

STUDIES ON *Acaena* (ROSACEAE):

IV. DISTRIBUTION AND ECOLOGY OF THE SUB-ANTARCTIC SPECIES

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ABSTRACT. The world distribution of the four *Acaena* taxa found on the sub-Antarctic islands is given together with detailed distribution of species on South Georgia. The general ecology of *Acaena* in the sub-Antarctic and similar areas of southern South America is examined. Habitat preferences and performance on South Georgia are examined in detail, the field observations being compared with experimental results. Some micro-climatic data are presented for a mature stand of *A. magellanica* and its significance is discussed in terms of plant environment.

Acaena is a genus largely restricted to the Southern Hemisphere, the few species occurring in the Northern Hemisphere being of very limited distribution. In the Southern Hemisphere it is found in South America, South Africa, Australasia and on numerous islands including all those in the sub-Antarctic, Tristan da Cunha, Gough Island, New Amsterdam and St. Paul, and the New Zealand shelf islands.

Distribution has been examined in two ways. First, the world distribution of *A. magellanica* (Lam.) Vahl, *A. tenera* Alboff and *A. minor* (Hook. f.) Allan has been mapped and, secondly, the detailed distribution of the three taxa *A. magellanica*, *A. tenera* and their hybrid (Walton and Greene, 1971) has been plotted for South Georgia. The ecology of *Acaena* species in the sub-Antarctic and southern cool-temperate zones is described with particularly detailed observations on South Georgian communities.

GEOGRAPHICAL DISTRIBUTION

World distribution

A. magellanica is more widely distributed than any other species in the genus. As Fig. 1 shows, it ranges from c. lat. 25° S. in northern Chile southward along the Andes to Tierra del Fuego, and across the Southern Ocean on the Falkland Islands, South Georgia, Prince Edward and Marion Islands, Iles Kerguelen, Iles Crozet, Heard Island and Macquarie Island. An early report of its occurrence in New Zealand (Hooker, 1867) is unsubstantiated.

A. tenera, on the other hand, has a very restricted distribution, occurring in South Georgia, Isla de los Estados and the mountains behind Ushuaia in Tierra del Fuego (Figs. 1 and 2). As in the case of *A. magellanica*, all distribution records for these maps are based on specimens examined and unpublished information provided by Prof. D. M. Moore, literature records being thought too unreliable in view of the confused state of taxonomy in the genus. One important literature record for *A. tenera*, for which it has not been possible to find any specimen, is that of Skottsberg (1916), who recorded this species from the vicinity of Lago Nahuel Huapi, lat. 41° S. in Prov. Rio Negro, Argentine.

A. minor, previously described as a variety of *A. sanguisorbae*, is found only on Macquarie Island, Campbell Island and the Auckland Islands.

A. magellanica has been found in Great Britain growing as a wool adventive and a specimen was also recently found in the Santiago herbarium (Fuentes s.n., SGO Herb. no. 077803), collected in 1911 from the Juan Fernandez Islands. Curiously, Skottsberg (1922) mentioned only *A. masafuerana*, *A. ovalifolia* and the inter-generic hybrid *Margyracaena* in his flora of these islands. No other specimens of *A. magellanica* have been found from there and it is tempting to conclude that the material found by Fuentes may have been a temporary introduction from Chile.

Although it might be imagined that *A. magellanica*, with such a wide geographical range, would also show wide climatic tolerances, this is true to only a limited extent. All the sub-Antarctic islands, the Falkland Islands, Tierra del Fuego and southern Patagonia share a

