

SOME STUDIES ON THE GENUS ACAENA

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by

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"The inner parts of the Country South Georgia was not less savage and horrible: the Wild rocks raised their lofty summits till they were lost in the Clouds and the Vallies laid buried in everlasting Snow. Not a tree or shrub was to be seen, no not even big enough to make a toothpick. I landed in three different places, displayed our Colours and took possession of the Country in his Majestys name under a discharge of small arms. Our Botanists found here only three plants, the one is a coarse strong bladed grass which grows in tufts, Wild Burnet and a Plant like Moss which grows on the rocks".

The Journals of Captain Cook : vol. 2 -
The Voyage of the Resolution and
Adventure in 1772-1775. Cambridge
University Press (1961).

SUMMARY

The species of Acaena (Rosaceae) growing on the sub-Antarctic island of South Georgia have been examined from two different aspects - the world level and the insular level.

A revision of the taxonomy and synonymy of the two sections of the genus containing A.tenera and A.magellanica has resulted in the reduction to synonymy of many species, and a complete synonymy for Sect. Acrobyssinoideae Bitt. and for A.magellanica (Lam.) Vahl (which comprises most of Sect. Ancistrum Bitt.) is provided. Morphological descriptions are given for A.magellanica and A.tenera, and for plants from South Georgia which are judged to be the hybrid A.magellanica x tenera.

An examination of aspects of generic morphology together with consideration of relevant biogeographical literature has resulted in the conclusion that the genus probably arose from tropical ancestral stock which may have been common to Poterium. Speciation within South America has resulted in a spectrum of types, from primitive woody species with racemic inflorescences and multispined fruits to more highly evolved species with less woody stems, few spined fruits and compact globular heads. Dispersion of the genus from South America has taken place at various times, resulting in different stages of generic evolution.

The majority of the Australasian species are found in New Zealand and appear to have a common ancestor. The relationships of other disjunct species were traced and relatively recent long distance dispersal was found to be a satisfactory explanation for most of their distributions.

The taxa on South Georgia were shown to ^{be} highly evolved. The inter-relationships between them are given in terms of breeding patterns and it is suggested that F_1 hybrids are normally formed with

A.tenera as the female, whilst F_2 and any subsequent generations are probably due to backcrossing to A.magellanica as the male. A.magellanica appears to be generally outcrossing whilst the reverse is true of A.tenera.

Examination of floral development showed no evidence of preformation of flowers in the previous season, initiation occurring simultaneously with snow melt at most sites. The rate of floral development appeared to be linked to site aspect. Seed germination studies showed a warm day/cold night regime to be the most effective. A.magellanica seedlings grew at a much higher rate than those of A.tenera, but seedling production on a per head basis was similar for both species. Under a given light regime there was a linear rate of leaf production for both taxa. Rates for seedling establishment in various soils at different sites were seen to correspond to a pattern predictable from the general ecological data for the species.

Measurement of changes in standing crop of an A.magellanica community showed it to be highly productive, although the **major part** of dry matter production was for vegetative rather than flowering tissue. Initial measurements of photosynthetic rates demonstrated marked differences between geographically isolated populations of A.magellanica. A significant rate of photosynthesis was found to occur at and below 0°C . in all the South Georgian taxa.

These data were discussed in terms of adaptation of the taxa to South Georgia and the other sub-Antarctic islands, whilst the information gathered on these and other species was used to propose a hypothesis for the origin, evolution and distribution of the genus.

CONTENTS

		<u>Page</u>
Chapter 1	Introduction	1
Chapter 2	Taxonomy and Nomenclature	
	The Genus	7
	Section Acrobyssinoideae Bitter	10
	Section Ancistrum Bitter	15
Chapter 3	Morphology	
	General morphology	
	Materials and methods	20
	<u>Acaena tenera</u> Alboff	22
	<u>Acaena magellanica</u> (Lam.) Vahl	24
	<u>Acaena magellanica</u> x <u>tenera</u>	28
	Anatomy	35
Chapter 4	Cytology and Hybridisation	40
Chapter 5	Geographical Distribution	
	Distribution on South Georgia	43
	World distribution	44
	Biogeography of the genus	46
Chapter 6	Growth of the Seed	
	Germination	55
	Establishment of the seedling	60
	Development of the seedling	66
	Dry matter production by the seedling	69
Chapter 7	Growth of the Adult Plant	
	Standing crop and dry matter production	75
	Floral induction	80

Contents (Continued)

	<u>Page</u>
Floral development	83
Scape growth	86
Chapter 8 Physiology	
Composition of plant parts:	
I. Water organic and ash content	90
II. Chemical content	94
III. Calorific values and efficiency	99
Pigment content	104
Photosynthesis	110
Chapter 9 Ecology	
General ecology	117
Microclimate measurements	133
Chapter 10 Discussion	138
Acknowledgements	151
References	152
Appendix 1 Complete synonymy of <u>A.tenera</u> , <u>A.masafuerana</u> and <u>A.antarctica</u>	A1: 1-2
Appendix 2 Notes on the identification of type collections	A2: 1-11
Appendix 3 Complete synonymy for <u>A.magellanica</u> including literature citations	A3: 1-8
Appendix 4 South Georgian site descriptions	A4: 1-5

The origin of the floras of both islands and continents has excited botanical interest for over a hundred years. Interest was originally stimulated by the major palaeontological discoveries in the early and mid-nineteenth century. Ettinghausen (1850) pointed out various similarities between fossil genera of the Cretaceous in Europe and modern day genera in the Australasian flora. From this basis he argued that a homogeneous flora with a world-wide distribution existed during the Tertiary period and the relics of this distribution are today seen as discontinuous distributions in present bipolar species. This monotopic theory has been attacked by various authorities (Briquet, 1901; Reitz, 1940; Florin, 1940) and now seems unlikely to be a reasonable explanation. The polytopic origin theory, supported by Briquet (1901), Schultz (1903), van Steenis (1962) and others, favoured migration from boreal populations to the austral zone via land bridges. Rietz (1940) examined both these hypotheses and concluded that any migration theories should be treated with a certain scepticism until a more firm understanding had been gained of the evolution of taxonomic units.

Any theory attempting to explain the present discontinuities of many Southern Hemisphere plant distributions has to provide a method for transferring plant material across what are now considerable areas of sea. Land bridges were proposed by Hooker (1844-47) to meet this difficulty and were supported by both Candolle (1855) and Darwin (1859). Wallace (1880) took a different point of view and proposed that long distance dispersal in its various forms could adequately account for the floras of remote oceanic islands. He therefore did not attach as much importance as

Hooker (1855-60) to the Panama break in the high mountain chain between North and South America. Godley (1967), using Juncus and Hebe as examples, has stated that whatever land bridges might have once existed, trans-oceanic dispersal of some species will also have occurred. Carlquist (1966) recently reviewed the available information and concluded that the theory of long-distance dispersal was well supported, especially if Wallace's hypothesis was taken together with Darwin's emphasis (1859) on the importance of high mountain chains. He suggested that relict flora patterns, such as those obtained under Hooker's hypothesis of a greatly increased land area, are markedly different from the immigrant patterns produced by a long-distance dispersal theory.

The polar regions of the world present marked contrasts in the variety of their floras and faunas. In the Antarctic most groups consist of many individuals of a few species, whilst the converse is true of the Arctic. This situation appears to be largely attributable to the geographical isolation of Antarctica from large continental areas and to the permanent icecap which covers most of it. Yet at one time the distribution of land in the Southern Hemisphere was greatly different from that at present, and at that time the climate of the polar area was warm enough to support a much more highly diversified flora and fauna than is possible at present.

The original idea postulating the existence of a huge southern land mass, put forward by du Toit (1937), has received a considerable amount of vindication in recent years. Evidence supporting the existence of the super-continent Gondwanaland has come from several sources, but the most significant have been the discovery of the fossil remains of the reptile Lystrosaurus at Coalsack Bluff, Victoria Land (Barrett, Baillie & Colbert, 1968), a better knowledge of the Glos^sopteris flora of the Southern

Hemisphere (Schopf, 1970) and the accumulation of considerable geophysical data supporting the new theory of plate tectonics which attempts to explain continental movement through geological time (Tarling & Tarling, 1971).

Finds of Tertiary microfossils and pollen (Cranwell, 1959) have shown that the flora of the Antarctic Peninsula area, which now consists of mosses, lichens and two phanerogams, contained a variety of species of conifers and angiosperms before the last major glaciation.

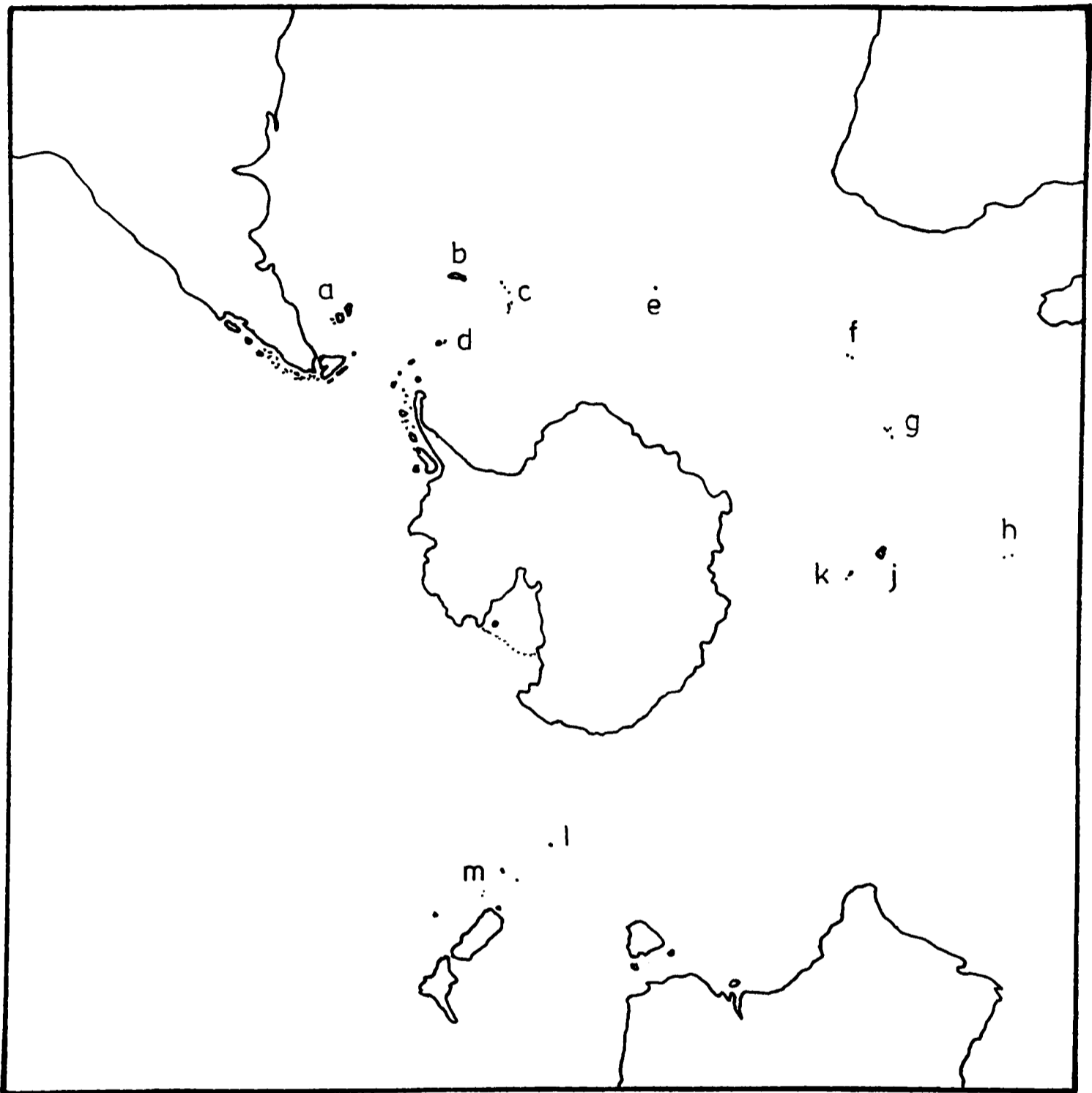
The Antarctic continent today is ringed by a number of islands, all of which now experience sub-polar or cool temperate climates. These islands generally lie on submarine ridges which often appear to form parts of extensive mountain systems either underwater or on nearby continental areas. These ridges are believed to have formed by plate tectonic movement, the ridges resulting from an upwelling of rock at the interface between two plates. The Scotia Arc is one such ridge, forming a link between the southern part of the Andes and the mountains of the Antarctic Peninsula. Adie (1964) has examined its probable origins in some detail. Along it lie a number of islands - South Georgia, South Sandwich Islands, South Orkney Islands and the South Shetland Islands. Of these islands only South Georgia and the South Orkney Islands are composed of pre-Tertiary rock, all the remaining islands being of volcanic origin. Two groups - South Sandwich and South Shetland Islands - still show numerous signs of continuing volcanic activity (Baker et al, 1964; Clapperton, 1969). Amongst the other sub-Antarctic islands - Îles Kerguelen, Îles Crozet, Prince Edward and Marion Islands, Macquarie and Heard Islands - only Îles Kerguelen is of non-volcanic origin.

In any discussion of plant migrations between South America and Australia-New Zealand, the floras of the sub-Antarctic islands must be taken into account. These islands, lying between the latitudes 45°S and 55°S, have a number of features in common. They are all small, all possess cool oceanic climates, and all are or have been glaciated to a considerable extent. All are far from continental land, and possess limited native floras. They appear to offer a series of stepping stones between South America and Australasia (Figure 1) and studies of their floras might help to suggest which of the various theories of discontinuous distribution is the most likely explanation.

If populations of a species with a wide distribution become spatially isolated from each other for a long period of time, it is likely that some degree of genetical isolation will also occur. This will increase with time, and over sufficiently long periods evolution may result in the formation of morphologically distinct species. The period of time required for this is considerable. However, if the populations concerned are only isolated for a short time, provided their local environments are sufficiently different, changes can occur to produce physiological ecotypes. This has recently been demonstrated conclusively for a number of polar species, e.g. Oxyria digyna (Mooney and Billings, 1961) and Phleum alpinum (Callaghan, 1972).

The sub-Antarctic islands represent the southernmost distribution of many species. Information on the performance of the species which have colonised these remote islands might well be of considerable assistance in assessing the importance of various features in the success of a species under such a rigorous subpolar climate. Comparisons between material from the islands and collections from other parts of a species range might shed interesting light on the possibilities of long distance dispersal, and of

Figure 1. Map of the distribution of land in the Southern Hemisphere (Polar Projection)



- Key:
- | | |
|-----------------------------------|-------------------------------------|
| a. Falkland Islands | g. Iles Crozet |
| b. South Georgia | h. New Amsterdam & St. Paul Islands |
| c. South Sandwich Islands | j. Iles Kerguelen |
| d. South Orkney Islands | k. Heard Island |
| e. Bouvet Island | l. Macquarie Island |
| f. Prince Edward & Marion Islands | m. New Zealand shelf islands |

speciation in isolated populations. To attempt to do this and to collect information which might offer some insight into the floristic connections between South America and Australasia the circum-polar genus Acaena was chosen for study.

In a check list of the sub-Antarctic vascular flora (Greene and Greene, 1963) only two species are shown as occurring on all the islands - Acaena adscendens and Callitriche antarctica. Other species such as Blechnum penna-marina and Ranunculus biternatus also have widespread distributions but are missing from at least one of the islands. Since Acaena adscendens was also known from the Falkland Islands and Patagonia, and since its position on most of the islands was that of a community dominant, this species was selected for intensive study.

Detailed field work was restricted to South Georgia, but the species was observed in the Falkland Islands and Tierra del Fuego where living material was collected.

The island of South Georgia lies south of the Antarctic Convergence and near the northern limit of the pack ice. Its climate is cool oceanic (Greene, 1964) with an average rainfall of about 1500 mm., and a temperature range of -15°C to $+15^{\circ}\text{C}$. More detailed meteorological data are provided in Pepper (1954) and Smith (1971). The limited flora consists of 24 native phanerogams (Green^e, 1964) with a number of introduced alien species (Walton and Smith, 1974). Cryptogams are numerous, with about 150 species of lichens (D. C. Lindsay, pers. comm.) and about 150 species of bryophytes (B. G. Bell, pers. comm.). A number of authors have shown the general distributions of the various phanerogamic species found on South Georgia and the other sub-Antarctic islands in map form, (Lourteig and Cour, 1963;

Korotkerich and Petrov, 1966; Huntley, 1971), whilst others, for instance Skottsberg (1915, 1936), have discussed generic distribution at length.

The wide geographical distribution of A. adscendens together with a very considerable range of morphological variation suggested that it might show some physiological adaptations to the variety of habitats covered in its range. Its apparent ability to spread to all the sub-Antarctic islands, and its importance as a major constituent of their plant associations showed clearly that this species was better adapted than most others to the rigorous subpolar and alpine climates of the southern end of the world.

A study of Acaena adscendens was therefore undertaken in which its taxonomy and morphology were examined for its whole range, whilst field studies of productivity and development were carried out on South Georgia. Laboratory studies yielded further information about seed germination, anatomy and rates of photosynthesis and respiration. Another species of Acaena, A. tenera, also occurs on South Georgia and this species, together with a naturally occurring hybrid between the two, was used in many of these studies. In an attempt to explain distribution patterns in the genus, all species were reviewed in a biogeographical context, and this has led to a suggested assessment of evolutionary trends within the genus.

The Genus

The genus Acaena belongs to the family Rosaceae (Subfamily Rosoideae, Tribe Sanguisorb^eae), its closest relatives being Polylepis R. & P., a South American genus, and Poterium L., a widespread Northern temperate genus. It was described by Linnaeus (1771) from a specimen of A.elongata from Mexico. In 1776 J.R. and G. Forster described the genus Ancistrum on the basis of material that they had collected from various islands in the Southern Ocean. Lamarck (1791) accepted Ancistrum for his new species whilst Ruiz and Pavón (1798) ascribed their new taxa to Acaena. Before the situation could become more confused Vahl (1804) reduced Ancistrum to synonymy with Acaena and incorporated all of Lamarck's species within the one genus.

The thirteen species described by Vahl (1804) showed considerable differences in morphology and it became obvious to Candolle (1825) that the genus should be divided into sections. He proposed two, Euacaena DC. and Ancistrum (Forster et Forster) DC., based on the position of spines on the cupule (Figure 2). However, the sense in which Reiche (1898) used the two subgenera Euacaena and Ancistrum did not correspond to that of the two original sections of Candolle, since Reiche used, as the primary difference, the type of inflorescence. Reiche put 15 species in Euacaena and 10 in Ancistrum, with 4 taxa not specified. Again using the type of inflorescence as the primary character Citerne (1897) divided the genus up into seven sections. The most detailed examination of the sections within the genus was however undertaken by Bitter (1911). Whilst he accepted the type of inflorescence as an important character, Bitter used its position to divide the genus into two series - Axillares and Terminales. Within each series there were then further divisions into sections, ten in all, and then into

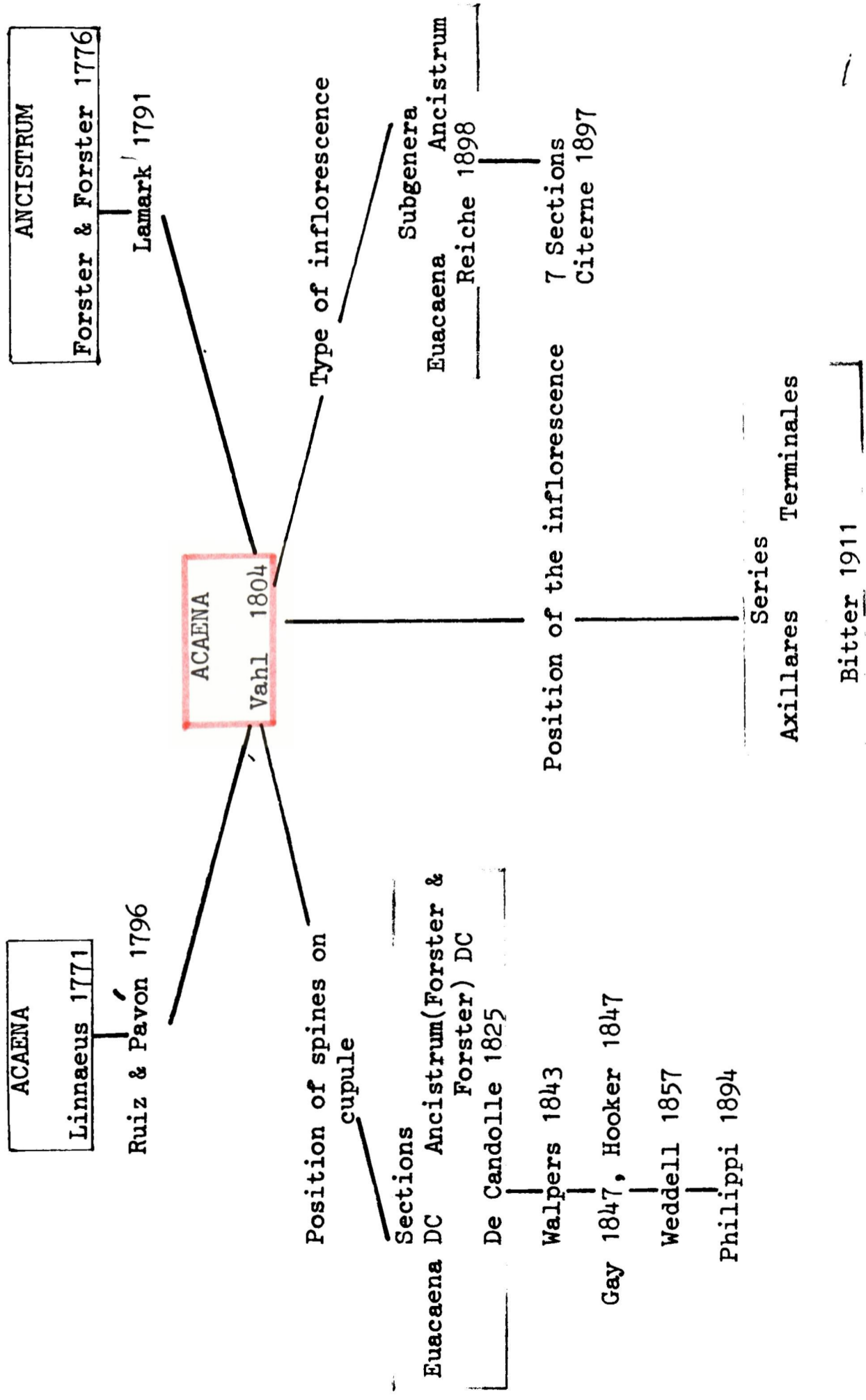


FIGURE 2. Usage of three different principal characters by various authors to define sections within the genus Acaena

subsections. The number within each division varied widely from only one species in a whole section to 22 in a subsection.

The taxonomic position up to and including Bitter (1911) is summarised in Figure 2. Since that monograph there have been only two publications which deal with more than one or two species of Acaena. Allan (1961) largely accepted the work of earlier authors for the New Zealand species, the only innovations being a number of new combinations. Grondona (1964), who dealt with the species occurring in Argentina, placed the 20 species in 5 sections. The connections between the various sections as used by Citerne, Bitter and Grondona is shown in Figure 3. The sections Lachnodia and Anoplocphala of Citerne are not represented in Argentina and were therefore not included in Grondona's revision. The connections shown between the various groups are based on the species placed in each group by the three authors.

It is clear that there have been differences of opinion as to which species should be grouped together. This is not surprising since the number of workers has been small and most have examined only a limited amount of material often covering only a part of the genus. It is also clear, from an examination of the criteria for delineation of sections, that the authors also have different opinions about the degree of difference necessary for a separate section to be described. Further confusion can arise if an important character is wrongly described. For instance, Sect. Eupatoriopsis (Bitt.) Grond. is not, as Grondona claims, synonymous with Subsect. Eupatoriopsis Bitt. since Grondona includes A.stricta Griseb. and A.myriophylla Lindl. in his section, these species being placed by Bitter in Sect. I Elongatae and Sect. VII Euacaena subsect. Pinnatifidae respectively. Further difficulty arises over A.stricta since Bitter described its flowering scape as axillary whilst Grondona stated that it was terminal.

BITTER (1911)

CITERNE (1897)

GRONDONA (1964)

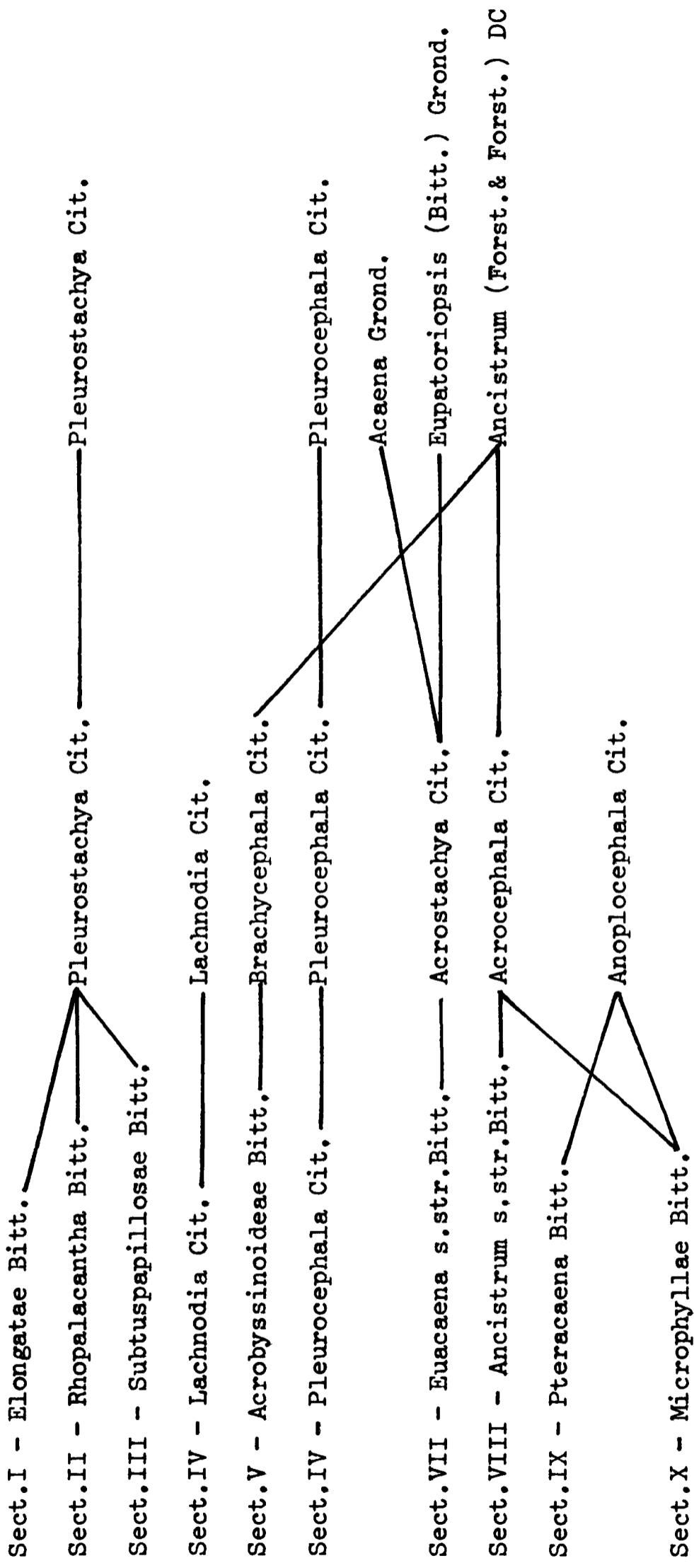


FIGURE 3. Relationships between the sectional classifications used by three principal reviewers of the genus Acaena

If the division of a genus into sections is to indicate the relationships between the species as many features as possible must be taken into account when delimiting the groups. As Davis and Heywood (1965) have pointed out the circumscription of natural sections may be difficult, many of the species being related to several sections. This is illustrated to a certain degree in Acaena, more obviously in Bitter's divisions than in that of other workers.

The primary characters used for grouping the species have differed in the various revisions. However, some overall agreement can be obtained if three characters are used - the type of inflorescence, the point of production of the flowering scape and the number and arrangement of spines on the fruit. In the author's opinion these characters together produce apparently natural groupings. On this basis Citerne's classification works well, Acrostachya, Acrocephala and Anoplocephala all having terminal inflorescences whilst the other four sections have axillary ones. Each group contains species which have a combination of globose or spicate inflorescences with many or few spined fruits. This would appear to be a better system than that adopted by Grondona where the two largest sections, Ancistrum and Acaena, both contain a mixture of terminal and axillary inflorescences. Bitter's classification is similar to that of Citerne at the section level. His subsectional classification is misleading since many of his descriptions were based on limited or cultivated material. The differences he describes between subsections and species often break down when population variability is taken into account.

The two South Georgian species of Acaena occur in Sects. Acrobyssinoideae and Ancistrum of Bitter's classification, although they were grouped in the single Sect. Ancistrum by Grondona, and in Sects. Brachycephala and Acrocephala by Citerne.

Section V Acrobyssinoideae Bitt.

Acaena tenera Alboff was placed by its author in Sect.

Ancistrum. This was presumably Ancistrum (Forst. & Forst.) DC. based on the position of spines on the cupule rather than Ancistrum sensu Reiche based on the type of inflorescence. Citerne (1897) did not see this species but placed a related one, A.microcephala Schlect. (= A.antarctica Hook.f.), in his Sect. Brachycephala. Bitter (1911) did see it and placed it in Sect. Acrobyssinoideae together with A.antarctica, A.pearcei Phil., A.microcephala, A.tenuifolia Bitt., A.valida Bitt. and A.tasmanica Bitt. Another species A.masafuerana Bitt., then placed in Sect. Subtuspapillosae, was removed by Bitter (in Skottsberg, 1922) to this section. Of these species Grondona (1964) dealt with three, placing them in Sect. Ancistrum, a section which otherwise contained only species with terminal inflorescences.

Until Skottsberg (1905) reported the presence of Acaena tenera on South Georgia it had been thought that only one species of Acaena grew on the island. Since then a certain amount of confusion has existed over the exact nomenclature of each taxon, and this has been further complicated by the recent recognition of intermediate forms.

The plant listed as A.tenera Alboff in Greene (1964) was first collected by Alboff in 1896 on Tierra del Fuego.

Bitter (1911) described two subspecies of A.tenera, ssp. epilis and ssp. pilosella. He separated these mainly on differences in the size and distribution of hair types and stated that one subspecies, ssp. pilosella was more compact and had a more robust rhizome than the other one. Whilst he examined five collections for the ssp. epilis he only examined one for the ssp. pilosella. Subsequent examination of his type collections and several other collections from South Georgie and Tierra del Fuego by the author has shown that these subspecies are unnecessary and untenable, since normal variation within a single population can encompass the hair and rhizome characters used by Bitter.

It is necessary to consider other species within this section which are related to A.tenera, especially A.antarctica Hook.f. and A.microcephala Schlect. both of which have been confused with each other and with A.tenera in the past. Dusen (1900) in his survey of plants from Magallanes even gave A.microcephala Schlect. as a synonym of A.ovalifolia R & P., a case of synonymy which defies explanation since the two species only have one character, a capitulate inflorescence, in common. Bitter (1911) recognised both species and distinguished them from A.tenera on the basis of their having purplish articulated hairs between the cupules and hairs on the leaflets. Bitter remarked that Skottsberg had already noted the close similarities between the three species.

A.antarctica was first described by J. D. Hooker (1847) from his collection made on Hermite Island, and one made by A. Menzies in 1787 on Staten Island. These specimens designated syntypes by the author were apparently sterile but close examination has shown the Menzies specimen to have a single ripe fruit, which was apparently missed by Hooker. The other species, A.microcephala, was described by Schlectendal (1856). His type specimen comprised two collections made by Lechler (Lechler 2951, 3029) in 1854 in the Cordillera de Ranco, Chile. The syntypes at Kew were examined by the author and on the basis of a character comparison shown in Table 1, A.antarctica and A.microcephala were found to be identical. Thus in accordance with Article 11 of the International Code of Botanical Nomenclature, the name A.antarctica Hook.f. takes precedence.

A.masafuerana was first described from a sterile collection made in the Juan Fernandez Islands by Skottsberg (Bitter, 1911) but later collections allowed Bitter to amplify his description with details of the

flowers and fruits (in Skottsberg, 1922). He contrasts it with A.antarctica and A.microcephala, distinguishing it from the former by the presence of one or two leaves on its scapes and from the latter by the hairs on its leaves being more delicate and never yellow.

Table 2 compares A.tenera (using South Georgian material), A.antarctica and A.masafuerana (using isotype specimen C. & I. Skottsberg 395).

As this table shows, A.masafuerana possesses some of the characters of each of the other two species. In overall appearance it resembles A.tenera more than A.antarctica. On the basis of this comparison it is thought by the author that this species is distinct enough to be retained with specific rank.

Grondona (1964) erroneously reduced A.tenera Alboff to a synonym of A.microcephala. The other synonym he quoted was A.pumila Phil. (non Vahl), a name later changed to A.pearcei Phil. (Philippi 1864). Examination of the holotype in Santiago (Pearce s/n, Herb. no. 49890) by the author showed that it should be assigned to A.antarctica, possessing pilose leaves and brownish articulated hairs at the base of its fruits. It is noteworthy that Grondona mentions specifically that A.antarctica was not included in his study.

To summarise, there are three species which show very close affinities to each other. A.tenera Alboff occurs only on South Georgia, Staten Island and mountains near Ushuaia (a reported occurrence near Lago Nahuel Huapi in Skottsberg (1916) is impossible to verify since the specimen is believed to have been lost, and the species has never been collected again in that locality). It is distinguished by its bright green glabrous leaves, glabrous scape and golden-yellow sessile glands at the base of the fruits. A.masafuerana is restricted to Masatierra in the Juan Fernandez Islands and is distinguished by its bright green slightly penicillate leaves, sparsely hairy scape and brown to purple articulated hairs at the base of the

Table 1 - A morphological comparison of *A.antarctica* and *A.microcephala*

Character	<u><i>A.antarctica</i></u>	<u><i>A.microcephala</i></u>
Leaflets	Very hairy above with long yellow-white hairs, becoming barer with age. Pencillate though hairs below mainly on veins. Mean number of leaflets 9.	More or less hairy above depending on age. Hairs long, whitish. Markedly pencillate though hairs below mainly on veins. Mean number of leaflets 9.
Scape*	Pilose, bract absent.	Pilose, bract usually present.
Fruit	Having 4 spines with gloccids per fruit; fruit 2 mm. long, with purplish articulated hairs at its base.	4 spines with gloccids per fruit; fruit 2-3 mm. long, with purplish articulated hairs at its base.

* Since only one scape was present on the *A.antarctica* type specimens and several scapes on *A.microcephala*, the presence or absence of such a variable character as a scape bract is not thought to be significant.

Table 2 - A morphological comparison of *A.tenera*, *A.antarctica* and *A.masafuerana*

Character	<u><i>A.tenera</i></u>	<u><i>A.antarctica</i></u>	<u><i>A.masafuerana</i></u>
Scape	Glabrous with 1 or 2 leaf-like bracts.	Densely pilose often with leaf-like bract.	Almost glabrous with 1 or 2 leaf-like bracts.
Leaf	Bright green above, usually glabrous. Leaflets not pencillate.	Dark green above densely hairy with long yellow hairs. Leaflets markedly pencillate.	Apparently bright green above, sparsely hairy. Slightly pencillate.
Fruiting Head	Golden yellow subsessile glands (manna) at base of cupules.	Brown to purple articulated hairs at base of cupules.	Brown to purple articulated hairs at base of cupules.

fruits. A.antarctica, which is distinguished by its densely pilose leaves and scape with brown-purple articulated hairs at the base of the fruits, is found in southern Andean Patagonia, Staten Island, Tierra del Fuego and the Falkland Islands.

The other species within this Sect. V of Bitter's classification are A.tasmanica Bitt., A.tenuifolia Bitt. and A.valida Bitt. The holotype of A.valida was in Berlin and has been destroyed. However, from Bitter's description and notes, plus an earlier determination of the collection he used for his type material as A.pearcei, it seems probable to the author that this species is conspecific with A.antarctica. Fortunately type material of A.tenuifolia is preserved at Munich and examination of this shows the collection to be A.antarctica, having pilose leaves and scapes, and the typical brown hairs at the base of the fruits.

A number of specimens labelled A.tasmanica from Tasmania have been seen during this study. This species was originally described under the name A.montana by Hooker (1844-46) from a collection made on the summit of Mt. Wellington by Gunn, but in his Flora Tasmaniae (Hooker, 1855-60) he reduced it to a variety of A.sanguisorbae. Bentham and Muller (1863-78) did not agree with this and maintained it as a separate species. Bitter (1911) decided that since he had not seen the type material he would redescribe the species from material in Berlin and Munich. He described it under a new name to ensure that no confusion would occur with a dwarf alpine form of A.sanguisorbae which had been reported from the same area. Examination of both Hooker's holotype from Kew and Bitter's holotype from Munich shows them to be the same species. The material is quite distinct from A.anserinifolia (= A.sanguisorbae) both in vegetative and floral characters. It most closely resembles A.antarctica in the author's opinion but should be retained as a separate species. Its correct name is A.montana Hook f.

Appendix 1 gives details of the complete synonymy of A.antarctica, A.tenera and A.masafuerana.

Sect. VII Ancistrum Bitt.

Bitter (1911) described 62 species in this section, dividing them up into 6 subsections, of which 52 were new species, in some cases comprising whole subsections. The second species on South Georgia falls in this section but has been referred to by so many different names that severe nomenclatural confusion now exists over its correct binomial.

This species of Acaena was first referred to under the name Ancistrum decumbens in a paper presented by G. Forster in September 1777 to the Royal Society of Göttingen. The paper was not published until 1789 and the name as used by Forster was a nomen nudem, since no description was included. J.R. and G. Forster had collected a specimen of this taxon on the 17th January, 1775 in Possession Bay, South Georgia, during Captain Cook's second voyage. This specimen, in the British Museum (Nat. Hist.) is labelled on the front lower right-hand corner with the handwritten name Ancistrum decumbens; the back of the sheet has "Insula Georgiae Australis. Oceani Atlantici JR and G Forster" written on it: it bears several capitula although none are composed of ripe fruits.

The name Ancistrum decumbens was first validly published by Gaertner (1788), although only a fruiting head was described to characterise the species. No type material or locality was quoted, although the material was said to have originated from the herbarium of Sir Joseph Banks. Since it is known that much of the Forster's material passed through Banks' herbarium it is possible that the fruiting head used by Gaertner could have originated from the South Georgian collection. Gaertner's herbarium is now at Tübingen and was checked by the author for the holotype which unfortunately appears to have been lost (Pers. comm. K. U. Leistikow).

On the basis of this evidence a new combination was made by the author (in Walton & Greene 1971) which resulted in the South Georgian plant being named as Acaena decumbens (Gaertner) D. W. H. Walton. Unfortunately this has since been found to be invalid due to a prior use of the epithet for another species, originally described under the name Agrimonia decumbens by Linnaeus f. (1781) and which was transferred to the genus Ancistrum as A. decumbens by Thunberg (1807) in his Prodomus Flora Capensis. The use of this name for a South African species was illegal since it had already been used by Gaertner. This usage of the specific epithet decumbens apparently remained largely unknown since the South African material was described later by Aiton under the name Acaena latebrosa in 1810. The South African species was generally referred to as A. latebrosa Ait. until G. C. Druce in 1917 published the new combination Acaena decumbens (Linn.f.) Druce which listed as synonyms Agrimonia decumbens Linn. f., Ancistrum decumbens Thunb., Acaena latebrosa Ait. and Ancistrum latebrosum Willd. This combination legalised the originally illegal name of Thunberg's and pre-empted its usage for a transfer of the Gaertner taxon from Ancistrum to Acaena. Thus the authors combination became a later homonym and another name had to be found for the South Georgian taxon. The earliest available name now becomes Ancistrum magellanicum Lam. (Lamarck, 1791) which was transferred to Acaena by Vahl (1805). The name Acaena adfendens (Lam.) Vahl (Vahl, 1805) is based on Lamarck's Ancistrum magellanicum var. β (Lamarck 1791) and does therefore not take precedence over A. magellanica.

A number of other names have been commonly used for this taxon. In the collections made by Will during the German South polar Expedition

to the island in 1882-83 material is variously identified as Acaena adscendens and A.laevigata. Bitter took the view that the material was sufficiently different to be described as a separate subspecies - Acaena adscendens Vahl ssp. Georgiae-australisⁱ with two forms, majuscula and minuscula. Greene (1964) kept this subspecies but did not use the forms, whilst Grondona (1964) and Moore (1968) both referred the material to Acaena magellanica (Lam.) Vahl. This raises the question of synonymy within this section of the genus.

Yeo (1973) has suggested that A.magellanica sensu Grondona (1964) is too broad an interpretation and has split the group into three taxa. On his treatment the South Georgian taxon become Acaena affinis Hook.f., and is said to be also found on all the other sub-Antarctic islands, the Falkland Islands and in the Magellan region. The related taxa becomes A.macrostemon Hook.f. and A.magellanica (Lam.) Vahl ssp. magellanica Bitter, both of which are restricted to South America, and A.magellanica (Lam.) Vahl. ssp. laevigata (Aiton) Bitter which is said to be endemic to the Falkland Islands. Considerable nomenclatural problems surround the application of the names A.magellanica and A.affinis and these are dealt with in detail in the appendix to his paper.

