral apices in the winter samples of this species, which has well-developed flowers shortly after melt, suggests inadequate sampling rather than no pre-formation of flowers. A further difficulty is the recognition of the earliest stages of floral development in some species (Sørensen, 1941; Mark, 1970). If induction takes place in February–March with initiation shortly after, development time before winter will be too short to allow a significant degree of differentiation to occur. Thus some species may overwinter apparently vegetative apices which are ready to begin floral development immediately winter ends.

The predominance of anemophilous flowers is not surprising in view of the limited insect fauna of South Georgia (Gressitt, 1970). Werth (1911) found a similar situation on Iles Kerguelen and noted that even in those species, such as *Galium antarcticum,* which were apparently entomophilous, autogamy could not be ruled out. He found cleistogamy to be very common and recorded that over 60% of the flora was normally self-pollinated. Indeed, on South Georgia it seems quite possible that entomophilous cross-pollination in any species can be regarded as an unusual event. Cross-pollination in the anemophilous species (especially the gynodioecious *Acaena magellanica*) must be quite common.

For the majority of species, the main period of flowering is December and January but a few species with overwintered inflorescences (e.g. *Poa flabellata*) flower mainly in October and November (Fig. 6). Species flowering earlier than usual in exceptionally favourable sites often have a smaller second flush of flowers in late summer. This relatively long flowering period is in sharp contrast to the behaviour of Arctic species.

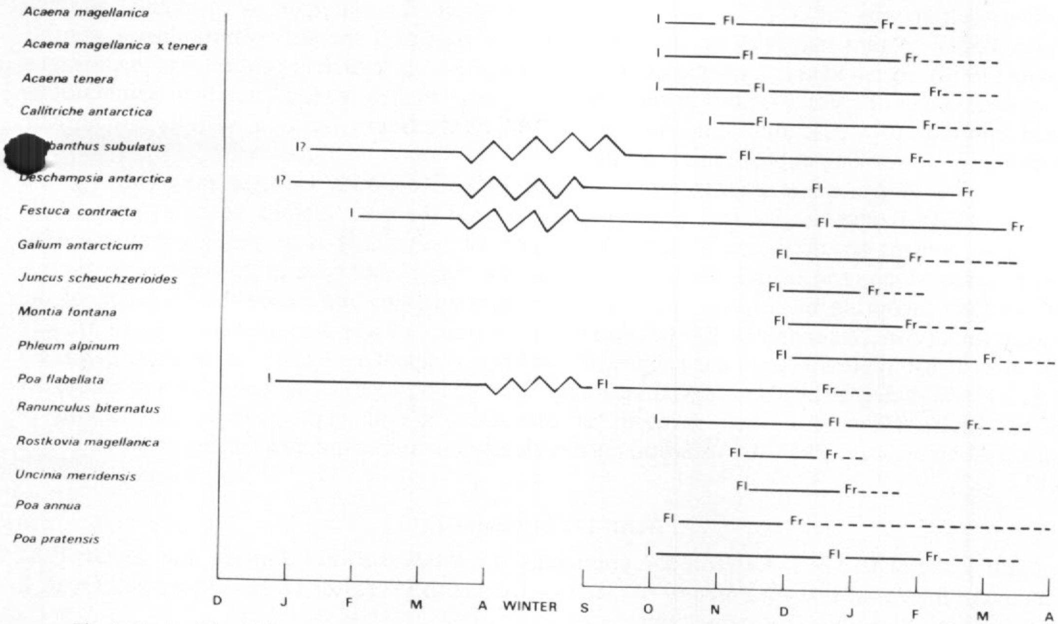

Fig. 6. Typical flowering periods for the South Georgian flora if snow melt occurs in September–October. I Floral initiation; Fl Flowering; Fr Fruiting.
Solid line denotes main flowering period; dashed line denotes period of occasional flowering.

Flowering times have been based on communities in the most favourable areas of the north-[illegible]st coast of South Georgia. A comparative assessment in 1974 of communities around the island showed that most sites on the south coast were generally 2–3 weeks behind Cumberland Bay sites in floral development. This was especially marked when comparisons of particular slope aspects were made. Many south-facing sites on the south coast still had snow patches in January, whereas these had melted in the Cumberland Bay area up to 2 months previously.

Although the effect of snow banks on floral development has not been studied in detail for the South Georgia species, the few observations that have been made suggest a similar pattern to that found in alpine situations (Billings and Bliss, 1959; Canaday and Fonda, 1974). In *Acaena magellanica* (Walton, 1976), plants from a late snow-bed site showed a telescoping of development which allowed them to complete their floral cycle before the end of the summer. This is clearly not possible for all species since, despite pre-formation of flowers, *Festuca contracta* apparently requires almost the whole summer to complete its flowering. This, together with its limited geographical distribution on the island, suggests that the species is at the limit of its environmental range on South Georgia. Edwards (1973) transplanted many South Georgian species to Signy Island, South Orkney Islands. His observations on these plants show that *Poa flabellata, Phleum alpinum, Deschampsia antarctica* and both species of *Colobanthus* are able not only to overwinter successfully but also to produce new inflorescences initiated on Signy Island. The aliens *Poa annua, Ranunculus repens* and *Achillea millefolium* also flowered the summer after transplanting. Seed germination was observed in several species but no established seedlings were found. He concluded that, of the species tested, *Poa flabellata* and *P. annua* seem the only new species capable of establishing themselves in the maritime Antarctic.

In the Arctic flora, many of the species are polyploid and show reproductive specializations such as pre-formation of flower buds (Hodgson, 1966), apomixis and cleistogamy. Mosquin (1966) has commented that all these features tend to decrease the genetic variability within a species and has suggested that the population uniformity may be an essential part of the life strategy of species in a polar environment. The price for retention of a highly adapted physiological system may well be the loss of a large part of a species' evolutionary potential. Savile (1972) accepted this hypothesis and suggested that lack of competition has encouraged the development of specializations in reproductive biology to ensure seed-set, which would not be tenable in the crowded communities of temperate habitats. South Georgia, with its low floristic diversity, presents ideal opportunities for this.

There are chromosome counts for 14 of the 25 native South Georgia taxa (Moore and Walton, 1970; Bennett and others, in press). Only four of these are diploid, giving at least a 40% polyploid content for the island's flora. This degree of polyploidy is as yet less than the 61% reported for Macquarie Island (Moore, 1960) but the majority of species do show reproductive adaptations favouring inbreeding and vegetative reproduction, and hence the retention of the present genotype. Callaghan (1974) has shown the existence of physiological ecotypes in *Phleum alpinum*, whilst Walton (1976) has suggested that the ecological diversity of *Acaena magellanica* is due to a high degree of phenological flexibility. The life strategies of successful South Georgian species, quite different in their methods of operation, are all dependent on adaptations in reproductive biology. The sub-Antarctic flora is clearly an interesting area for future work in this field.

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