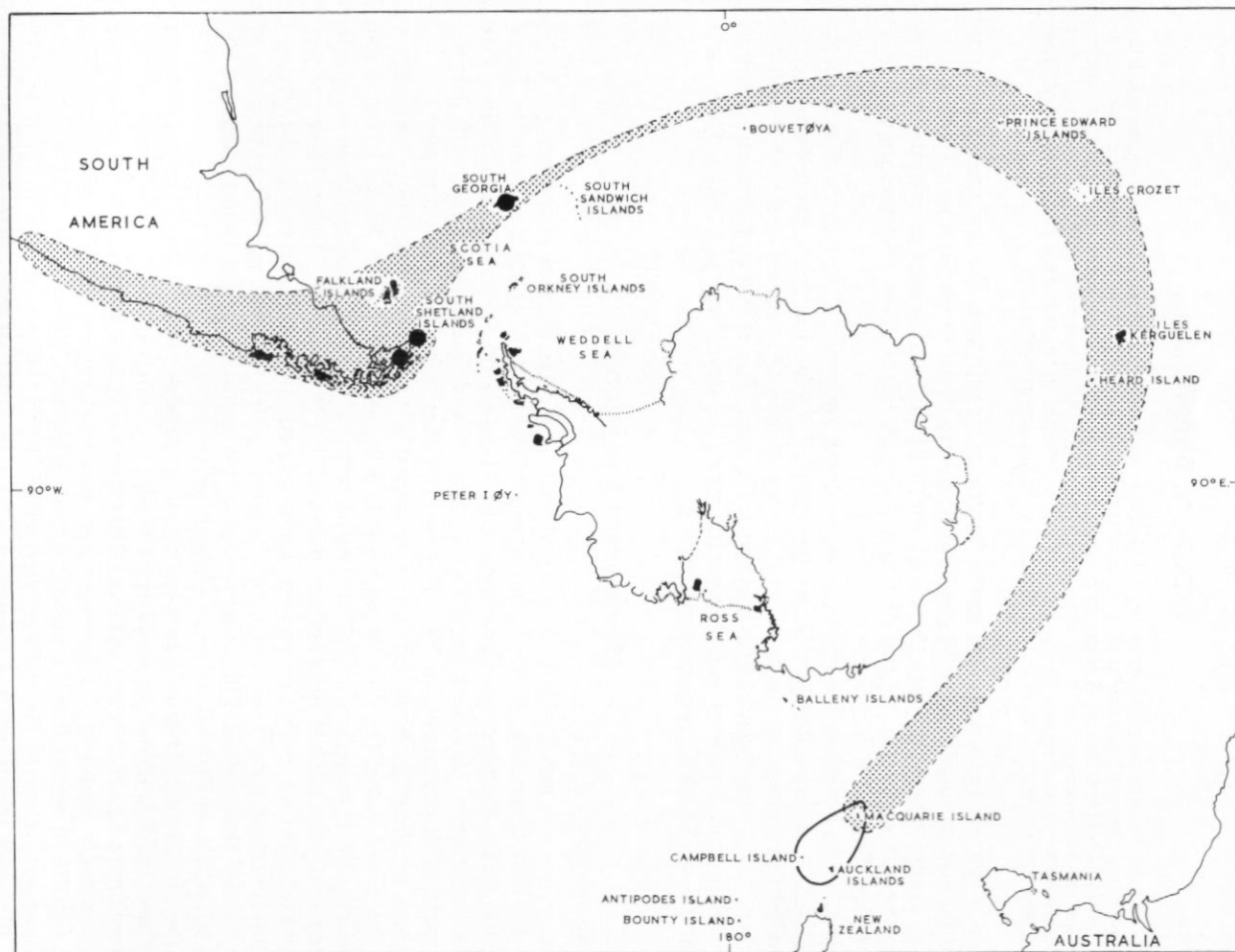


Fig. 1. World distribution of *A. magellanica* (stippled area), *A. minor* (—) and *A. tenera* (●).

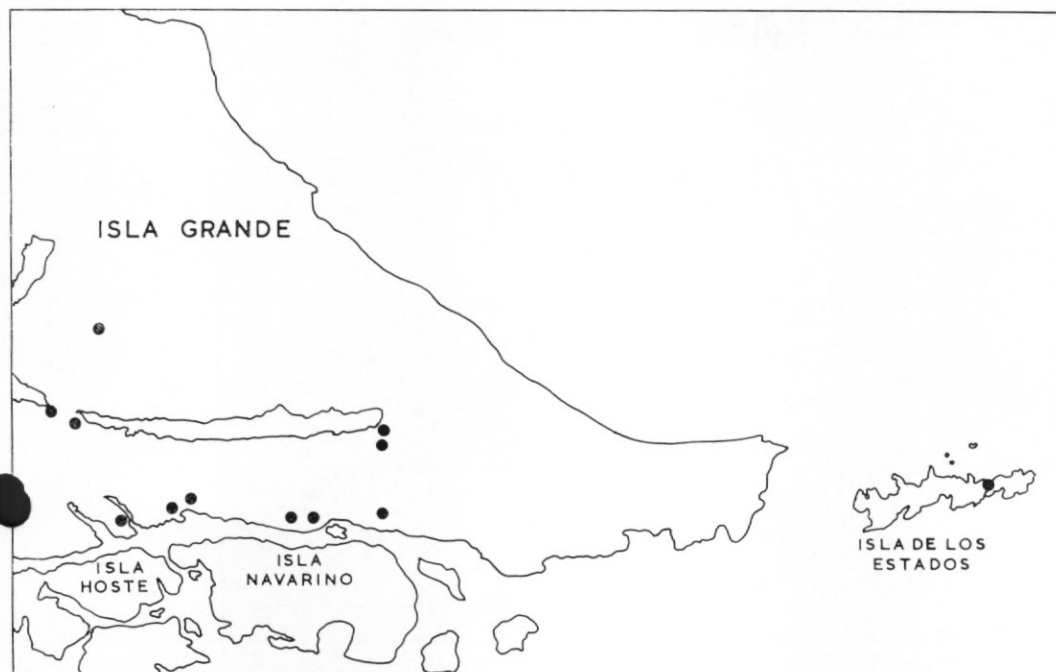


Fig. 2. Distribution in Tierra del Fuego of *A. tenera* (from herbarium specimens and unpublished records of D. M. Moore).

broadly similar cool-temperate climate. Farther north in South America this type of climate exists only at steadily increasing altitudes in the Andes. The limitation of *A. magellanica* to this climate is confirmed by the data in Fig. 3. The scarcity of data between lat. 32° and 44° S. is not a reflection of the frequency of occurrence of the species, rather of a lack of altitude data on all the collections studied. The distribution of *A. tenera* is too limited to show any similar trends but provisional studies on the closely related species *A. antarctica* Hook. f. showed an even more marked correlation between latitude and altitude.

Distribution on South Georgia

The data for the distribution map (Fig. 4) are derived from the records held in the British Antarctic Survey data bank (see Greene, 1972) and include all records up to June 1974. The mapping of the South Georgian flora was begun by Greene (1964) on the 5 km. grid system and most of the coastal areas of the island have now received a reasonable primary survey for phanerogams. *A. magellanica* is the most widespread of the three *Acaena* taxa, occurring in 150 squares, ten of which do not have *A. tenera* records. *A. tenera* has been recorded from 140 squares all having *A. magellanica* records. The records for the hybrid are more limited, since recording of this as a separate taxon did not begin until 1967. Its variability can cause difficulties for field recorders, so as far as possible all the records on this map have been checked by the author. The hybrid has been recorded reliably from 84 squares, two of which do not contain either *A. magellanica* or *A. tenera*. If this is correct, it suggests that the hybrid may have spread into these areas from neighbouring squares by seed. Normally, hybrid populations are found close to plants of one of the parent species and, since they do not show very great seed viability, it is assumed that spread must be largely by vegetative means.

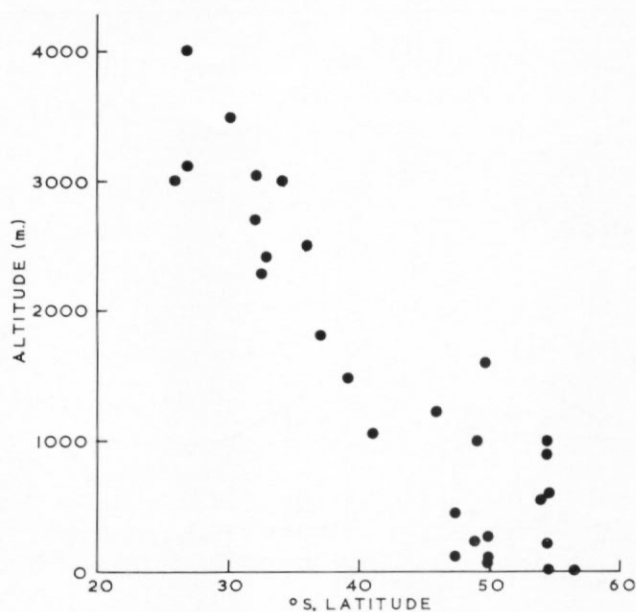


Fig. 3. Diagram of the altitude of occurrence of *A. magellanica* at different latitudes (from herbarium specimens).