Yeo (1973) designated a Hooker specimen at Kew as the lectotype of A.affinis, the material having been collected on Îles Kerguelen. Whilst he agrees that this taxon has traditionally been called A.adscendens^f he states that this was a wrong application of the name. He uses considerable ingenuity to prove the identity of the original specimens of Lamarck's and justify his usage of A.affinis and A.magellanica. Unfortunately his work is based mainly on a small collection of living material from the Cambridge Botanic Gardens supplemented by an examination of a small number of

herbarium specimens largely from British Museum (Nat. Hist.). The much wider range of material examined in this survey has shown that the characters he used to delimit his taxa are inadequate. A complete range or variation can be seen within the group A. magellanica sensu Grondona and attempts to split off separate species are constantly thwarted by the overlapping of definitive characters from one 'species' to another. Although the author agrees with Yeo that it ought to be possible to split up the wide range of variation within A. magellanica into distinct species in practice it has not proved possible to delimit satisfactory taxa. That is not to say however, that the plants at each end of the range of variation do not show some clear differences. It is thought that more information is required on character plasticity, chromosome numbers and breeding cycles within this complex before any realistic judgements can be made regarding the delimitation of categories within it. Accordingly, the present author believes that the description of A. magellanica (Lam.) Vahl as given by Grondona (1964) is currently satisfactory for general taxonomic purposes.

Grondona (1964) listed 54 synonyms (including subspecies and varieties) for A. magellanica. From the material examined in the present survey and a close examination of the descriptions of species falling within the Sect. Ancistrum it became clear that a number of other synonyms also existed. Appendix 2 gives details of a further 32 synonyms together with the reasons for the reduction to synonymy in each case. This appendix also contains a list of the taxa for which type material has been lost together with some notes on certain species. Appendix 3 gives a complete synonymy of the species within A. magellanica (Lam.) Vahl together with literature citations.

The taxonomy and nomenclature of Section VII *Ancistrum* Bitter can be summed up as follows: a highly variable taxon with a very wide distribution has suffered from repeated redescription at a local level resulting in severe nomenclatural and taxonomic chaos at a world level. Material covering a considerable degree of variation has been grouped together by Grondona (1964) and the author under the name *A. magellanica* (Lam.) Vahl since it is believed that this will prove the most useful solution in the present state of knowledge. The taxon is however believed to consist of a number of interbreeding but diverging groups which may well merit subspecific recognition at some time in the future.

Chapter 3

MORPHOLOGY

General Morphology

Materials and Methods:

Despite numerous previous descriptions of various taxa in the same or very similar groups within the genus to the South Georgian species, it was considered essential that detailed morphological investigations were made. This was partly to assist in the taxonomic assessment of the relationships of the species and partly to investigate the intermediate character of certain populations found on South Georgia.

Material from a large number of herbaria was used for taxonomic purposes. Notes were made on morphology from many of these specimens whilst a number of collections were submitted to a very detailed investigation for all characters.

Collections from the following herbaria were used in the survey (abbreviations as in Lanjouw & Stafleu, 1964; for AAS see Greene, 1972):

A	BAB	FI	M	SGO
AAS	BAF	G	MVM	SI
BREM	BM	K	NA	UPS
BA	E	LTR	P	Z
BAA		LY	S	

The detailed scorings for South Georgian material were based largely on over 70 collections from ASS, BM and K. Over 100 extra South Georgian gatherings were also scored for the A. magellanica complex although many more collections were examined but not scored in detail.

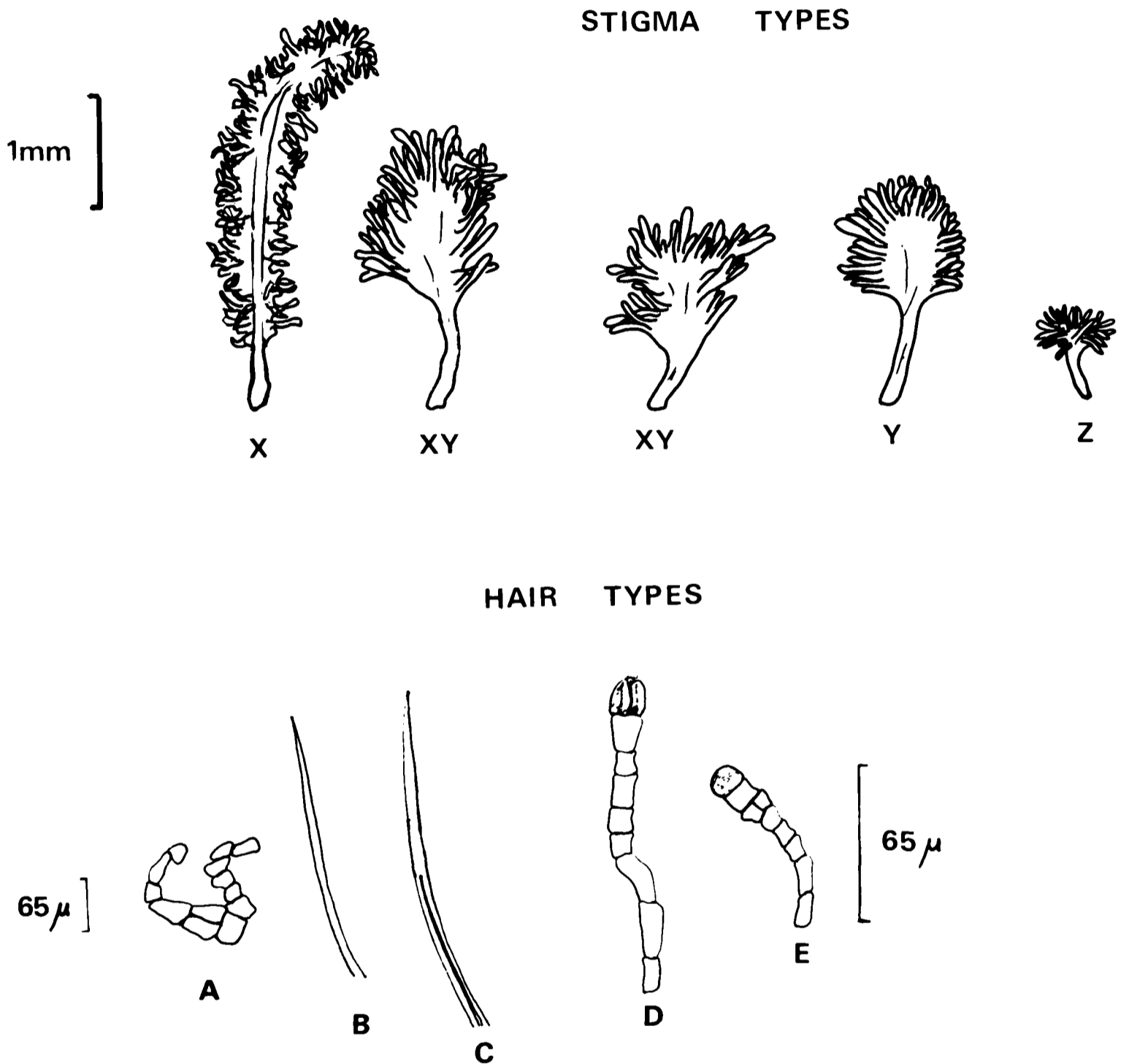
Very few sheets of A.tenera were available other than those from South Georgia. The only hybrid material was in South Georgian collections. The characters chosen for scoring were those that had been used by various authors to delineate species in the past. Certain other characters were also included ^hwhere it seemed likely to the author that they would prove useful in characterising the degree of variability present in a particular taxon.

Leaf characters: three measurements were made on the largest leaf in each collection - length, maximum width and length of terminal leaflet. Leaf length was measured from the base of the stipules to the top of the terminal leaflet. The position of the maximum width of the leaf was noted. The length of the terminal leaflet was taken from the base of the petiolule to the leaflet tip. All measurements were made to the nearest mm. A leaf ratio of length/width was calculated. Leaf pilosity and distribution was scored on a seven point scale. Two types of hairs were found (see Figure 4). Although leaf colour is a definitive character in the field it could not be scored accurately for herbarium material.

Scape characters: on flowering and fruiting specimens the presence or absence of a scape bract (Figure 5) was noted and the presence of any flowers or secondary capitula in the axil was recorded. Every complete scape was measured from the base of the second leaf to the bottom of the capitulum. Note was taken of any hairs on the scape.

Capitulum characters: the developmental stage and diameter to the nearest mm. (including spines) of all capitula were recorded. The number of spines per fruit, occurrence of glochids, hairs and, in some instances, numbers of fruits per head were also recorded. Slides were made of floral parts, the flowers being soaked in 30% ethanol for 30 minutes before they were dissected ^sand mounted in Gum Chloral. Stigma type was then scored (Figure 4) and measurement made under the microscope

Figure 4. Hair and Stigma Types found on A. magellanica and A. tenera



Key: Stigma Types X, Y and Z from South Georgian collections. Types XY from Moore 1689 & 2149, Tierra del Fuego.

Hair Types - Type A from A. tenera, multicellular ("manna")
 Types B & C from A. magellanica, uniseriate
 Types D & E from A. tenera, multicellular glandular

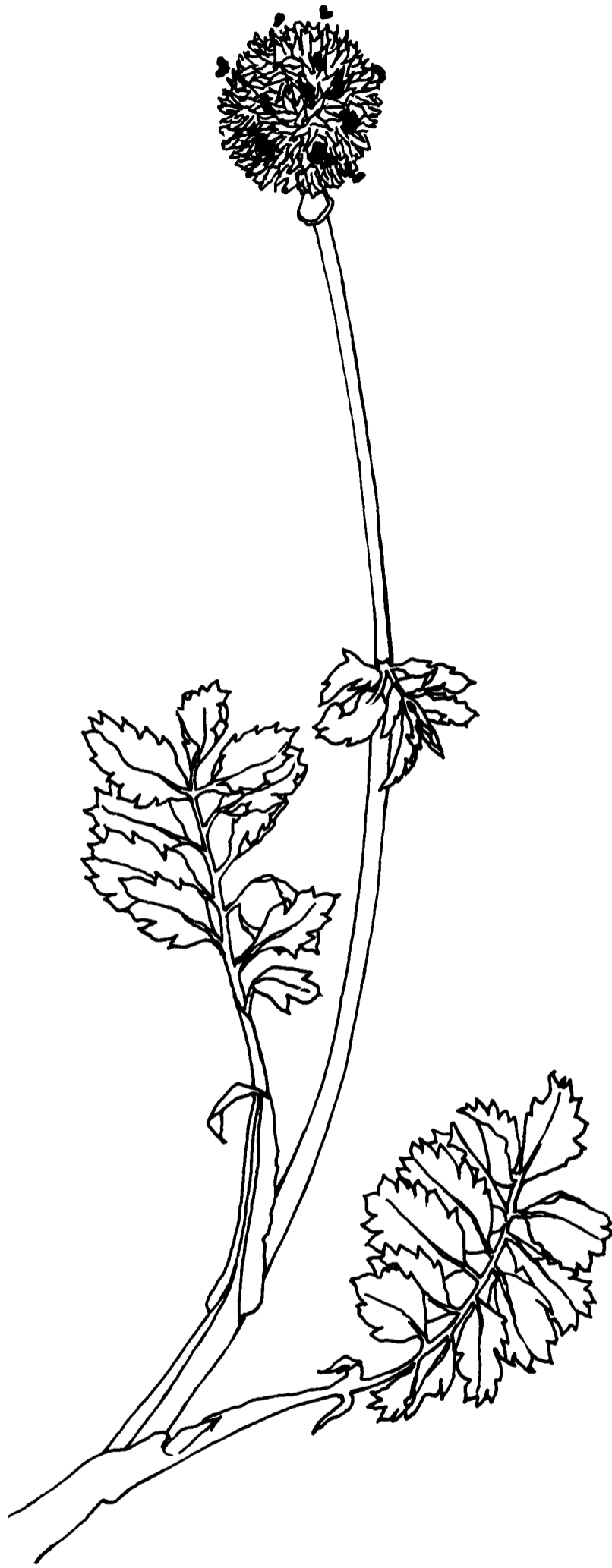


Figure 5. Flowering shoot of *A. magellanica* (Lam.) Vahl from South Georgia

of maximum length and width of stigmas, dehisced anthers and sepals.

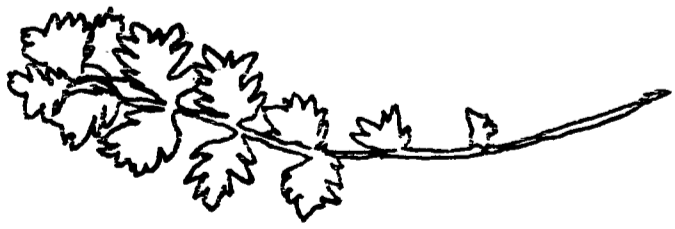
Ratios of length/width were calculated for all three organs.

Yeo (1973) used certain other characters such as the size of the distal leaflets, axillary shoots elongate or rosetted, the presence or absence of supplementary spines on the fruits and the number of stipule lobes. These were used together with the measurements described above when scoring extra-South Georgian populations.

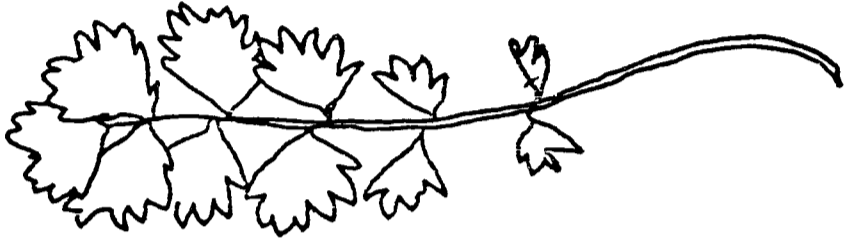
Acaena tenera Alboff

South Georgian material:

Leaf shape was similar in all collections (see Figure 6) and although leaf lengths up to 13.5 cms. have been found, these were very exceptional. The leaflets were always a bright glossy green with bright red tips to the leaflet dentations (see photograph in Figure 8). Leaflet number was fairly constant at 11-13. The leaves normally appeared glabrous, very exceptionally with a few hairs on the ventral surface of the main vein. Careful examination with a lens has usually disclosed the presence of a few hairs in the angle of each leaflet dentation. These small hairs were of the glandular type (Figure 4) and were apparently similar in all except size to those which formed a distinct yellowish clump at the junction of the petiole and the base of the leaflet. Leaf ratio ranged from 2.60-5.47 (\bar{x} =3.79, SD 0.77), which was much higher than that for A. magellanica. The scatter diagram in Figure 9 of terminal leaflet length/leaf ratio shows considerable horizontal but little vertical spread. Stipules were always present. They were small and entire, generally with a small but definite point, and usually did not exceed the sheathing part of the petiole by very much.



A. tenera



Hybrid

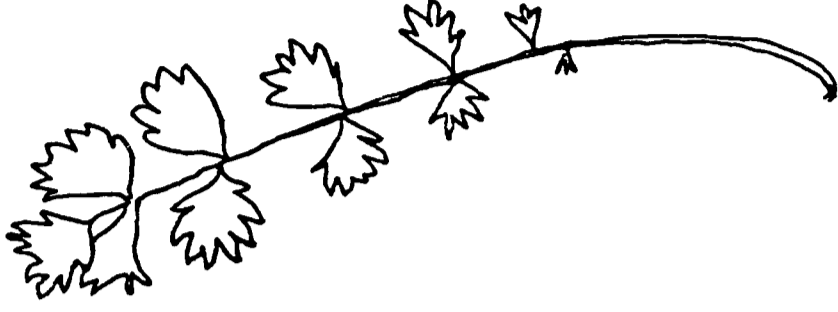


Figure 6. Leaf shape in *A. tenera* Alboff and the hybrid *A. magellanica* x *tenera*

A very noticeable feature of some A.tenera plants was that the young leaves were sometimes completely red when first produced. This pigmentation was not persistent and had normally become restricted to the leaflet tips by the time the leaf was fully grown and unfurled. This phenomenon is discussed in more detail in Chapter 8. The size range of mature fruiting scapes was 1.2-12.5 cms. Scape length appeared to be directly related to habitat in that plants from exposed fellfield sites had very short scapes whilst those from sheltered lowland sites had the longest scapes. A field survey showed that a scape bract was present in about 90% of all the scapes examined, and the majority of these had a single flower in its axil. No specimens were found with more than one flower in the bract axil or with any secondary capitula. All the flowers examined were normal. It is important to point out that during mounting of herbarium material this axillary flower is often lost, a feature which must be borne in mind during scoring of specimens. Whilst mature scapes always appeared glabrous it was sometimes possible to find some glandular hairs on young growing scapes. The scape is axillary in this species, its base normally being surrounded by dead leaf bases from previous years.

The flowering and fruiting capitulum in A.tenera was much smaller than in either of the other two taxa. This was partly due to the smaller size of the flowers themselves, but also to a smaller number of flowers per head.

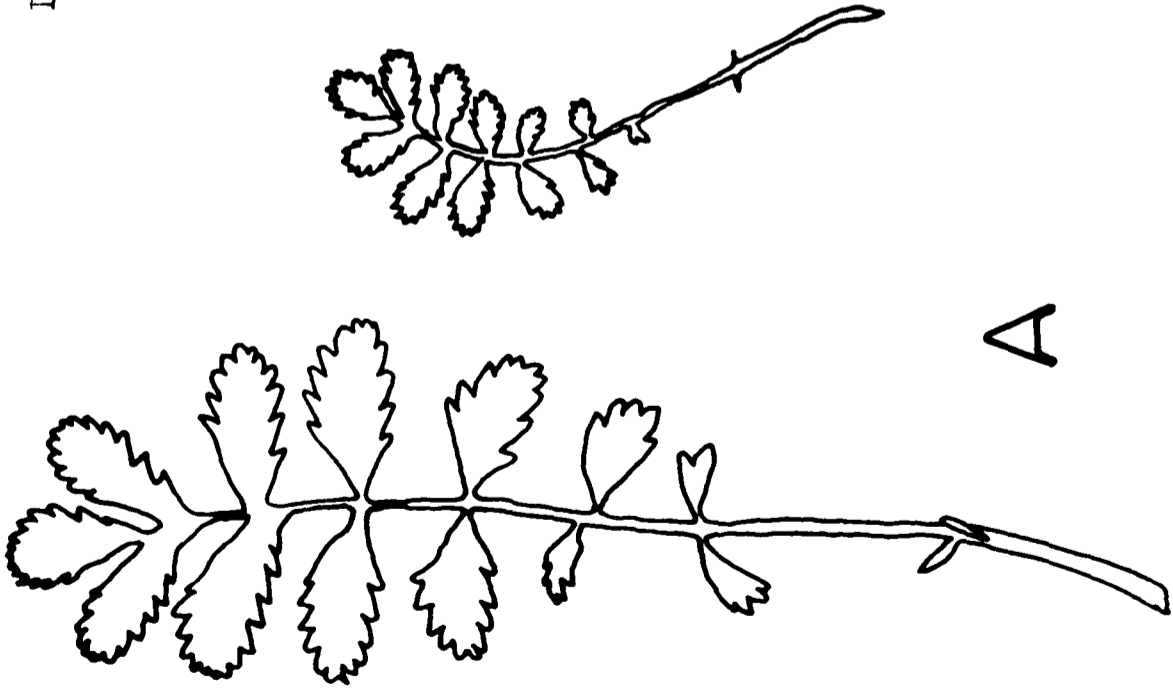
Stigma type was always Z (see Figure 4) and stigma length was usually within the range 0.79-1.40 mm. Sepal size was also of the same order: 1.6-3.1 mm. long by 0.7-2.0 mm. wide. The sepal ratio of 1.86 (SD 0.06) was much less than that for A.magellanica, reflecting the shorter, fatter shape. The scatter diagrams in Figure 9 show tight clusters of points for A.tenera when contrasted with the other two taxa. The close grouping of the points for A.tenera shows a low degree of variability in its characters, the

Key: A. South Georgia

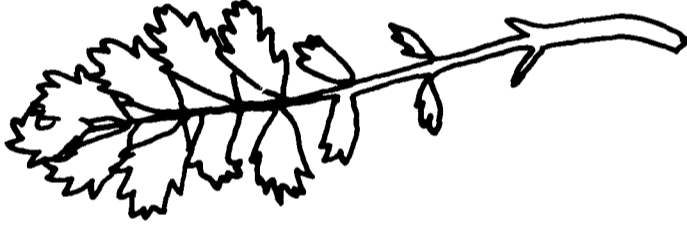
B. Falkland Islands

C. Cambridge Bot.Garden (A.magellanica)

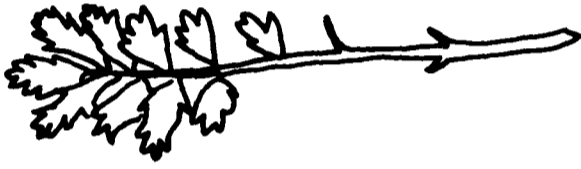
D. Cambridge Bot.Garden (A.laevigata)



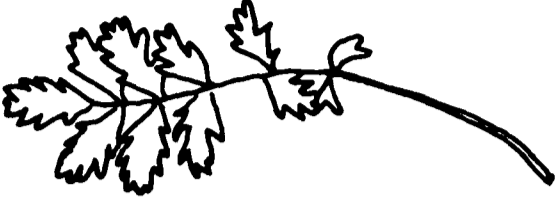
A



B



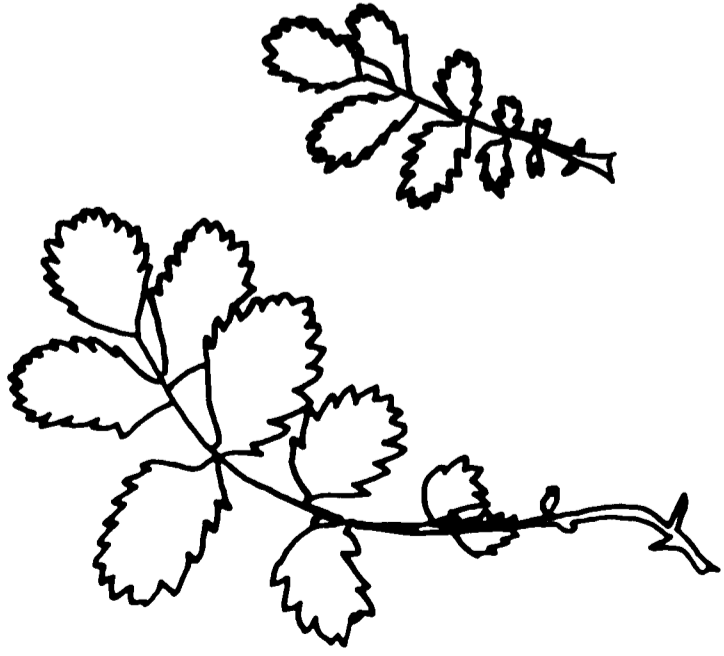
C



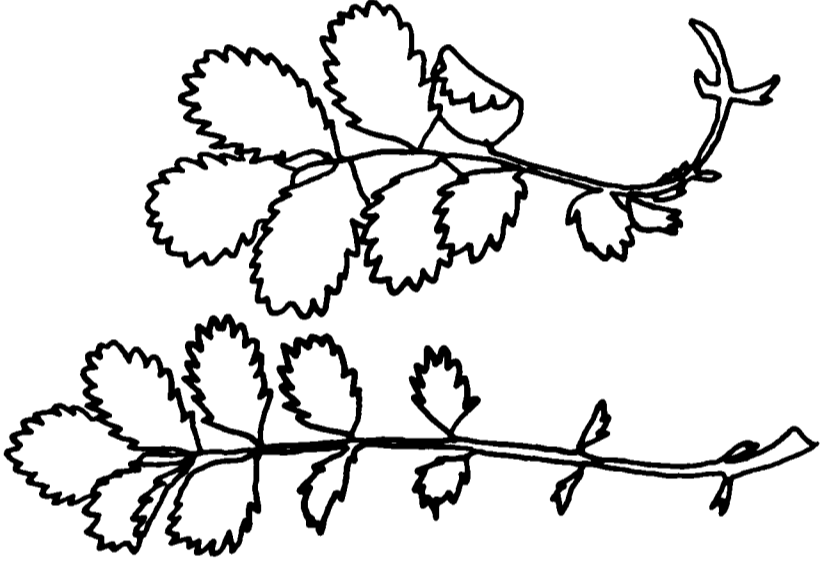
D



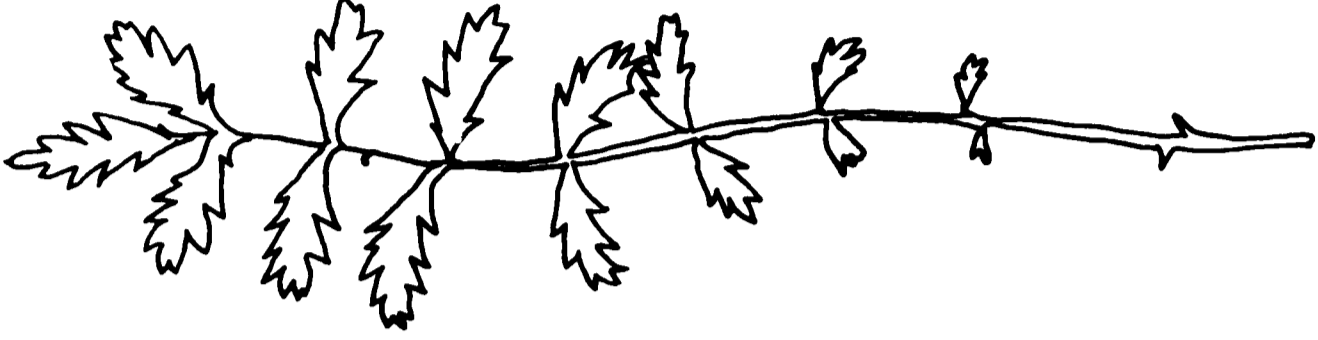
Figure 7a. Leaf shape in A.magellanica (Lam.) Vahl



A



B



C

- Key: A. Tierra del Fuego (Moore 62043)
B. Nothofagus forest, Tierra del Fuego
C. Cambridge Bot. Garden (A. macrostemon)

Figure 7b. Leaf shape in A. magellanica (Lam.) Vahl

A. magellanica



Hybrid

A. tenera

Figure 8. Photograph illustrating leaf colour in the three South Georgian taxa of Acaena

separation of this taxon from A.magellanica being clearly shown by the location of the clusters themselves.

The scatter diagrams for perianth ratio and leaf ratio (Figure 9) show greater constancy for perianth shape in A.magellanica and for leaf shape in A.tenera. Both the sepals and the floral bracts have uniseriate hairs. Those on the bracts were abundant but largely limited to the margins. "Manna" hairs (see Figure 4) were always found to be present at the base of the flowers. The normal number of spines per cupule was 4, always with several downward pointing glochids. The fruits themselves were always glabrous.

A summary of definitive characters for this taxon is presented in Table 4.

A.magellanica (Lam.) Vahl

South Georgian material:

The scatter diagrams in Figure 9 show clearly that this taxon was far more variable than A.tenera even within the one island. The variational disparity was more marked when material from the whole range of the species was plotted. On South Georgia the leaf ratio normally falls between 2.0 and 3.5 with few points outside these limits. A detailed series of measurements on a few populations, using several leaves from each, gave a mean ratio of 2.69 (SD 0.57) for 67 leaves. Using only the largest measurable leaf from each herbarium collection gave a mean leaf ratio of 2.84 (SD 0.51) for 22 leaves. Maximum leaf size was very variable and appeared to be closely linked to the degree of exposure of the habitat specimens from fellfield areas having must smaller leaves than those from protected sites. Mature leaves ranged in length from 2.5 to 15 cms.

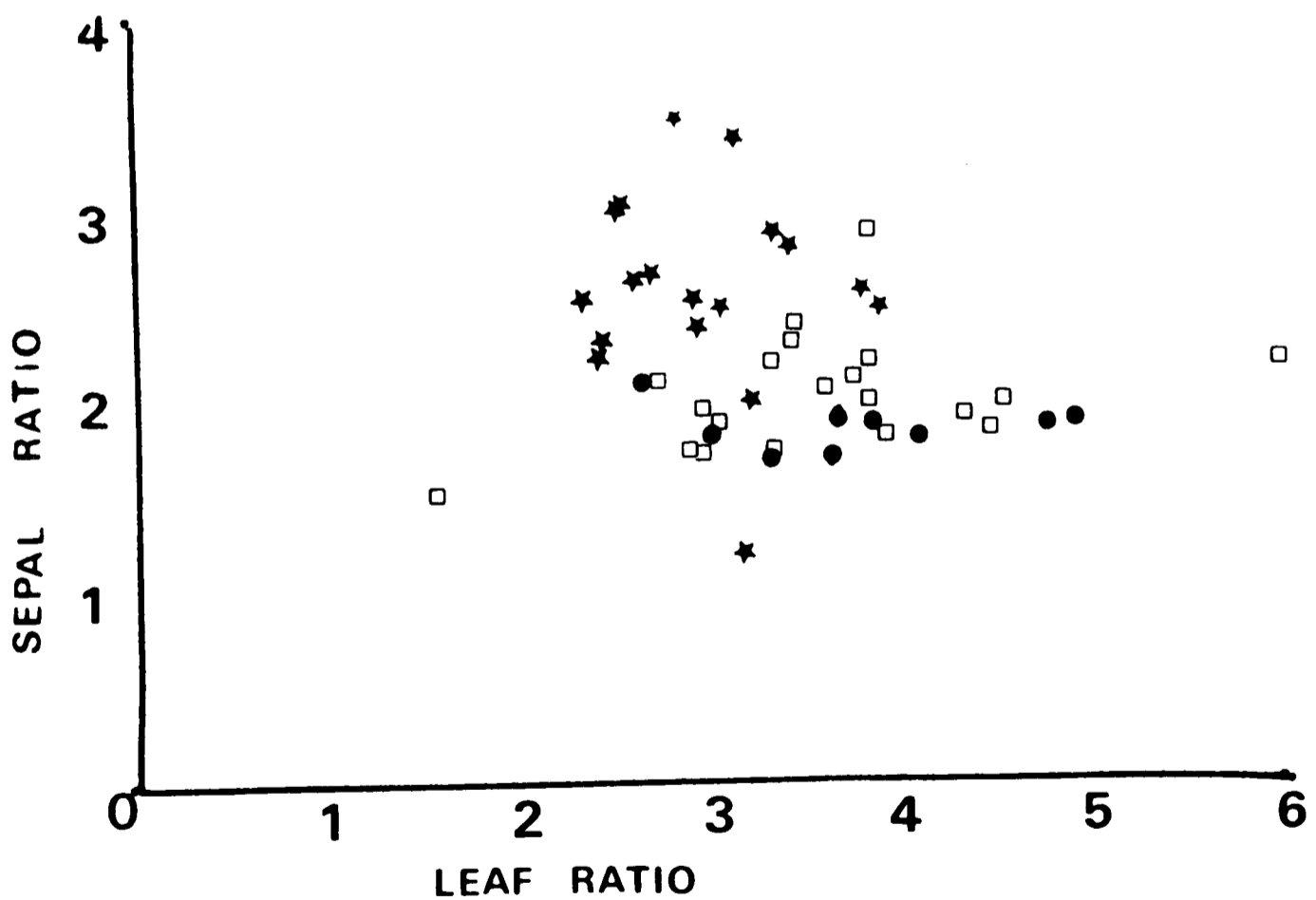
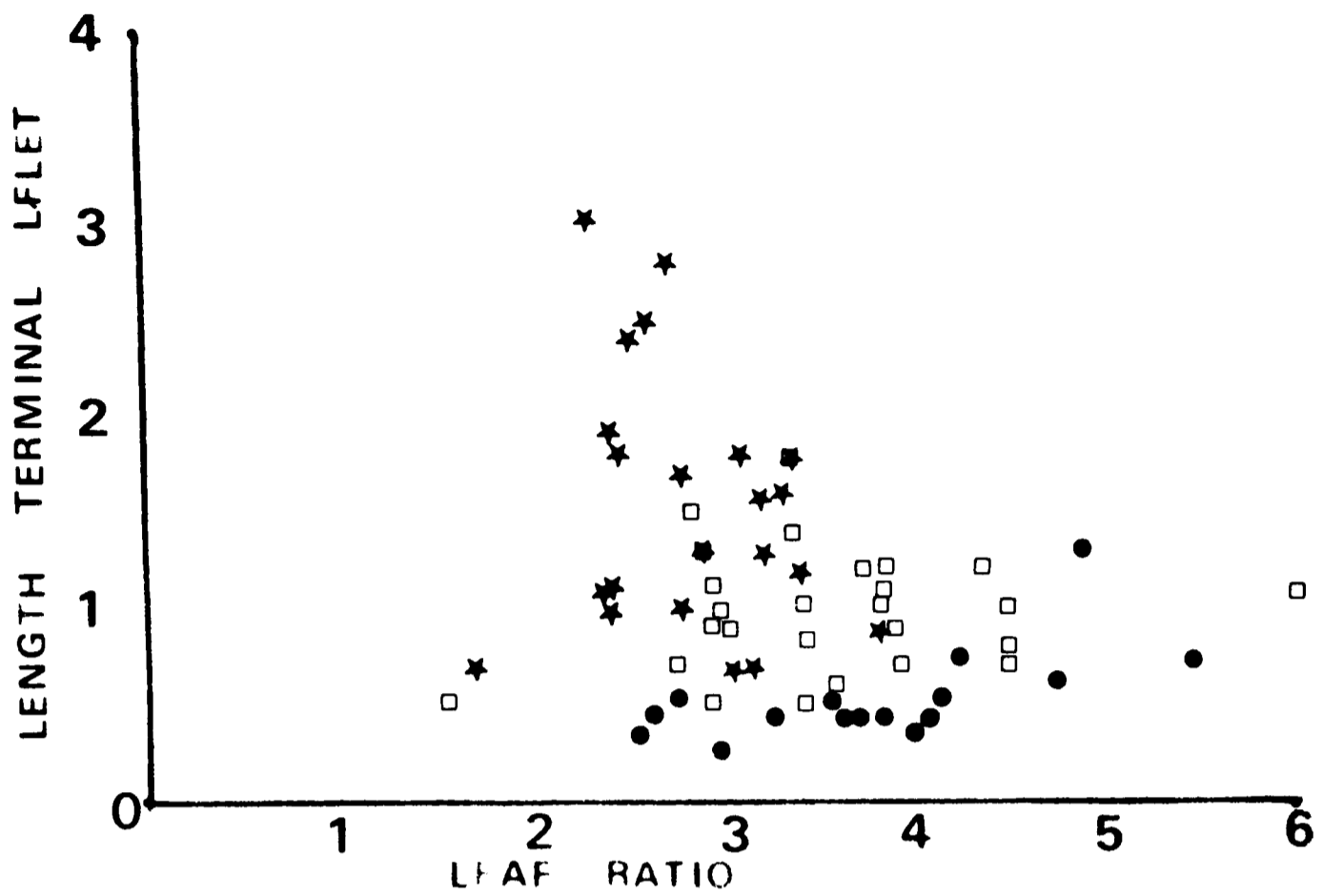


Figure 9. Scatter diagrams of morphological measurements

Key: ● A.tenera ★ A.magellanica
 hybrid on overlay

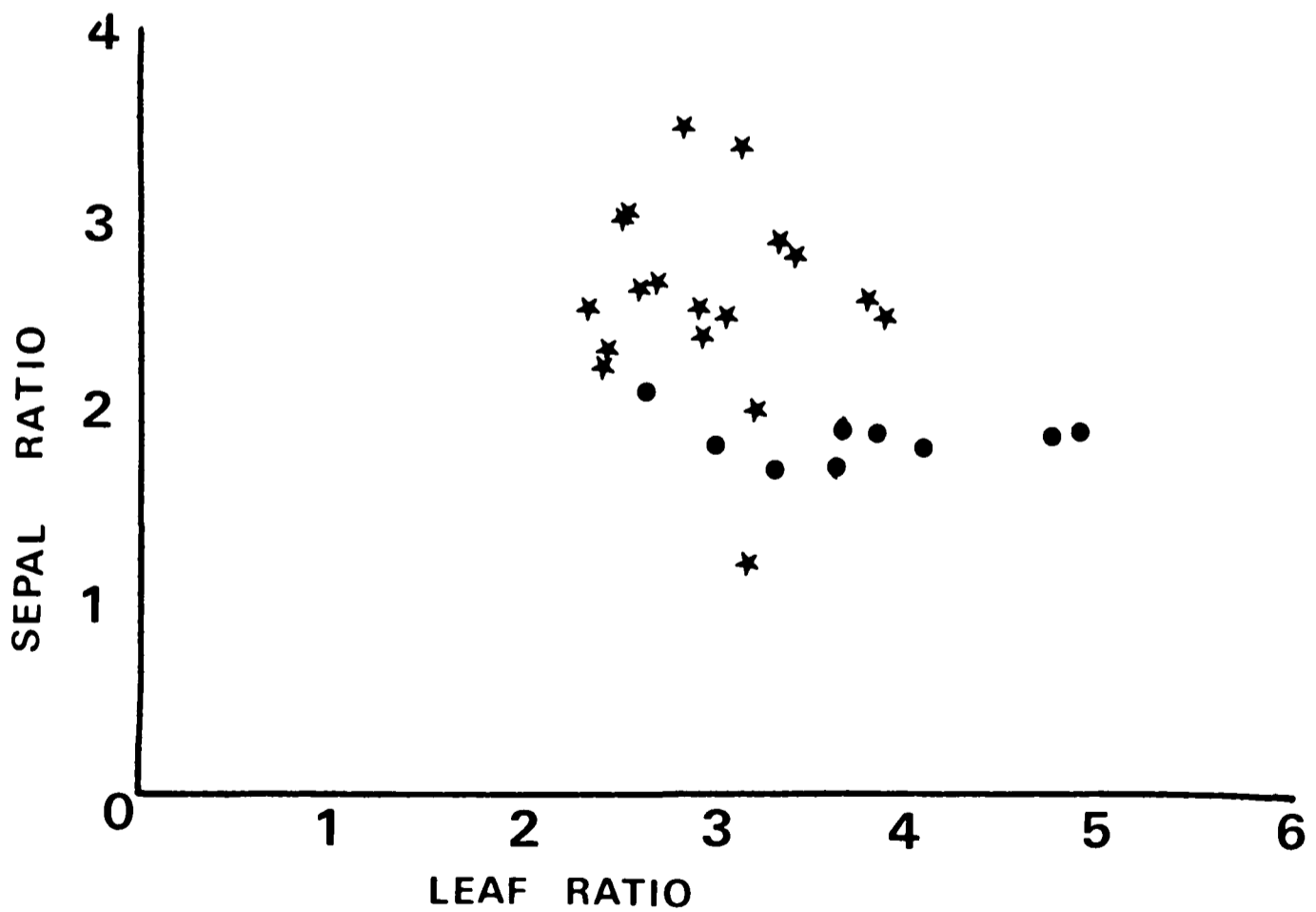
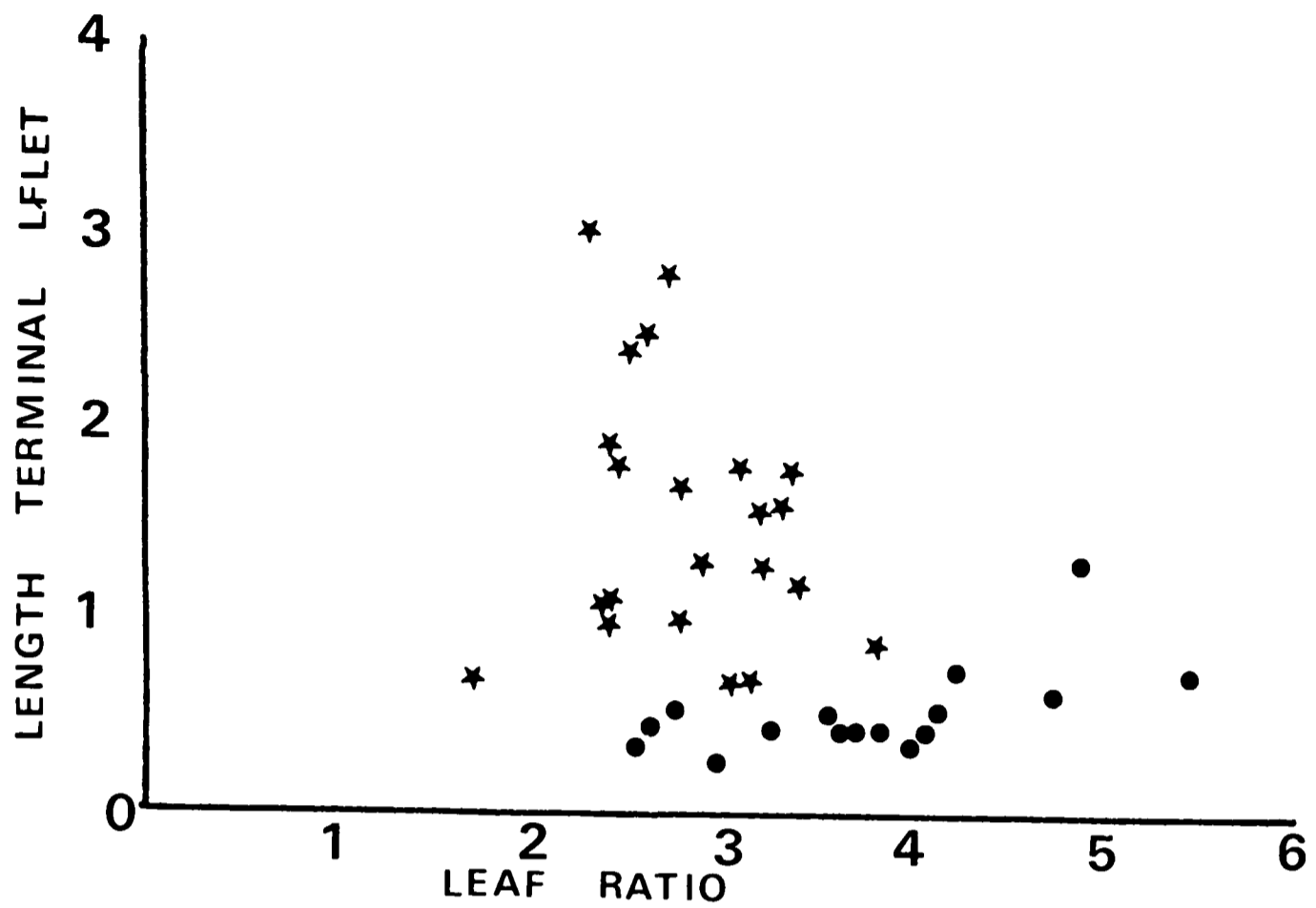


Figure 9. Scatter diagrams of morphological measurements

Key: ● A.tenera * A.magellanica
 hybrid on overlay

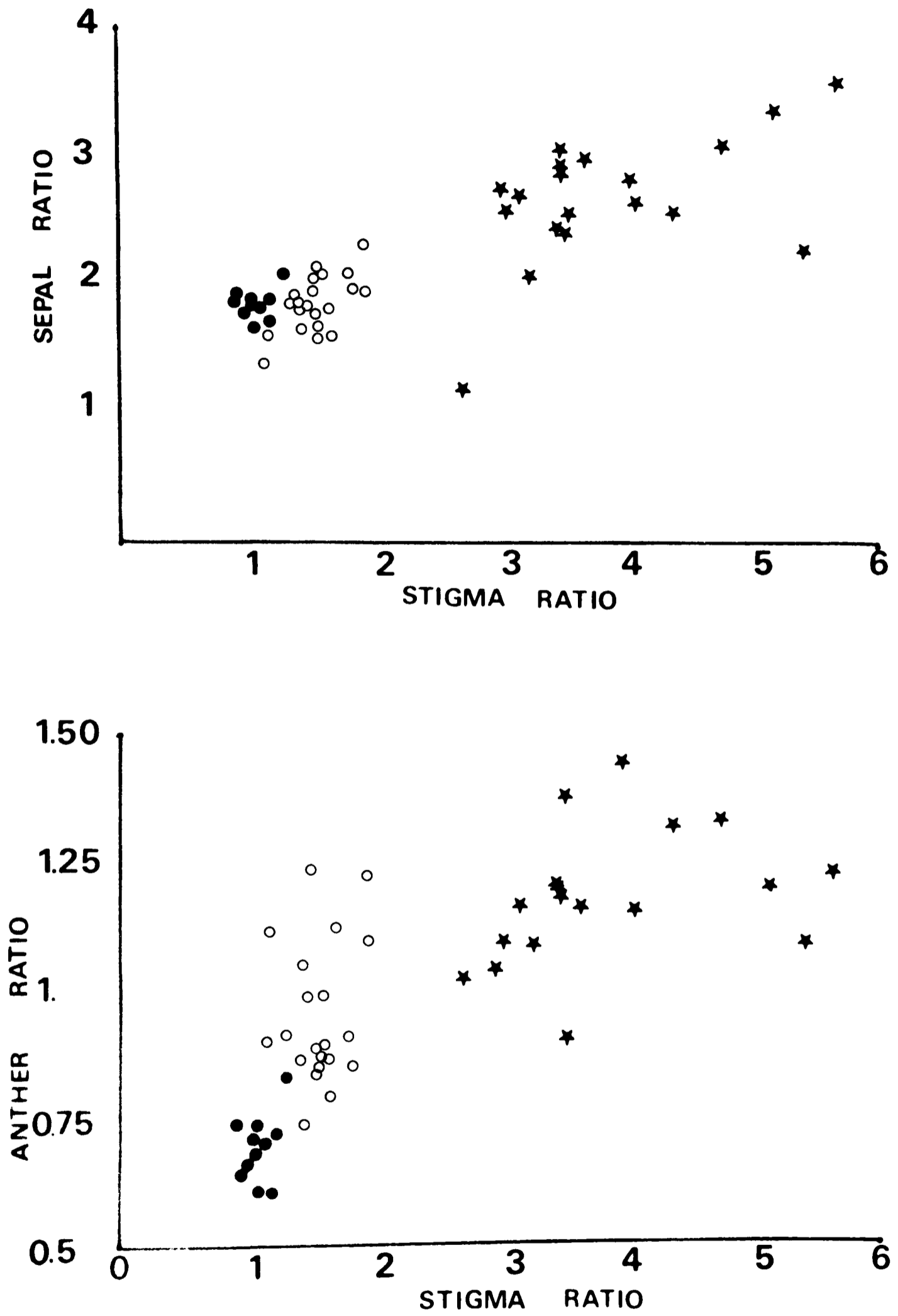


Figure 9. Scatter diagrams of morphological measurements

Key: ● *A. tenera* ★ *A. magellanica*
 hybrid on overlay

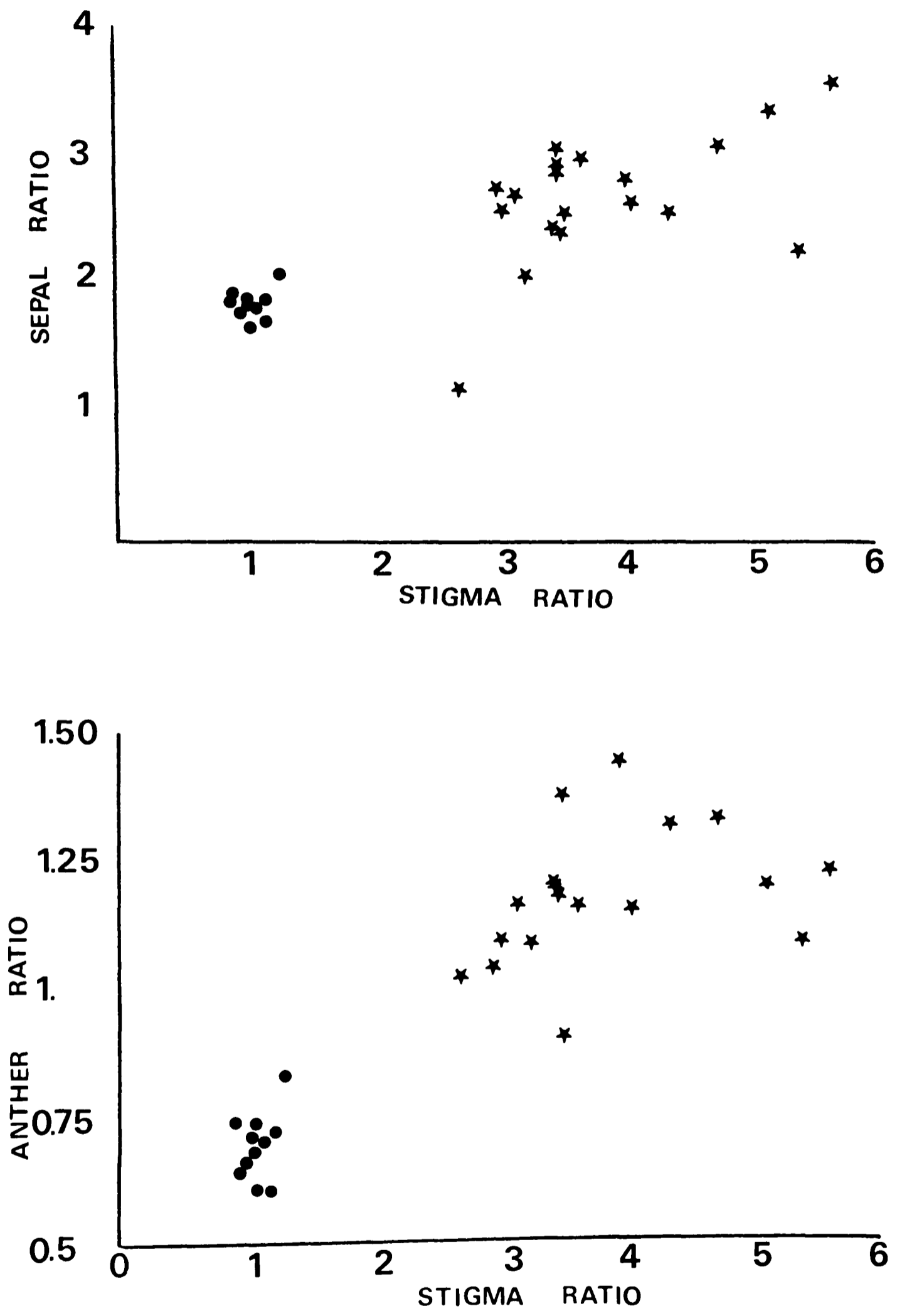


Figure 9. Scatter diagrams of morphological measurements

Key: ● A.tenera ★ A.magellanica
 hybrid on overlay

Table 4 - A comparison of A. magell^{an}ica, A. tenera
and Acaena hybrid on South Georgia

	<u>A. magellanica</u>	<u>Hybrid</u>	<u>A. tenera</u>
Leaf colour	glaucous	intermediate green	bright glossy green
Number leaflets	mainly 11-13	mainly 11-13	mainly 11-13
Leaf ratio	2.84(SD 0.51)	3.65(SD 0.81)	3.79(SD 0.77)
Mean length terminal leaflet	1.50	1.10	0.59
Leaf pilosity	vh-sh/b	sh/b or nh	nh
Hair types	uniseriate	uniseriate & glandular	uniseriate, glandular and 'manna'
Scape	terminal	terminal	axillary
Scape bract	frequently present	normally present	normally present
Axillary flowers -heads	single flowers frequent	flowers &/or heads normally present	single flowers normally present
Stigma type	X	Y	Z
Mean stigma length mm.	3.24	1.97	2.04
Stigma ratio	3.86(SD 0.79)	1.56(SD 0.21)	1.08(SD 0.11)
Anther ratio	1.18(SD 0.48)	0.94(SD 0.14)	0.69(SD 0.07)
Sepal ratio	2.63(SD 0.50)	1.97(SD 0.26)	1.86(SD 0.06)
Fruiting head diameter cms.	2.0-3.1	1.1-1.5	0.6-0.9
Fruit length mm. (inc. spines)	8.0-15.0	3.0-5.5	2.0-3.5
Mean No. fruits/head	90 (range 54-146)	43 (range 33-57)	23 (range 20-26)
Pollen fertility	92-98%	50-55%	90-95%
Normal seed germination at 20°C	40-80%	0-1%	50-95%

The length of the terminal leaflet was positively correlated with total leaf length, but not very closely with leaf shape (as exemplified by leaf ratio).

The point of maximum breadth was always $\frac{1}{3}$ of the length from the tip. The numbers of leaflets per leaf varied both within and between populations but was generally 11-13. Typical leaf shape and dentation of the leaflets is shown in Figures 7a & 7b which also show leaf shapes of A. magellanica populations from elsewhere. Leaf shape in A. magellanica was very variable and is extensively illustrated in both Bitter (1911) and Yeo (1973), with some further drawings in Grondona (1964). Pilosity is equally variable. Young leaves always appear more pilose than fully mature ones, although in both young and old leaves a wide range of pilosities can be found. The hairs are largely restricted to the ventral leaf surface although a few occur on the dorsal surface and then either in the leaflet dentations or on the main veins. In almost glabrous specimens hairs are restricted to only the main ventral veins. On South Georgia no completely glabrous specimens or densely pilose material has been found. The hairs are always uniseriate (Figure 4), type A in Nordborg's (1968) classification. Leaf colour is normally a glaucous green (see Figure 8), often with red-tipped points to the leaflet dentations. Stipules are always present, broadly sheathing at the base, and either entire and pointed or leaf-like at the apex.

The scape is terminal and its final length appears to be linked to exposure in the same way as leaf size. The tallest one found on the island was growing in the lee of a building at Grytviken and measured 26.5 cm.



Figure 10. Specimen of A. magellanica from the Falkland Islands showing ovate terminal capitula and many subsidiary capitula.



Figure 11. Specimen from Punta Arenas showing abnormal capitulum.

The scape bract is of frequent occurrence, sometimes with a flower but never a capitulum in its axil. Examination of 300 flowering scapes from one population gave the following data:

Scapes with bract	78%
Scapes with rudimentary flower in axil of bract	51%
Scapes with fully developed flower in axil of bract	11%

It is only rarely that more than one flower is found in the axil of the bract, and in these cases all the flowers were fully developed. The rudimentary flowers appear to begin development normally but shrivel up and die soon after the flower opens. The bract flowers are always similar to those in the terminal capitulum, so that female heads also have female flowers only in the bract axil. The hairs found on the scape are always uniseriate.

Both hermaphrodite and gynodioecio^us plants are found throughout South Georgia. The female flowers correspond closely with the description and drawings in Grondona (1964). In both types of flowers the floral bracts and sepals have many long uniseriate hairs on the outer surface and margins. The fruit varies from completely glabrous to a sparse covering of white uniseriate hairs. The fruits normally have 4 spines, although subsidiary ones are occasionally found, and these always have gloch^hids. The size of the mature fruit can vary considerably as can the number of fruits per head. This appears to be closely connected with plant habitat, plants in more favourable sites producing larger fruits. The number of fruits ranges from 54-150 per head, with a range in fruiting head diameter of 2.0-3.1 cm. Fruit type is illustrated in Figure 13.

Stigma length varies but is always longest in the female flowers (4 mm. and over). Stigma type in the South Georgian material is always X (Figure 4) and the mean value for the collections scored was 3.24 mm. The stigma ratio (Figure 9) varies considerably, much more than in either of the other two taxa, and the same is generally true of the anther ratio. This variability in anther ratio is not correlated with the aborted anthers in the female flowers, their proportions showing the same degree of variability as those in hermaphrodite flowers. Sepal size, 1.9 - 4.6 mm. long by 0.8 - 1.7 mm. wide, is greater than in the other two taxa.

It is quite clear that A. magellanica, even in a South Georgian context only, shows a high degree of morphological variability. This is further emphasised by the number of abnormalities collected on the island. Small capitula are frequently found in which flowers are not evenly produced over the whole head, and one instance has been found of a breakdown of developmental control in which single flowers spiralled down the scape below the capitulum. Other examples of abnormalities include incomplete elongation of the petiole, "rosetting" of abnormal leaves around the base of a scape and the production of shoots with a very low chlorophyll content. Fused cupules, as illustrated by Grondona (1964), have also been found. Table 4 summarises the important characters for this taxon.

A. magellanica x tenera

South Georgian material:

Plants showing characters intermediate between those of A. magellanica and A. tenera have been found only on South Georgia. Most of this material, now present in various herbaria, was collected by the author. Earlier collections were usually identified as A. adscendens.

The scoring of hybrid material is inevitably complicated if any back-crossing occurs. Leaf colour, one of the best field characters, is shown in Figure 8. Leaf shape is variable and although generally appeared similar to A. magellanica (Figures 6 and 7), the leaf ratio is closer to A. tenera (Figure 9). The occurrence of red tips on the leaflet dentations is variable even within one population. Leaf length ranges from 2.0-13.5 cm. with a mean ratio of 3.65(SD 0.81) in the collections scored. Uniseriate hairs (Figure 4) are normally present on the lower leaf surface but are never dense. Occasional glandular hairs are found in the axils of leaflet dentations whilst there is normally a considerable clump of these golden hairs in the axil of the leaflets. Stipules are always present and are either entire or bifid.

The scape is terminal and although its final length appeared to be linked to the degree of exposure of the habitat, it rarely exceeded 15 cm. When young glandular hairs were sparsely distributed over the whole scape but these had generally disappeared by the fruiting stage. One or more bracts were found on the scape and these could be very leaf-like. The bracts almost always subtended either a number of florets or secondary capitula on their own scapes. These secondary heads were one of the most characteristic features of the hybrid plants. The secondary capitula began development after the main capitulum but often overtopped the main scape when fully grown.

The main capitulum diameter when fruiting was usually 1.1-1.5 cm. All flowers were hermaphrodite with stigma type Y (Figure 4) with a mean stigma length of 1.9 mm. The stigma ratio (Figure 9) showed a very close similarity to A. tenera whilst anther ratio was intermediate between the two parents. Sepal size, 1.6-3.1 mm. long x 0.7 - 2.0 mm. wide, gives a mean ratio of 1.97 (SD 0.36) which shows again a close similarity to A. tenera (Figure 9).

The floral bracts were covered on their outer surface with long uniseriate hairs, and these were also found on the sepals. Both uniseriate and glandular hairs were found sparsely distributed over the fruit.

Fruit type is illustrated in Figure 13. Spine number was rather more variable than in the parental taxa with subsidiary spines occurring in some collections. The normal number of spines was 4. Glochids were always present. Although the fruit type was basically the same as A. magellanica the fruits were always smaller for the same habitat. Table 4 summarises the main characters for this taxon.

Extra-South Georgian material:

From a general examination of over 250 collections and a more detailed inspection and scoring of over 80 other collections of A. magellanica s.l. from South America and the Falkland Islands a number of general comments can be made about the morphological variation in this taxon.

Leaf size varied very widely and appeared to be closely linked to climatic factors such as altitude and the degree of wind exposure, material from high exposed areas having much smaller leaves than that growing in low sheltered areas. Leaf shape was also affected as shown by a length/breadth ratio ranging from 2.6-8.1. There appeared to be a tendency for the higher values of the leaf ratio to be associated with the elongate shoot form rather than the rosette type. This is to be expected since the greater internode length in the elongate type obviously allowed a greater degree of leaf expansion than in the rosette form. A further qualification is necessary since the rosette form appeared to be much more common in the exposed higher altitude areas, the type of habitat which caused the greatest reduction in leaf size.

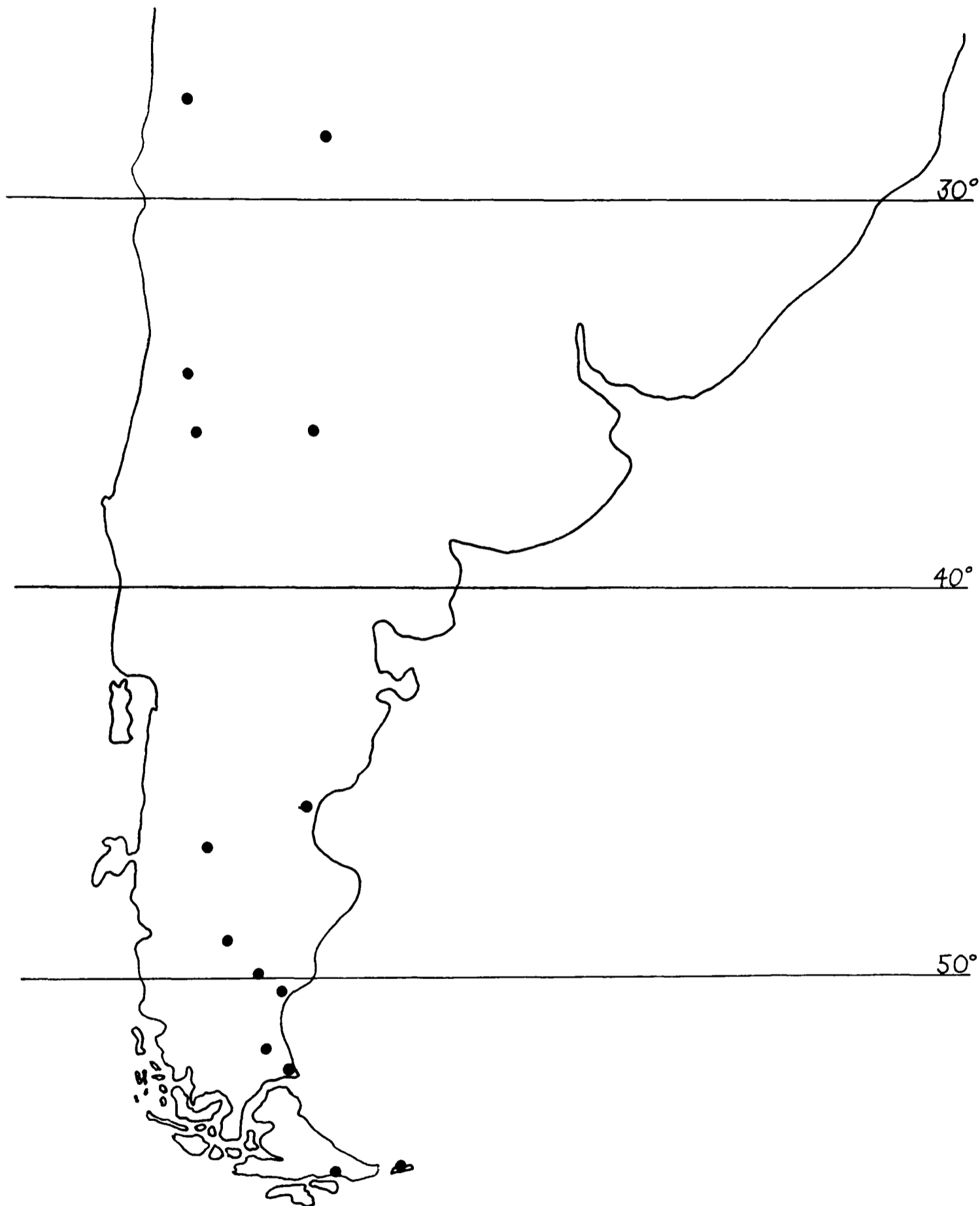


Figure 12. Distribution in South America of female populations of *A. magellanica* (Lam.) Vahl (from herbarium specimens)

All leaflets were found to be decurrent to some extent, even if only by 0.5 mm., whilst generally the specimens had entire stipules, the exceptions to this usually being collections from female populations. There appeared to be a gradient in leaf pilosity, diploid material from the sub-Antarctic islands and Tierra del Fuego having the least hairs whilst presumed tetraploid specimens from the Chilean Andes, were very pilose. Whilst the general tendency was for an increase in pilosity from South to North, numerous single collections were found which did not fall easily into this pattern. The altitude at which this species occurs increases from South to North and the increase in pilosity may well be associated with a general increase in the severity of the local climate at these higher altitudes. In any locality there are however more favourable and less favourable sites for any individual species and specimens which do not appear to follow the general trend of increasing pilosity may well be those from the more favourable and sheltered sites.

The number of flowers per head varied being least in the depauperate plants from exposed habitats. Actual figures are not available as that would have meant destroying the specimens. Scapes were frequently quite pilose in all material when young, but only persisted like this when fully grown in specimens from northerly localities. Specimens with very pilose scapes normally also had very pilose leaves. Stigma type and size also varied. The XY type of stigma was frequent although the X type was the commonest. The X type was always found in female flowers, which had very small undeveloped anthers similar to those found in South Georgian material. Some specimens have been seen with unusually small stigmas and very large anthers, suggesting that flowers which are more functionally male than female can also be produced. They appeared to be very rare however, and since the stigma was always of a functional size the flowers must be treated

as hermaphrodite and the species cannot be described as dioecious. Comparisons of stigma and anther dimensions in various collections are given in Table 3.

From the differences in length/breadth ratios for the two organs it is obvious that a considerable diversity of shape existed in both. The contrast in size between the aborted or undeveloped anthers and normal anthers is immediately obvious in Table 3. It is not always the female flowers that had the largest stigmas though, with maximum stigma length ranging from 0.77 mm. in the Falkland Islands to 5.53 mm. on Îles Kerguelen. Holdgate no. 642 from the Falkland Islands was an unusual specimen with almost cleistogamous flowers, the reduced size of the stigma giving the flowers a predominantly male appearance. Grondona (1964) illustrated a comparable specimen from Chubut, Argentina. It is interesting that the size and the proportions of the aborted anthers was similar in all the areas whilst those of the functional anthers varied quite widely. The female populations of this species are as widely distributed as the hermaphrodite ones (Figure 12) which suggests they may be of multiple origin.

The genetic control system for determining the shape of the inflorescence in this species does not seem to be too secure. In hybrid material the production of secondary capitula from the axils of scape bracts is a constant character. Specimens of A. magellanica have been found on South Georgia and in Argentina where the inflorescence has broken down to a transitory phase between capitulate and racemic with a small terminal head and a series of individual flowers spiralling down the scape. In material from the Falkland Islands the terminal heads have been found to be markedly ovate, whilst a specimen from Punta Arenas (Herb. no. 049843, SGO) showed two flowering heads in which all the flowers had been produced on long individual pedicels (Figure 11).

Table 3 - Anther and stigma measurements from various populations of A. magellanica

		ANTHER			STIGMA		
		max	max	ratio	max	max	ratio
		length	breadth		length	breadth	
<u>South Georgia</u>							
	(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
<u>Marion Island</u>							
	(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
<u>Kerguelen</u>							
	(Osten, 8668; MVM)	0.77	0.77	1.0	3.19	1.06	3.0
	(Proctor, 15; BM)	0.30	0.30	1.0	5.53	1.06	5.2
<u>Macquarie Island</u>							
	(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
<u>Falkland Islands</u>							
	(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
<u>Tierra del Fuego</u>							
	(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
<u>Argentina</u>							
San Juan	(Canplin & Ralph 31; K)	1.53	1.06	1.4	2.13	0.43	4.9
Mendoza	(Moseley, sn.; 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
<u>Chile</u>							
	(Bridges, 1192; K)	0.43	0.38	1.1	3.40	1.60	2.1
	(Werderman, 598; K)	0.21	0.26	0.8	3.40	0.85	4.0

All measurements in mm. Abbreviations for herbaria follow Lanjouw & Stafleu (1964).

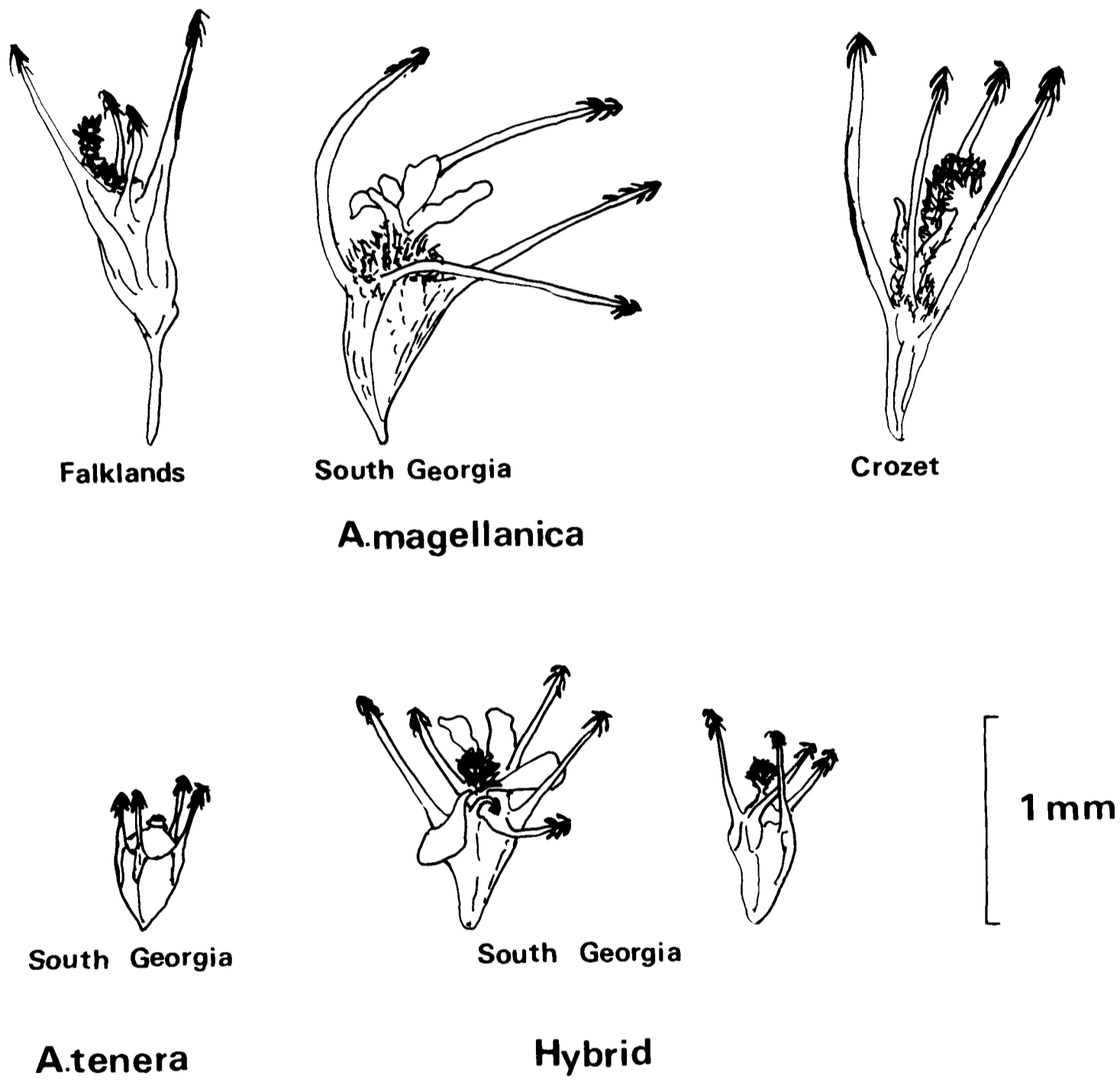


Figure 13. Fruit types in the South Georgian taxa of Acaena

Specimens originally referred to various species in the A. magellanica complex have been examined from numerous localities in South America and the sub-Antarctic islands. Many of the specimens constituted type material for species described by Bitter (1911) and other authors. Attempts were made to identify particular specimens using the keys in Bitter (1911), Grondona (1964) and Yeo (1973). The only satisfactory key was Grondona's which correctly identified material to A. magellanica in all except a very few cases. Bitter's keys proved totally inadequate as a specimen could be identified as three separate species merely by using different parts of the same plant. The key in Yeo (1972) together with his descriptions was much better than this but since it was based mainly on a small sample of living material it did not work satisfactorily when presented with the true range of variation shown in this complex.

Moore (pers. comm.) has found that the diploid populations in S. America appear to be restricted to the eastern tip of Tierra del Fuego. Using herbarium material from two of these diploid populations comparisons were made with other collections falling well within what appears to be the tetraploid area. As many as possible of 24 characters, both vegetative and sexual, were used for each specimen.

Sorting of sheets by eye for groups based on overall general appearance gave two main groups together with a large number of individual sheets. The examination of the two large piles showed them to be based largely on leaf colour, pilosity and growth form. When detailed measurements were made of various characters the two groups were found to overlap considerably. Analysis of the collection locations for the specimens falling in the same group as the diploid collections showed it

to contain all the material from the sub-Antarctic islands together with material from Staten Island and a variety of sheets from various parts of South America. It did not prove possible however to satisfactorily describe clearly defined taxa which corresponded to diploid and tetraploid material due to overlap of most important characters.

The general conclusions to be drawn from this appear to be as follows: A. magellanica s.l. comprises a species complex with two ploidy levels. It is unlikely that the diploid and tetraploid interbreed although it appears that their ranges overlap to some extent. The diploid appears to be slightly less variable than the tetraploid in most characters but the range of variation overlaps so much that it appears difficult to describe accurately separate species or subspecies at the moment. In a complex such as this where both self and crossfertilisation can occur it does not seem worthwhile for general taxonomic purposes to try and delineate subspecific taxa, which could often be based only on small populations. Many of Bitter's species are probably referable to this level. Whilst the diploid populations appear to be restricted to the eastern tip of Tierra del Fuego and the sub-Antarctic islands from chromosome counts carried out so far, specimens from Staten Island and other parts of South America show a close morphological correspondence.

Anatomy

Materials and Methods:

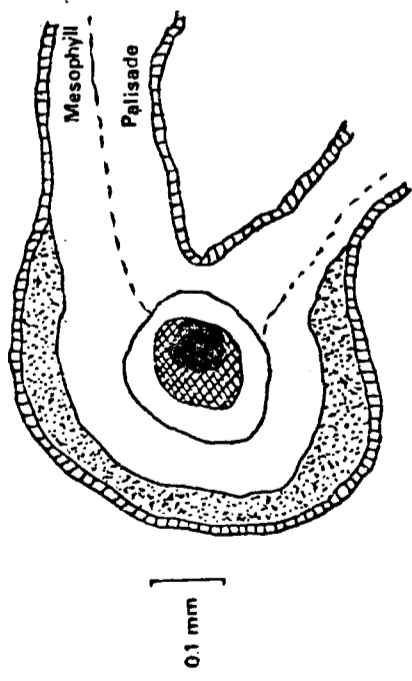
Collections were made of all three South Georgian taxa and the material preserved in formalin acetic alcohol. Samples of particular organs were dehydrated and embedded in paraffin wax before sectioning on a rocking microtome. The sections were normally stained in Safranin and either

Aniline Blue or Light Green. The majority of sections were transverse although some longitudinal ones were cut of rhizome material. Starch content was tested for using Iodine in KI, whilst crystal inclusions were searched for in sections using polarised light.

Results:

In the collections examined mean leaf thickness was generally greatest in A.magellanica and least in A.tenera. Normally the palisade layer was 2 cells deep although a short third layer was apparent in some A.magellanica leaves (Figure 14). Stomata were found on both leaf surfaces in A.magellanica and the hybrid, but only on the adaxial surface in A.tenera. There were usually about c. 30% of the total number of stomata on the abaxial surface in A.magellanica whilst in the hybrid it was generally only c. 20%. There appeared to be a direct relationship between stomatal number per unit area and the size of the leaflets in any particular specimen, this latter character being correlated with plant habitat and exposure. The cuticle in all three taxa was twice as thick on the abaxial as on the adaxial surface of the leaflets. The cells of the upper epidermis were normally quite regular in size and flat, whilst those of the lower epidermis were irregular in size for all three taxa and often slightly papillose. Crystals were seen frequently in the transverse leaf sections of A.magellanica, rarely in those of the hybrid and not at all in those of A.tenera. When present they were nearly always associated with the vascular bundle sheaths. Crystal distribution was seen much more clearly in cleared material of whole leaflets.

In the petioles of all three taxa the vascular bundles were normally arranged in a single arc, each bundle with a sheath. In A.magellanica these sheaths, and in some cases the vascular bundles themselves, contained



KEY

Xylem
Phloem
Collenchyma
Epidermis

Main vein of *Amagellanica* leaflet

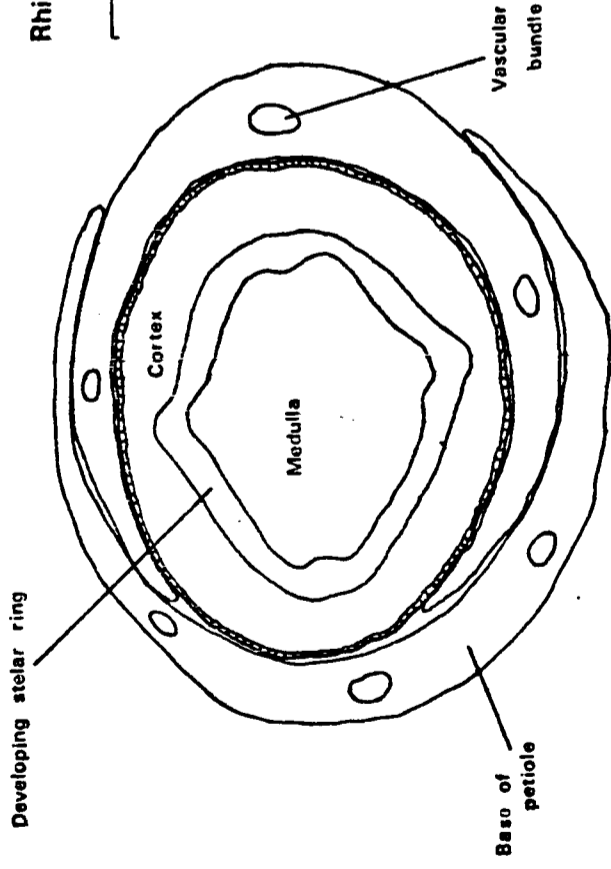
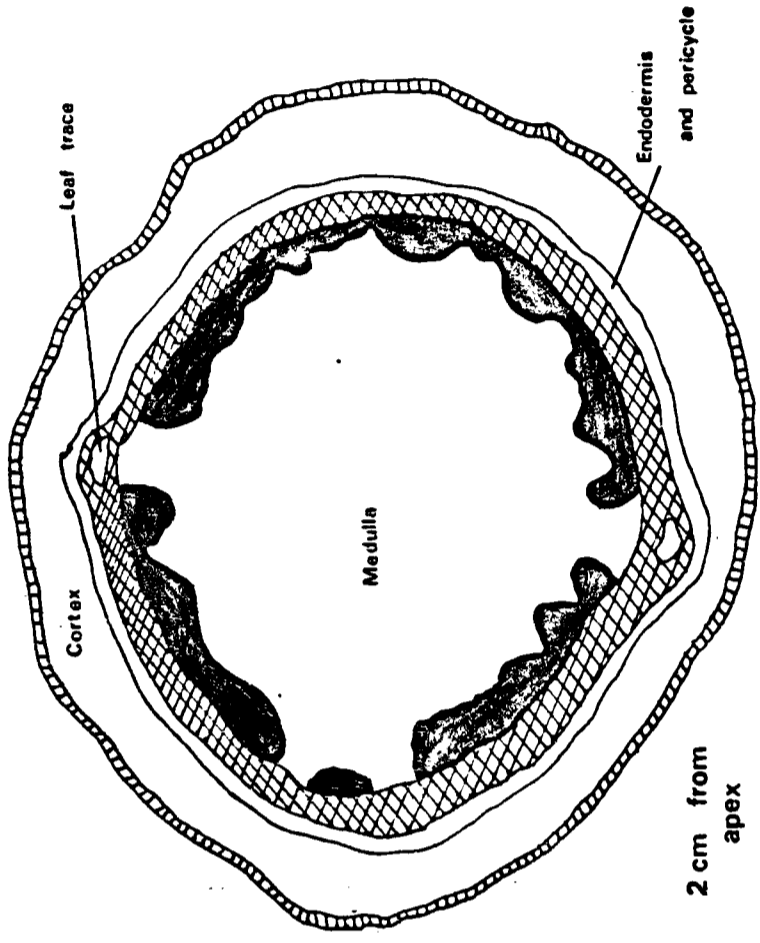
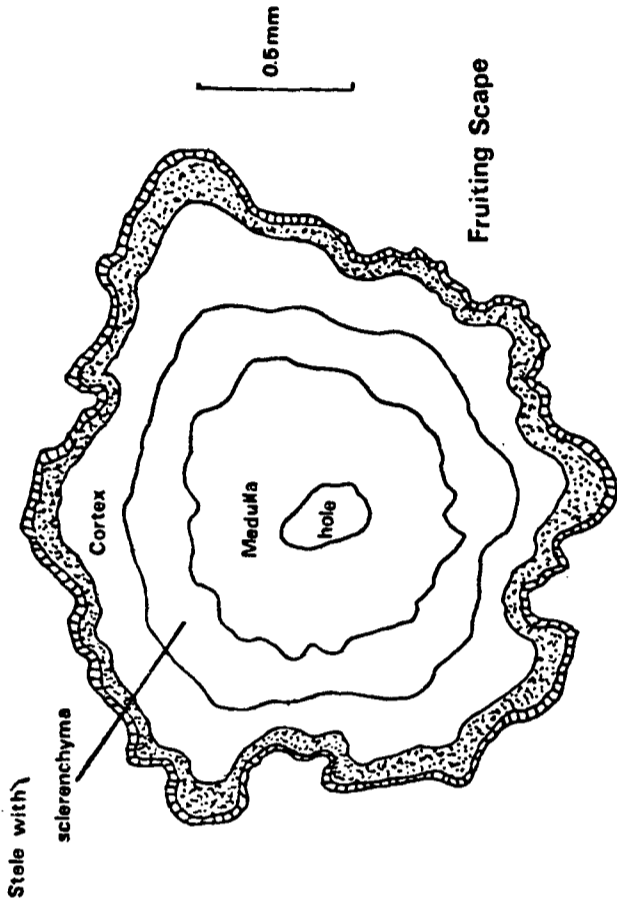


Figure 14. Transverse sections of leaf, scape and rhizome anatomy in *A. magellanica*

considerable quantities of tannins. These were present to a limited extent in the hybrid but absent from the petioles of A.tenera.

In all three taxa stomata were found in the scape epidermis. The principal strengthening tissue in the scapes was collenchyma which formed an external ring just below the epidermis. It was up to 8 cells thick in A.magellanica but only 1-3 cells thick in A.tenera. Further strengthening was provided by the development of a ring of sclerified cells around the vascular bundles, extending up the scape as it matured.

Rhizome anatomy was basically similar in all three taxa (Figure 14), although the maximum diameter of the rhizome was always greatest in A.magellanica and least in A.tenera for a given age of plant. The differentiation of 4 vascular bundles occurred less than 1 cm. back from the apical bud in A.magellanica rhizome. Secondary vascular bundles had formed within 2 cm. of the apex and these united to form a complete ring of xylem. By the end of the first year the rhizome was over 2 mm. in diameter. Secondary thickening then began and during the second year a periderm was formed and a cork layer produced to replace the fragmented epidermis. Medullary cells frequently became lignified during the early stages of secondary thickening and as the production of secondary xylem proceeded medullary rays were formed. All the tissues in the rhizome except the periderm were found to be used for starch storage. The periderm was found to contain large amounts of tannins whilst the outer cells of the secondary xylem usually contained considerable numbers of crystals. This developmental sequence appeared to be similar in all three taxa, although differences existed in the thickness of certain layers of cells. Since secondary thickening was annual it was expected that some evidence of annual rings would be found in the secondary xylem. This was not so in any of the A.tenera specimens examined, but in some sections of both hybrid and

A. magellanica there appeared to be annual rings present. A number of attempts were made to use counts of annual rings for aging of plants but such difficulties were often experienced in making objective ring counts that the method could only be said to give a general estimate of plant age rather than an exact one.