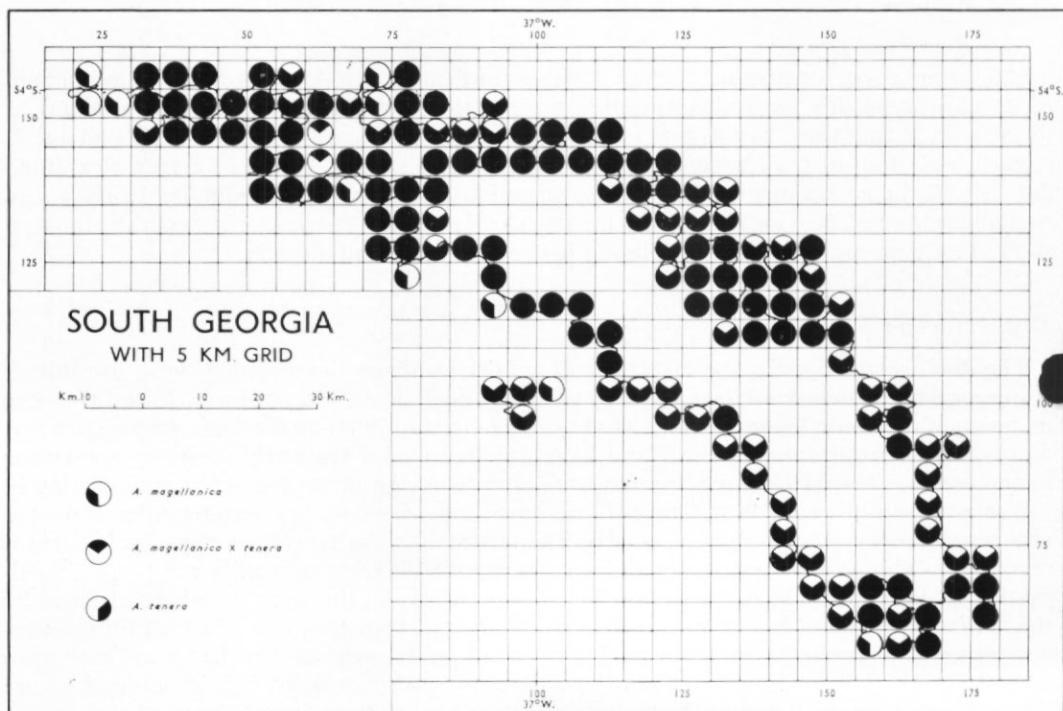


Fig. 4. Distribution of the three taxa of *Acaena* on South Georgia.

GENERAL ECOLOGY

A characteristic feature of the flora of the sub-Antarctic islands is the low species pressure. On most of these islands, a range of habitats exists which is sufficient to allow clearly defined communities to form. A few species are restricted to certain habitats because of absolute edaphic or hydrological requirements, e.g. *Callitriche antarctica* is only found in wet areas, but most species appear to have sufficiently wide ecological tolerances to be able to flourish in a variety of habitats and communities. Plant communities on South Georgia show little species fidelity in any of the associations, which appear to comprise a continuum of interrelated nodes (Smith and Walton, 1975). On South Georgia *Acaena magellanica* occurs in most communities, whilst *A. tenera* is much more limited in its occurrence, generally being restricted to the more montane habitats.

The following account is concerned with the species on the sub-Antarctic islands, although remarks on other species are included. The information is derived from literature, personal communications and the author's observations.

New Zealand shelf islands. Johnson and Campbell (1975) recorded *A. minor* var. *minor* and *A. minor* var. *antarctica* (Ckn.) Allan from the Auckland Islands. Allan (1961) noted the habitat of the latter variety as turfy grassy places and suggested that it might be only a luxuriant habitat-induced form. Johnson and Campbell found it to be "Common, especially near the coast, sometimes growing near the high-water mark". *A. minor* var. *minor* is said to be less common and found mainly on cliffs. They also recorded *A. anserinifolia* (J.R. & G. Forst.) Druce from one locality on the main island.

In Meurk's (1975) list for Campbell Island both varieties of *A. minor* were given together with *A. anserinifolia*. He described *A. minor* var. *minor* as the alpine meadow taxon and *A. minor* var. *antarctica* as occurring at lower altitudes. He suggested that there may be considerable interbreeding between taxa on the island partly as a result of the destruction of much of the natural vegetation by introduced herbivores. It is quite certain that *A. minor* var. *antarctica* is not synonymous with *A. antarctica* as he suggested might be the case.

Macquarie Island. *A. magellanica* (= *A. adscendens*) was reported by Taylor (1955) as growing only in wet peat or gravel. It occurs as isolated plants but more commonly forms mats on creek gravels where it reaches its largest size. It flowers from September to February and, since it is a favourite food of the rabbits, they have been instrumental in a wide dispersal of the fruits. Costin and Moore (1960) and Johnston (1966) have reported that in some areas rabbit grazing has resulted in the establishment of *A. magellanica*-dominated communities in place of the original *Pleurophyllum hookeri* Buch. and *Stilbocarpa polaris* A. Gray associations. Taylor (1955) noted that many leaves and stems in this species were very purplish in spring and, although fruits were found in all habitats, they were most prolific in the mat communities. The other species of *Acaena* on the island, *A. minor* (= *A. anserinifolia* var. *minor* Hook. f.), is much more common at higher altitudes and is an important constituent of the dry *Azorella selago* Hook. f. fellfield (Ashton and Gill, 1965), an association in which *A. magellanica* occurs only rarely. Gillham (1961) reported *A. magellanica* as an important colonizer in the disturbed drier areas of bird colonies and elephant seal wallows and she suggested that on the New Zealand shelf islands this niche was occupied by *A. minor*. Despite Meurk's (1975) suggestion, there is no evidence from studies of herbarium material that there is any hybridization between the two species, a point upheld by field observations (personal communication from J. F. Jenkin).

Heard and Macdonald Islands. Very little has been published on the flora of Heard Island. *Acaena magellanica* was previously found only in the Spit Bay area, where it was reported to

be not abundant and usually occurring in small isolated patches among *Azorella selago* cushions (Law and Burstall, 1953). More recent visits have increased the area from which it is known, Budd (1970) reporting it from Long Beach in 1963 and 1965, and in 1969 it "was found to be prolific at Skua Beach and to occur as far north-west as the Compton Glacier".

Macdonald Island was visited for the first time by a scientific expedition in 1971. Budd (1972) reported the vegetation to be very similar to that on Heard Island but no specific comment was made on *A. magellanica*.

Marion and Prince Edward Islands. Huntley (1971) has investigated the communities occurring on these islands in some detail. He found that heavy salt deposits from spray usually caused blackening of the leaves of *A. magellanica*. It apparently grows best in well-drained eutrophic soil in sites sheltered from the wind. Although it occurred in 45 per cent of the 457 quadrats that he examined, it was only a minor constituent of the *Crassula moschata* Forst. f. and the *Cotula plumosa* Hook. f. associations, whilst it was not found at all in bog areas but occurs occasionally in the *Agrostis magellanica* Lam. mire. Inland stands of *Poa cookii* Hook. f. often contained *Acaena magellanica* growing between the tussocks, whilst in two communities—*Acaena*-*Pringlea* spring association and the *Acaena* herbfield—it was always the dominant species. The herbfield normally had a carpet of *Rhynchostegium brachypterum* (Hornsch.) Jaeg. (given as *R. brachypterygium*) and *Drepanocladus uncinatus* as an understorey. *A. magellanica* is also found as an important constituent of the fernbrake *Blechnum penna-marina* (Poir.) Kohn. association.

Huntley (1971) noted that young vegetative buds appeared in July, leaves in late August, growing to form a canopy by October when the first flower buds appeared. Pollination occurred in early December.

Iles Kerguelen. The ecology of the islands in this group has been covered by Chastain (1958). He reported that *Acaena magellanica* occurs in both wet grassland and dry habitats. It is replacing *Azorella selago* Hook. f. on most of the main island and this may be partly due to spread by rabbits. He suggested that two forms of the species are distinguishable: form A, found in grassland and drier habitats is better developed and larger than the other form; form B, found in bogs and fens, with small leaflets often with red coloration. He noted that he saw material similar to the latter from the Falkland Islands and Patagonia. He also pointed out that the two forms that he described are connected by a complete range of intermediate plants.

Iles Crozet. In an account of the flora of Ile aux Cochons, Dreux (1964) stated that it differs very little from that of Ile de la Possession. In the south and east of the island, large areas between 100 and 300 m.² are covered by *Acaena magellanica*, whilst this species also occurs in the vegetation of the coastal fringe.

Davies and Greene (1976) stated that *Acaena magellanica* is common throughout Ile de la Possession, normally growing on a peaty substrate and only rarely on bare scree slopes. It is an important constituent of the *Agrostis magellanica* and the *Poa pratensis* grasslands, as well as of the *Blechnum penna-marina* association. It is found only at the edges of bog communities. In the fellfield communities it occurs up to 170 m. as isolated plants in the gravel and more frequently on peaty islands of vegetation.

Falkland Islands. Five species of *Acaena* occur on these islands: *A. lucida*, *A. ovalifolia*, *A. antarctica*, *A. pumila* and *A. magellanica* (Moore, 1968). *A. antarctica* and *A. pumila* are both limited to mountain areas and are very rare, whilst *A. ovalifolia* is found only in one area of West Falkland. Both of the other two species are widespread, although *A. lucida* is normally found only in coastal communities. *A. magellanica* also occurs in these communities but it extends farther inland in some areas. As both Skottsberg (1913) and Moore (1968) have remarked, it seems to prefer moist habitats, a point also made by Vallentin and Cotton (1921).