Discussion:

There are very few papers dealing with the anatomy of Acaena. Metcalfe and Chalk (1950) noted that the leaf epidermis in A. adscendens (= A. magellanica) was papillose on both surfaces and that a transverse section of the petiole showed that the vascular bundles were arranged in a single arc. The leaves of A. minor have also been reported to have a papillose epidermis (Herriot, 1905), whilst those of A. caesiglauca apparently have not. From the material examined in the present survey it was possible to verify that some papillosity did occur in the epidermis of A. magellanica and that the vascular bundles were arranged in a single arc in the petiole. The leaf anatomy of the South Georgian material of A. magellanica was apparently very similar to South American collections of the same species (under the name of A. subnitens, Pyykkö, 1966). Calcium oxalate crystals were also present in the South American material but the sparse glandular hairs reported for those collections have not been seen in South Georgian material. Pyykkö (1966) has suggested that the cells of the lower epidermis might be partly mucilaginous but this feature was not seen in the South Georgian material. She placed the A. magellanica material in her 'Group 3. Antennaria magellanica type', whilst the other 12 species of Acaena went into 'Group 10. Acaena integerrima type' and 'Group 11. Acaena pinnatifida type'. These groups 10 and 11 are very similar and differ

only in a tendency for leaves of the latter to be isolateral. Both groups differ from group 3 in having stomata restricted to the lower surface, and in slight differences in cell size and mesophyll thickness. It is difficult to see in some instances what justification Pyykkö had for grouping species together in this way since many of her characters appear to show considerable overlap.

No published information is available on the anatomy of any other plant parts except for some on floral development in Acaena sanguisorbae (A. anserinifolia) (Kania, 1973) and in A. pinnatifida (Bonne, 1928). This subject has not yet been investigated for the South Georgian species.

The importance of the rhizome as a starch store is quite clear from the anatomical evidence. The accumulation of tannins and crystals in both the petioles and the rhizome is clearly very interesting, especially as it occurs in many species in the genus. These materials have been suggested to perform a variety of functions although there is general agreement that crystals represent storage of unwanted inorganic material whilst tannins may either be linked with starch metabolism or present to protect cells against desiccation and decay (Esau, 1965). The location of the tannins in the outer layers of the rhizome periderm would fit this theory well but it is not clear why they should be found in the petiole. If crystals are indeed only waste products it might be expected that they would be found in all parts of the plant. This appears to be the situation at the moment in the species of Acaena examined.

Chromosome counts for this genus have been provided by Moore (1960,1964,1967,1972), Moore and Walton (1970), Dawson (1960) and Favarger and Huynh (1965), (Table 5). Of all the species with published counts all except three have $2n=42$ (Moore, 1972) including the hybrid material on South Georgia (Moore and Walton, 1970). The three species with the higher ploidy levels are A.saccaticupula, in New Zealand, A.californica in California and A.magellanica in the Falkland Islands and most of South America except the eastern tip of Tierra del Fuego. At the moment A.magellanica is the only species in this genus known to show chromosomal variation.

Large scale hybridisation appears to be limited to certain New Zealand species (Buchanan, 1871; Dawson, 1960; Allan, 1961), where hybrid swarms are a common feature on disturbed ground and in unstable habitats such as dune areas. An intergeneric hybrid is also known - Acaena argentea x Margyricarpus setosus - but 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 for F_2 populations (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 A.myriophylla and A.anserifolia.

A.magellanica and A.tenera are the only South American species known to hybridise. The chromosome morphology of the hybrid, which is only found on South Georgia, does not show any abnormalities, but it is apparently almost infertile. The lack of hybridisation 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 (see

Table 5). Indeed, the area in which A.magellanica and A.tenera occur together in Tierra del Fuego falls outside the part of the island in which diploid populations of A.magellanica are known to occur (D. M. Moore, pers. comm.). It would therefore seem unlikely that any further examples of the South Georgian hybrid will be found elsewhere.

The seed collected from hybrid populations on South Georgia for testing has given germination results of 0-1%. The establishment of F_2 populations would therefore seem a rare occurrence. However it has proved possible to grow F_1 plants from A.tenera seed, but never from A.magellanica seed. In the course of germination and seedling productivity studies three F_1 plants have been produced from around 1500 seeds. A similar number of A.magellanica seeds have not produced any hybrid plants. Bearing in mind its distribution (see Chapter 5) there obviously exists a high likelihood for the independent origin of hybrid populations in different parts of South Georgia.

Table 5 - Chromosome numbers in *Acaena*

Species	Locality	Number	Reference
Magellanica	Macquarie Island	2n=42	Moore (1960)
	South Georgia	2n=42	Moore & Walton (1970)
	Falkland Islands	2n=84	Moore (1967)
	Magallanes, Chile	2n=84	Moore (1964)
	East T. del F.	2n=42	unpub. Moore
Tenera	South Georgia	2n=42	Moore & Walton (1970)
Magellanica x Tenera	South Georgia	2n=42	Moore & Walton (1970)
Ovalifolia	Llanquihue, Chile	2n=42	Moore (1964)
	Magallanes, Chile	2n=42	Moore (1964)
	Chile	2n=42	Favarger & Huynh(1965)
Lucida	Magallanes, Chile	2n=42	Moore (1967)
Minor	Macquarie Island	2n=42	Moore (1960)
Saccaticupula	New Zealand	2n=84	Moore (1964)
Novae-zealandide	New Zealand	2n=42	Dawson (1960)
Pallida	New Zealand	2n=42	Dawson (1942)
Anserinifolia	New Zealand	2n=42	Dawson (1960)
	Tasmania	2n=42	Moore (1964)
	New South Wales	2n=42	Moore (1964)
Californica	California	2n=126	Moore (1964)

Chapter 5

GEOGRAPHICAL DISTRIBUTION

Introduction

Acaena is a genus largely restricted to the Southern Hemisphere, the few species occurring in the Northern Hemisphere being very limited in their 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, New Amsterdam and St. Paul and the New Zealand shelf islands. Distribution has been examined in three ways. Firstly, the detailed distribution of the two species and their hybrid on South Georgia has been plotted to see if there is any clear pattern or discontinuities on an island basis. Secondly the world distribution of A.magellanica and A.tenera has been mapped and lastly, the whole genus has been examined from a biogeographical point of view and maps of the world distribution of certain character, e.g. inflorescence type, are given to illustrate an argument proposing a centre of origin for the genus.

Distribution on South Georgia

The data for the distribution map (Figure 15) 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 taxon of the three ^{Acaena taxa} occurring in 150 squares, 10 of which do not have A.tenera records. A.tenera is 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 also makes it

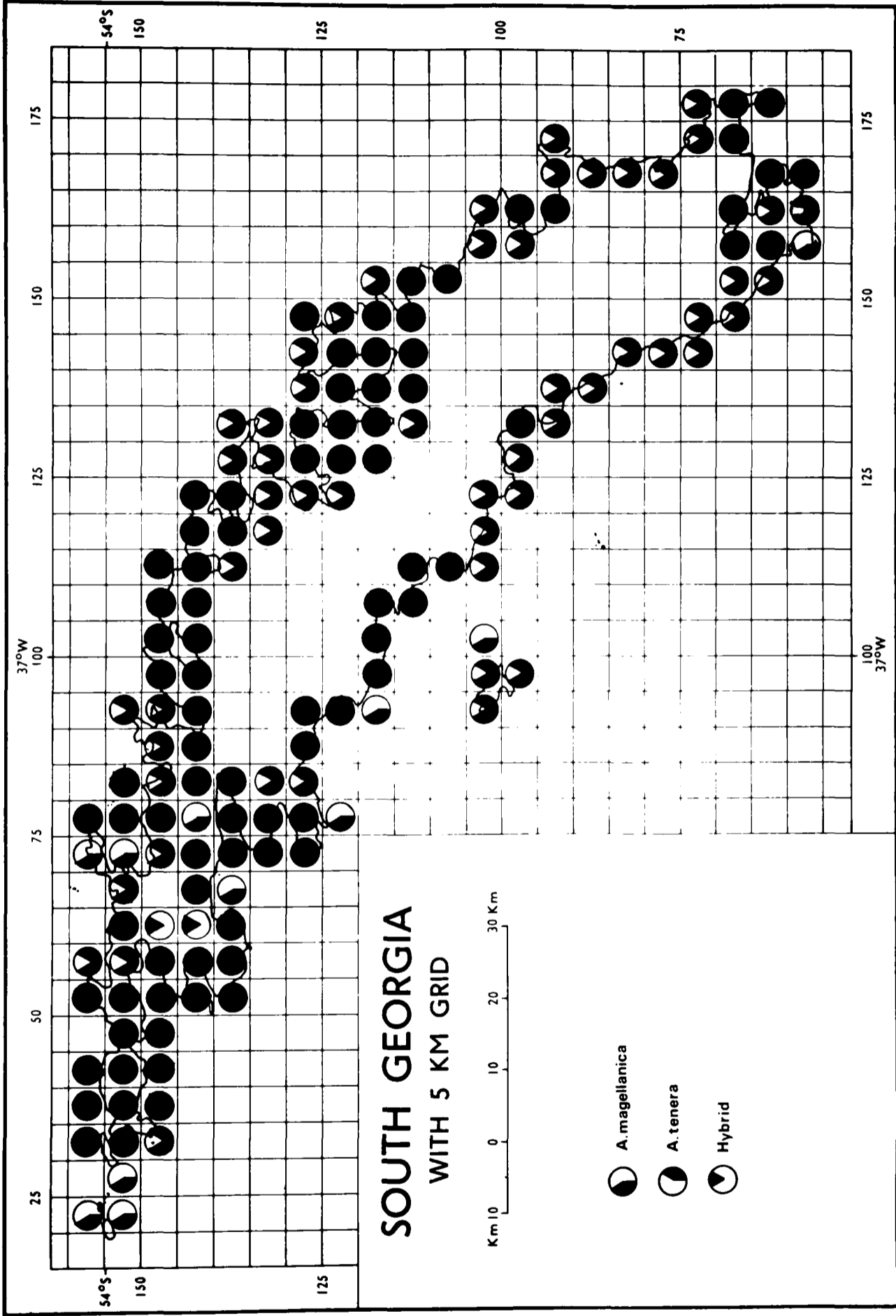


Figure 15. Distribution of the three taxa of *Acaena* on South Georgia

difficult for field recorders to be absolutely certain what they are recording, so as far as possible all the records on this map have been checked by the author. The hybrid is recorded reliably from 84 squares, two of which do not contain either A.magellanica or A.tenera. If this is a true state of affairs it suggests that the hybrid may have spread into these squares from neighbouring squares. 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.

World Distribution

A.magellanica is more widely distributed than any other species of Acaena. As Figure 16 shows it ranges from c. 25°S in northern Chile southwards along the Andes to Tierra del Fuego, and across the Southern Ocean on the Falkland Islands, South Georgia, Prince Edward and Marion Islands, Kerguelen, Iles Crozet, Heard Island and Macquarie Island. Despite earlier reports (Hooker, 1867) of its occurrence in New Zealand no specimens of this species have been seen from New Zealand in any of the collections.

A.tenera, on the other hand, has a very restricted distribution (Figure 16) occurring in South Georgia, Isla de los Estados and the mountains behind Ushuaia in Tierra del Fuego (Figure 17). As in the case of A.magellanica, all distribution records for these maps are based on specimens examined and unpublished information provided by Dr. D. M. Moore, literature records being thought too unreliable in view of the confused state of taxonomy in the genus. One 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 the Andes.

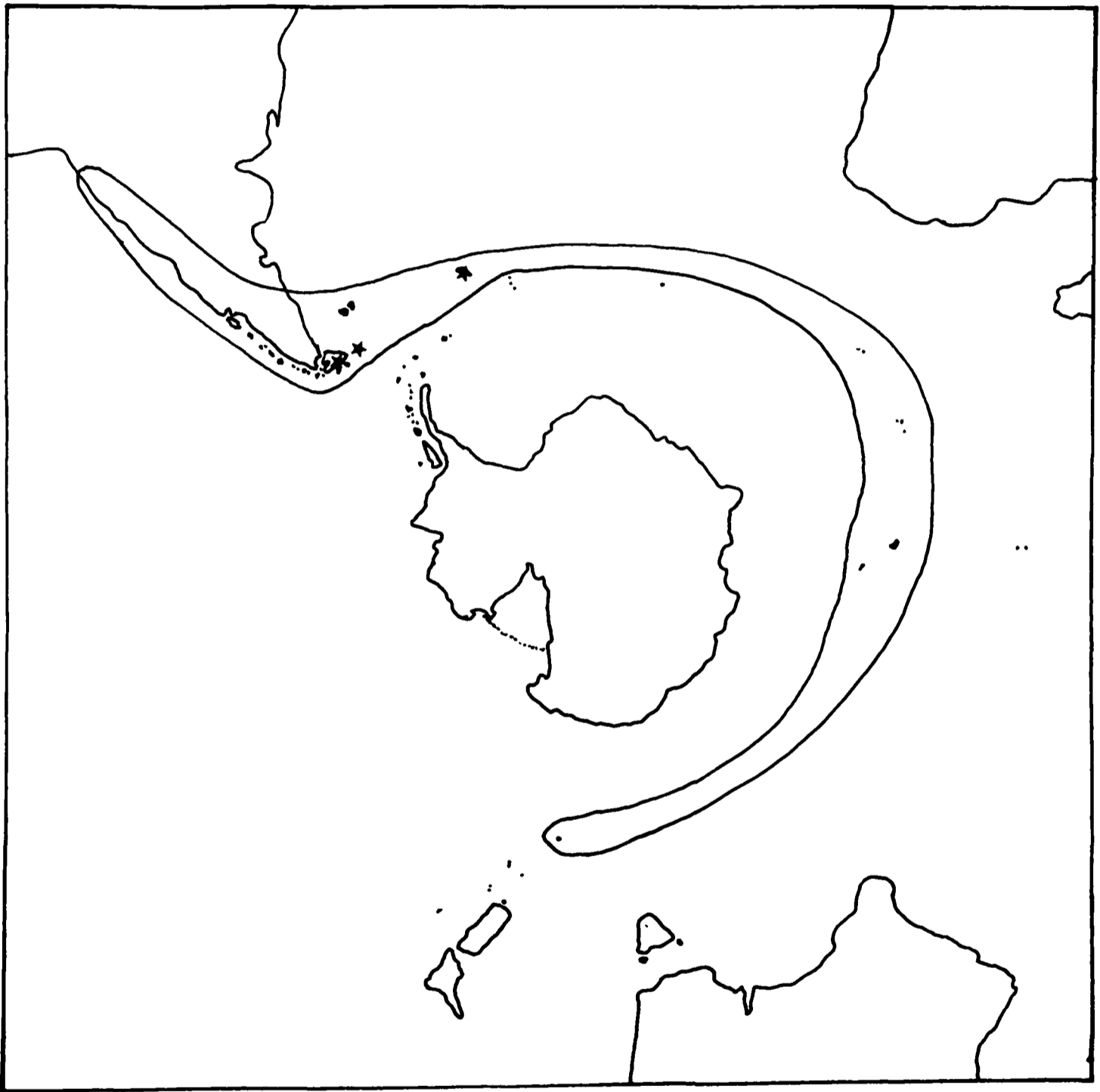


Figure 16. World distribution of A.tenera Alboff (★) and A.magellanica (Lam.)Vahl (—)

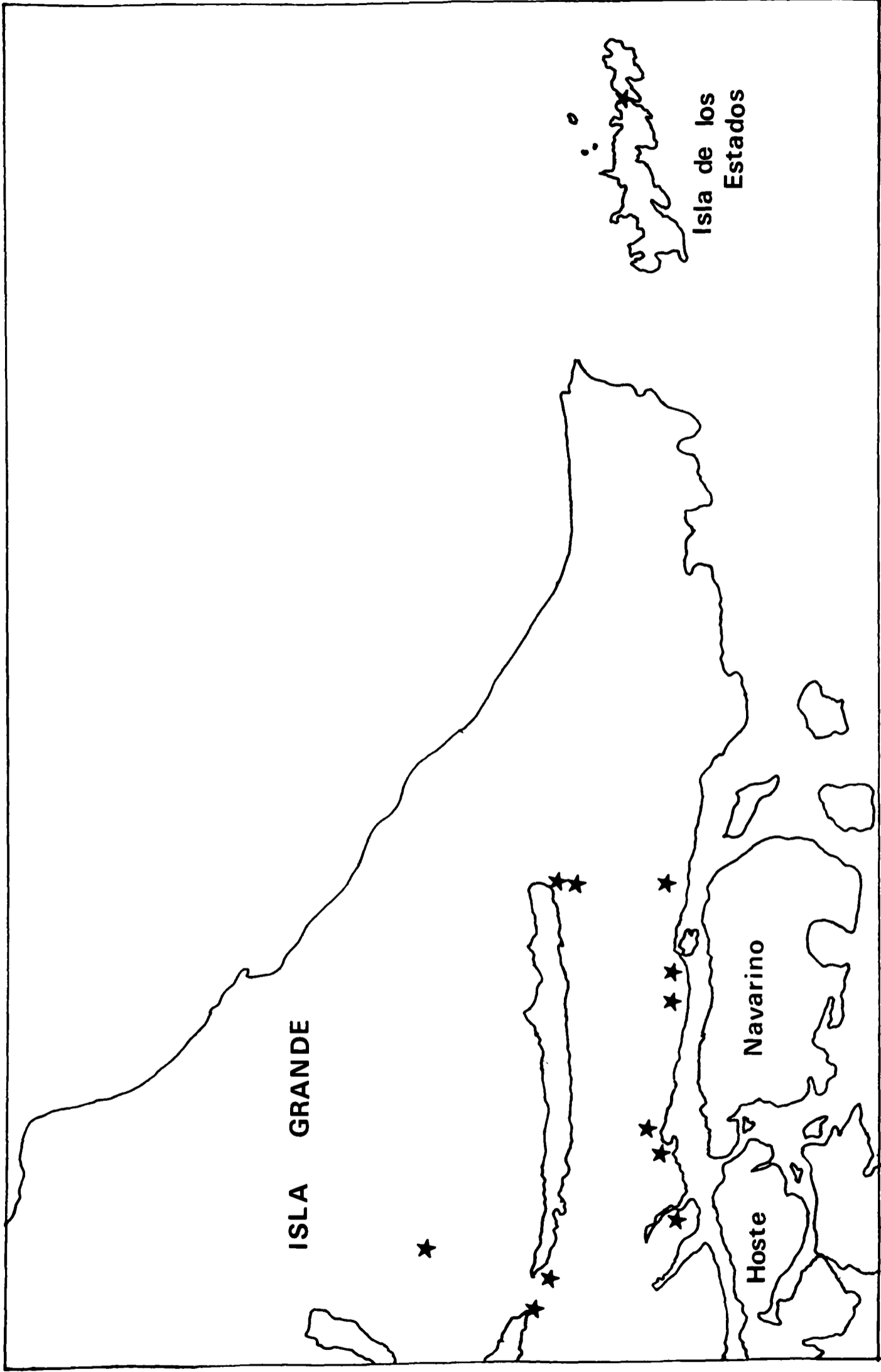


Figure 17. Distribution in South America of A. tenera Alboff (from herbarium specimens and unpublished records of D.M. Moore)

Despite searches in Swedish and Finnish herbaria for this specimen no trace of it could be found. Nor were any specimens of A.tenera from this region found in any of the South American herbaria examined. Despite Skottsberg's undoubted taxonomic reputation this record, so isolated from all others for this species, must be treated as dubious at the moment.

A.magellanica has been found in Great Britain growing as a wool adventive and a specimen was also recently found in Santiago (Fuentes s.n., SGO Herb. no. 077803) collected in 1911 from the Juan Fernandez Islands. Curiously Skottsberg (1922) mentions only A.masafuerana, A.ovalifolia and the inter-generic hybrid Margyracaena in his flora of these islands. No other specimens of this species have been found from there and it is tempting to conclude that the material found by Fuentes may have been an 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 certain extent. All the sub-Antarctic islands, the Falkland Islands, Tierra del Fuego and southern Patagonia share a broadly similar climate, probably best classed as cool temperate. Further north in South America this type of climate only exists at steadily increasing altitudes in the Andes. Thus it might be expected that the further north A.magellanica occurs the higher the altitude is likely to be. That such a view is correct is confirmed by the data shown in Figure 18. The scarcity of data between latitudes 32°-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 showed an even more marked correlation between latitude and altitude.

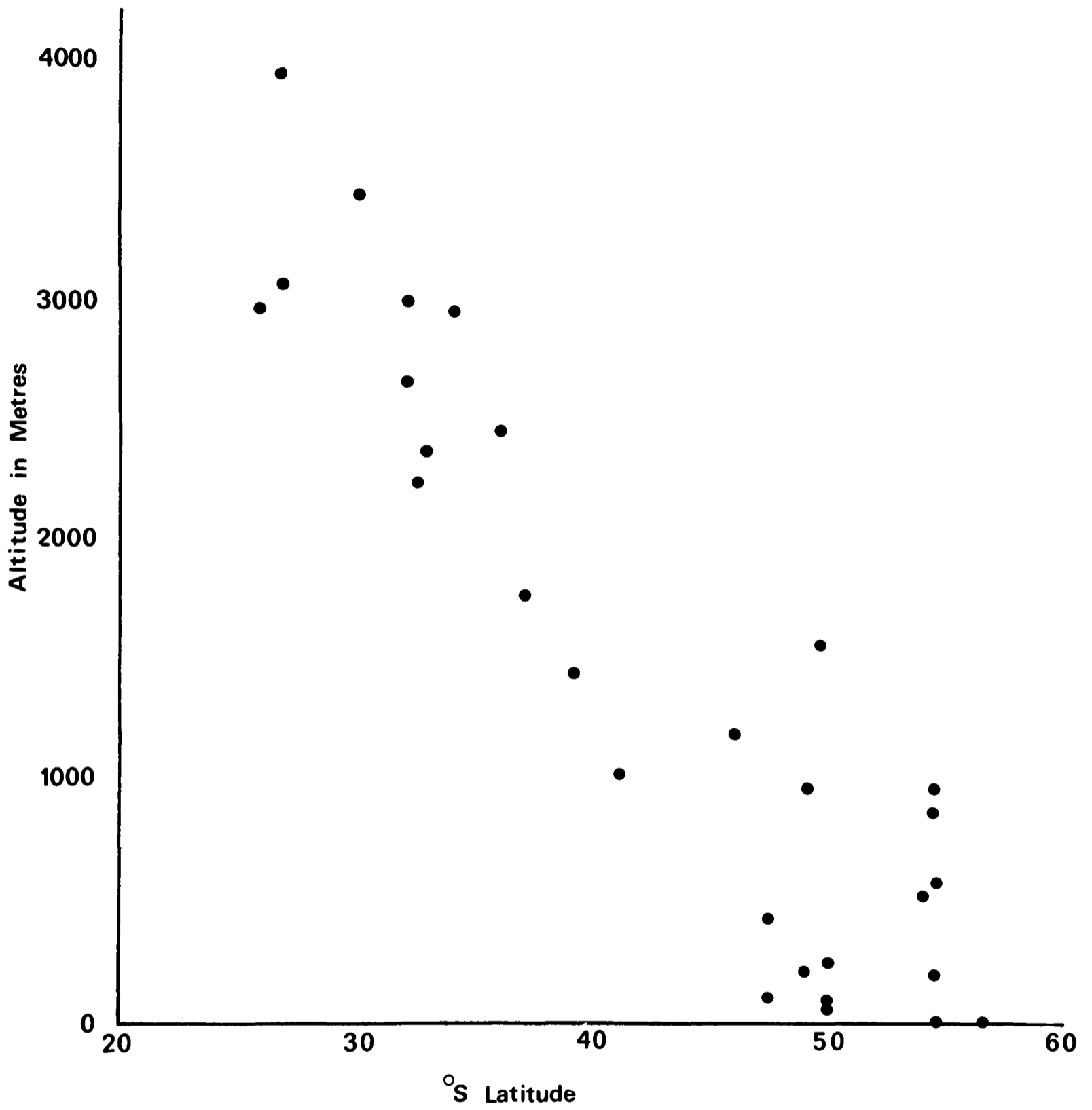


Figure 18. Diagram showing the altitude of occurrence of *A. magellanica* at different latitudes

Biogeography of the genus Acaena

The genus Acaena has been subdivided in several ways to show major groupings based on morphological characters. Candolle (1825) used the position of the spines on the cupule to divide the genus into two sections, whilst Reiche (1898) used inflorescence type as a primary division. There are two basic types of inflorescence - an interrupted racemic spike and a compact globose or cylindrical head. A number of species fall between these two extremes, thus forming a connecting series. Apparently correlated with the form of the inflorescence are the number and arrangement of spines on the fruits. If the small number of species which have greatly reduced spines are ignored, all the other racemose species have fruits with many spines, e.g. A.elongata, A.myriophylla, whilst most of the capitate species have fruits with less than 6 spines.

Phylogenetically the primitiveness of any character is always difficult to determine. Within any one taxon all the characters have not necessarily evolved at the same rate; Delphinium for example has primitive follicles but an advanced zygomorphic corolla. However, evolutionary trends within groupings of various sizes, from families down to species, all tend to follow one direction, that of reduction in plant parts either by loss, fusion or by contraction (Hutchinson 1959). In these terms it seems likely that a compact globose inflorescence has been derived from a loose racemic spike rather than the reverse. A concomitant of this would seem to be that the multispined fruits so common with racemic inflorescences evolved into the few-spined fruits of the capitate species. The restriction of spines to the top of the cupule obviously allows fruit density to be increased in a head of a given size.

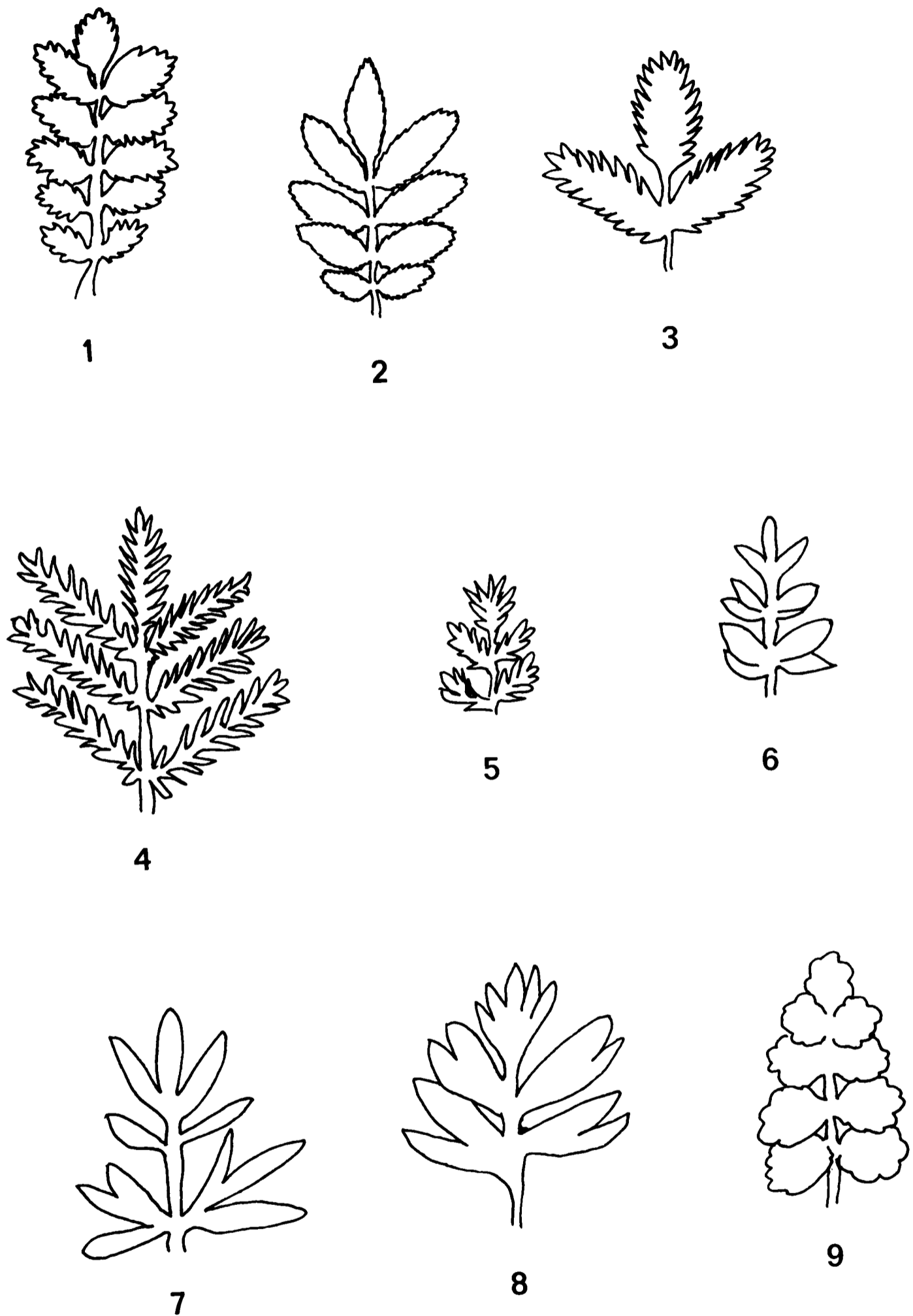


Figure 19. The basic leaf shapes in the genus Acaena

Key: 1.Antarctica; 2.Argentea; 3.Eupatoria; 4.Myriophylla;
 5.Macrocephala; 6.Lucida; 7.Platyacantha; 8.Caespitosa;
 9.Pumila

(not to scale)

Hutchinson (1959) has suggested that as a general rule simple leaves probably precede compound leaves, though Davis and Heywood (1965) believe this is subject to many exceptions, since it may often be difficult to decide if a simple leaf is evolutionally simple or if it is derived from a simple - complex - simple series of changes. Eames (1961) has shown that in at least some cases stipulate leaves are likely to be more primitive than exstipulate. Figure 19 shows the basic leaf types in the genus and Table 6 gives details of the occurrence of stipules in most species. All the leaves in this genus are compound but detailed leaflet structure varies quite widely between species.

The characters of inflorescence position and type, the number of spines on the fruit, the leaf type and the presence or absence of stipules are the only characters which are examined here by the author from an evolutionary point of view. Obviously, many other characters could have been used and these may well have presented rather different patterns for interpretation. The choice of these particular characters has been dictated by several considerations: they exist largely within two states in the genus (except for leaf type), they show little variability within taxa except under exceptional circumstances, and they appear to be important from an adaptation or life cycle point of view (this is excluding stipules). This last criterion might well appear more subjective than it is in fact. Characters such as number of spines on fruit are of major importance if a species is reliant on animal dispersal. The production of terminal inflorescences, as against axillary, markedly influences the growth pattern and often the rate of production of inflorescences per unit area. Leaf type is again of considerable importance in its link with growth form.

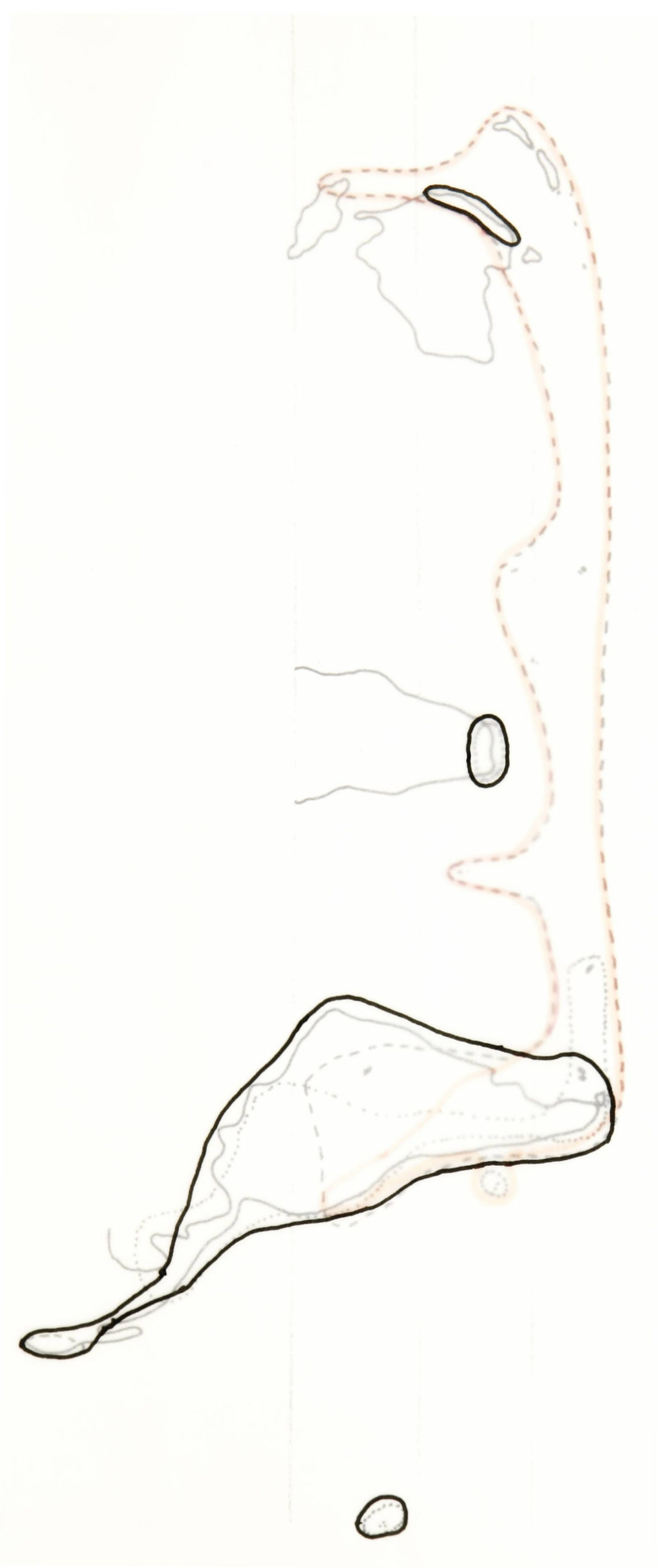


Figure 20. Distribution of inflorescence types in the genus Acaena L.

- Key: figure - terminal flowering type
 auxiliary flowering type
 overlay - capitate
 racemose

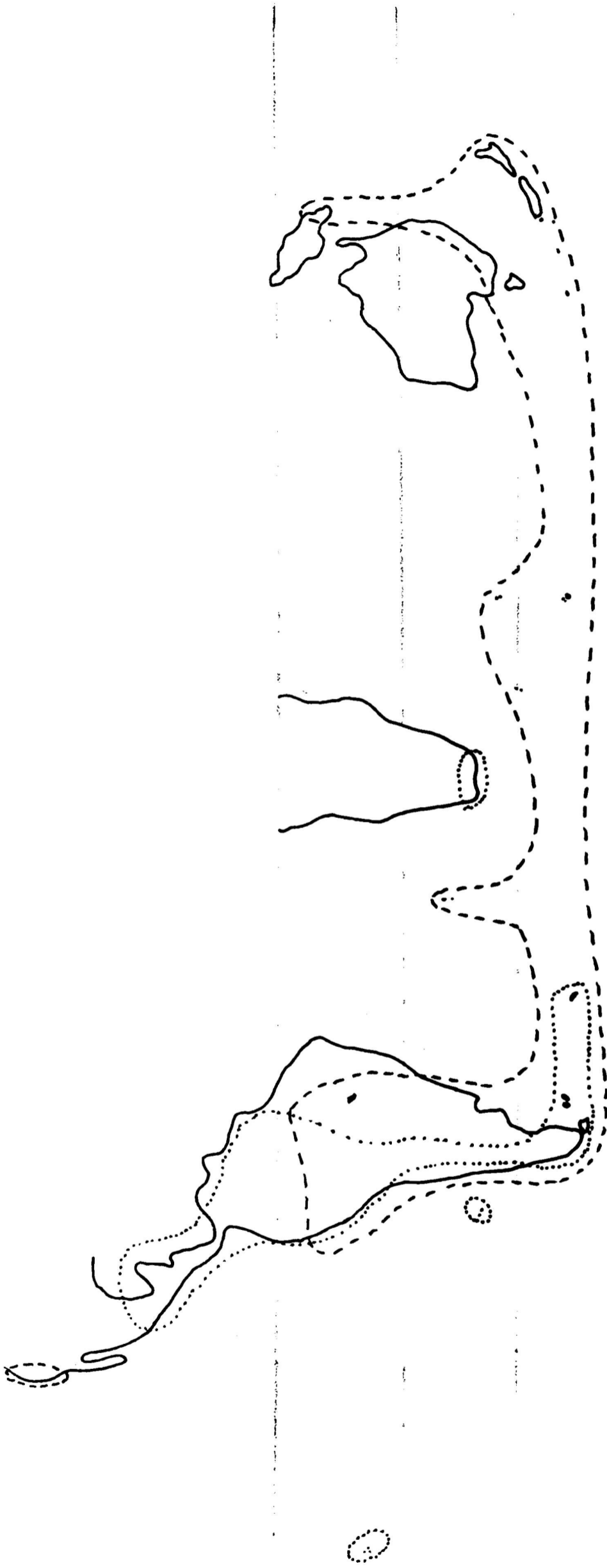


Figure 20. Distribution of inflorescence types in the genus Acaena L.

Key: figure - terminal flowering shoot - - - - -
axillary flowering shoot
overlay - capitata inflorescence — (red)
racemose inflorescence — (black)

Other characters which have been considered by the author include anther and stigma colour, stigma type, hair types and flower morphology but, aside from the difficulties of recording some of them satisfactorily, none appeared to the author to be of very great evolutionary importance.

The distribution of the two inflorescence types is shown in the overlay to Figure 20. The capitate species have a continuous distribution, basically Andean - Southern Circumpolar - Australasian, whilst the racemic types have a main group in South and Central America with several disjunct species (A.exigua, A.californica, A.latebrose and A.ovina). ^{distribution of the two} The types of inflorescence insertion is shown in Figure 20, and it is clear that the terminal type has a very similar distribution to that of the capitate headed species, although there is one disjunct species in California. Leaf type appears to be quite variable (Table 6) but of the 47 species listed over 70% have leaf types 1-3. Whilst it would appear from Table 6 that there are far more species with terminal inflorescences than axillary, 40% of the species with the terminal type are New Zealand species. This New Zealand group all possess stipules and again make the distribution of this character within the genus seem unbalanced. If the New Zealand group are treated as one species group there are then about equal numbers of species with and without stipules.

Although inflorescence type has been recorded as capitate or racemic for the purpose of mapping this slightly oversimplifies the situation since some species could be described as having more or less spicate inflorescences, these having been recorded as racemic rather than capitate. All except two species within Acaena normally have glochids on their fruit spines. Again, by scoring the remaining species for fruits with few spines (6 or less) or fruits with many spines two clear groups emerge in which the majority of the multispined fruits are associated with racemic (or spicate)

inflorescences whilst the few spined fruits are always found in capitate inflorescences. In a few instances multi-spined fruits do form capitate heads, e.g. A. macrocephala and A. leptacantha, but these are the exception and their heads have a low fruit density compared to capitate species such as A. magellanica. There are certain species which appear to show a transitional stage of development between the 4 spined fruit of a capitate head (A. magellanica) and the multispined fruit of a true racemic inflorescence (A. elongata). Instead of having spines distributed uniformly over the whole fruit, these species, e.g. A. pinnatifida, have an angled fruit instead of a round or oval one and the spines are often restricted to the edges of the angles. It would therefore appear that a connecting series of types exists for inflorescence type, leaf type, fruit type and stipules although each category can usually be characterised by a small number of states into which the majority of species fall.

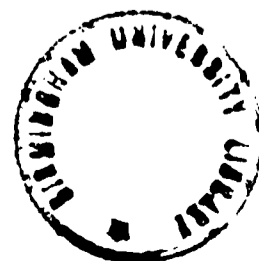
Having examined the geographical distribution of these characters it is now necessary to connect them with the distribution of individual species and groups of species. In this way the suggested evolutionary trends within the genus may throw some light on the possible earlier paths of distribution of species. The genus has two main areas of importance, southern South America and New Zealand, the species composition of each area being quite different. The New Zealand species all have general morphological similarities, with capitate terminal inflorescences, usually with two stamens per flower (anthers and stigmas being white in the majority of species), 4 spined fruits and a similar stipulate leaf shape throughout. The species are not easily distinguished from each other in some instances. To date the most common chromosome number recorded for these species has been the diploid, $2n=42$ (Moore, 1964, 1972) and several workers have remarked on

Table 6 - Leaf type, the occurrence of stipules and the position of the inflorescence in *Acaena*

Species with stipules			Species without stipules or with rare rudimentary ones		
Leaf type		Inflor. position	Leaf type		Inflor. position
1	Anserinifolia	T	1	Integerrima	T
1	Buchananii	T	1	Sericea	T
1	Caesiglauca	T	2	Splendens	T
1	Fissistipula	T	4	Pinnatifida	T
1	Glabra	T	5	Leptacantha	T
1	Hirsutula	T	5	Macrocephala	T
1	Inermis	T	5	Poeppigiana	T
1	Insularis	T	6	Confertissima	T
1	Magellanica	T	7	Platyacantha	T
1	Microphylla	T	8	Alpina	T
1	Minor	T	8	Caespitosa	T
1	Novae-Zelandiae	T	8	Californica	T
1	Ovalifolia	T			
1	Pallida	T	2	Cylindristachya	A
1	Pusilla	T	6	Lucida	A
1	Saccaticupula	T	9	Pumila	A
1	Sarmentosa	T		Latebrosa	
1	Stangii	T			
1	Viridior	T			
2	Argentae	T			
3	Eupatoria	T			
3	Ovina	T			
3	Stricta	T			
4	Myriophylla	T			
8	Trifida	T			
1	Antarctica	A	The numbers refer to the leaf type of each species (see Figure 20).		
1	Montana	A	The letters refer to the position of the inflorescence: T = terminal;		
1	Masafuerana	A	A = axillary.		
1	Tenera	A			
2	Elongata	A			
3	Exigua	A			

the frequency of hybridity (Buchanan, 1871; Cockayne and Allan, 1934; Dawson, 1960; Allan, 1961). All this suggests very strongly that there was a close ancestral connection between all the currently recognised New Zealand species and that speciation may still be occurring to some degree. The two Australian species, A.ovina and A.montana, have no connection with the New Zealand species. A.ovina is very similar to the South American A.eupatoria. Orchard (1969) regarded this species as a complex of clearly definable species, a statement which is not accepted by the author. There is however evidence that speciation is currently occurring within A.ovina and it is of particular interest that this species, with a racemic inflorescence, has been found to hybridise with a capitate New Zealand species, A.anserinifolia, (Buchanan, 1871). A.montana is much rarer than A.ovina being restricted to alpine regions in Tasmania. It appears to be related to the A.tenera/A.antarctica/A.masafuerana group and its habitat restriction is similar to that imposed on the other species of the group. This type of connection between South American species and those endemic to Tasmania and Australia is not uncommon (Skottsberg, 1915).

The South American species have both racemic and capitate inflorescences, borne generally in a terminal position. Some species show a considerable amount of morphological variation, e.g. A.magellanica, A.pinnatifida, but most species are quite clearly distinct. The species show much greater diversity of leaf shape than the Australasian species and are about equally divided between those with stipules and those without. Hybridisation in the field is apparently very rare (Grondona, 1964; Walton and Greene, 1970), and although diploid and tetraploid chromosome numbers have been found diploid appear to be the most common at the moment.



A number of isolated endemic species need to be accounted for to complete the survey of the genus. A.latebrosa (= A.decumbens (Linn.f.) Druce) is a rare plant found in Cape Province. It has an axillary racemose inflorescence and multispined fruits, linking it with the South American species. Bitter (1911) treated it separately in a section of its own, and suggested that it came somewhere between A.elongata/A.stricta and A.pumila/A.exigua. This view has yet to be investigated by the author.

A.sarmentosa and A.stangii, the two Tristan da Cunha species, are very closely related and appear to be derived from the same ancestor, in the opinion of the author. They occupy very similar ecological niches on the island to those of A.magellanica and A.tenera on South Georgia, A.sarmentosa being the more common lowland species whilst A.stangii is the alpine species. There appears to be no hybridisation between the two species (N. Wace, pers. comm.). The Tristan species appear to fall within the A.anserinifolia group rather than the A.magellanica group and this relates them to the species found on New Amsterdam and St. Paul, A.insularis, an endemic described by Citerne (1897). The Tristan flora shares several species with New Amsterdam and St. Paul including two species of Uncinia, Phyllica arborea and ten pteridophytes.

The species from Hawaii, A.exigua, is a very rare alpine limited to only a few islands in the archipelago. With its axillary scapes and multispined fruits its closest relative is A.pumila, a species not apparently occurring any further north than 39°S in Chile. The connection between the floras of California and Chile (Raven, 1963) is evidenced by the similarity between A.californica and the South American species A.pinnatifida and A.trifida.

On the basis of the data presented above some provisional hypotheses can be put forward to explain the present distribution of Acaena and suggestions can be made about some possible lines of evolution in the genus. The greater range of variation shown by the South American species together with the occurrence in tropical latitudes of species with primitive racemic axillary inflorescences (A.cylindristachya, A.elongata) suggest an origin for the genus in the tropical Andean part of South America, possibly from a common ancestor with Poterium. The ancestral species probably had a basal rosette of leaves, possibly with a leaflet type 1-3, a lax racemic inflorescence of multispined fruits and a chromosome number $2n=42$. It also seems likely that the inflorescence was axillary rather than terminal. Speciation seems to have produced a number of groups within the genus as it extended out from the tropics into cooler temperate latitudes. Reduction in the inflorescence making it capitate with few spined fruits appears to have been one major line of evolution. This group has spread, possibly via the sub-Antarctic islands to New Zealand where the diversity of ecological niches (Raven, 1973) has allowed considerable speciation from a narrow base. Since the speciation in A.ovina is much less developed it is considered that this was a later introduction from material now attributable to the A.eupatoria group. Speciation within South America has resulted in a continuation of the ancestral line with probably few changes in a tropical environment (A.cylindristachya), whilst a number of intermediate stages between racemic and capitate inflorescences are still in evidence. Probably running concurrently with the change from racemic to capitate has been the change from axillary to terminal inflorescences. The position of A.latebrosa both morphologically and geographically suggests that its introduction

to South Africa may well have taken place before much speciation had occurred in South America. On the other hand, A.californica must have been introduced to California by long-distance dispersal from Chile at a late date because of its close similarity to A.trifida.

Whatever may have been on the sub-Antarctic islands before the last major glaciation was most probably largely removed during the glacial period and the present flora is due to re-introduction by long-distance dispersal. This does not mean, of course, that the islands did not act as 'way stations' or 'stepping stones' for species moving between South America and Australasia in the earlier interglacial periods. Indeed, earlier suggestions by Skottsberg (1936) that the distribution of the genus can only be accounted for by an Antarctic origin and spread northwards do not seem very likely in view of what is now known of the breakup of Gondwanaland. The two species of Acaena on South Georgia are unlikely to have been there for much longer than 10,000 years and must be regarded as separate introductions direct from Tierra del Fuego. A concomitant of this is that the hybrid must have arisen during that period, probably independently in a large number of sites given its apparently very low seed viability. The period of time available on South Georgia has not been sufficient to allow any degree of speciation to occur, unlike the situation on Tristan where the exposed rock has been dated at c. 1 million years (Baker et al. 1964), this apparently being sufficient to allow the evolution of two distinct species of Acaena.

Chapter 6

GROWTH OF THE SEED

Seed Germination

Materials and methods:

The effect on germination of a number of climatological treatments was investigated. Only seeds of A.magellanica and A.tenera were used because a number of trials with the hybrid showed it to give only 0-1% germination.

(1) Effect of varying temperatures:

Seed which had wintered in the field was germinated in controlled temperature chambers on filter paper in plastic petri dishes, each dish containing fifty seeds. There were two replicates for each treatment. Seeds were removed as they germinated. The criterion adopted for deciding when a seed had germinated was that the length of the extending radicle must have been at least twice as long as its basal width. Nine different temperature regimes were used. The requirements of other phytotron users meant that the light period was split into two periods of 8 hours, whilst the dark period was one period of 8 hours. The effects of light and dark on germination will be dealt with later.

The temperature treatments used were as follows:- (temperatures in °C).

		Treatment symbol								
		5/5	5/10	5/20	10/10	10/5	10/20	20/20	20/5	20/10
Light	8 hours	5	5	5	10	10	10	20	20	20
	8 hours	5	10	20	10	5	20	20	5	10
Dark	8 hours	5	10	20	10	5	20	20	5	10

(2) Effect of cold treatments:

The seed used for this experiment was collected at the end of summer in March 1968. For the cold pre-treatment batches of 50 seeds were put into two sections of a dark refrigerator at -4°C . or -11°C . The seeds were in small, dry, glass tubes. Samples were taken from the -4°C . ^{regime} at weekly intervals and from the -11°C . ^{regime} at fortnightly intervals. They were sown on filter paper in petri dishes and incubated at 20°C . Three control sowings of unvernalsed seed were made during the experimental period and another one six months later.

(3) Other treatments:

Initial experiments on germination suggested that there was probably no difference between light and dark germination in both species. A second set of experiments was carried out using lots of 50 seeds and two different temperatures, 20°C . and 10°C . Overwintered seed was used, all dark dishes being kept in light-tight copper containers.

In an effort to increase the rate and decrease the delay in onset of germination, tests were done using pre-treatments in 50% H_2SO_4 or 50% ethanol, since it was thought that they might remove any germination inhibitors present. Treatments of up to four minutes in the acid and alcohol were tried on overwintered seed. Germination of seeds totally immersed in distilled water was also tested. Three continuous temperatures were used, 5°C ., 10°C ., 20°C ., with 3 replicates of 25 seeds/species/temperature.

Results:

(1) Effect of varying temperatures:

The results are shown in Figs. 21 & 22. Comparison of these graphs shows that the two species differed considerably in their

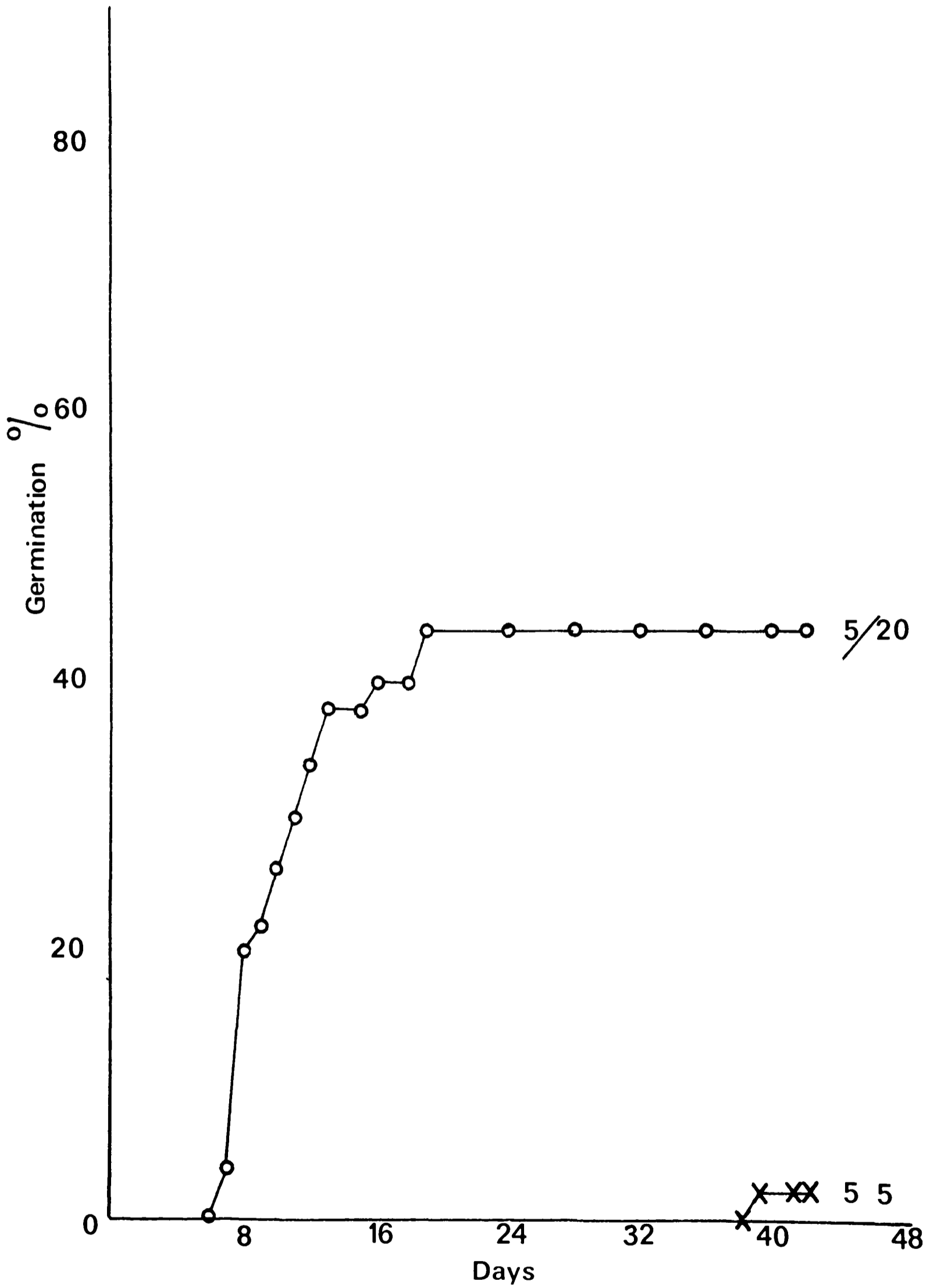


Figure 21a. Germination of A. magellanica seed in 5/5, 5/10 and 5/20 treatments

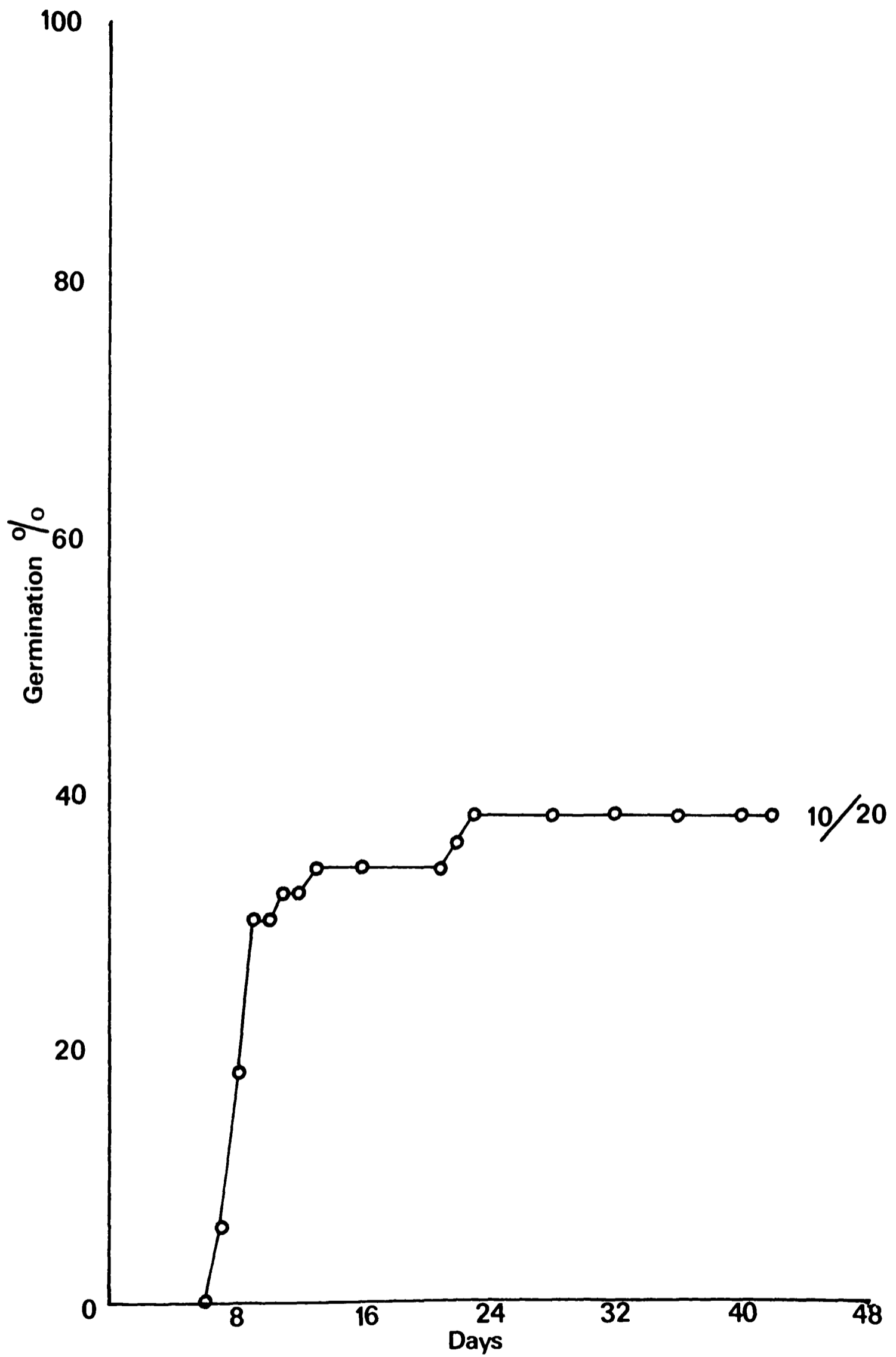


Figure 21b. Germination of A. magellanica seed in 10/5, 10/10 and 10/20 treatments

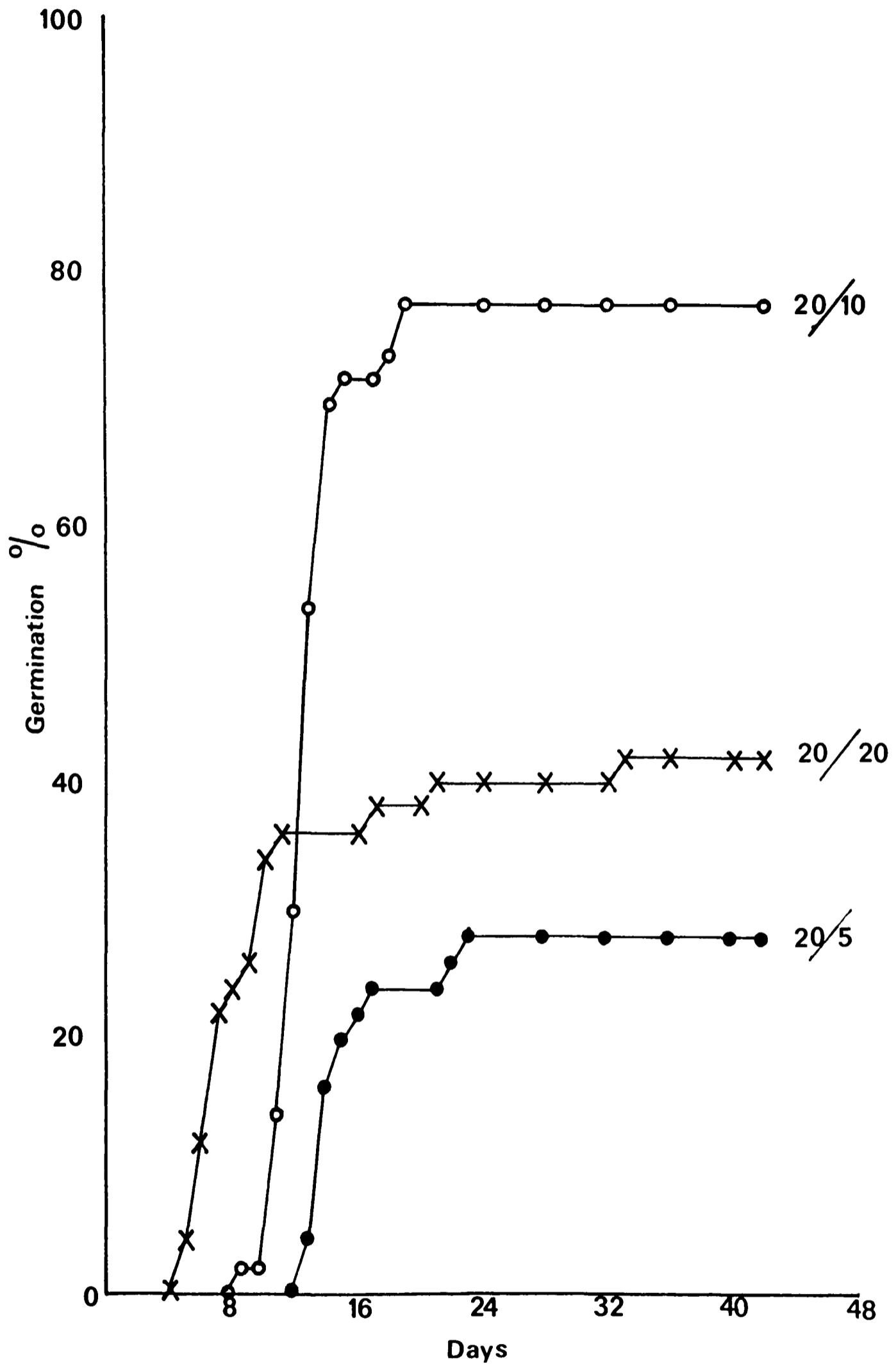


Figure 21c. Germination of A. magellanica seeds in 20/5, 20/10 and 20/20 treatments

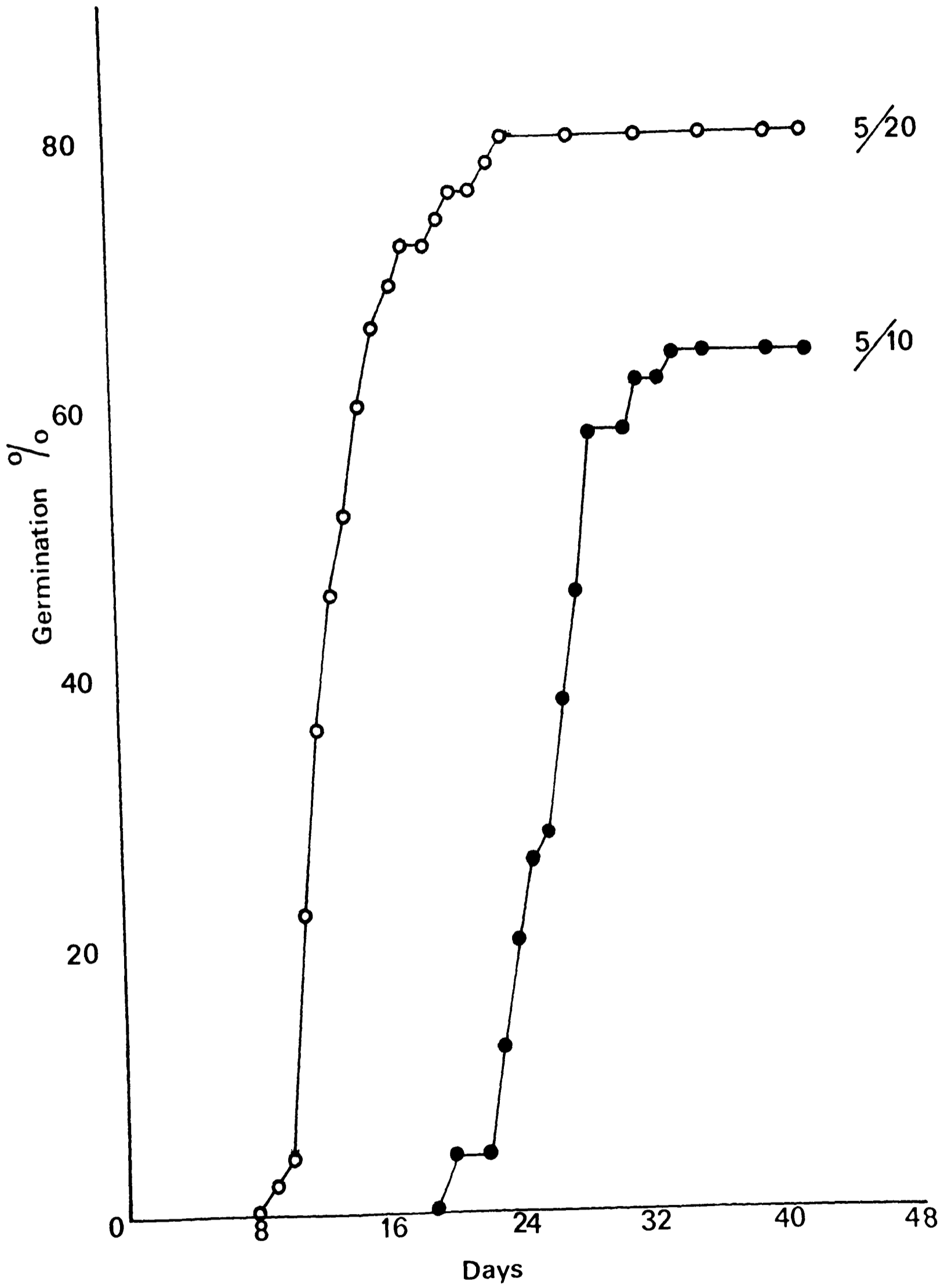


Figure 22a. Germination of A.tenera seed in 5/5,5/10 and 5/20 treatments

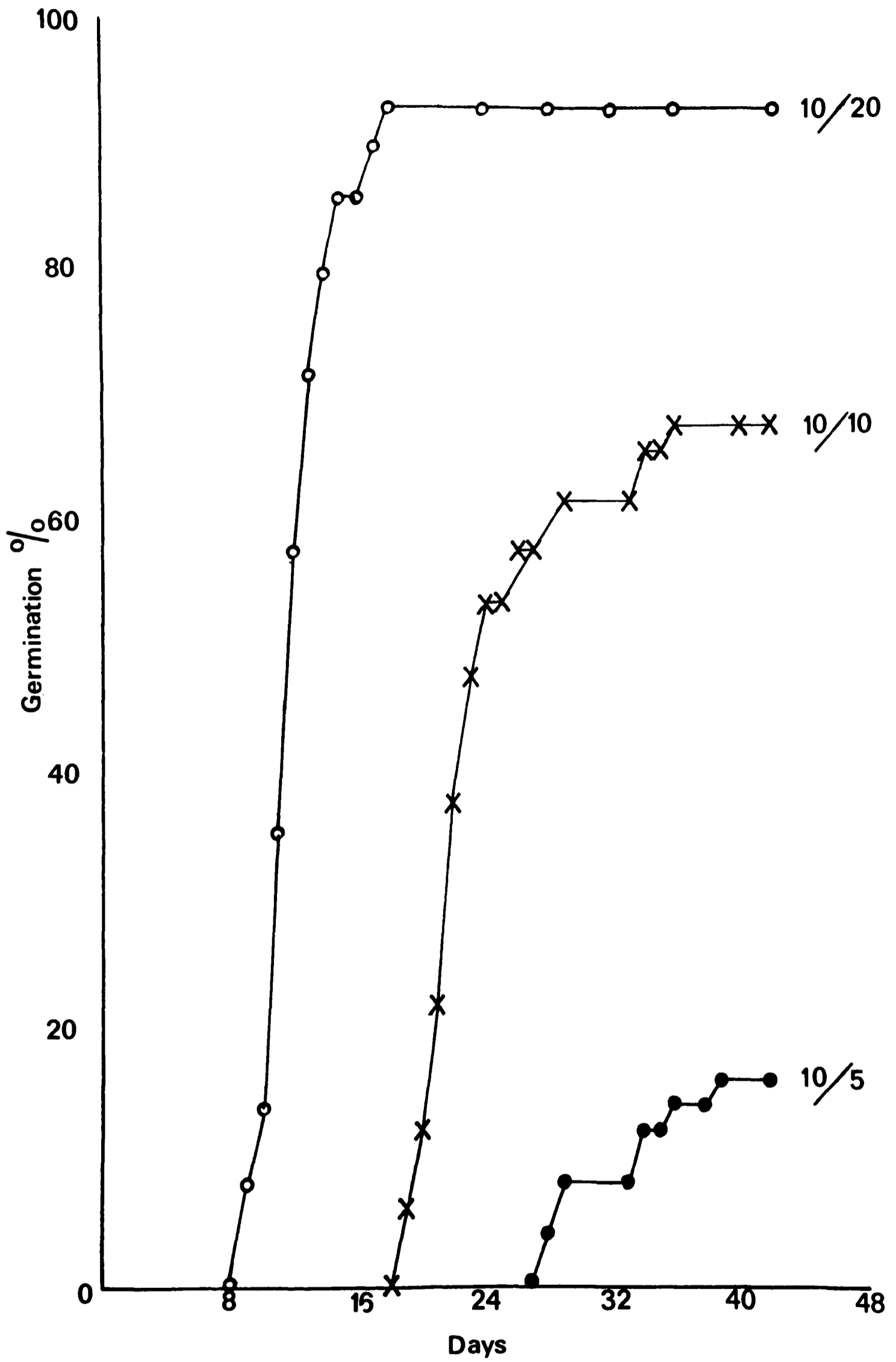


Figure 22b. Germination of A.tenera seeds in 10/5, 10/10 and 10/20 treatments

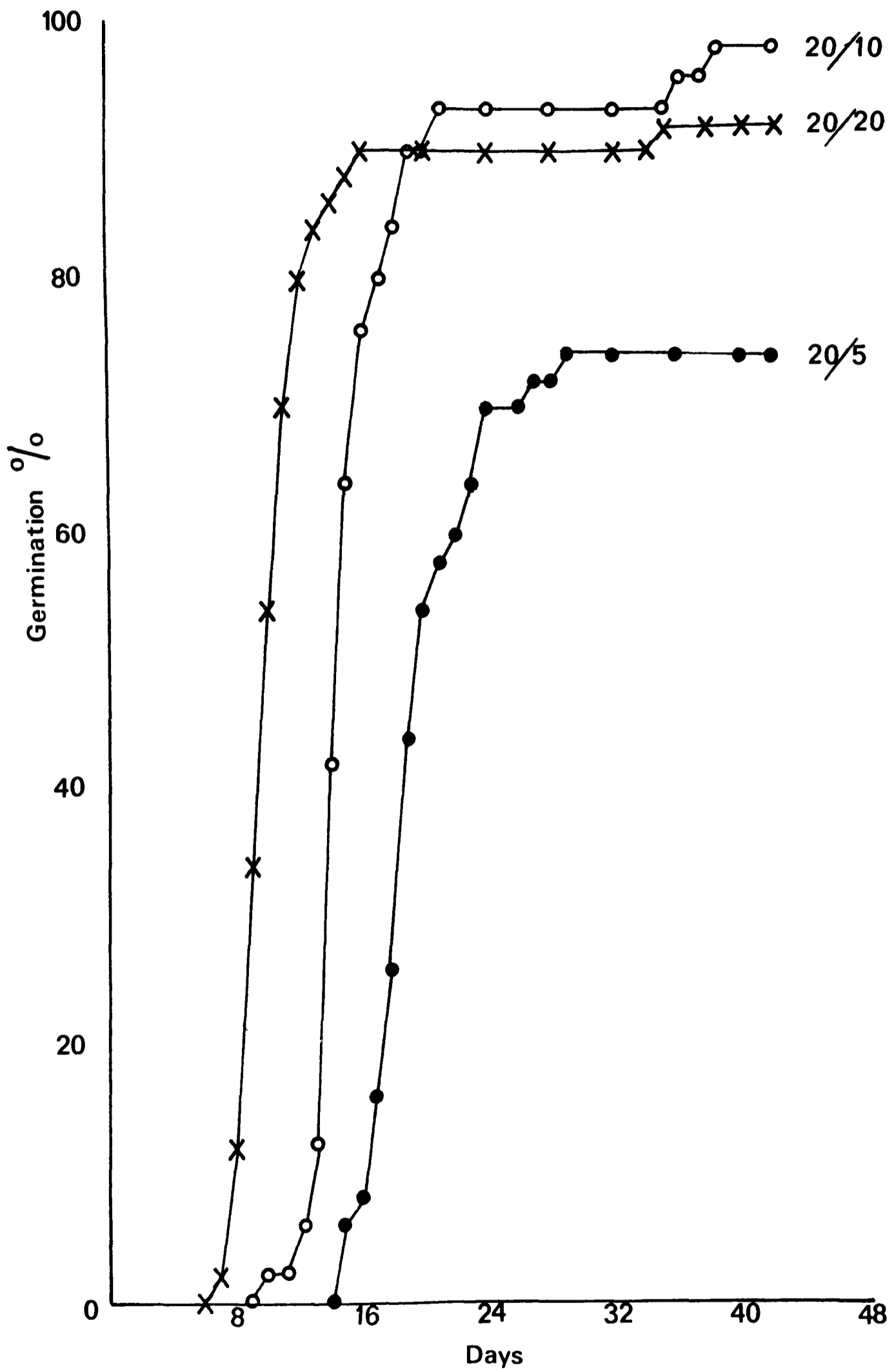


Figure 22c. Germination of A.tenera seeds in 20/5,20/10 and 20/20 treatments

response to temperature. A.tenera germinated in 8 of the 9 treatments, whilst A.magellanica only germinated in 6 treatments. In all treatments the final percentage was higher in A.tenera, though the rate was approximately the same for both species. The 20/10 i.e. warm day, cool night, gave the highest rate for A.magellanica, this being equalled by A.tenera in 20/20, 20/10 and 10/20. The graphs show the time of onset of germination for each treatment. The period between sowing and germination is never less than 4 days and can be 38 days or more. If the delay time is plotted against the daily degree hours total for each treatment the points shown in Fig. 23 result. The degree hours total is calculated by adding together the mean temperatures for all the hours of a day, e.g. treatment 20/10 has 8 hours at 20°C. and 16 hours at 10°C. so the degree hour total for the day is $(20 \times 8) + (10 \times 16)$ equals 320. Fig. 23 shows that for every treatment in which both species germinated A.magellanica always germinated before A.tenera. Although it is possible to predict from the figure the approximate time delay that should have ensued before germination of the 5/10 and 10/5 samples of A.magellanica, i.e. 5/10 c. 16 days and 10/5 c. 22 days, neither of these samples showed any germination even after 40 days. The reason for this is not clear, though a number of explanations are possible. It may be that below a certain level of degree hours per day metabolic activity is too low to allow germination to occur, or it is possible that although the degree hour total per day can be kept low, it must be differently divided within the day to allow germination to take place. For instance, the 160 degree hours made up of 8 hours at 10°C. and 16 hours at 5°C. which did not allow germination might allow it if it was composed of 4 hours at 20°C. and 20 hours at 4°C.

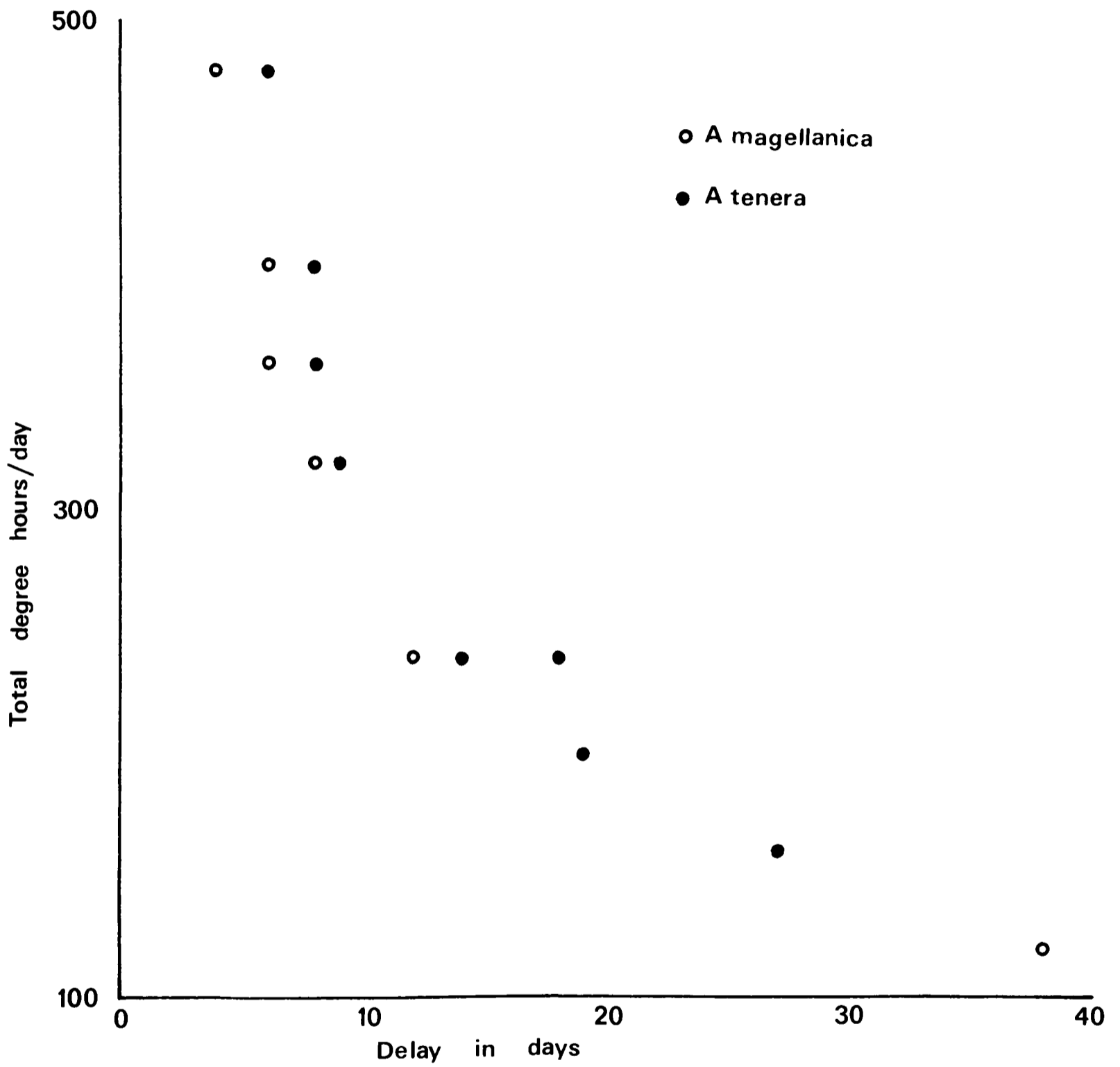


Figure 23. The delay in the onset of germination at various temperatures

The major germination differences between A.magellanica and A.tenera would seem to be that although A.magellanica usually germinates earlier, A.tenera has a much wider latitude in its temperature requirements and normally has a higher final germination percentage.

(2) Effect of cold treatments:

The results are shown in Fig. 24. These do not give the exact date of the onset of germination but the graphs do show the rate of germination in each sample and the final percentage germination. The samples treated at -4°C . show an increasing rate up to week 6 for A.magellanica and up to week 7 for A.tenera, which then begins to fall off to a very low point at week 10 for both species. The -11°C . samples show a rather similar trend, with the best rates from the 6 week sample for A.magellanica and for A.tenera. Overall, the 4 and 6 week cold treatments gave the best results.

The results of the four controls show how variable unvernalsed seed can be in germination potential. The first controls showed no germination even after 28 days. The second controls are shown on the graphs. The third controls showed a higher initial rate than the second ones, but had to be abandoned early due to their becoming infected with fungus. The fourth controls set up about six months after the end of the experiment, are also shown on the graphs.