TABLE I. FLORISTIC COMPOSITION OF SOUTH GEORGIAN COMMUNITIES CONTAINING *Acaena* TAXA

	Site I (Point)	Site II (Dwarf Shrub)	Site III (Shackleton)	Site IV (Dam)	Site V (Hope)	Site VI (<i>Acaena</i> Fellfield)	Site VII (<i>Acaena</i> - <i>Rostkovia</i>)	Site VIII (IBP <i>Festuca</i>)	Site IX (IBP Primary)
<i>Acaena magellanica</i> (Lam.) Vahl.	100/60·2	100/95·0	100/96·4	45/18·3	44/12·4	—	92/21·8	92/14·5	93/30·2
<i>A. tenera</i> Alboff	—	—	2/0·2	70/17·0	40/3·0	96/12·2	—	14/0·8	—
<i>A. magellanica</i> × <i>tenera</i>	—	—	—	45/19·0	80/38·4	20/3·0	—	—	—
<i>Phleum alpinum</i> L.	36/7·7	—	—	—	64/11·0	80/11·4	88/6·6	58/5·2	52/0·8
<i>Festuca contracta</i> T. Kirk	—	4/0·3	—	45/9·8	88/19·0	92/13·6	2/+	98/32·3	100/67·8
<i>Deschampsia antarctica</i> Desv.	72/13·6	—	—	—	12/1·6	—	—	—	—
<i>Poa flabellata</i> Hook. f.	—	—	—	40/7·0	8/1·8	—	—	—	—
<i>Poa annua</i> L.	86/23·1	—	—	—	—	—	—	—	—
<i>Rostkovia magellanica</i> (Lam.) Hook. f.	—	—	—	—	80/13·5	—	100/36·7	46/2·6	8/0·3
<i>Juncus scheuchzerioides</i> Gaud.	—	—	—	—	28/12·8	—	48/4·0	—	—
<i>Tortula robusta</i> Hook. et Grev.	18/2·6	98/77·0	88/29·8	75/24·0	36/7·4	8/+	96/88·4	4/0·4	45/7·0
<i>Polytrichum alpinum</i> Hedw.	—	—	—	40/6·8	16/2·6	100/37·2	—	94/9·0	69/7·8
<i>P. alpestre</i> Hoppe	—	—	—	10/+	48/5·8	—	—	—	12/3·8
<i>P. piliferum</i> Schreb. ex Hedw.	—	—	—	—	—	24/2·7	—	—	—
<i>P. juniperinum</i> Willd. ex Hedw.	—	—	—	—	4/+	—	—	—	—
<i>Chorisodontium aciphyllum</i> (Hook. f. et Wils.) Broth.	—	—	—	20/2·0	—	—	—	100/40·0	13/0·8
<i>Drepanocladus uncinatus</i> (Hedw.) Warnst.	—	—	—	—	—	—	18/6·0	—	—
<i>Bartramia patens</i> Brid.	—	2/+	—	70/10·0	32/4·2	—	2/0·2	—	2/+
<i>Ceratodon</i> sp.	6/1·0	—	—	—	—	—	—	—	—
<i>Psilopilum trichodon</i> (Hook. f. et Wils.) Mitt.	—	—	—	10/1·5	—	—	—	—	—
<i>Philonotis</i> spp.	—	—	—	5/0·5	—	—	—	—	—
<i>Grimmia</i> sp.	—	—	2/0·2	—	—	—	—	—	—
<i>Rhacomitrium</i> sp.	—	—	—	—	—	—	—	2/+	—
<i>Conostomum pentastichum</i> (Brid.) Lindb.	—	—	—	—	—	—	—	2/0·1	—
<i>Bartramia subsymmetricum</i> Card.	—	—	—	—	—	44/3·4	—	—	—
<i>Barbilophozia</i> spp.	—	—	—	45/9·8	36/11·6	—	—	98/11·9	96/6·7
<i>Cephaloziella</i> spp.	—	—	—	5/+	—	96/+	10/3·0	—	—
<i>Lophocolea</i> spp.	—	4/0·4	2/+	10/2·5	12/+	96/+	—	4/+	—
<i>Riccardia</i> spp.	—	—	—	—	—	—	2/0·4	—	—
Fungi	—	—	—	—	—	—	2/+	—	—
Lichens	—	—	—	15/+	12/0·6	100/27·6	—	100/21·0	44/1·2
Bare ground	38/9·0	—	14/2·0	45/6·4	8/1·2	100/24·0	—	2/1·0	1/0·3

Data given as frequency/mean cover per 100 random quadrats.
+ Denotes presence with minimal cover.

It has, however, been found growing on well-drained sandy areas, the plants from this habitat being much less glaucous than usual and also producing smaller flower heads than those in wetter habitats. Skottsberg (1913) recorded it as beginning to flower in early November, in full blossom by mid-December and in fruit by January, a point corroborated by Moore (1968), who also noted its altitudinal range as up to 215 m.

Tierra del Fuego and Isla de los Estados. Roivainen (1954) recorded four species of *Acaena* from Tierra del Fuego in his major paper on the ecology of Isla Grande. He classified the moorlands there in nine categories and listed *A. tenera* as occurring in two and *A. magellanica* in six. His cover values for *A. tenera* rarely rose above three (Domin scale), whilst those for *A. magellanica* reached ten in some places. It is important to note that Roivainen made no reference to either *A. antarctica* or *A. microcephala*. Examination of herbarium material has suggested that *A. antarctica*, a species frequently confused with *A. tenera* in the past (Walton and Greene, 1971), may well have accounted for most of the material Roivainen recorded as *A. tenera*. In Tierra del Fuego until recently *A. tenera* was only known from the mountains where Alboff made the type collections. D. M. Moore (personal communication) made the following comments about its ecology there: "The altitudinal range is variously 550–650 m., tree line upwards, 1,800–3,000 ft. In no case have I seen it below tree line (almost consistently 1,500 ft. here) and it has been found in open, damp soil of snow-patch areas, among *Azorella selago* hummocks, in damp patches with *Ourisia fuegiana* and in amongst cushions of *Plantago barbata*. It grows pretty close to *A. magellanica* in most places but there is no evidence of hybridization—as one might expect. It does not occur as far east as the diploid *A. magellanica*."

Five species—*A. antarctica*, *A. magellanica*, *A. ovalifolia*, *A. pumila* and *A. tenera*—are known from Isla de los Estados. *A. antarctica* and *A. pumila* appear to be fairly common in fellfield areas between 100 and 600 m. but *A. tenera* is known only from a single collection (Puerto Cook, Staten Island. Leg. Castellanos, s/n. 8/3/1934. Herb. no. 12925. BA), no plants of this species being seen during a recent collecting trip to the area (personal communication from T. R. Dudley). *A. magellanica* appears to be common between sea-level and 35 m. in areas such as *Empetrum* heaths and on cliff ledges by the sea (Dudley, in press).

Other islands. Two species, *A. sarmentosa* Carm. and *A. stangii* Christoph., occur in the Tristan da Cunha–Gough Island group (Wace and Dickson, 1965). They occupy much the same niches as the two species on Macquarie Island and the two species on South Georgia, with *A. stangii* being the more montane species. These two species are closely allied to the Australasian *A. anserinifolia* group, as is *A. insularis* Cit., described from New Amsterdam and St. Paul (Citerne, 1897).

South Georgia. Greene (1964) has given some general information on the floristic content of the various South Georgian plant communities. To illustrate some of these communities in more detail, quantitative species lists were obtained for a range of *Acaena*-dominated stands (Table I). These lists (derived from 100 random quadrats of 25 cm. by 25 cm. per site) give relative frequencies and mean cover details for a number of different sites chosen to cover a range of floristic content and edaphic variation. Descriptions of the sites have been given by Walton (1974, 1977).

Only two sites contained all three *Acaena* taxa, sites IV and V. At site IV the three taxa had about equal cover ratings but *A. tenera* was twice as frequent as either of the others. At site V the hybrid had by far the greatest frequency and the highest cover rating. The only other stand in which the hybrid was recorded was site IV, this being the only one from which *A. magellanica* was absent. *A. tenera* occurred at five out of the nine sites but it was an important constituent at only two, sites IV and VI. *A. magellanica*, on the other hand, occurred in eight sites and

was more or less prominent in them all. Table I shows clearly the floristic poverty of well-established *A. magellanica* stands (sites I–III).