From the foregoing results it would seem possible to make a number of tentative deductions. It appears from the graphs that the requirement for a cold pre-treatment of seed before germination is only facultative, and that it may diminish with age. Seeds are most unlikely to be subject to continuous temperatures of -11°C . in the South Georgian winter in any area with continuous snow cover (Longton and Greene, 1967), although ground temperatures of -4°C . are probable. Ten weeks exposure

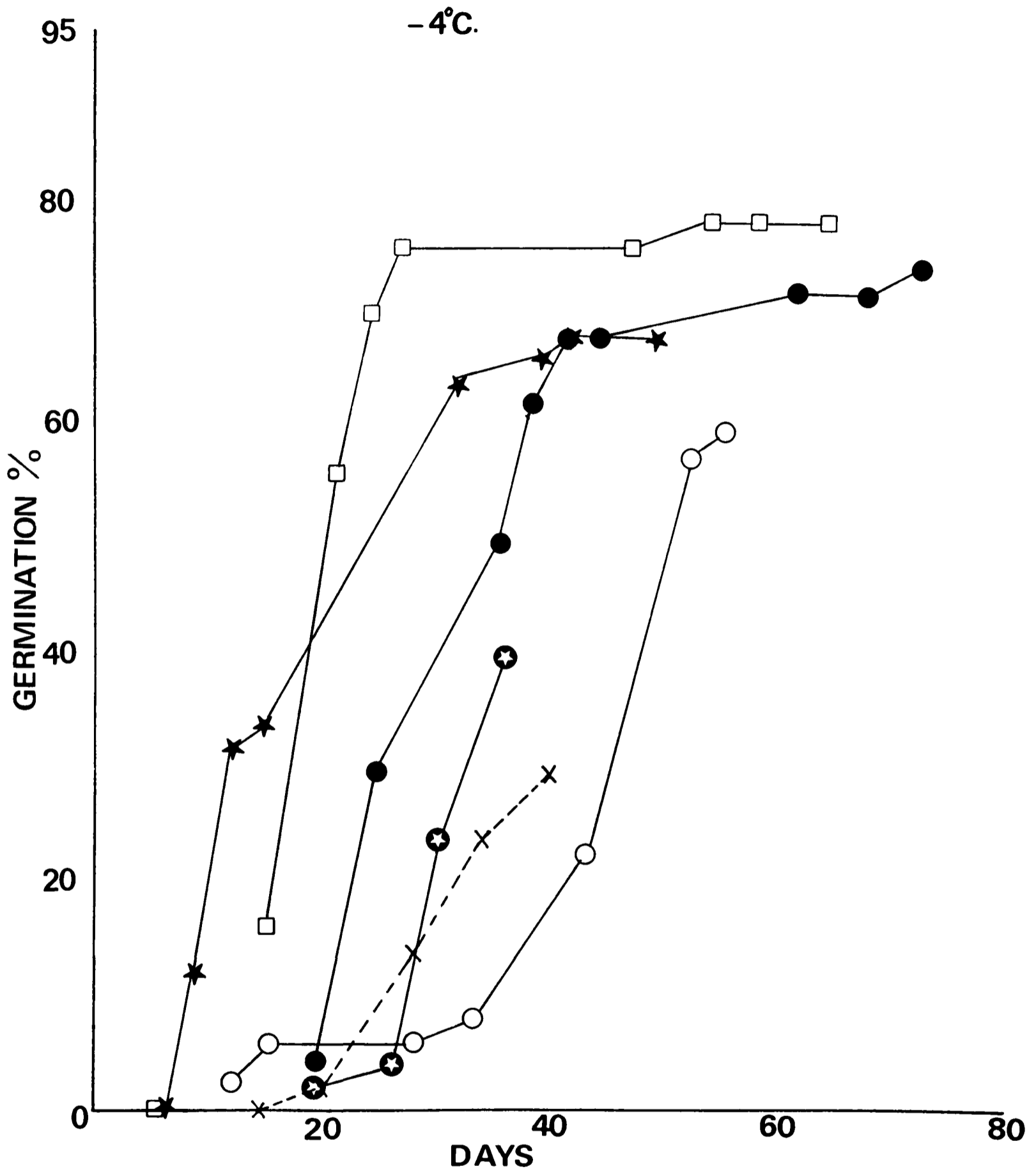


Figure 24a. Germination of *A. magellanica* seeds subjected to varying periods of cold pre-treatment at -4°C

Key: number of weeks at -4°C

- 2 weeks
- 4 weeks
- 6 weeks
- ★ 8 weeks
- ⊛ 10 weeks
- × control

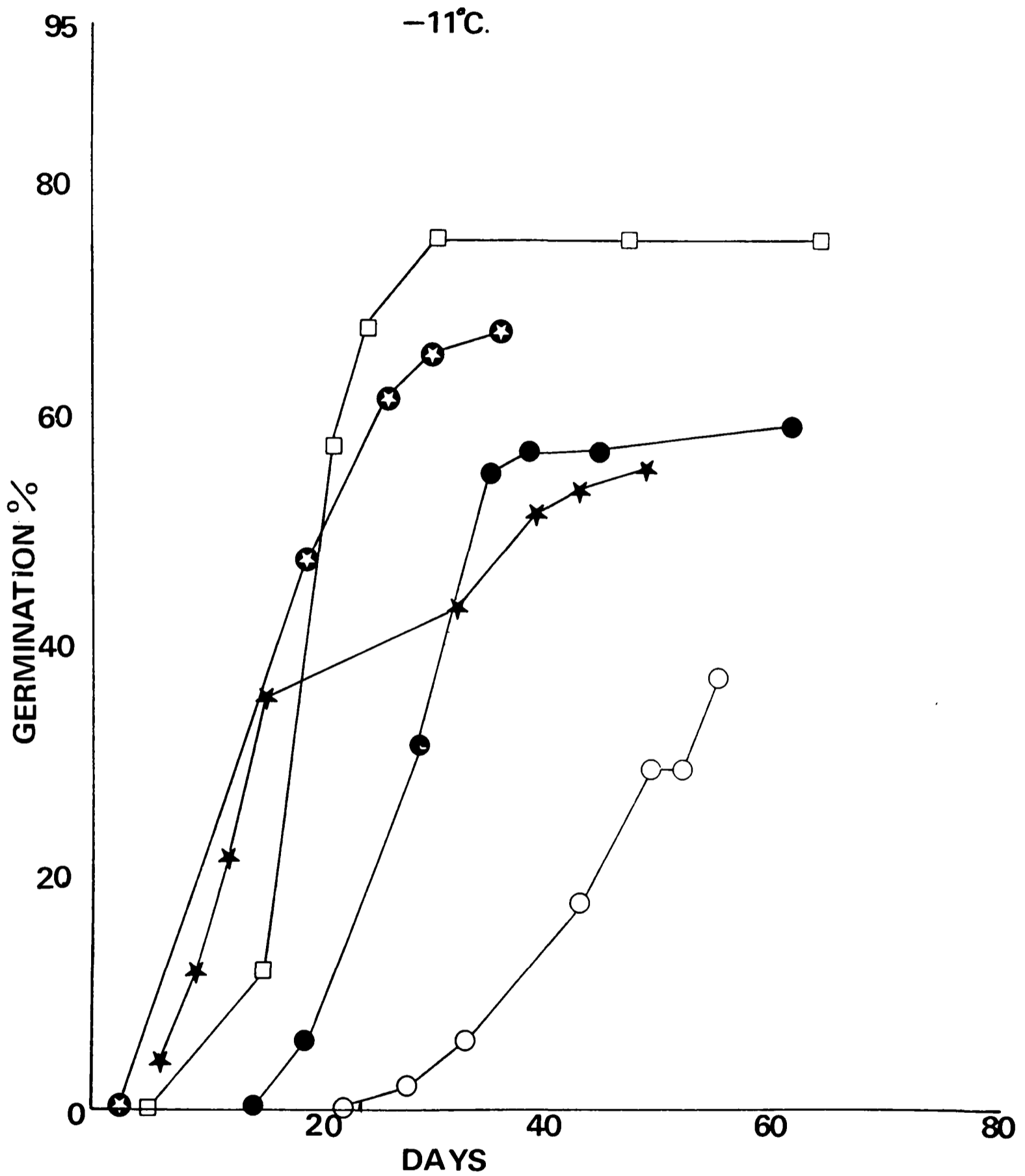


Figure 24b. Germination of *A. magellanica* seeds subjected to varying periods of cold pre-treatment at -11°C
 Key: as in Fig. 24a

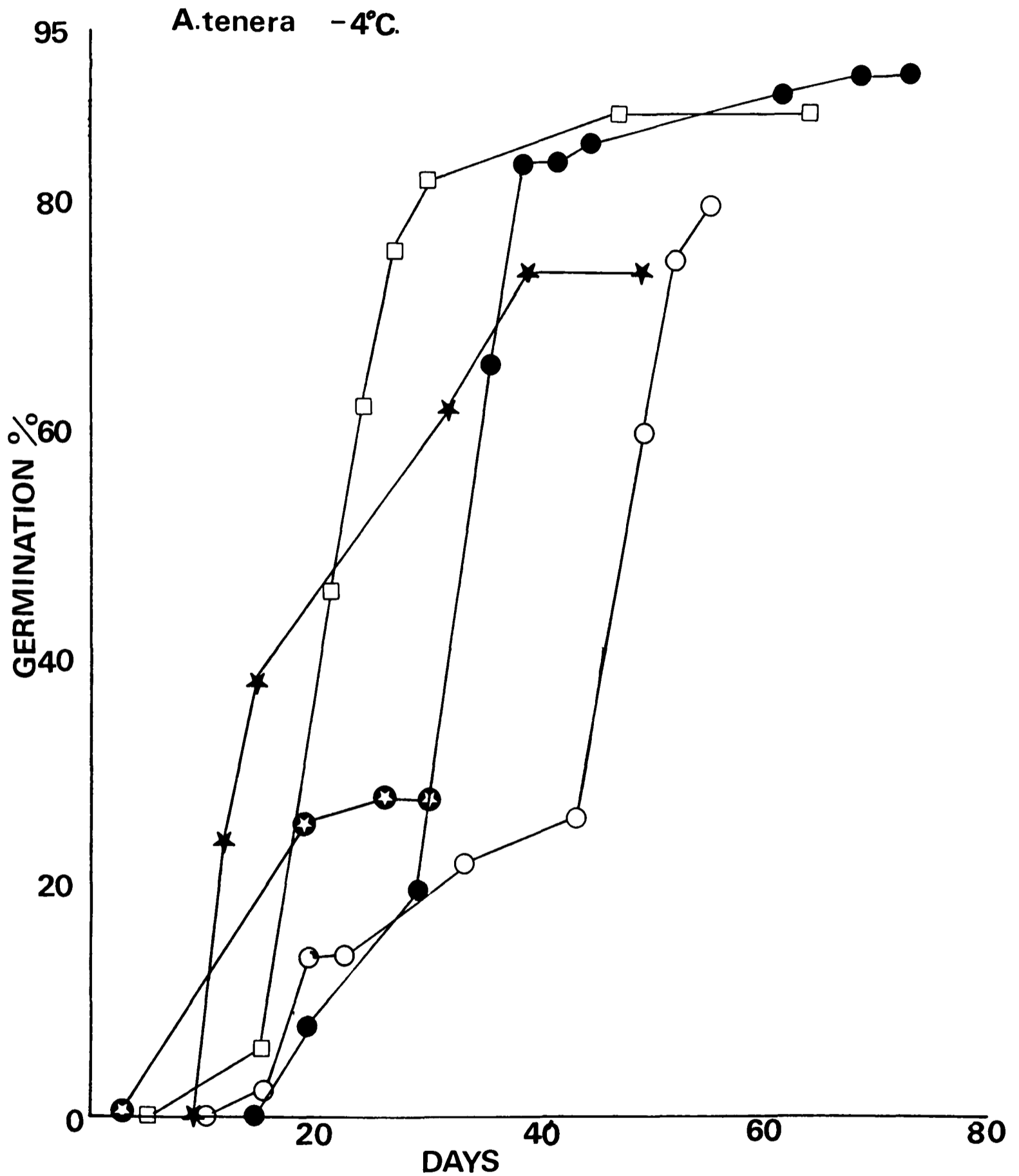


Figure 24c. Germination of *A.tenera* seeds subjected to varying periods of cold pre-treatment at -4°C

Key: number of weeks at -4°C

- 2 weeks
- 4 weeks
- 6 weeks
- ★ 8 weeks
- ⊛ 10 weeks

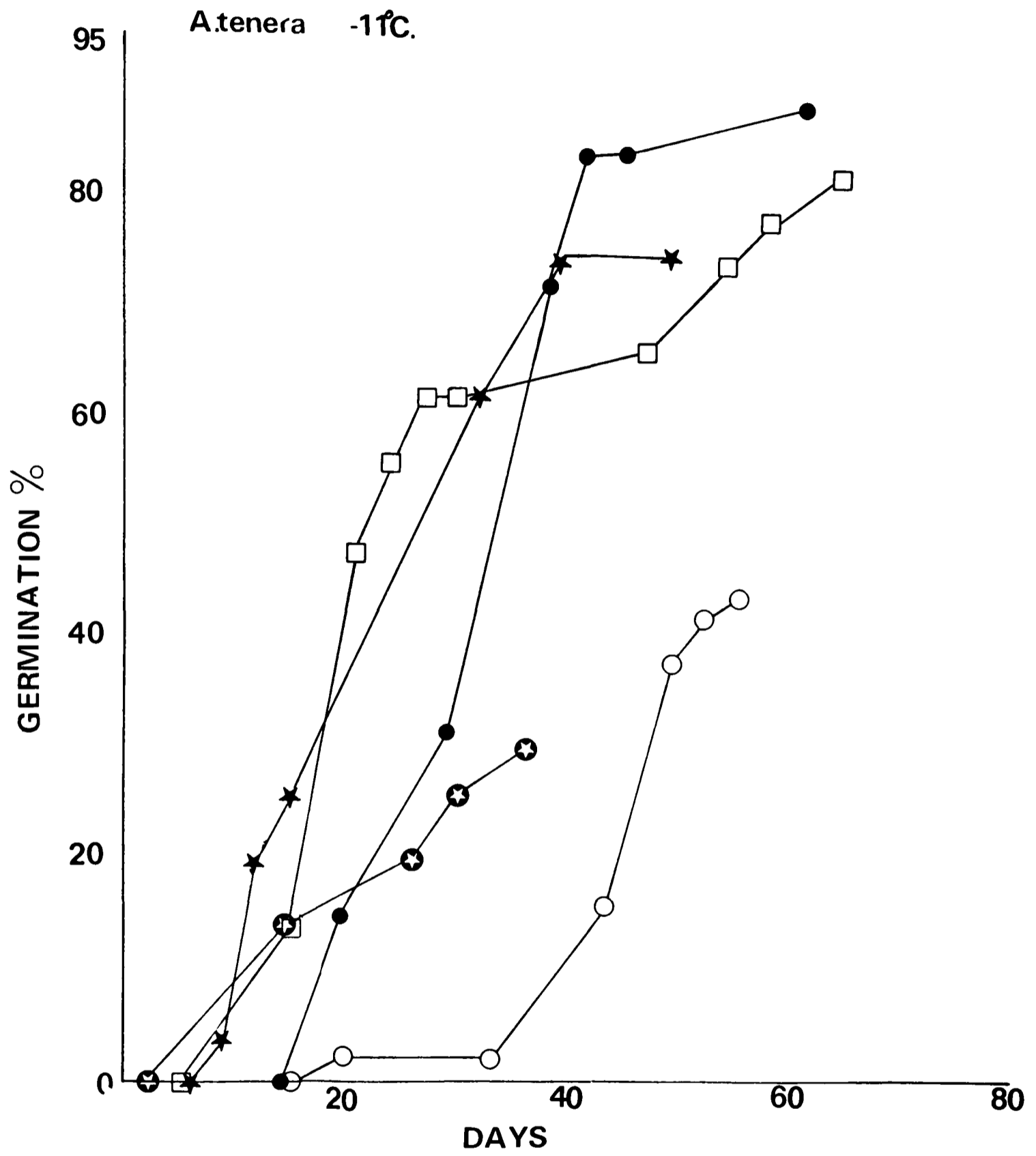


Figure 24d. Germination of *A.tenera* seeds subjected to various periods of cold pre-treatment at -11°C
 Key: as in Fig.24c

to a temperature of -11°C . seemed to depress germination a little but the final percentages for both species showed that the seeds could survive the worst conditions that South Georgia is likely to experience in winter, as long as they remain ungerminated.

(3) Other treatments:

Treatments in acid proved uniformly ineffective in hastening germination. Ethanol treatments gave variable results none of which showed any significant hastening of germination or increase in the rate. The germination experiments in distilled water also gave variable responses which are summarised below. In most cases the maximum percentages achieved were as high as in the normal germination experiments.

Seed Germination in Water.

Days after sowing	<u>A. magellanica</u>		<u>A. tenera</u>	
	10°C.	20°C.	10°C.	20°C.
7	0	8-28%	0	0-6%
11	0	26-80%	0	0-40%
17	0	36-84%	6%	24-50%

It was noticed that the extrusion of the radicle by the seeds immersed in water was somewhat abnormal. Normally after the radicle appears it grows quickly to a length of a centimetre or more. In many of the immersed seeds the radicle either grew very slowly or stopped altogether after about 3 mm. This was particularly so in seeds of A. tenera. Attempts have also been made to remove the outer coats of the seeds in both species, but this has proved difficult without causing some damage to the seed.

Most of the seeds from which the testas were successfully removed succumbed to fungal infection in a very short time, making it impossible to discover if the operation resulted in enhanced germination rates.

The experiments at 20°C. and 10°C. to test for differences between light and dark germination showed that although germination onset was normally at the same time in both light and dark considerably higher final percentages were achieved in the light rather than the dark by both species. This was consistent in both temperature treatments.

Establishment of the Seedling

Finding the right ecological niche to germinate in does not automatically lead to each seed producing a fully-fledged plant. If the seed should germinate in an already established plant community it will have to compete with all the species present for essential nutrients, water and light. If, on the other hand, it falls on to bare ground much of the likelihood of establishment will depend on the local microtopography of the soil surface and the type of soil. It is at this point that the size of the seed and of its cotyledons can be critical (Salisbury, 1942) whilst the rate of growth of the seedling during its first summer may well determine whether the plant will become permanently established.

Materials and Methods:

Acaena seedlings have been found germinating both in moss and on areas of bare ground. Since the seedlings establishing on bare ground were colonising a new area and increasing the distribution of the species it was decided to test for germination and establishment of both

A. magellanica and A. tenera in two soil types at various sites on South Georgia.

Accordingly, ungerminated seeds of the two species were planted at 10/pot at six sites in early February 1970. Six pots of each species were planted for each soil type, a loam from beneath Festuca grassland and a mineral soil from a frost heave area. The six sites used were: Grassland, Heath, Fellfield, Acaena sward, Acaena Fellfield, and Rostkovia bog. All pots were sunk into the ground to their rims. The seeds were planted c. 5 mm. below the soil surface. No water or nutrients were given to the pots.

Results:

The pots were examined in March, November and December 1970, and in February and March 1971. The first seedlings were seen in December 1970 in mineral soil pots at the Acaena sward site. Apparently no seeds had germinated at the end of the last season and over-wintered. Table 7 shows the number of seedlings present in February and March 1971 together with an assessment of their growth as shown by the mean number of leaves per plant for each treatment.

When the pots were examined in February 1971 clear evidence of frost action could be seen, especially in the mineral soil pots. This had brought many small stones to the surface and in many cases seedlings were gaining considerable advantage from the protection afforded by them. This sorting was most in evidence at the Fellfield and Heath sites, where it has also had the effect of bringing the planted seeds to the surface.

The high water table in the pots at the Rostkovia bog site apparently precluded any germination, although by the end of the experiment some mosses had begun to colonise the soils.

At the Acaena sward site the A.magellanica plants afforded a high degree of shelter to the pots and had to be regularly cut back to prevent them being overgrown. At the end of the experiment the leaves of both species at the Acaena Fellfield site were small with reddish tips, with the cotyledons apparently still in use, whilst^{at} the Acaena sward site the cotyledons had almost all died and only the A.tenera seedlings had red tips to their leaves. The leaves of both species were bigger at this site than at the Acaena Fellfield one. At all sites the root systems of all seedlings in loam were much shorter and more branched than those in mineral soil. Table 8 shows the percentage of the seeds planted that were actually present as plants at the end of the experiment, after almost 14 months.

For both species higher percentages were achieved in all cases for the mineral soil rather than the loam. Out of twelve treatments for each species only four succeeded for A.magellanica but seven succeeded for A.tenera. It is very interesting to observe that both species were most successful at the Acaena sward site, but that A.tenera also achieved considerable percentages at the Grassland and Heath sites. In all treatments in which plants were established A.tenera had a higher percentage than A.magellanica.

The apparently greater suitability of the mineral soil over the loam for germination and establishment was not unexpected since it offered a more variable microtopography than the loam. A.tenera, which tends to grow in the more exposed situations could be expected to do better on mineral soil than A.magellanica would. The protection afforded by the small stones in the mineral soil could well play a decisive part here, since

Table 7 Establishment and development of seedlings at various sites

	<u>A. magellanica</u>				<u>A. tenera</u>			
	loam		mineral		loam		mineral	
	\bar{x} lf.no.	no. plants	\bar{x} lf.no.	no. plants	\bar{x} lf.no.	no. plants	\bar{x} lf.no.	no. plants
17 FEBRUARY 1971								
Grassland	0	0	0	0	2.8	4	2.1	15
<u>Acaena</u> sward	4.0	2	3.4	9	2.5	4	2.7	25
<u>Acaena</u> Fellfield	2.0	1	1.1	7	0.8	2	1.0	5
Heath	0.5	1	2.3	11	2.2	5	2.0	15
<u>Rostkovia</u> bog	0	0	0	0	0	0	0	0
Fellfield	0	0	0	0	0	0	0	0

30 MARCH 1971								
Grassland	0	0	0	0	4.0	3	2.6	15
<u>Acaena</u> sward	5.5	2	5.3	8	3.3	3	3.1	22
<u>Acaena</u> Fellfield	0	0	3.0	3	0	0	2.0	4
Heath	0	0	3.3	9	1.8	6	2.0	15
<u>Rostkovia</u> bog	0	0	0	0	0	0	0	0
Fellfield	0	0	0	0	0	0	0	0

Table 8 Percentage of seeds planted present as plants in March 1971

	<u>A. magellanica</u>		<u>A. tenera</u>	
	<u>loam</u>	<u>mineral</u>	<u>loam</u>	<u>mineral</u>
Grassland	0	0	5.0	25.0
<u>Acaena</u> sward	3.3	13.3	5.0	36.7
<u>Acaena</u> Fellfield	0	5.0	0	6.7
Heath	0	15.0	10.0	25.0
<u>Rostkovia</u> bog	0	0	0	0
Fellfield	0	0	0	0

the slower-growing A.tenera seedlings were always much smaller than those of A.magellanica. In March 1971 although A.tenera had more plants established than A.magellanica the mean number of leaves per plant was always higher in the latter species. The likelihood of loam soil being available for colonisation without competition is remote but large areas of mineral soil with minimal plant cover are frequent. Comparison of the figures shown in Table 7 for the February and March scorings show that whilst some treatments were originally successful, e.g. loam at the Fellfield and Heath sites for A.magellanica and loam at the Acaena Fellfield site for A.tenera, the seedlings in these had died by the end of March. The number of plants in some of the other treatments also decreased between the two scorings, even at such favourable sites as the Acaena sward.

No clear conclusion can be drawn over the favourability for development of one soil type against another. At a sheltered site such as the Acaena sward A.magellanica grew well in both soil types, although at the Grassland site the A.tenera plants produced appreciably more leaves in loam than in mineral soil. In comparison between species, A.magellanica obviously grew faster in terms of leaf production than A.tenera.

The overall pattern that emerges suggests that A.tenera is capable of colonising a wider range of habitats than A.magellanica, and that more seedlings of A.tenera will survive in a given habitat than of A.magellanica. Against this must be set the considerably higher rate of growth shown by A.magellanica seedlings.

To test this the establishment figures for the germinated seedlings used in all the dry matter production experiments were extracted and are presented in Table 9. The numbers after the species name correspond to particular plantings so the percentage figures for each species at a

Table 9 Establishment of germinated seedlings planted in all growth experiments

Species	Expt. no.	No. seeds planted	% establishment	Growth medium
<u>A. magellanica</u>	1	200	43	Vermiculite
	2	176	65	"
	3	120	27	"
	5	96	38	Soil
	6	75	35	Vermiculite
	7	75	20	"
	<u>A. tenera</u>	1	280	66
2		176	78	"
3		120	79	"
4		96	94	"
5		120	37	Soil
6		75	46	Vermiculite
7		75	50	"

particular planting can be compared to give a measure of establishment in the standardised medium of vermiculite. In all the vermiculite plantings A.tenera had a higher percentage establishment, in some cases twice that of A.magellanica. Only in planting 5 which was in soil did the two species show about the same percentage.

It would seem therefore that, normally, more A.tenera seedlings will appear in a particular treatment if equal numbers of seeds from both species are present to start with. This is unlikely in a natural situation since A.magellanica is much more widespread on the island than A.tenera (when considering the ground area covered by the species) and is almost certainly producing a much greater number of seeds per season.

Development of the Seedling

Materials and Methods:

Observations were made on leaf production in the seedling stages. Scorings were made on seedlings sown in both vermiculite and natural soil on South Georgia, and on seedlings grown on John Innes No. 2 compost in three controlled environment chambers in Birmingham.

Only unfolded leaves were scored. A development index was calculated by multiplying the percentage of seedlings at each leaf stage by standard factors - x1 for one leaf, x2 for two leaves, etc. - and adding the results. If for instance, 50% had one leaf and 50% two leaves the development index (DI) would be 150. This method was used for all the seedling observations. The results were plotted against days since sowing and linear regression lines fitted using a programme developed by T. V. Callaghan.

Results:

The slope of the fitted linear regressions gave the mean number of days required to produce a leaf in each experiment. These figures are shown in Table 10. Quite clearly A.magellanica has a much higher rate of leaf production than A.tenera at all three temperatures. A figure of 15 days per leaf obtained for A.tenera growing in the Alpine House is similar to the value obtained for this species in the 20°C. chamber. The plants in the chamber began to show signs of stress by the time the second leaf had appeared, with the leaves being larger than normal on very long petioles. Although the rate of production was higher in the Alpine House the plants there produced normal leaves and were still in good condition at the 5 leaf stage. This was probably due to the temperature cycle in the greenhouse which gave high daytime temperatures but low night temperatures. This would seem to allow the plant a respite at night which is denied it in the constant temperature chamber. It has already been established that germination is improved by conditions of fluctuating temperature which are more natural than constant temperatures. It would therefore seem reasonable to expect overall plant growth of tundra and alpine species to respond in a similar fashion.

If the results obtained in the U.K. are compared with figures calculated from field growth experiments the inhibiting effect of South Georgian weather conditions can be clearly seen (Table 10). The rate of leaf production in experiment 8a was slightly higher than was achieved in the 20°C. chamber although this planting was eight days later than in experiments 1/2, which only achieved a rate comparable with the 10°C. chamber. In all the experiments A.tenera showed remarkable constancy with

Table 10 Mean number of days required to produce a leaf under various conditions

Species	Temperature regimes in Birmingham			
	20°C.	10°C.	5°C.	Alpine greenhouse
<u>A. magellanica</u>	8.5	16	27	-
<u>A. tenera</u>	17	22	36	15.5

	Experiment number in South Georgia*			
	1/2	6/7	8a	5
<u>A. magellanica</u>	18.5	15	7	-
<u>A. tenera</u>	33	33	-	33

* planting times of South Georgian experiments:

1/2	4.12.69
6/7	26.12.69
8a	12.12.69
5	30.12.69

a rate only slightly above that of the 5°C. chamber. These results are curious since all these experiments were grown at the same site and therefore experienced approximately the same microclimate. Experiment 6/7 were grown in local soil whilst all the rest were grown in vermiculite. It was expected that the earlier planting (expt. 1/2 at 4.12.69) in vermiculite would show better growth than those planted in natural soil (expt. 6/7) at a later date (26.12.69).

Dry Matter Production by Seedlings

Materials and methods:

A number of experiments were carried out in 1967-68, 1969-70 and 1970-71 growing both A.magellanica and A.tenera from seed. In all cases the seeds were germinated first on damp tissues in the laboratory before planting about 5 mm. deep in pots of vermiculite or local soil. A standard number of 8 per pot was used. Black plastic pots were used for all experiments. Material in vermiculite was watered with modified Hoagland's solution once every two or three days; material in soil was given no water or nutrients. The soil used was taken from under a Festuca grassland in King Edward Cove.

Two plantings were made for each species in 1967 but final data were only obtained for the first planting of A.magellanica. For these experiments seedlings were matched in pairs, one of the pair being taken at the first harvest whilst the other was taken up to the I.B.P. Grassland site for the growth period from 22.12.67-7.3.68. The majority of the seedlings used were at the three leaf stage. The first planting of A.tenera did not reach this stage until the middle of March and was

therefore not used. The same applied to all the material in the second planting. Thirty seedlings were used per harvest for A. magellanica. Leaf areas were found by printing on Ammonax paper and weighing the cut-out leaf prints.

Two plantings were made in 1969-70 but again due to poor growth and death of seedlings in both vermiculite and soil no harvests were taken in that season, leaving the seedlings to overwinter. Almost none were left alive by the following summer so this experiment was abandoned.

The plantings in the 1970-71 season were made very early, 15.11.70. Four random harvests were taken on 12.12.70, 16.1.71, 20.2.71 and 27.3.71 at both the I.B.P. Grassland and Cryptogamic sites. For all experiments the plants were carefully washed before being divided into root, shoot and leaves which were then dried in an oven for several days before weighing.

Results:

The data for A. magellanica and A. tenera seedlings in 1970-71 are presented in Tables 11 & 12. The difference in dry weight production between the two species is striking. The growth of A. tenera was extremely slow even under what were judged to be favourable conditions. From previous germination experiments the rate of leaf production was expected to be lower in A. tenera than A. magellanica, and branches were only expected in the latter species. The earlier experiments in 1967-68 gave the following results for A. magellanica:

Relative Growth Rate (R_w) 0.29 gm/gm/week

Net Assimilation Rate (E_A) 0.61 gm/dm²/week

Leaf Area Ratio (F_A) 0.53 dm²/week

The A.tenera seedlings in this planting had only reached the 3 leaf stage after 10 weeks so that no growth values were obtained for them. On the basis of these two experiments and the observations made in the establishment experiment it would appear that in either soil or vermiculite A.tenera seedlings are unlikely to produce more than 5 leaves during their first summer or weigh much more than 10 mgs. On the other hand A.magellanica can produce up to 30 leaves under non-limiting nutrient conditions and weigh up to 350 mg. in a single season. This must make a considerable difference to the abilities of the seedlings to overwinter successfully, the A.magellanica seedling having already produced some rhizome material as an overwintering food store by the end of the first summer with a large number of leaves to allow adequate photosynthesis to take place above that necessary merely for immediate growth. The very small A.tenera seedlings on the other hand have no rhizome at the end of the first summer and it is remarkable that sufficient extra material can be made and stored by these small plants to bring them safely through the winter period.

Frequently whole heads of ripe A.magellanica fruits become detached and are dispersed as a single entity. If one of these heads lands in a suitable area all the fruits may begin to germinate. A head like this was collected from gravelly ground covered by Deschampsia antarctica and mosses in 1971. It had germinated earlier that season and contained 53 seedlings. Whilst most were at the 5-8 leaf stage of development, suggesting that most of the seeds had germinated at the same time, a few seedlings were found with smaller numbers of leaves and even one with cotyledons. Each seedling was dried and weighed. The mean dry weight of the seedlings was 5.4 mg. (SE. 2.3) showing very slow growth for that stage of development. Another head had apparently landed nearby during a previous season and had germinated

in situ. The young plants resulting from this were collected and dried. Only 15 plants survived from the original number of seedlings produced by this head and their mean dry weight was 97.6 mg. (S.E. 72.9). The range of individual weights was very high, from 6.2 mg. to 247.2 mg. These seedlings appeared to be up to two years old and it was obvious from the wide disparity in sizes and weights that competition effects would soon eliminate many of the remaining plants.

Table 11 Data for A.magellanica seedlings grown in vermiculite on
South Georgia in the 1970-71 season

I.B.P. Grassland Site	Harvests			
	1	2	3	4
Mean no. leaves	2.7	8.3	17.2	29.0
Mean no. branches	0	1.1	1.9	2.9
Mean d.wt. leaves (mgs.)	2.2	6.2	35.0	109.7
Mean d.wt. shoot (mgs.)	0.7	2.5	10.0	45.4
Mean d.wt. root (mgs.)	1.8	8.5	39.4	140.6
Mean total d.wt. (mgs.)	4.7	17.2	84.5	295.6
I.B.P. Fellfield Site				
Mean no. leaves	2.7	7.3	14.1	30.1
Mean no. branches	0	0.8	1.3	3.8
Mean d.wt. leaves (mgs.)	2.2	6.8	26.9	123.3
Mean d.wt. shoot (mgs.)	0.7	2.7	7.9	62.6
Mrs. d.wt. root (mgs.)	1.8	6.2	30.7	159.1
Mean total d.wt. (mgs.)	4.7	16.5	65.6	345.1

Table 12 Data for A.tenera seedlings grown in vermiculite on
South Georgia in the 1970-71 season

I.B.P. Grassland	Harvest			
	1	2	3	4
Mean no. leaves	1.5	3.7	4.8	4.6
Mean no. branches	0	0	0	0
Mean d.wt. leaves (mgs.)	0.9	0.8	2.1	1.7
Mean d.wt. shoot (mgs.)	0.5	1.8	2.9	3.8
Mean d.wt. root (mgs.)	0.5	1.0	2.5	3.3
Mean total d.wt. (mgs.)	1.9	2.7	7.5	8.9
I.B.P. Fellfield site				
Mean no. leaves	1.5	3.3	4.0	4.3
Mean no. branches	0	0	0	0
Mean d.wt. leaves (mgs.)	0.9	0.7	1.2	1.4
Mean d.wt. shoot (mgs.)	0.5	1.3	1.2	2.9
Mean d.wt. root (mgs.)	0.5	0.7	1.2	1.9
Mean total d.wt. (mgs.)	1.9	2.7	3.6	6.2

The floristically impoverished herb and dwarf shrub tundra of the polar and high alpine regions has been considered to have net annual primary production rates of a much lower magnitude than the phanerogamic vegetation of temperate regions (Bliss, 1962; Rodin & Bazilevich, 1964). Scott and Billings (1964) have shown, however, that although annual productivity may be low, daily productivity at favourable sites during the short growing season can approach that of cultivated crops in temperate regions.

The native phanerogamic species on South Georgia are necessarily adapted to growth, flowering and colonisation of new habitats under the fairly severe climatic regime that prevails during the summer growing season. In any community, dry matter production is inextricably linked both with the edaphic factors of soil type, nutrient availability and decomposition rates, whilst the energy value of the system (calorific value) can be used together with the radiation receipt to determine the photosynthetic efficiency of the plant. Measurements were made of dry matter production in a A. magellanica community during one summer, along with assessments of calorific values and chemical content of both plants and soil. The first two sections will be treated separately in this chapter whilst chemical content is discussed in chapter 8.

Standing Crop and Dry Matter Production

Materials and methods:

The area used was a shallow depression about 10 m. above sea level on the south side of King Edward Cove, Cumberland East Bay.

The community was analysed for homogeneity of species composition and distribution using 100 random quadrats, (25 x 25 cm.) and was found to be an almost pure Acaena magellanica/Tortula robusta stand. Since the site had a northerly aspect and was partly sheltered by its surrounding ridge from the wind, conditions for growth were very favourable. Again, due to its nearness to the shore and its sunny aspect there was no indication that snow lie might be prolonged at the end of winter.

This site was extremely damp, attracting run-off water from higher up the hill. The soil within the depression was almost completely organic. The maximum depth of the peat was not determined but it appeared to be in excess of 75 cms. over the whole site. Since the community appeared almost uniform throughout its upper two thirds only this area was used for sampling. Five random quadrats 25 cm. x 25 cm. were harvested each month. Numbers for the quadrats to be harvested were taken from a table of random numbers and were then applied to a grid system superimposed on the site. Each quadrat was clipped to the ground using secateurs and all material taken back to the laboratory for sorting.

The leaf area of each quadrat was estimated by taking a subsample of about one tenth of the total living Acaena leaves. The leaf area of this sample was measured accurately on an airflow planimeter (Jenkins 1959). After drying, the subsample weight as a proportion of the total leaf weight was used to calculate the total leaf area of each quadrat. A mean leaf area was then calculated for each month from these totals.

The material harvested was sorted into 12 categories:

- a. living leaves, b. leaf litter, c. living rhizome, d. rhizome litter, e. living flowering and fruiting heads (i.e. this years),
- f. flowering and fruiting head litter (i.e. previous years),
- g. living scapes, h. scape litter, i. Tortula, j. other litter,
- k. Galium antarcticum, l. living flowers and scapes (only used when material was too small to sort into separate categories).

Sampling dates ^{for the summer 1970-71} were as follows: 30 October, 1970, 27 November, 24 December, 29-31 January, 1971, 26 February, 30 March.

Results:

Table 13 shows the standing crop results on a g./m^2 basis for the six months from October 1970 to March 1971. Since the proportion of other species beside Acaena magellanica and Tortula robusta was so small, the community could be studied in terms of these two species alone. The proportion of Tortula varied during the season and appeared to be closely related to leaf production in Acaena. Figure 25, showing leaf area index (LAI) of Acaena and the mean dry weight of Tortula per square metre, suggests that the moss used the periods, a. between snow melt and leaf expansion and, b. after leaf fall began at the end of summer, for its periods of maximum production. Despite the slight peak caused by the increase in Tortula weight for December the trend was obviously downwards until well after the maximum leaf area was attained by the Acaena, although recovery of the moss during March was both substantial and rapid. Clarke, Greene & Greene (1971) showed that growth of Tortula did occur between December and February but since this was not under the same conditions of seasonal leaf shading as described here, moss production in the two assessments is not easily comparable.

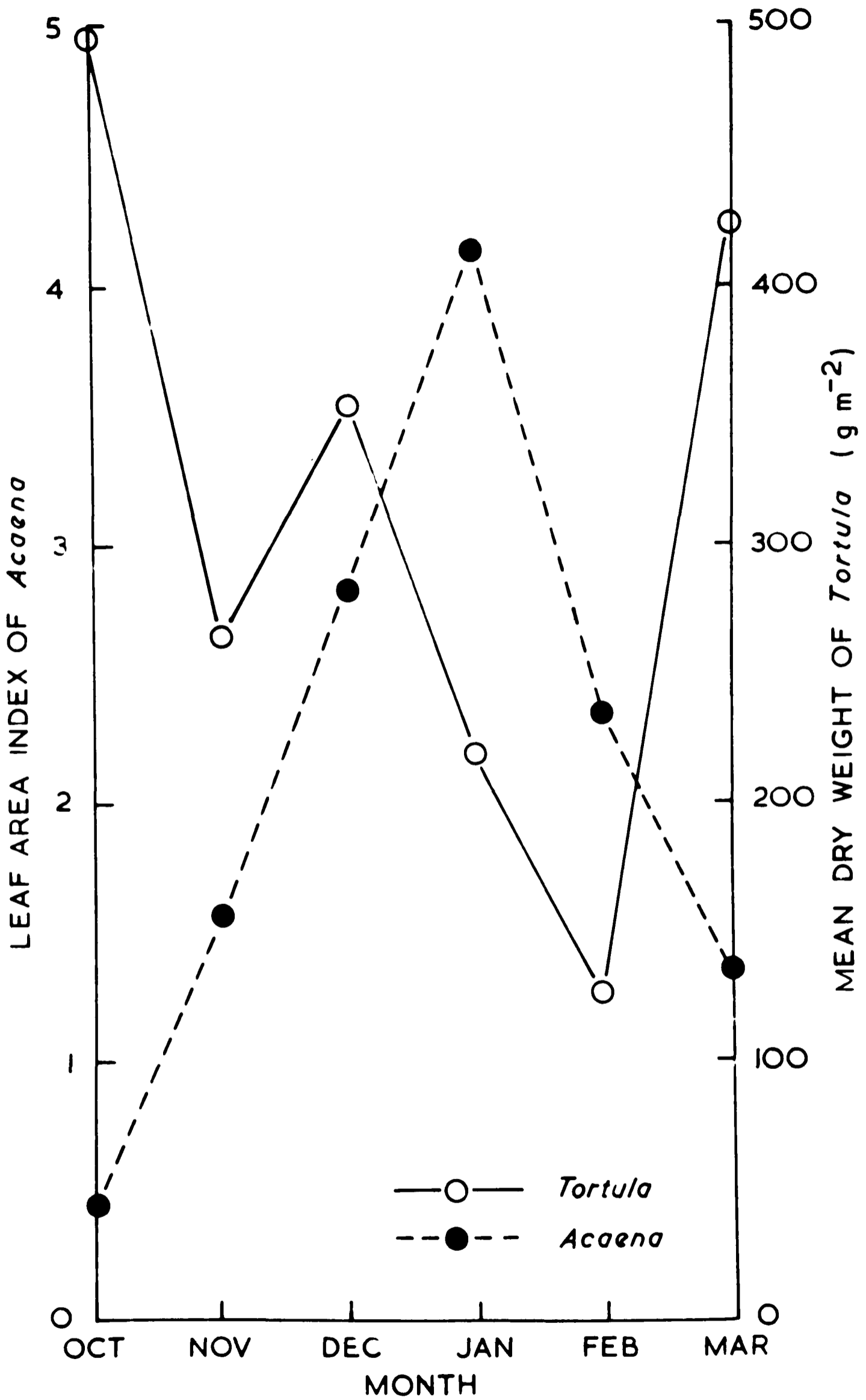


Figure 25. The relationship between the Leaf Area Index of Acaena magellanica and the growth of Tortula robusta

Table 13 Above ground standing crop in an Acaena magellanica sward

	October	November	December	January	February	March
Living leaves	38.9	140.3	227.5	310.6	190.1	109.9
Leaf litter	83.7	134.9	156.0	301.0	276.3	212.5
Living rhizome	434.7	517.9	508.5	755.4	937.8	660.0
Rhizome litter	275.4	421.8	180.6	195.0	296.6	146.7
Living scapes	-	-	6.1	17.9	7.5	9.4
Scapes litter	13.8	9.8	11.8	10.4	5.0	4.3
Living fls./frs.	-	-	5.9	32.6	13.3	17.8
Old fls./frs.	5.1	3.8	5.9	10.1	2.7	-
Tortula robusta	496.5	264.2	355.0	220.5	124.5	424.8
Other litter	3.0	3.5	3.7	1.6	0.5	0.6
Living fls. & scapes	-	4.0	0.2	-	-	-
Total living <u>Acaena</u>	473.6	658.2	748.2	1116.5	1148.8	797.0
Total <u>Acaena</u> litter	378.1	570.4	354.4	516.6	580.6	363.5
Total <u>Acaena</u>	851.7	1228.6	1102.6	1633.1	1729.4	1160.5
weight	1351.2	1496.3	1461.3	1855.2	1854.4	1585.9

All values are mean dry weights in grams/m².

\bar{x} No. flowering hds per m ²	-	89.6	86.4	140.8	54.4	105.6
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Leaf production at this site began in early October shortly after snow melt. On most shoots the first small leaves to unfold were affected by local frosts and had blackened by the end of the month. The LAI for October is likely to be up to 20% too high since many of the individual leaflets on the leaves had not properly unfolded in the field. The leaf litter component of the October sample contained both the new leaves shrivelled by frost and the remains of last year's leaves both still attached to the rhizome and on the ground. The ratio of living leaves to dead leaves reaches a peak in December whilst the LAI reaches its maximum in January. If simply assessed on the evidence of dry weight, leaf production only exceeds leaf death for two months of the year, namely December and January.

The rate of breakdown of leaf material within a closed sward such as this one could be quite high. The leaflets were quickly destroyed by wind, rain and decomposers once the leaf had begun to die. All that then remained was the petiole. This dried and withered away only slowly, many petioles persisting attached to the rhizome over the winter period. These old petioles composed the bulk of the leaf litter material found in the October sample. They had a fairly thick cuticle, and often contained considerable crystal inclusions in the cells around the vascular bundles.

There were considerable difficulties in allotment of rhizome material to the living and litter categories. Material that was soft or was decaying in any way was treated as litter but it is thought that some of the material put into the living category may well have been more dead than alive. It is unlikely that any living material found its way into the litter category. This should be borne in mind when assessing the values for the rhizome. The living to dead ratio has two dips, both

of them due to high values for litter in the months concerned. Reference to the original figures for each quadrat showed that in November the high litter value was due to two abnormally littered samples and that of February to a single sample with exceptionally high litter content. The dry weights show the expected increase in living rhizome weight during the season, with the maximum being reached in February. The decline between February and March of almost 30% is unexpected and unlikely just before the onset of winter. Since the ratio of living to dead rhizome is still rising at this point it is thought that the decline in the absolute value for living rhizome weight may appear more important than it really is.

Flowering heads first appeared in the November samples and were only in the early stages of development. The mean number of heads/m². varied from month to month (Table 13) giving an overall mean of 96. This site is believed to be above average in its production of flowering heads but the dry weight of material involved in the reproductive structures is much less than 1% of the total for living Acaena. There is no doubt that almost all the energy of the plant, at least in these closed sward situations, is directed primarily at vegetative rather than at sexual reproduction.

Flowering

Field observations on South Georgia and observations on plants grown in Birmingham indicated that the extent of flowering in any particular plant could vary considerably between seasons, and also that a plant was unlikely to be capable of flowering at least within the first two years when grown from seed. The number of flowers produced

per unit area apparently depended to a considerable extent on ecological factors, and could be expected to vary between the species due to the difference in the point of insertion of the scape.

Examination of shoot apices collected on South Georgia has given an indication of the conditions necessary for floral induction. Field measurements of scape growth and flower development have shown differences between the three taxa, which have an important bearing on the occurrence of cross-pollination between A.magellanica and A.tenera. The morphological development of the flowers in capitula has been studied and assessments made of pollen viability in the three taxa and seed production in various habitats.

Floral induction:

The stimulus required to change a vegetative shoot apex to a floral one can be either a temperature change or a change in the day length to which a plant is subjected. The latter appears to be by far the most common stimulus. To determine the effect of photoperiod, cuttings were taken off stock plants of A.magellanica growing in Birmingham, and rooted in a mist propagating bed. The plants were potted and kept overwinter in a partly heated greenhouse. The 40 best plants were moved into controlled environment chambers (5°, 10° and 20°C.) with two daylengths in each chamber - long-day 16 hrs. and short-day 8 hrs. The experiment was terminated after 2½ months when no plants had flowered. The most likely explanation for this would be that the plants were not sufficiently large to be able to flower.

Field observations on South Georgia showed that inflorescences could be found on plants clear of snow about the middle of October.

This applied to all three taxa. The daylength at this time of the year was about $13\frac{1}{2}$ hours. This was corroborated by the appearance of flowers on stock material grown in Birmingham during late April, the daylength being between 13 and 14 hours. Since material of A. magellanica collected on South Georgia in late September showed no floral initiation, and no evidence has been found of the over-wintering of partly developed **flower** buds as is common in the Arctic flora (Sørensen, 1941), it seems reasonable to assume that the species is neither day neutral nor an obvious short day plant. It is possible in some instances that sufficient light might penetrate the overlying snow during October to stimulate floral initiation before the plant itself had actually emerged.

Flowering is however not only controlled by day length. It also appears that plant age is an important factor, whilst temperature, through its control of growth and leaf production, can obviously exert a considerable secondary effect. The cuttings used in the photoperiod experiment were all of recently produced rhizome, and none of these flowered in the year after they were struck. Material grown from seed has shown that plants must be over 3 years old before they are likely to flower even under favourable conditions and it seems likely that the age limitation is correlated with the size of the rhizome system and consequently the size of the carbohydrate reserve available.

On South Georgia, although there is a distinct flush of flowering in spring, many plants especially in South-facing sites produce inflorescences later in the season. Under these circumstances it would appear that the photoperiod necessary for floral induction may simply be one in excess of 13 hours.

Floral development

Materials and methods:

To score the development of each head accurately floral development was broken down into a number of stages. These were as follows:

- Stage I - head evident but no flowers open
- Stage II - flowers opening
- Stage III - all flowers open, stigmas exerted
- Stage IV - anthers exerted,
- Stage V - fruiting (anthesis finished, spines evident).

Stages II, III and IV were broken down further into thirds, e.g. Stage II - 2/3 to show how much of the head had reached that particular stage. It only proved possible to apply this detailed scheme to the heads of A.magellanica and the hybrid, the flowers of A.tenera being too small for accurate scoring.

Using this scheme floral development of A.magellanica was examined at the Point Site (I), Sward Site (II) and Shackleton Site (III), using both individual marked heads and the whole communities. The hybrid was examined at the Hope Site (V) and A.tenera at the Dam Site (IV), though at these last two sites only individually marked heads were used. For further details about these sites see Appendix 4. Twenty marked scapes were used at the Point, Sward and Shackleton sites and twenty-five at the Hope and Dam sites. The data were transformed to a Floral Index so that the mean development stage at each scoring could be plotted. Each development stage was given a Floral Index number as follows:-

Stage I FI = 1, Stage II - 2/3 FI = 3, Stage III - 2/3 FI = 3,
etc to Stage V FI = 11.

In studies of community development the same Floral Index stages were used. Ten random quadrats were thrown and all the heads falling inside them were scored. The data were then calculated to give the percentage of heads in each development stage at each site.

Results:

When the Floral Index totals for the three A. magellanica sites were plotted against time the resulting graphs were found to be very similar (see Fig. 26). The graph obtained for the hybrid was slightly different (Fig. 26), although this may have been due to the test period being rather later in the season than for A. magellanica. Estimates can be made from the graphs of the mean length of time taken to complete each stage in floral development. Table 14 shows these estimates. At all the sites the stigma exertion stage (Stage III) appeared to be the shortest, lasting only 5-7 days, whilst ^{pollen liberation} (Stage IV) was 9-12 days long.

The rate of development of A. magellanica and the hybrid would seem to be fairly similar. It is not possible to offer comparative data on A. tenera however due to a difference in the position of the capitulum during the period when the flowers are opening. In both A. magellanica and the hybrid the flowering head develops whilst the scape is elongating (see next section), carrying the head clear of the surrounding leaves by the time the individual flowers begin to open. In A. tenera virtually all the floral development occurs whilst the head is very small and before any significant scape elongation has occurred. The same sequence of stages appears to occur but no estimate of the time required for each stage has been possible.

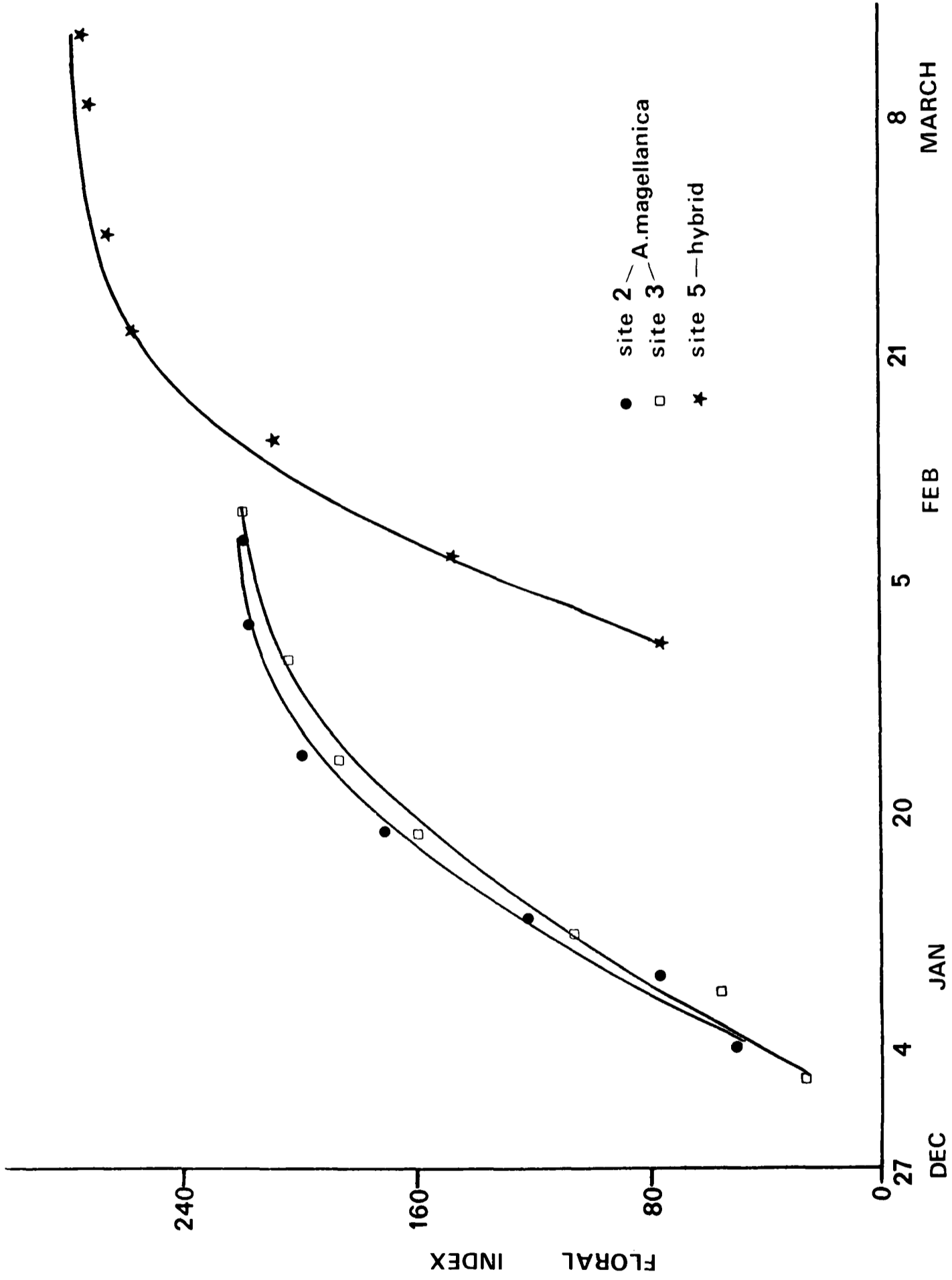


Figure 26. Floral development in A. magellanica and the hybrid

Table 14 Estimated Length in Days of Floral Development Stages

	Site	Species	Floral Development Stage		
			II	III	IV
I	(Point Site)	<u>A.magellanica</u>	13	7	12
II	(Sward Site)	<u>A.magellanica</u>	14	5	9
III	(Shackleton Site)	<u>A.magellanica</u>	9	6	12
V	(Hope Site)	Hybrid	c.7	6	9.5

Observations on ten heads of A.magellanica in cultivation in Birmingham has shown that the overall length of floral development is shorter than at any of the South Georgian sites. Stage II is normally 5-6 days, Stage III 5-7 days and Stage IV 7 days.

The histograms in Fig. 27 show the mean floral development for the A.magellanica communities at three sites. There were obvious differences between the sites, the capitula at Site I apparently having developed much earlier than at the other two sites. The date of onset of flowering at any particular site was undoubtedly influenced by topographical and ecological features. In this case, Site II which was North-facing developed much earlier and much more quickly than Site III which was South-facing. Snow lie is dependent to a considerable extent on the local topography and aspect of any site. Observations in September and October 1970 showed that there could be two or three weeks difference between North and South Facing sites for a complete melt to occur.

To check the effect that aspect might have on flowering a survey was carried out on sites of different aspects. Two sites were used per aspect and the four cardinal points were covered. All scoring was done on the same day. All heads were scored in 20 random quadrats per site and

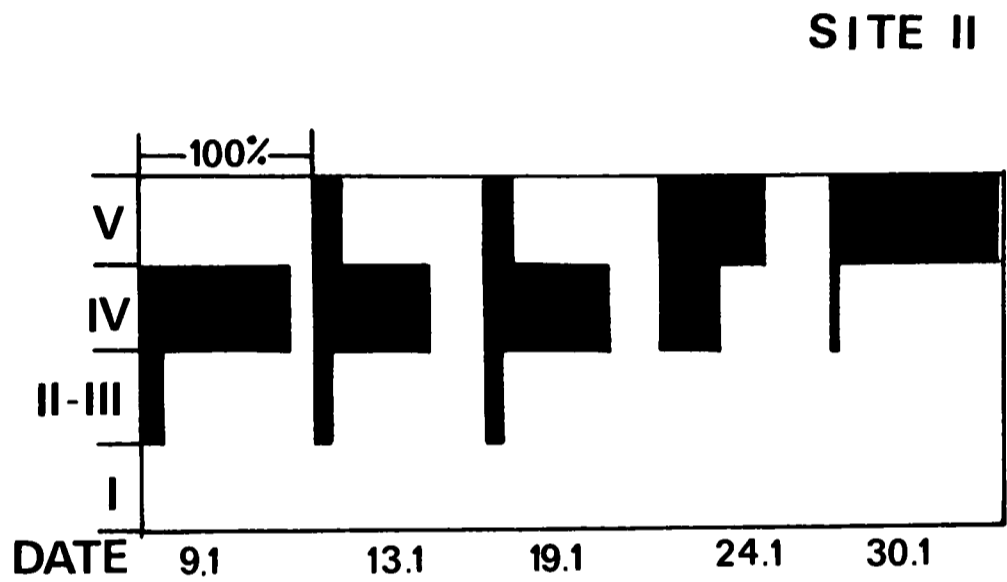
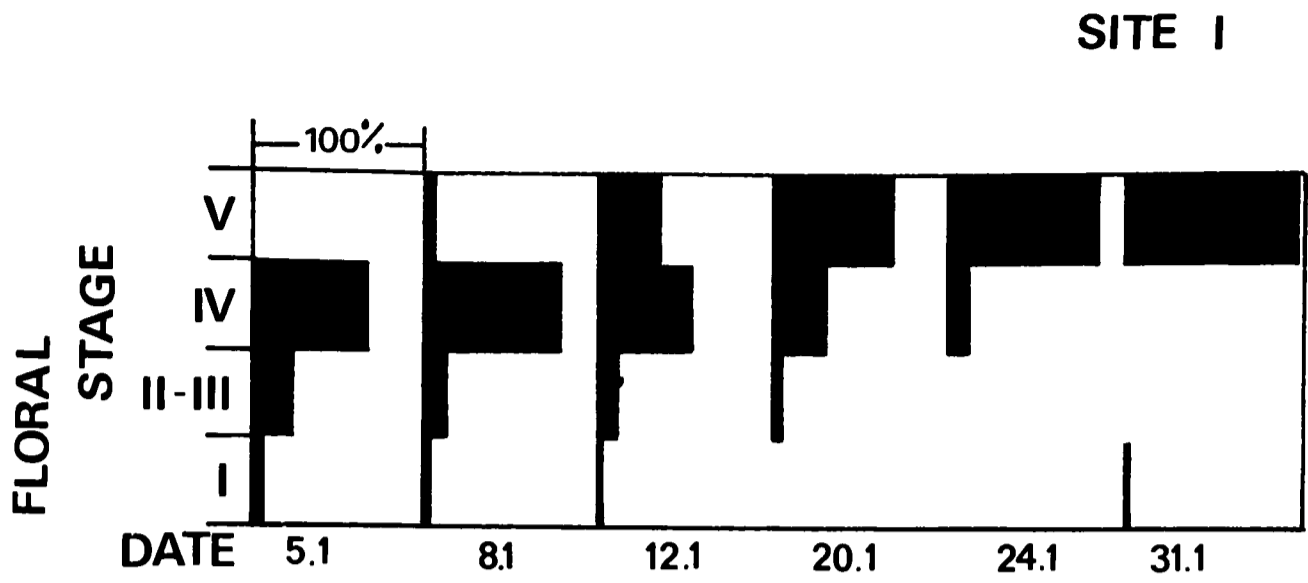


Figure 27. Histograms of floral development of A. magellanica communities at three sites

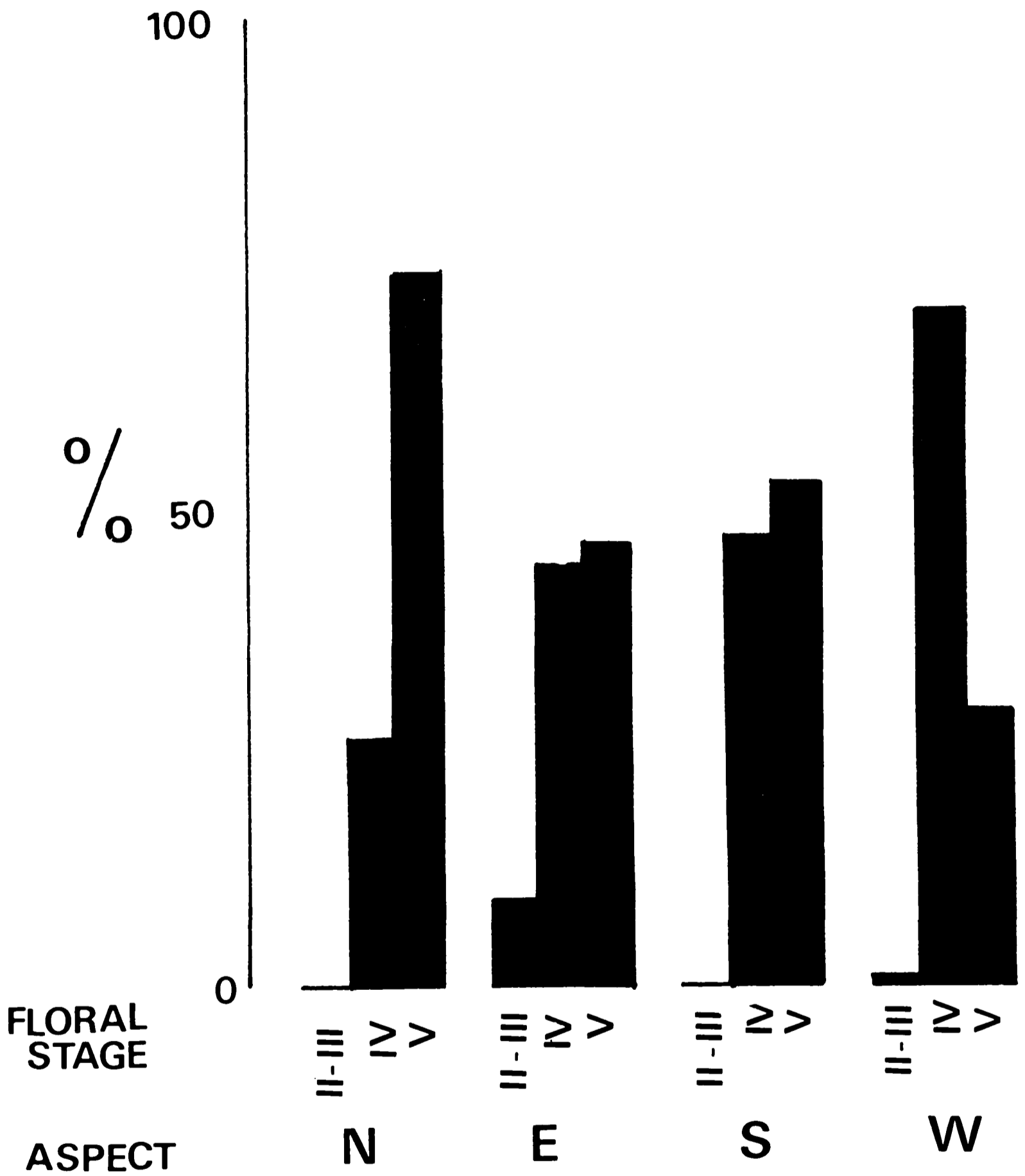


Figure 28. Histogram showing the effect if site aspect on the floral development of A. magellanica communities

a mean value found for each stage in sites of the same aspect. The histograms in Fig. 28 are not conclusive but do offer some support to the theory that A. magellanica on North-facing sites tends to flower earlier and develop more quickly than on sites of other aspects.

The histograms in Fig. 27 show the appearance of a small percentage of heads at Stage 1 on 31 Jan. at Site I. This denotes the onset of a second flush of flowering which is only well marked in those sites which flower early. At this time Site III has all its heads in or about to enter ^{the stage of pollen release}. The second flush is much less extensive than the first and may well take advantage of all the pollen still being produced by the other late developing sites.

Scape Growth

Materials and methods:

Scapes were selected which appeared to be at a comparable early stage of growth. Twenty marked scapes were used at each A. magellanica and A. tenera site, whilst twenty-five were used at the hybrid site. Scape length was measured from the base of the flowering head to the point where the stipular sheath of the second leaf fused to the stem (see Fig. 5). All measurements were made to the nearest millimetre at intervals of approximately one week. The periods during which the measurements were made differ for the three taxa, this being due to difficulty in finding a suitable site for the hybrid and to the late onset of elongation at the A. tenera site. Three sites were used for the A. magellanica measurements (Sites I, II and III), one site for A. tenera (Site IV) and one for the hybrid (Site V). (These sites are all described in Appendix 4). Curvilinear regressions were fitted to the data by a stepwise procedure

which tested the significance of the reduction in total variance due to the fitting of progressively higher value equations, (program developed by T.V. Callaghan).

Results:

The mean values for scape growth at each site, together with their appropriate curvilinear regressions are shown in Fig. 29. It was found that quartic regressions produced a significantly greater reduction in variance for all sites than any lower value regressions. The three A. magellanica sites show close similarities in the shapes of their curves. It is clear that the time taken for the scapes to reach their maximum size at these three sites was approximately the same but that the rate of growth during this period varied considerably. Mean scape length increased more rapidly at both of the sheltered sites (Sites II & III) than at the shore site (I). The higher insolation at Site II (north-facing) undoubtedly helped to increase its rate of growth over that at Site III (south-facing). In the other taxa the growth period was much longer, particularly so in the case of the hybrid.

The growth curves for both A. tenera and the hybrid extend over a much larger part of the summer than any of the ones obtained for A. magellanica. There appears to be a correlation here both with the typical habitats of the three taxa and with their flowering cycles. Elsewhere it has been recorded that in A. magellanica the flowers do not open until the scape has carried the head clear of the leaf canopy. A. magellanica is the only one of the three taxa to form pure stands with almost 100% leaf cover. Obviously, if anthesis occurred whilst the capitulum was below the level of the leaf canopy the chances for effective cross-fertilisation occurring would be much reduced. On the other hand, A. tenera, which normally occurs as isolated plants often in

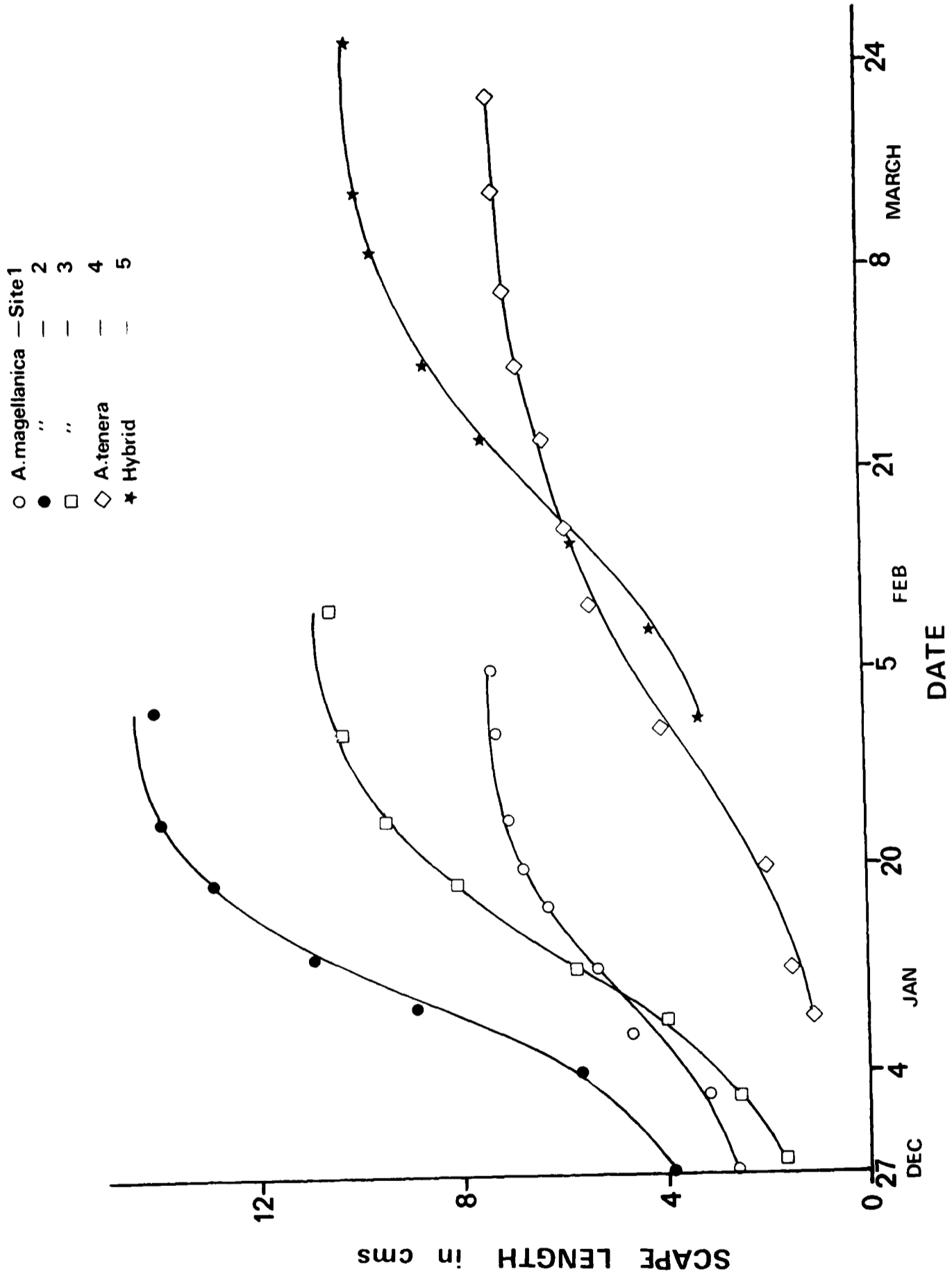


Figure 29. Fitted regressions of scape growth against time for A. magellanica, A. tenera and the hybrid

only sparse vegetation, apparently completes fertilisation before the scape has elongated very far. Most of the elongation in this species occurs during the period of fruit ripening. The hybrid occupies intermediate habitats and whilst it can form extensive patches nowhere does it produce a closed sward like A.magellanica. Its lengthy scape growth period appears to be a compromise between those of its parents. Since most of the hybrid scapes used also bore axillary capitula it is possible that the use of material for their development contributed to a reduction in the main scape elongation rate.

As a check that the scapes used for the growth studies on A.magellanica were representative for the plants 100 fruiting scapes were collected on a random basis during February from each site. These figures together with the means for the marked scapes are given in Table 15. The random scapes from all sites gave a higher mean length than the marked scapes but it is interesting to see that the sites still fall in the same order, with the longest scapes at Site II and the shortest at Site I. The standard errors, with two exceptions, are all between 19% and 23% of their respective means suggesting that each sample shows approximately the same degree of variability. The two exceptions are A.tenera (34%) and the random scapes of A.magellanica at Site I (27%). No obvious explanation can be given for Site I but at Site IV the high variability is thought to be related to the topography, the plants growing between stones and in the lee of large boulders.

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

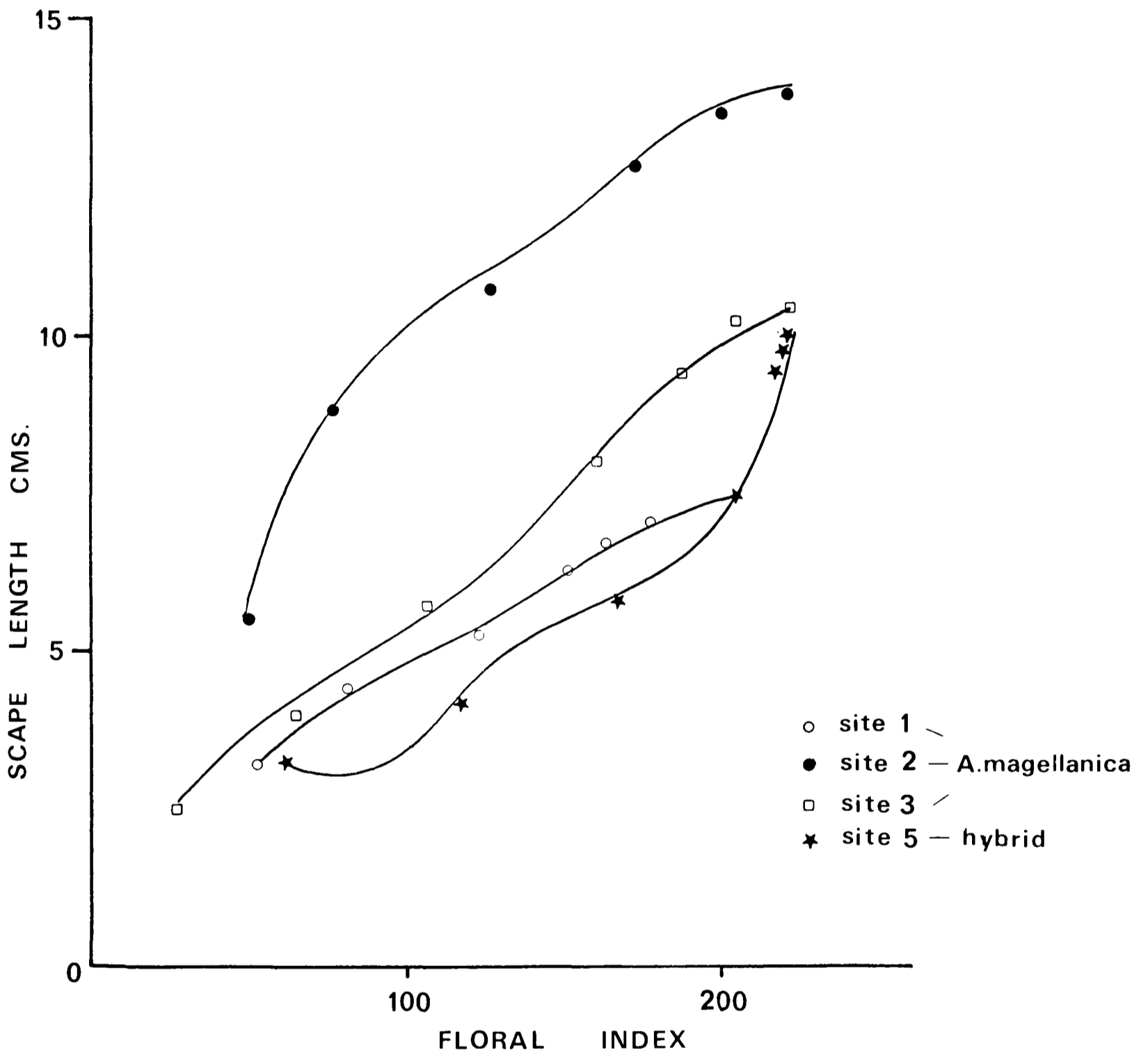


Figure 30. Fitted regressions of scape growth against floral development for *A. magellanica* and the hybrid

at the three A.magellanica sites and the hybrid site. The curves are shown in Fig. 30. Quartic curves were used for all the sites since the calculated F values showed these to be significantly better fits than the lower order curves. These patterns 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.

Table 15 Mean Scape Length at Various Sites

	<u>A.magellanica</u>			<u>A.tenera</u>	<u>A.hybrid</u>
	Site I	Site II	Site III	Site IV	Site V
Marked scapes	8.1(1.9)	15.1(3.2)	11.4(2.4)	7.6(2.6)	10.6(2.2)
Random scapes	11.8(3.2)	16.0(3.1)	13.0(3.1)	-	-

All lengths in cms. with standard error in brackets. The lengths of the marked scapes differ from those shown in Fig. 29 since they have been corrected to include that part of the scape inside the head which is only measurable after the fruiting head has been removed.

Chapter 8

PHYSIOLOGY

The Composition of Plant Parts

I. Water, Organic and Ash Content

Since each of the Acaena taxa apparently shows a marked preference for certain types of habitats, each differing in water availability, and all exhibit a tendency to accumulate crystals in various tissues, an analysis of the relationships between water, organic matter and ash was undertaken.

Other workers have used a variety of temperatures and methods for determination of these factors in plants. Odum, Marshal and Marples (1965) noted that ash determination by calorimetry appeared to always underestimate the amount of ash present. Reiners and Reiners (1972) investigated this and showed that whilst a charring/muffle furnace technique gave the best results, simply heating material at 575°C. in a muffle furnace was sufficient to obtain acceptable results. They also investigated the effect of different drying temperatures prior to ashing and concluded that lower temperatures, e.g. 55°C, were not apparently detrimental to the final results, and might even be more beneficial in calorimetric investigations since volatile compounds were not destroyed. A recent survey by Isaac and Jones (1972) on the effects of various ashing temperatures on the determination of nutrient content concluded that dry ashing at 500°C. for 4-15 hours gave the best results.

Material and methods:

Material of all three taxa was collected from a site near to the laboratory. Whilst it would have been possible to use fairly open dry

sites for A.tenera and the hybrid, all material was collected from one area where the water availability was apparently similar for all three. The site was on a wet peaty area. Due to restrictions on oven usage all material was not processed completely at the same time, although all material for each category e.g. leaves, was collected and dried for water content on the same day. Material was collected in the late morning after any dew had disappeared.

Immediately after collection the material was sorted in a cold room and weighed for fresh weight, using five samples for each determination. The samples were dried in an oven at 65°C. for several days until a constant dry weight was obtained. Samples were then ashed in an oven at 550°C. for 12 hours, and stored in a dessicator to cool before weighing.

Material in the following categories was collected, although not all categories were collected for each species: leaf, petiole, flowers stage II - III and scape, flowers stage IV and scape, flowers stage V and scape, rhizome.

Results:

The results obtained are shown in Table 16. The data are expressed in each category as percentages of the mean dry weight of the samples. A number of points are immediately apparent. The water content in each species was at a maximum in the petiole and a minimum in the rhizome. The differences were large, over 200% for both A.tenera and the hybrid. In all categories which are comparable A.magellanica had a higher water content than either of the other two, often with A.tenera occupying the intermediate position between A.magellanica and the hybrid. The high water content of the petioles may have been connected

Table 16 The relationships between Water content, Organic content and Ash in the South Georgian species of Acaena

	Leaf	Petiole	Flowers II-III	Scape	Flowers IV	Scape	Flowers V	Scape	Rhizome
Water Content									
<u>Acaena magellanica</u>	389.6	689.4	450.8	549.0	412.3	605.8	435.8	451.7	-
<u>Acaena tenera</u>	321.5	496.6	-	-	-	-	283.6	443.1	252.9
Hybrid	294.4	421.0	-	-	367.2	459.4	-	-	205.9
Organic Content									
<u>Acaena magellanica</u>	93.0	86.9	95.3	95.0	95.7	94.7	94.8	95.6	-
<u>Acaena tenera</u>	95.0	94.2	-	-	-	-	95.9	95.2	96.8
Hybrid	95.5	92.2	-	-	96.1	94.0	-	-	97.6
Ash Content									
<u>Acaena magellanica</u>	7.0	13.1	4.7	5.0	4.7	5.3	5.2	4.4	-
<u>Acaena tenera</u>	5.0	5.6	-	-	-	-	4.1	4.8	3.2
Hybrid	4.5	7.8	-	-	3.9	6.0	-	-	2.4

All data are expressed as percentages of mean dry weight, and are means of five samples.

with the importance of maintaining rigidity even though strengthening tissue was only poorly developed. There appeared to be little change in the water content of the flowers as they ripened to fruits, and, except for one anomaly in the A.magellanica scapes (605.8%), the values for scapes appear to be quite stable. The fruits of A.tenera - flowers V 283.6% - were markedly drier than those of A.magellanica whilst there was little difference between the scapes at that stage.

The organic content varied very little compared to the water content. The lowest value was the A.magellanica petiole and the highest value the hybrid rhizome. The higher values for the A.tenera and the hybrid rhizomes were expected since they were presumably due to the large quantities of starch stored in these organs. Besides the value of 86.9% for the A.magellanica petiole the values for the petioles of the other taxa were also slightly lower than those obtained for other plant parts. This must be due to the high values for water content and ash content in the petioles.

The comparison between the highest and lowest figures for ash content shows clearly where the bulk of the crystals were formed in the plant. The value of 13.1% for the A.magellanica petiole was almost twice as high as any of the other determinations. It is interesting to note that in all three taxa the highest ash values were obtained for the petioles, followed by the leaves, whilst both the lowest values were for rhizome material. Anatomical studies have shown that crystals are very common in leaves, often filling the cells alongside the veins, whilst they normally appear in the bundle sheaths in the petioles. A comparison with the percentage increases in calorific values when ash is excluded from the calculations (see Table 22) underlines the absolute data obtained in the

ash determinations since the largest increases are seen to be in the leaves, whilst the smallest increases in all cases are in the rhizomes.

II. Chemical Content of Plants and Soils

The elements present in any plant fall generally into three groups. The largest of these in terms of dry weight comprises carbon, hydrogen and oxygen; together these elements make up about 94% of the plant. The remaining 6% is composed largely of nitrogen, potassium and phosphorus together with the other essential macronutrients, whilst the various trace elements together make up the third group amounting to only a fraction of 1%. Carbon, hydrogen and oxygen are lost when plant material is ashed and only the elements in the second and third categories remain.

It is known that plants do not necessarily take up elements from the soil in the proportions in which they are present. Some plants even selectively accumulate elements to concentrations which would be toxic for most other species, e.g. selenium in Astragalus sps. Sutcliffe (1962) has suggested individual species tend to have a characteristic salt content which is relatively independent of the composition of the medium in which they are grown. A knowledge of nutrient cycling is an essential part of any attempt to understand ecosystems or their individual constituent species.

Materials and methods:

Samples were collected of all three taxa at approximately one month intervals throughout the summer 1970-71, beginning in early November. The same sites were used for each harvest of each species. The A. magellanica was taken from a north-facing Acaena-Tortula community growing on moist peat.

The hybrid was from a steep north-facing hillside broken by small rock outcrops, with Festuca, Phleum and bryophytes as the other principal plant cover. The A.tenera site was on the edge of a damp north-facing hollow in Festuca grassland, the soil being a typical grassland one.

After harvesting the material was brought back to the laboratory where it was sorted into categories, washed and dried in an oven at 55°C. for several days. It was then stored in paper bags until it was analysed. All the analyses were done by The Chemical Service, The Nature Conservancy, Merlwood Research Station, Grange-over-Sands, Lancashire. Nitrogen is recorded as total, all other elements as extractable.

Results:

The results of the chemical analyses are shown in Tables 17-19. It is unfortunate that all the figures are based on single determinations only and that material of each species is not available from a variety of habitats. Some seasonal trends are discernible in certain instances but overall the data present a rather confusing picture.

One very obvious trend was the decline in the N content of A.magellanica leaves throughout the summer. This was paralleled to some extent by the flowers and scapes, whilst levels in the leaf litter and rhizome remained almost static throughout the season. There was some evidence for a similar trend in the hybrid leaves, but not in A.tenera.

In most cases the levels of K and Na in leaf litter increased throughout the season, whilst holding fairly stable or fluctuating irregularly in rhizome and flowers. In all three species the leaf content of Na showed an unusual pattern where it built up a peak at harvest 4 and then declined quite sharply. The Mg level was fairly constant in most cases throughout the season. The amount of fluctuation was especially low

Table 17 Chemical content of Acaena magellanica

		N	P	Mg	Ca	K	Na	
Harvest	1	4.0	0.59	0.51	1.24	3.13	0.12	LEAVES
	2	3.3	0.47	0.49	1.48	1.56	0.24	
	3	2.8	0.48	0.46	1.48	1.64	0.28	
	4	2.2	0.36	0.42	1.93	1.17	0.88	
	5	1.4	0.27	0.55	3.07	1.70	0.50	
Harvest	1	1.19	0.20	0.37	2.68	0.19	0.05	LEAF LITTER
	2	1.38	0.22	0.39	3.00	0.17	0.03	
	3	1.33	0.29	0.60	2.46	0.61	0.18	
	4	1.09	0.26	0.56	2.63	0.52	0.38	
	5	1.16	0.26	0.49	0.31	0.33	0.34	
Harvest	1	1.17	0.26	0.27	0.99	0.98	0.11	RHIZOME
	2	1.25	0.23	0.33	1.29	0.47	0.10	
	3	1.14	0.24	0.37	1.15	0.67	0.12	
	4	0.92	0.25	0.29	0.56	0.64	0.14	
	5	1.00	0.23	0.30	1.04	0.61	0.07	
Harvest	2	3.75	0.63	0.43	0.71	2.64	0.08	FLOWERS/ FRUITS & SCAPES
	3	2.41	0.48	0.34	0.69	1.64	0.11	
	4	2.06	0.51	0.30	0.69	1.52	0.20	

Table 18 Chemical content of Acaena tenera

		N	P	Mg	Ca	K	Na	
Harvest	1	0.89	0.10	0.42	0.51	2.70	0.15	
	2	3.90	0.48	0.31	0.53	1.80	0.31	
	3	2.10	0.32	0.38	0.65	0.30	0.43	LEAVES
	4	2.81	0.38	0.44	1.22	1.17	0.81	
	5	2.80	0.36	0.39	1.00	1.10	0.55	
Harvest	1	0.80	0.094	0.14	0.76	0.36	0.041	LEAF LITTER
	2	2.00	0.19	0.22	0.94	0.33	0.056	
Harvest	1	2.50	0.20	0.20	0.34	0.88	0.13	
	2	1.40	0.30	0.18	0.31	0.48	0.11	
	3	2.80	0.54	0.16	0.29	0.46	0.12	RHIZOME
	4	1.45	0.30	0.20	0.45	0.50	0.10	
	5	1.60	0.25	0.17	0.38	0.46	0.091	
Harvest	2	2.60	0.54	0.23	0.28	1.90	0.18	
	3	2.30	0.26	0.23	0.27	1.40	0.22	FLOWERS/ FRUITS & SCAPES
	4	2.38	0.40	0.24	0.48	0.98	0.30	

Table 19 Chemical content of the hybrid

		N	P	Mg	Ca	K	Na	
Harvest	1	3.5	0.59	0.61	0.84	2.59	0.12	
	2	0.85	0.11	0.23	0.56	2.00	0.11	
	3	2.80	0.37	0.44	0.56	2.00	0.25	LEAVES
	4	2.66	0.35	0.56	0.94	2.03	0.55	
	5	1.90	0.26	0.68	1.11	1.70	0.39	
Harvest	1	1.80	0.37	0.41	0.99	0.16	0.041	
	2	1.00	0.19	0.38	1.00	0.31	0.038	LEAF LITTER
	3	2.20	0.34	0.47	0.86	0.59	0.13	
	5	2.70	0.21	0.58	1.00	1.00	0.38	
Harvest	1	1.56	0.31	0.33	0.63	0.61	0.05	
	2	1.90	0.21	0.22	0.34	0.55	0.034	
	3	3.00	0.26	0.26	0.41	0.68	0.066	RHIZOME
	4	1.20	0.26	0.26	0.31	0.48	0.05	
	5	1.70	0.20	0.27	0.39	0.65	0.078	
Harvest	2	2.30	0.39	0.41	0.41	0.18	0.063	FLOWERS/ FRUITS & SCAPES
	3	2.20	0.31	0.39	0.32	2.10	0.18	

in the rhizome samples. P appeared to be reasonably constant in rhizomes and leaf litter, but with irregular fluctuations in the other parts, whilst Ca showed a slight upward trend in the leaves and remained relatively stable in most other parts.