The *Acaena*–*Tortula* association, which can be considered as the sub-Antarctic equivalent of a dwarf-shrub community, is best exemplified by site II. It is undoubtedly one of the major colonizing communities on the island. Primary colonization of an area remote from established plants normally occurs by seedling establishment in a moss patch. Greene (1964) stated that the presence of *Tortula robusta* was essential if a sward was to be formed and that it was only rarely that *A. magellanica* could become established without the moss. Walton (1977) has suggested that this is not generally true, other mosses or the basal leaves of phanerogams often providing a suitable micro-climate for the seed to germinate and establish. Furthermore, once a large plant or sward is established, the spread of the *Acaena* canopy appears to precede the spread of the *Tortula*. Field observations by R. E. Longton (personal communication) support these conclusions. Peat formation below these communities is often considerable, depths of over 1.5 m. having been found. It is not clear to what extent *A. magellanica* has always been the dominant species in the sites with peat formation. Rhizomes of *A. magellanica* found at a depth of 1.5 m. were apparently undecomposed but it is impossible to say whether they originated at that level or had grown down into it from higher up the profile.

The best-developed *Acaena*–*Tortula* associations are on north-facing slopes, often of wet peat. This association can also develop on dry scree slopes and on flat out-wash areas of morainic debris. Flowering appears to be influenced most markedly by site exposure (Walton 1979) but it may be affected by water availability. Sites facing due south flower later than those facing due north in any given locality.

The associations containing *A. magellanica* and *Festuca contracta* (sites VIII and IX) can have either species dominant or the two co-dominant. This is a widespread community type on the northern side of the island, especially in the areas around Cumberland Bay and Stromness Bay. Generally, this community contains a high proportion of dead *Festuca contracta* (Walton and others, 1975) and this, together with the tufted growth form of the grass, appears to restrict the rhizomatous growth of the *Acaena* plants. The sites with a high proportion of *Festuca* are found on well-drained and generally dry brown earth soils. *A. magellanica* does not flower as profusely nor have such long scapes in this community as in the pure *Acaena* stands. The cryptogamic content of the grass-heath association is considerable. The proportion of *Tortula robusta* is low, whilst species of *Polytrichum*, *Chorisodontium*, *Drepanocladus* and *Barbilophozia* can be major constituents. Most lichens generally belong to the genera *Cladonia*, *Pseudocyphellaria* and *Stereocaulon*.

Only one wet community (site VII) is shown in Table I. The dominant phanerogam is *Rostkovia magellanica*, although a small amount of *Juncus scheuchzerioides* is present. *A. magellanica* has a high frequency but low overall cover. *A. magellanica* leaves in this type of wet community are normally small and more tightly clustered than in drier communities (Walton, 1976). Often the leaves are tinged with red. Bliss (1975) found that red leaves produced by Arctic plants of *Dryas integrifolia* had both higher leaf temperatures and greater photosynthetic activity than green leaves. Whilst there are no data for this in South Georgia, several species besides *A. magellanica* and *A. tenera* do show red pigmentation in their leaves, especially just after snow melt. Flowering is infrequent and when it does occur the scapes and heads are both small. The rhizome or stem is only visible where it produces leaves, the remainder being hidden under moss. Site VII contains an overwhelming proportion of *Tortula robusta* but communities with a high content of *Drepanocladus uncinatus* and *Chorisodontium aciphyllum* are also common where the site is less eutrophic. Not surprisingly, these mire communities are underlain by peat deposits often of considerable depth, especially where they lie in a basin.

No example of the *Poa flabellata* tussock community is included in Table I. *A. magellanica*, an important constituent when the tussock stools are far apart, sometimes forms a continuous

cover between the stools, in some cases growing on to stools damaged by seals. *A. magellanica* does not tolerate trampling, being quickly affected by the establishment of penguin rookeries or seal populations. It is normally the only *Acaena* species occurring in this community and so the only one likely to suffer this kind of pressure. In one part of Royal Bay *A. tenera* was found to have replaced *A. magellanica* in the area between the tussocks but this only occurred on steep slopes well away from the beach. In the flat beach areas where standing water is common between tussocks *A. magellanica* does not occur. The growth form of *A. magellanica* in the tussock community is similar to that in the pure stands but flowering is limited to the most open areas, often seeming to follow drainage channels.

The fellfield community (site VI) is typified by a high cryptogam content, considerable bare ground and having all its phanerogamic constituents dwarfed. *A. tenera* is an important constituent together with *Phleum alpinum* and *Festuca contracta*. A wide variety of foliose and crustose lichens are present, along with species of *Polytrichum* and, frequently, *Rhacomitrium*. The *Acaena* hybrid may also occur but plants often appear to grow very slowly. *A. tenera* often flowers prolifically in this habitat, especially in the protection of stones and large boulders. In the most exposed areas virtually all the phanerogams are confined to colonies of moss at the base of boulders where they are adequately protected from the wind.

A. tenera does not commonly form dense mats. It is a rare constituent of most of the *Acaena*-*Tortula* communities and generally uncommon in the *Festuca* grassland, its commonest habitat being bare scree in exposed situations. In almost all cases the plant will be rooted in a moss turf or cushion, usually of *Polytrichum* spp. in the drier habitats and species of *Chorisodontium* or *Brachythecium* in the wet sites. However, young plants obviously derived from seed have been observed growing directly in the soil at the base of stones and boulders (Walton, 1977).

The *Acaena* hybrid normally occurs in areas at the edge of a population of one or other of its parent species, especially where populations of *A. magellanica* and *A. tenera* overlap. It does not form closed stands like *A. magellanica* or appear only as scattered plants like *A. tenera* but tends to adopt the intermediate form of an open clump. In border situations flowering is frequent. Its sites are usually well drained and may be floristically rich (site V). It appears to be unable to compete particularly well with either of its parents but to have rather better tolerance of exposure than *A. magellanica*, being more frequent in fellfield communities and other exposed situations than that species. On a transect up Mount Duse from sea-level to 180 m. the hybrid began to form an important part of the community at c. 100 m., the point at which *A. magellanica* became a less important constituent. What is not clear is whether the hybrid is restricted to the intermediate sites because its parents are sympatric there, or if this restriction is an effect of competition.

Animal pressure on South Georgia comes from several sources. The effect of birds other than penguins appears to be largely beneficial, both from the point of view of manuring and the probable incidental spread of fruits. Penguin rookeries normally eliminate most phanerogams quite quickly. Rats appear to have little effect but reindeer, the other introduced mammal, have a marked effect on *A. magellanica* and the hybrid in two areas of the island (Lindsay, 1973; Kightley and Smith, 1976). These taxa are grazed back to the rhizome and apparently have little opportunity to flower. *A. tenera* is less affected, presumably because its effective ground cover is too low to make grazing worthwhile. The effect of elephant seals is limited to communities growing on flat beach areas. Although normal seal activities tend to eliminate both *A. magellanica* and the hybrid, *A. magellanica* is an early colonizer of the bare areas of deserted wallows.

In many parts of the island *A. magellanica* becomes infected by a fungus, *Ovularia* sp. (personal communication from R. Watling), towards the end of the summer. Yellow necrotic spots appear on the leaves, often affecting every leaf in a stand. It has not been determined whether this fungus has any inhibitory effect on the growth of the plant.

MICRO-CLIMATE

The formation of large stands dominated by *A. magellanica*, often leading to the suppression of the original vegetation, and the necessity for relating laboratory measurements of photosynthesis to field conditions made it necessary to investigate the micro-climate of a mature community. The high summer leaf-area index of this dwarf shrub ensures that little light reaches the ground, moss growth being restricted to early spring and late autumn. A mature stand often reaches 30 cm. in height and must have a significant effect on radiation balance and soil heat flux. Quantification of the temperature profile was required as a preliminary step in relating biological activity to environment.

Material and methods

A Grant automatic micro-climate monitoring station, with temperature probes (thermistors) and a Kipp and Zonen solarimeter, was run from 17 February 1971 until 9 March 1971 at the dwarf-shrub site. The accuracy of the recording system was $\pm 0.5^\circ \text{C}$ at best. Recordings were made hourly of the following:

- i. Air temperatures at 50, 25, 10, 5 and 0 cm. above ground level.
- ii. Soil temperatures at 5, 10, 20 and 40 cm. below ground level.
- iii. Incoming short-wave radiation.

The air probes were arrayed on an aluminium mast with shields of white-painted perforated gauze. The height of the *Acaena magellanica* shoots around the mast was 15–20 cm., whilst at the base of the mast was a layer of *Tortula robusta* up to 5 cm. deep. The soil at this site was pure peat, usually very wet.

Three Piche evaporimeters were also run for this period near to the micro-climate mast. They were set up at 50, 25 and 7.5 cm. above ground level and were read as frequently as possible.

Results

Extracts from the data collected are shown in Fig. 5. The temperature profiles have been plotted against time and points of the same temperature joined together to give an isothermal diagram. The period chosen runs from one hot clear day through a cool cloudy day to another hot day. The official meteorological records for screen temperature are also given in Fig. 5. Rain fell on all 3 days (12.6 mm., 0.7 mm. and a trace).

The top of the leaf canopy between 15 and 20 cm. and the moss layers 5 cm. deep both have a marked effect on changes in the temperature profile with time. Movement of air within the canopy is almost negligible and this allows the development of hot and cold spots. The hottest areas appear to be located at the top of the moss mat although, at times, these areas can extend upwards to just above the leaf canopy. A similar situation exists for cold spots produced during cloudless nights by radiative cooling. Temperatures within the plant cover can fall to several degrees below the ambient air temperature with frost pockets forming just inside the canopy.

Although the sunshine record was very similar for both of the hot days, the mean wind speed was much lower on 17 February (3.9 kt.) than on 19 February (8.3 kt.). This is reflected in the measurements of much higher temperatures, over 20°C , in the first hot spot than in the second (Fig. 5). During the intervening cloudy day the mean wind speed was very low (2.0 kt.) and this, together with the lack of radiative heating, resulted in the persistence of sub-zero temperatures in the air profile until late morning. The moss mat acts as an insulator so that even the major daily temperature fluctuations do not usually penetrate beyond 5 cm. into the soil. Indeed, it can be seen in Fig. 5 that it is only when pronounced temperature foci develop within the canopy that any change occurs in the soil-temperature profile. The space between the top of the moss layer and the top of the canopy experiences far greater extremes of tempera-

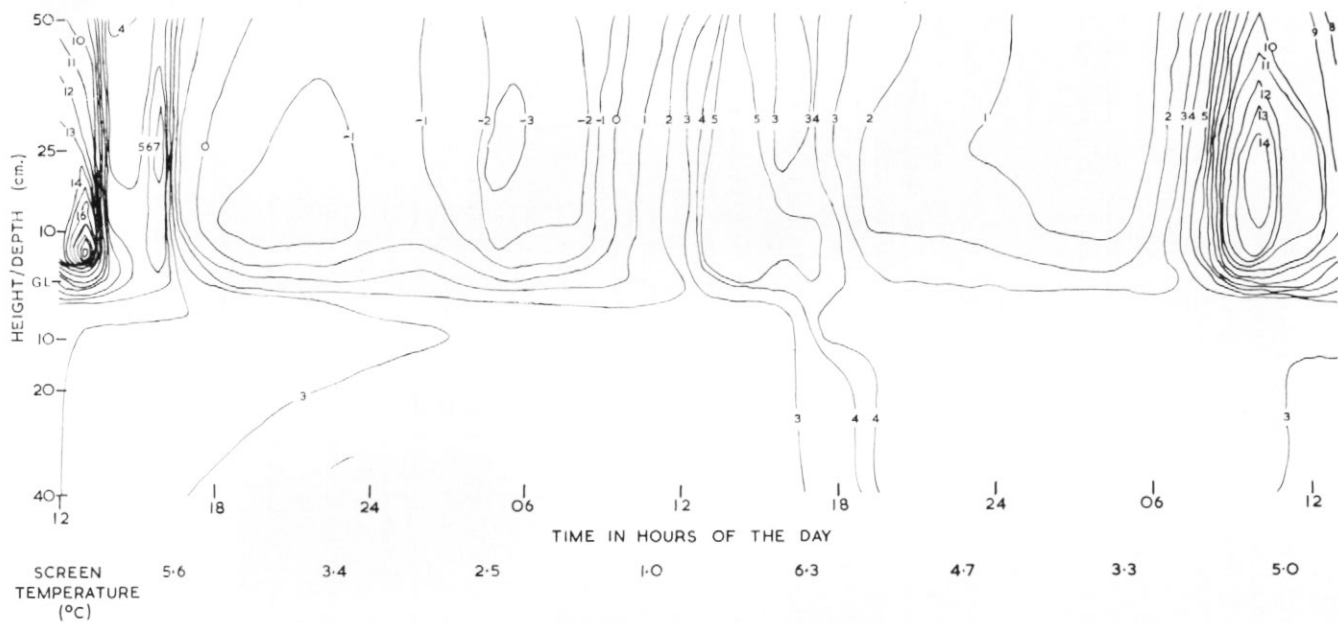


Fig. 5. The temperature pattern (°C) with time in a vertical profile through an *A. magellanica* community on South Georgia (17-19 February 1971). (GL is ground level.)

ture than those shown by ambient air temperature above the plants but, because of the moss layer, the stems and rhizomes are apparently subjected to only small temperature changes when growing at or below the soil surface.

The measurements given are for late February. It is to be expected that even higher temperatures would be experienced within the stand during December and January, whilst the frequency of frosts obviously increases as winter approaches. The results from the evaporimeters showed only a slight decrease in evaporation between 50 and 25 cm. but a very marked decrease at 7.5 cm. The leaf cover in this stand was 100 per cent and the rate of evaporation within the sward, even under quite warm conditions, suggests that air movement was very small at 7.5 cm. and that the atmosphere within the sward was generally very humid. This is of major importance for the growth of *Tortula robusta* and is likely to be highly significant as regards decomposition of litter.

DISCUSSION

Both species of *Acaena* range widely over South Georgia and records collected to date suggest that the hybrid is probably equally well distributed. The three taxa show a considerable degree of ecological amplitude, with *A. magellanica* exhibiting the widest degree of tolerance. One or both of the species occur in all the associations that are currently recognized on South Georgia, with the hybrid appearing as an important constituent generally only in areas where competition from its parent species is low.

Two major factors influencing the distribution and success of the taxa appear to be water availability and degree of exposure. In areas well supplied with water, protected from the wind and with a northerly aspect, *A. magellanica* can be expected to do exceptionally well, producing much larger leaves than normal and showing considerable vegetative growth, generally at the expense of flowering. *A. tenera*, when growing in sheltered flushes at low altitudes can also produce exceptionally large leaves. In exposed and dry habitats, both *A. tenera* and the hybrid appear to do better than *A. magellanica*. Flowering, as has been shown earlier (Walton, 1979), is considerably influenced by aspect, especially in exposed sites. The height of the flowering head is closely related to the degree of wind exposure in *A. magellanica* and the hybrid, but not as critically so in *A. tenera*. Germination and establishment of seedlings in bare earth in the shelter of a stone appears to be far more common in *A. tenera* than in *A. magellanica*, which shows a distinct preference for germination in moss mats (Walton, 1977). The field establishment of the hybrid from seed has not been seen.

The situation on South Georgia appears to be most similar to that on Macquarie Island, with its two species, and Marion Island, which contains only *A. magellanica*. On both these islands *A. magellanica* occurs in a wide range of communities but it does best in pure stands with a moss understorey. On Iles Crozet it appears to be limited to peaty soils, not being such an active colonizer of the scree slopes as on South Georgia, whilst on Iles Kerguelen its natural ecological position has been considerably changed by extensive rabbit grazing. In material from both Macquarie Island and Iles Kerguelen the red coloration in the leaves typical of plants growing in boggy areas of South Georgia has been remarked upon. The situation on Heard Island, where *A. magellanica* appears to be limited to a small number of localities, may be due partly to inadequate exploration of the island. Interestingly, Smith (1977) noted beetle grazing of *A. magellanica* on Marion Island. Although beetles are common on South Georgia, there is little evidence of this.

On both Isla de los Estados and Tierra del Fuego, where the ranges of *A. magellanica* and *A. tenera* apparently overlap, no specimens have been seen showing hybridism. It is possible that the *A. magellanica* populations on Isla de los Estados are diploid, in which case the apparent lack of hybridization may be due to the rarity of *A. tenera*. On this island, *A. magellanica* appears to be largely limited to coastal cliff areas, habitat details for *A. tenera* being lacking. On Tierra del Fuego, where both chromosome races occur, *A. magellanica* would

seem to be widely distributed from moorland to *Nothofagus* forest to the strand line. On the other hand, *A. tenera* is severely limited to fellfield areas above 500 m. and has only been found in areas with tetraploid *A. magellanica*.

Both chromosome races of *A. magellanica* appear to have wide ecological tolerances throughout their respective ranges, whilst *A. tenera* apparently shows a much wider range on South Georgia than in Tierra del Fuego. This may be due to the much greater species pressure and lack of fellfield habitats at sea-level in the latter, the growth form of *A. tenera* being a major limitation in terms of competitive ability (Walton, 1976).

The micro-climate at plant level in a mature *A. magellanica* stand is considerably more severe than suggested from standard meteorological data. The formation of hot spots and frost pockets within the boundary layer and the top few centimetres of the canopy ensures that fluctuations are of a considerable amplitude. Preliminary data for *A. magellanica* have indicated a significant rate of photosynthesis even at -2°C (Smith and Walton, 1975), and an upper compensation point above 30°C . *A. magellanica* would thus seem able to continue active photosynthesis over the wide temperature range to which the canopy leaves are likely to be subjected. The high humidity within the canopy is directly linked with the lack of air movement. This in turn allows the seasonal growth of *Tortula robusta* (Walton, 1973) which then provides an insulating layer between the centre of the most violent temperature fluctuations and the ground. *A. magellanica*, unlike *A. tenera*, is able to considerably modify much of its local environment as the plant grows. This may result in a feed-back mechanism, ensuring its permanent dominance in certain sites.

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