The relationship between the elemental content of the plants and that of the soil can be seen by comparing the data in Tables 17 and 18 with that in Table 20 where analysis data for the soils at two sites are presented. The soil at the A.tenera site in the Festuca grassland was much poorer in extractable nutrients than the peat beneath A.magellanica. The levels of all nutrients were higher in the plants (with the exception of Ca in A.magellanica) than in the soils. Some nutrients were selectively accumulated at higher rates than others. Table 21 shows the nutrient content of the plant parts as percentages of the soil nutrient levels at mid-season. Although the percentages are higher in A.tenera in every case reference back to Tables 17 and 18 shows that the absolute values for plant contents are closely similar for the two species. However, to reach this state A.tenera must accumulate more nutrient from its poor soil. This lends support to Sutcliffe's (1962) hypothesis mentioned earlier, since both species reach approximately the same nutrient content despite gross differences in the chemical contents of their respective soils.

III. Calorific values and efficiency of energy utilisation

Materials and methods:

The samples were taken from the same sites as for the chemical analysis material on 20-21 January, 1971. After sorting into

Table 20 Chemical content of soils from sites used for harvesting plants
for chemical analysis

	N	P	Mg	Ca	K	Na	% loss on ignition
<u>A. magellanica</u> site	1.84	0.033	0.35	5.42	0.143	0.121	43
<u>A. tenera</u> site	0.87	0.016	0.026	0.087	0.031	0.016	20.5

All data expressed as % of mean dry weight. All elements, (except N) as extractable only. N as total. All data mean of two samples. Analyses carried out by The Chemical Service of the Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.

Table 21 The selective accumulation of nutrients from the soil by
two species of Acaena

	N	P	Mg	Ca	K	Na
<u>A. magellanica</u>						
Leaves	52	1354	31	less	7718	131
Leaf litter	less	778	71	less	326	48
rhizome	less	627	6	less	368	0
flowers/fruits	31	1354	less	less	1046	less
<u>A. tenera</u>						
Leaves	141	1900	1361	647	4093	2587
Rhizome	221	3275	515	233	1383	650
Flowers/fruits	164	1525	784	310	4416	1275

Data is shown as % increase above the mid-season nutrient levels in the soil

categories the samples were washed thoroughly, oven-dried at c. 55°C. for several days and stored in paper bags. Calorific value determinations on an ash-free dry weight basis were made by The Chemical Service, The Nature Conservancy, Merlewood Station, Grange-over-Sands, Lancashire. The method of analysis is described in Smith & Walton (1973).

Results:

The calorific value data are shown in Table 22. It is unfortunate that there is only a single determination available for each sample, but the relatively small difference between the highest and lowest values obtained does suggest that no large errors have crept in. The percentage increase in caloric value by removal of the ash fraction shows that the greatest increases were in the values for the leaves, followed by the fruits, then the scapes and finally the rhizomes. Since exactly the same pattern is followed in all three taxa and the highest percentage increase for the rhizome is only 4.3% it is thought that soil contamination was negligible.

Comparing the values in Table 22 with those for various plant stands listed in Lieth (1968) the calorific values for Acaena species appear to be similar to that obtained by Bliss (1962) for various North American herbs and rather lower than his figures for deciduous shrubs. Comparison with the data obtained by Jenkin and Ashton (1970) for Macquarie Island show Acaena species to be very similar to Celmisia longifolia and slightly higher than Pleurophyllum hookeri. No lipid extractions have been made on Acaena but judging from the correlation shown by Bliss (1962) between high lipid content and high calorific value it appears likely that the lipid content of all three South Georgian taxa is not high.

Table 22 Calorific Values for South Georgia species of Acaena

		K cals/gm.	K cals/gm.	
		Dry Weight	Ash-free dry weight	% increase
<u>A. magellanica</u>	leaves	4.29	4.67	8.9
	rhizome	4.46	4.65	4.3
	scapes	4.30	4.49	4.4
	fruits	4.49	4.72	5.1
	(mean scapes/ fruits)	4.40	4.61	4.8
Hybrid	leaves	4.42	4.72	6.8
	rhizome	4.45	4.60	3.4
	scapes	4.20	4.45	6.0
	fruits	4.40	4.69	6.6
	(mean scapes/ fruits)	4.30	4.57	6.3
<u>A. tenera</u>	leaves	4.55	4.81	5.7
	rhizome	4.47	4.56	2.0
	scapes/fruits	4.50	4.66	3.6

Estimates of photosynthetic efficiency can be made using the calorific values of plants since these are to a certain extent a measure of the energy fixation ability of the plant. Zelitch (1971) has pointed out that photochemical efficiency is not directly related to productivity since the efficiency of light conversion is greatest at low irradiance. Using production data from Table 13 it is however possible to calculate an approximate figure for efficiency for above ground growth in a mature sward of Acaena magellanica. Using the data for the months December and January -

$$\text{mean radiation} = 400 \text{ cal/cm}^2/\text{day}$$

$$\text{photosynthetically active radiation (PAR)} = 178 \text{ cal/cm}^2/\text{day}$$

$$\text{but (Zelitch, 1971) only 12\% of PAR is absorbed} = 213.6 \text{ Kcal/m}^2/\text{day}$$

$$\text{actual above ground growth for 64 days} = 500 \text{ gm/m}^2$$

$$= 7.8 \text{ g./m}^2/\text{day}$$

if an allowance of 33% of gross photosynthesis is made for respiratory loss (Loomis and Williams, 1963)

$$\text{gross production} = 11.7 \text{ g./m}^2/\text{day}$$

$$\text{energy fixation} = 11.7 \times 4.66 \text{ Kcal/m}^2/\text{day}$$

$$= 54.52 \text{ Kcal/m}^2/\text{day}$$

thus, on a respiration corrected basis, for above ground production only, the efficiency of an A. magellanica sward is approximately

$$\frac{54.52}{213.6} = 25.5\%$$

If however the calculation is done on the basis of total radiation the efficiency falls to 0.14%, whilst on the basis of total PAR it is 0.31%. Assuming that 3.7 Kcal are required per gram of carbohydrate synthesised (Zelitch, 1971), the photochemical energy available has a potential

production of $213.6/3.7 = 57.7 \text{ g./m}^2/\text{day}$. The respiration corrected production figure is 20.3% of this. A comparison of these estimated efficiencies with the figures given by Zelitch (1971) for various crops in different parts of the world suggests that A. magellanica efficiency is somewhat similar to that of a temperate forest.

Comparison with the only other data available for the sub-Antarctic (Jenkin and Ashton, 1970) shows the efficiency of Acaena magellanica to be about 30% of that of a low altitude Macquarie Island grassland but very similar to a low altitude Pleurophyllum hookeri herbfield.

Pigment Content

Field Observations had shown that each of the three taxa had a distinctive leaf colour (Fig. 8). Furthermore, the occurrence of a red pigmentation in the petioles and especially the tips of the leaflet dentations was far from uniform, both between and within each taxon. As well as an investigation of pigment content in all three taxa, an experiment using seedlings of A. magellanica and A. tenera was carried out to study pigment production.

Materials and methods:

Mature leaves of the three Acaena taxa were collected on South Georgia during early February. Each sample was divided into two, the fresh weight found and then half the sample dried so that pigment content could be calculated on both fresh and dry weight bases. Half of the sample was homogenised in 85% Analar acetone using a Waring Blendor, magnesium carbonate being added to prevent acid breakdown of pigments. All samples and equipment were kept as cold as possible. The extracts were centrifuged

and then diluted to a standard level. Measurements of absorption were made in a Pye Unicam SP 600 Spectrophotometer at the following wavelengths - 750, 663, 652, 645, 630 and 475.

Calculation of chlorophyll content was done using equations from Arnon (1949). Estimates of anthocyanin content were made using the measurement at 550 (Billot, 1964) and of carotenoids using the measurement at 475 (Tieszen and Johnson, 1968).

The experiment to test the conditions of red pigment formation was carried out using seedlings of A. magellanica and A. tenera, grown in a greenhouse on South Georgia and on the ground outside during the 1970-71 summer. Pots of material grown inside were moved out and vice versa during the experiment.

Results:

The values for chlorophylls a and b, together with the carotenoid and anthocyanin ratios are given in Table 23. The a:b ratio is similar for all three taxa, as are the actual pigment contents on both fresh and dry weight bases. Important differences do occur however in the carotenoid and anthocyanin ratios. These ratios can only be taken as general guides to the leaf content of anthocyanins and carotenoids since the presence of the chlorophylls has a partial masking effect on the absorption determinations. The carotenoid ratio is the same in both A. magellanica and the hybrid but slightly higher in A. tenera. There are though marked differences in the anthocyanin ratios with A. magellanica being only 30% of the value for A. tenera. This is not altogether unexpected since the leaflets of A. tenera did have red tips to the dentations, which were not present in the A. magellanica material and only very small in the hybrid material.

Table 23 Pigment content of the South Georgian Acaena taxa

Species	Basis for calculation	Chlorophyll in mg./g.		a:b ratio	Carotenoid ratio	Anthocyanin ratio
		a	b			
<u>A. magellanica</u>	fresh wt.	0.80	0.20	3.9	2.0	0.14
	dry wt.	3.16	0.83			
<u>A. tenera</u>	fresh wt.	0.89	0.23	3.9	2.4	0.41
	dry wt.	3.00	0.79			
Hybrid	fresh wt.	0.79	0.21	3.8	2.0	0.23
	dry wt.	3.10	0.81			

From this analysis it would seem that the differences in leaf colour between the three taxa are not due to any differences in their chlorophyll a and b content. Difference in the content of the subsidiary pigments carotenoids and anthocyanins clearly delineate A. tenera from the other two taxa, the anthocyanin content apparently being linked to the occurrence of red tips on the leaflet dentations.

It is interesting that all three taxa show very similar values for chlorophyll content when sampled on the same day. These values are probably lower than the maximum attained during the season since the analyses were done in early February, a period of declining radiation. Low values for the a:b ratio are characteristic of species from low light intensities, a situation which Tieszen (1970) has found in Arctic grasses. The a:b ratio of 3.9 is similar to those reported by Bliss (1966) for alpine species on

Mt. Washington. Tieszen and Bonde (1967) have found that in Trisetum and Deschampsia an increase in light intensity resulted in an increase in the a:b ratio. The South Georgian values, attained under temperate latitude day length, are therefore more similar to those of alpine species or of an alpine environment and this lends further support to the suggestion that South Georgia should be treated as an alpine and not an arctic area.

The results of the experiment on the production of red pigmentation are given in Tables 24 and 25. In both species the maximum development of the red pigmentation that occurred in plants grown exclusively inside was restricted to a slight pink flush on the stem, although in many cases not even this developed. The cotyledons showed no trace of red when they first appeared above ground but developed it very quickly in the case of material grown outside. This red pigmentation occurred in several other species (Juncus, Ranunculus) especially during the period of snow melt at the end of winter.

Two factors differ between the conditions outside and the conditions within the greenhouse - a considerable temperature difference existed since the greenhouse was heated so that temperatures below 6°C. never occurred, whilst daytime temperatures were often above 20°C., and the glass in the greenhouse effectively excluded the UV component of the light. Ultra violet radiation increases with increasing altitude whilst the amount reaching the earth's surface is influenced by the ozone component and turbidity factors in the atmosphere. Since South Georgia is situated in a temperate latitude and these experiments were conducted at sea level, it is reasonable to assume that the material grown outside was not subjected to any unusually high levels of UV radiation.

Table 24 The Occurrence of Red Pigmentation in plants of A. magellanica

Date	INSIDE	IN → OUT	OUTSIDE	OUT → IN
31.12.69	No plants with red pigmentation	-	All plants with red pigmentation, on upper surface of cotyledons, all stems and petioles very red	-
20.1.70	Slight pink tinge on stems	-	All plants with red pigmentation, v. marked in the leaflet tips and stems	-
3.2.70	Still only slightly pink. All leaves larger than those on outside plants	All large leaves produced inside now all with red pigmentation, or dying. New leaves appearing with red pigmentation, these leaves smaller than those produced inside	All still pigmented as above.	Leaves produced outside remain unchanged. New leaves produced inside are larger and have no red pigmentation.
23.2.70	Only slight pink tinge on some stems. Plants with 10-16 leaves	Old leaves mostly dead or v. dark reddish. All plants with bright stems and all new leaves with red-tipped dentations.	All leaves small and still not fully unfolded. All with red-tipped dentations. Plants mostly with 4 leaves.	First leaf and cotyledons still dark green or slightly yellowish, with short petiole and red-tipped dentations. No red pigmentation in any new leaves
12.3.70	As before. Plants with 17-23 leaves, all healthy, and large. Petioles long.	All old leaves dead. New leaves smaller with red tips, similar to normal outside ones. Petioles short, leaves not completely unfolded.	Plants as before, with 5 leaves each.	The only red pigmentation left now at leaflet tips of first three leaves.

Table 25 The Occurrence of Red Pigmentation in Plants of A.tenera

DATE	INSIDE	IN → OUT	OUTSIDE	OUT → IN
31.12.69	No red pigmentation in cotyledons, leaves or stem.	-	Plants with margins and upper surface of cotyledons red. Some newly emerged cotyledons without red pigmentation.	-
20.1.70	Slightly red tinge on stems. Leaves large with long petioles.	-	Stem and leaf tips red. Leaves very small, not completely unfolded.	-
3.2.70	As before.	Most large leaves dead. Youngest large leaf with red tips and petiole. New leaves with red tips, much darker green than leaves produced inside, and smaller.	As before.	All new leaves larger than those produced outside and without red pigmentation. Red colour mostly gone from petioles and stem. First leaf still with red tips.
23.2.70	Pigmentation as before.	All oldest leaves dead. Youngest of leaves produced inside turned darker green with very marked red pigmentation in leaflet tips, petioles and stem. All new leaves small, dark green and with red tips.	Plant with 2-3 leaves. Pigmentation as before.	First leaves and cotyledons still dark green or yellowish, with short petioles and red tips to leaflets. No red colour in any new leaves.
12.3.70	As before, plants with 5-7 leaves.	All of leaves produced inside now dead. New leaves appear very similar to normal outside ones except that they are slightly bigger.	Plants now all with 3 leaves. Pigmentation unchanged.	All leaves produced outside now dead. No red colour in any new leaves or petioles.

If it is UV which stimulates the production of the red anthocyanins in the first place, the swift production of only the red leaflet tips in A.tenera plants moved outside is not explained since it would be expected that anthocyanins would be formed throughout the leaf. In Juncus ^{uch}~~scheuzerioides~~ the whole upper surface of the leaf frequently turns bright red when the plant emerges from under the snow. This colour is fairly rapidly lost however, not even the tips of the leaves retaining it. On emergence from snow banks A.tenera has sometimes shown completely red leaves, which change slowly until only the red tips and stem remain. This tip pigmentation was retained in the old leaves of the A.tenera plants transferred inside for 2½ months although no new leaves produced inside showed this. The production of this anthocyanin may be partly under a temperature control, with the low temperatures acting as a stimulus for production. Some support for this is gained by the observation that the red pigmentation is less marked in plants grown in the open in Birmingham than it is for those grown on South Georgia.

Photosynthesis

In species whose distribution covers numerous degrees of latitude or where considerable geographical isolation between populations is common, the formation of groups, distinct from each other on morphological or physiological grounds, is not uncommon. Bipolar species can show distinct differences between populations in the North and South on morphological grounds (Moore & Chater, 1971) or, as in Phleum alpinum, on physiological grounds (Callaghan, 1972). Acaena magellanica and A.tenera show differences in their geographical distribution patterns and in the

degree of variability of their morphological characters. A.magellanica is also known to show cytological differences. A preliminary investigation of photosynthesis in plants from South Georgia, and Tierra del Fuego was undertaken to assess if physiological differences existed both between and within the species.

Material and methods:

Material of A.magellanica was available from the following localities:

Tierra del Fuego: near shore, dry bare ground, Ushuaia.
: in Nothofagus forest, amongst grasses, above Ushuaia.

South Georgia: growing on moss mat, Shallop Bay.

Material of A.tenera used was:

South Georgia: growing in moss mat, Shallop Bay.

Material of the hybrid was also tested:

South Georgia: edge of A.magellanica sward, Maiviken.

All this material had been collected live in the field and brought back to Birmingham for growing on. All the species were kept under the same conditions in open frames. Material of A.magellanica and the hybrid had been grown in Birmingham for several years. The material of A.tenera had only been in the frames for 3 months, but the leaves used had been produced in Birmingham. The rate of photosynthesis of each population was measured at various temperatures and light intensities using an infra red gas analysis (IRGA) system. Detached leaves, their ends in a foam block filled with water, were placed in a chamber with a perspex lid. The light intensity and temperature were held constant and the rate of CO₂ uptake by the leaves

was measured once a steady state had been achieved. Air entering the chamber was maintained at a high humidity to alleviate any symptoms of water deficiency. Light intensity in the chamber was monitored with a Lambda Quantum Sensor which measured only the amount of photo-synthetically active light entering. To ensure that measurements were not made whilst the leaf was dying the photosynthetic rate at 10°C. was monitored at intervals throughout the experiment, and when the rate at this temperature showed signs of a decline the experiment was terminated.

Since the IRGA was set up as a differential instrument with a sensitivity of 1 scale deflection to 1 ppm CO₂, and since Rotameter flow meters were used to monitor the air flow, the calculation of the photosynthetic rate at each temperature and light intensity used the equation derived by Baker and Musgrave (1964) as given in Sestak, Catsky and Jarvis (1971):

$$F = \frac{\Delta C}{A} \times \frac{J \times 44}{22414} \times \frac{273}{T} \times \frac{P}{1013.23} \times \sqrt{\frac{T}{T_1}} \times \sqrt{\frac{P_1}{P}} \times 36 \times 10^5$$

- where
- F = photosynthetic rate as CO₂ uptake mg⁻¹cm⁻²h⁻¹
 - ΔC = CO₂ difference before and after chamber in ppm
 - J = gas flow rate cm³ sec⁻¹
 - A = area in cm² or weight in mg of leaves
 - T = temperature of flow meter at time of observation °A
 - T₁ = temperature of flowmeter when calibrated °A
 - P = barometric pressure at time of observation mb
 - P₁ = barometric pressure when flowmeter was calibrated mb

The area of the leaves was measured by cutting out and weighing photographic contact prints. The leaves were then dried at 70°C and weighed. Photosynthetic rates were calculated on both leaf area and leaf dry weight bases.

Results:

The results from all the populations tested are shown in Figs. 31 and 32. Due to limitations on the availability of the IRGA equipment only a small number of runs could be carried out and in view of this the data presented must be regarded as preliminary.

All three South Georgian taxa were run at two light levels, although the hybrid run at the lower light intensity had to be cut short before an optimum was reached. The optimum temperature for photosynthesis was apparently between 10-12°C for A.tenera at both light intensities and for the hybrid and A.magellanica at the higher intensity. No optimum was obtained for the hybrid at the lower light level whilst that for A.magellanica was between 20-25°C.

Comparison of the South Georgian A.magellanica with the two populations from Tierra del Fuego, all at the lower light level, is most interesting. The optima for the Tierra del Fuego material appears to be between 10-12°C., about 10°C less than the South Georgian. The shapes of the curves are also quite different, both the Tierra del Fuego ones being similar with sharp rises and falls about the optimum temperature. On the other hand the South Georgian material produced a curve with a comparatively slow rise and fall and a less clearly defined optimum. All three populations showed a similar rate of photosynthesis at 0°C but their upper compensation points differed greatly. It would seem likely that the upper point for the Tierra del Fuego populations was less than 25°C whilst

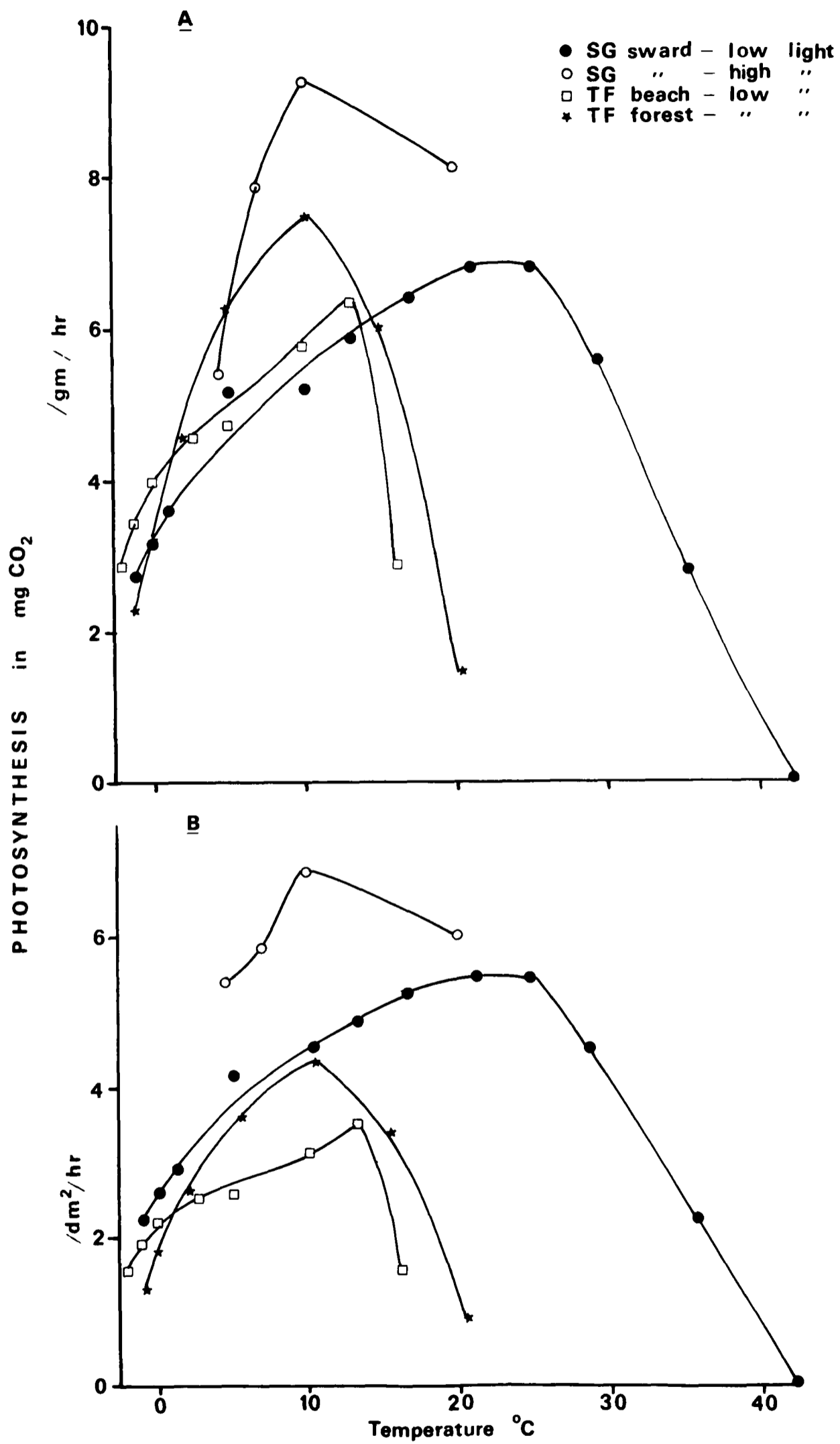


Figure 31. Rates of photosynthesis of detached leaves of A. magellanica from various populations
 A - expressed on a leaf dry weight basis
 B - expressed on a leaf area basis

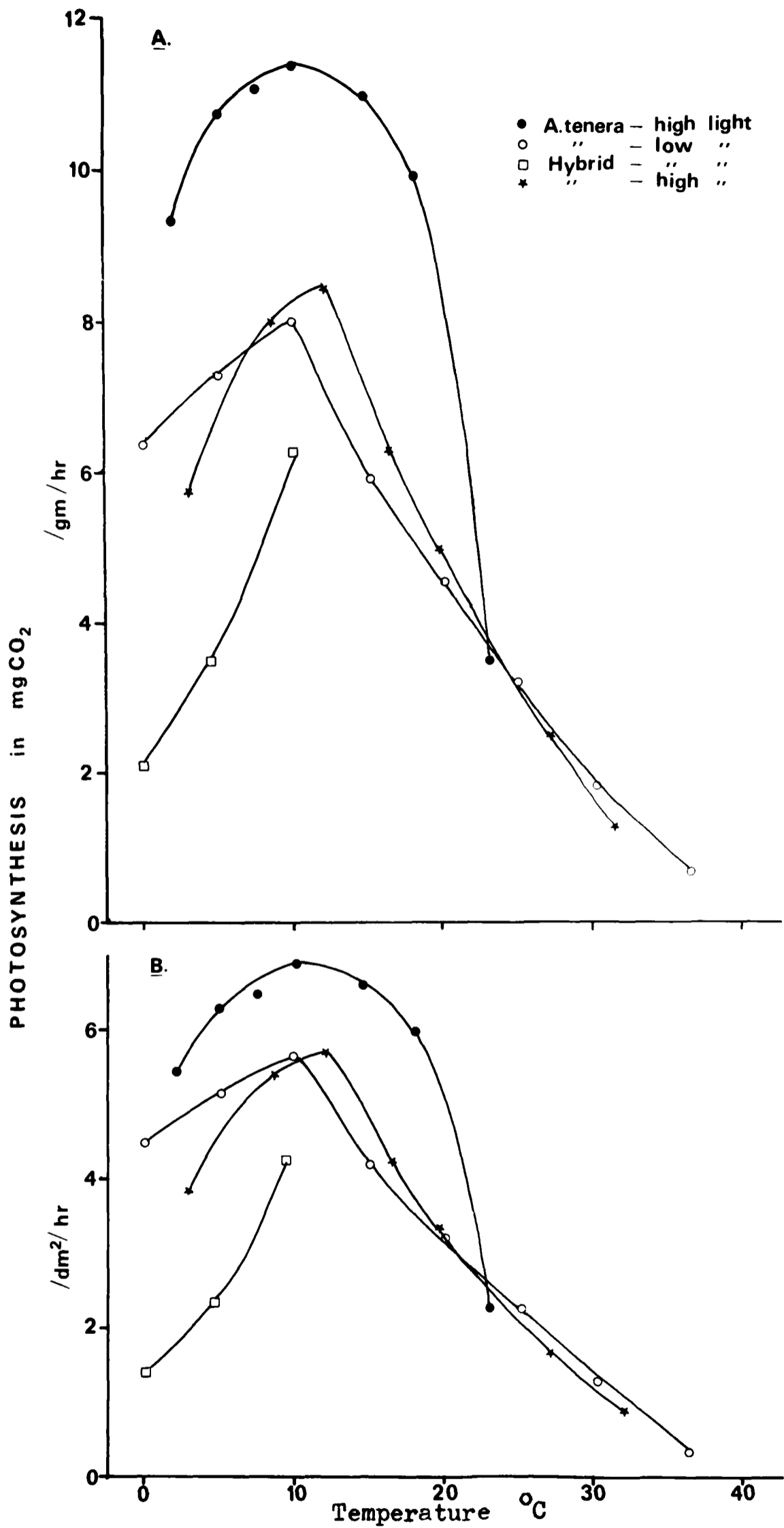


Figure 32. Rates of photosynthesis of detached leaves of *A. tenera* and the hybrid from South Georgian populations
 A - expressed on a leaf dry weight basis
 B - expressed on a leaf area basis

that for South Georgian material proved to be over 40°C.

The two Tierra del Fuego populations came from different habitats, the material from the Nothofagus forest being heavily shaded and, when collected, having rather larger leaves than the material from the roadside. It is therefore interesting that it appeared to be more efficient than the roadside material at the low light level of 136 micro-einsteins/m²/sec.

The upper compensation points of A.tenera and the hybrid can only be inferred from the graphs. For A.tenera it would appear to be around 25°C. at the higher light intensity and about 40°C. at the lower intensity. For the hybrid at the higher intensity it appears to be between 35-40°C. The lower compensation point was not reached for any of the taxa. Even at -2°C. one of the Tierra del Fuego populations was still photosynthesising at c. 40% of its maximum rate. There was some evidence of frost damage during low temperature runs but only if the material was returned to a temperature above freezing quickly. If the increase in temperature was slow and gradual no apparent damage was done to the leaf's photosynthetic ability.

The maximum rate of photosynthesis achieved by each of the populations varied somewhat. The data are shown plotted both on a leaf area basis and on a leaf dry weight basis. In all cases the photosynthetic rates appear higher on the leaf area basis. The relative positions of the curves also change when photosynthesis on a dry weight basis is studied. This is due to differences in specific leaf area between the populations used. It was highest in the material from the roadside and lowest for South Georgia for A.magellanica. The values for the hybrid were almost identical for both populations but those for A.tenera varied considerably.

Specific leaf areas in cm^2/gm for material used in
photosynthesis experiments

A. magellanica

Tierra del Fuego	Forest	176
	Roadside	183
South Georgia	Shallop Bay	124 and 135

A. tenera

South Georgia	Shallop Bay	142 and 166
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Hybrid

South Georgia	Maiviken	147 and 148
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This means that for A. magellanica the leaves of the Tierra del Fuego populations were considerably thinner than those from South Georgia. Indeed, they were thinner than those of any of the South Georgian taxa. The importance of examining photosynthesis on more than one basis is quite clear, although many workers still only present results on either a leaf area or leaf weight basis.

The maximum rate of photosynthesis achieved was that for A. tenera at high light intensity on a leaf weight basis. Interestingly, on a leaf area basis this rate falls to equal that of South Georgian A. magellanica. The contrasts produced by using leaf area and leaf dry weight as bases for the calculations of photosynthesis raise more problems than they answer. In the case of A. magellanica the Tierra del Fuego populations appear to be more efficient or at least as efficient as the South Georgian ones on a

specific leaf area basis. It is not known though if the differences in specific leaf area are caused by an increase in density of the leaf or an increase in volume. Each of these is likely to produce different effects on leaf temperature and the rates of gas exchange in the air spaces inside the leaf. From the information presented here it is only possible to say that marked differences exist between spatially isolated populations within A.magellanica and that inter-specific differences can be shown between the South Georgian taxa. Considerable further investigation is needed before it will be possible to pinpoint the reasons for the differences more accurately. There does however seem to be some evidence that physiological ecotypes exist within A.magellanica.

Chapter 9

ECOLOGY

General Ecology

A characteristic feature of the flora of the sub-Antarctic islands is the lack of species pressure due to the limited numbers of species able to survive successfully in such rigorous climates. On most of these islands a range of habitat types 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 very wet areas, but most species appear to have sufficiently wide ecological tolerances to be able to flourish in a variety of habitats and communities. R. I. L. Smith (pers. comm.) after a recent survey of plant communities on South Georgia, has suggested that there is little species fidelity in any of the associations which show complete intergradation to form a single continuous series. On South Georgia Acaena magellanica occurs in most communities, whilst A.tenera is much more limited in its occurrences, generally preferring the more montane habitats.

In Chapter 2 A.magellanica was shown to vary morphologically more than A.tenera, whilst in Chapter 8 physiological differences between geographically isolated populations of this species were illustrated. It is predominantly a plant of the Southern Cool Temperate and sub-Antarctic botanical zones, although it does extend north to 24°17'S in the Andes. A.tenera is however much more restricted in distribution, and much more stable in morphological characters.

Results:

The following account is large concerned with the species occurring 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 in the case of South Georgia, the Falkland Islands and some of the Tierra del Fuego observations.

Macquarie Island: A. magellanica (= A. adscendens) was reported by Taylor (1955) to grow only in wet peat or gravel. It occurred as isolated plants but more commonly as mats on creek gravels where it reached its largest size. It flowered from September to February and since it was a favourite food of the rabbits they were instrumental in a wide dispersal of the fruits. Johnston (1966) has reported that in some areas rabbit grazing was causing the establishment of A. magellanica dominated communities in place of the original Pleurophyllum hookeri and Stilbocarpa polaris 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 sward areas. The other species of Acaena on the island, A. minor, occupied rather more montane habitats, a similar position to that of A. tenera on South Georgia. It was also widely distributed by the rabbits but tended to prefer drier sites than A. magellanica. It was much more common at higher altitudes and was an important constituent of the Azorella selago feldmark, (Ashton and Gill, 1965), an association in which

A. magellanica occurred only rarely. This species is a constituent of the floras of the New Zealand shelf islands, Allan (1961) even recording a luxuriant form on Auckland and Campbell Islands as A. minor var. antarctica (Cockayne) Allan. Gillham (1960) reported A. magellanica as an important coloniser in the disturbed drier areas of bird colonies and elephant seal wallows and suggested that on the New Zealand shelf islands this niche was occupied by A. minor. In the herbarium material examined no evidence has been seen of hybridisation between the two species, a point upheld by field observations (J. F. Jenkin, pers. comm.).

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 that it was found at Long Beach in 1963 and 1965, and in 1969 "was found to be prolific at Skua Beach and to occur as far north-west as 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 A. magellanica was sensitive to heavy salt deposits from spray which usually caused blackening of the leaves. It apparently did best in well drained

eutrophic soil in sites sheltered from the wind. Although it occurred in 45% of the 457 quadrats that he examined it was only a minor constituent of the Tillaea moschata and the Cotula plumosa associations, whilst it was not found at all in bog areas but occurs occasionally in the Agrostis magellanica mire. Inland stands of Poa cookii often contained Acaena magellanica growing between the tussocks whilst in two communities it was always the dominant species- Acaena-Pringlea spring association, and the Acaena herbfield. This herbfield normally had a carpet of Rhynchostegium brachypterygium and Drepanocladus uncinatus as an understorey. Acaena also occurred in the fernbrake Blechnum penna-marina association as an important constituent.

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.

Îles Kerguelen group: the ecology of the islands in this group was covered by Chastain (1958). He reported that Acaena magellanica occurred in both wet grassland and dry habitats. It was replacing Azorella selago on most of the Main Island and this may have been partly due to rabbits which ate both leaves and stems whilst helping to spread the ripe fruits to new habitats. He suggested that two forms of the species were distinguishable; Form A, found in grassland and drier habitats was better developed and bigger than the other form; Form B, found in bogs and fens, with small leaflets often with red colouration. He noted that he had seen similar material to the latter from the Falkland Islands and Patagonia. He also pointed out that the two forms that he described were connected by a complete range of intermediate plants.

Îles Crozet group: The most recent published account of the flora of any of the islands in this group is that of Dreux (1964). In his account of the flora of Île aux Cochons he stated that it differed very little from that of Île de la Possession. In the south and east of the island large areas were covered by Acaena magellanica between 100 and 300 m., whilst this species also occurred in the vegetation of the coastal fringe.

Dr. L. Davies recently visited Île de la Possession and made the following observations on Acaena magellanica (pers. comm.). It was found throughout the island normally growing on a peaty substrate, and only rarely on bare scree slopes. It was an important constituent of the Agrostis magellanica and the Poa pratensis grasslands, as well as the Blechnum penna-marina association. It was not found actually in bog communities, only at their edges in less waterlogged areas. In the fellfield communities it occurred as isolated plants in the gravel and more frequently on peaty islands of vegetation. Found up to 170 m. on this island.

Falkland Islands: several 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 high alpine areas and are very rare whilst A.ovalifolia is found only in one area of West Falkland. Both the other two species are widespread although A.lucida is normally found only in coastal communities. A.magellanica also occurs in these communities but does extend further inland in some areas. As both Skottsberg (1913) and Moore (1968) have remarked, it does seem to prefer moist habitats, a point also made by Vallentin and Cotton (1921). 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) records 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 Staten Island: Roivanen (1954) recorded four species of Acaena from Tierra del Fuego in his major paper on the ecology of the Isla Grande. He classified the moorlands there into 9 categories and listed A.tenera as occurring in two and A.magellanica in six. His cover values for A.tenera rarely rise above three (Domin scale) whilst those for A.magellanica reached ten in some places. It is important to note that Roivanen makes no reference to either A.antarctica or A.microcephala in his paper. Examination of herbarium material suggested that A.antarctica, a species frequently confused with A.tenera in the past, may well have accounted for most of the material Roivanen recorded as A.tenera. Until recently in Tierra del Fuego A.tenera was only known from the mountains where Alboff made the type collections. However, Dr. D. M. Moore (pers. comm.) has now discovered a number of new localities further to the east and north than those known previously (see Fig. 17). He makes the following comments "The altitudinal range is variously 550-650 m., tree-line upwards, 1800-3000'. In no case have I seen it below treeline (almost consistently 1500' 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 hybridisation - as one might expect. It does not occur as far east as the diploid A. magellanica". (pers. comm., in letter 23/7/73).

Staten Island is largely an unknown area botanically. Examination of herbarium specimens has shown the presence of A. antarctica, A. magellanica and A. tenera. A. antarctica appears to be fairly common in fellfield areas of the island, 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). A. magellanica appears to be common at sea level in areas such as Empetrum heaths and on cliff ledges by the sea.

Other islands: two species of Acaena, A. sarmentosa and A. stangii occur in the Tristan-Gough 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 the species A. insularis, described from New Amsterdam and St. Paul (Citerne, 1897).

South Georgia: Greene (1964) has given some general information about the floristic content of the various South Georgian plant communities. To illustrate some of these communities in more detail the data in Table 26 were collected. These random quadrat surveys (100 random quadrats 25 x 25 cm) give relative frequencies and mean cover details for a number of different sites chosen to cover a range of floristic content, soil type, pH and water content. Descriptions of the sites can be found in Appendix 4.

Table 26

Frequency/Mean Cover Data from Random Quadrat Surveys at a Number of Sites on South Georgia

	Site I (Point Site)	Site II (Sward Site)	Site III (Shackleton Site)	Site IV (Dam Site)	Site V (Hope Site)	Site VI (Acaena Fellfield)	Site VII (Acaena Rostkovia)	Site VIII (IBP Festuca)	Site IX (IBP Primary)
<u>Acaena magellanica</u>	100/60.2	100/95	100/96.4	45/18.3	44/12.4	-	92/21.8	92/14.5	93/30.2
<u>A.tenera</u>	-	-	2/ 0.2	70/17.0	40/ 3.0	96/12.2	-	14/ 0.8	-
<u>A.hybrid</u>	-	-	-	45/19.0	80/38.4	20/ 3.0	-	-	-
<u>Phleum alpinum</u>	36/ 7.7	-	-	-	64/11.0	80/11.4	88/ 6.6	58/ 5.2	52/ 0.8
<u>Festuca contracta</u>	-	4/0.3	-	45/ 9.8	88/19.0	92/13.6	2/ +	98/32.3	100/67.8
<u>Deschampsia antarctica</u>	72/13.6	-	-	-	12/ 1.6	-	-	-	-
<u>Poa flabellata</u>	-	-	-	40/ 7.0	8/ 1.8	-	-	-	-
<u>Poa annua</u>	86/23.1	-	-	-	-	-	-	-	-
<u>Rostkovia magellanica</u>	-	-	-	-	80/13.5	-	100/36.7	46/ 2.6	8/ 0.3
<u>Juncus scheuzerioides</u>	-	-	-	-	28/12.8	-	48/ 4.0	-	-
<u>Tortula robusta</u>	18/ 2.6	98/77	88/29.8	75/24.0	36/ 7.4	8/ +	96/88.4	4/ 0.4	45/ 7.0
<u>Polytrichum alpinum</u>	-	-	-	40/ 6.8	16/ 2.6	100/37.2	-	94/ 9.0	69/ 7.8
<u>P.alpestre</u>	-	-	-	10/ +	48/ 5.8	-	-	-	12/ 3.8
<u>P.piliferum</u>	-	-	-	-	-	24/ 2.7	-	-	-
<u>P.juniperinum</u>	-	-	-	-	4/ +	-	-	-	-
<u>Chonosodontium aciphyllum</u>	-	-	-	20/ 2.0	-	-	-	100/40.0	13/ 0.8
<u>Dryopandocladus uncinatus</u>	-	-	-	-	-	-	18/ 6.0	-	-
<u>Bartramia sp.</u>	-	2/ +	-	70/10.0	32/ 4.2	-	2/ 0.2	-	2/ +
<u>Ceratodon sp.</u>	6/ 1.0	-	-	-	-	-	-	-	-
<u>Psilopilum trichodon</u>	-	-	-	10/ 1.5	-	-	-	-	-
<u>Philonotis sps.</u>	-	-	-	5/ 0.5	-	-	-	-	-
<u>Grimmia sp.</u>	-	-	2/ 0.2	-	-	-	-	-	-
<u>Racomitrium sp.</u>	-	-	-	-	-	-	-	2/ +	-
<u>Conostomum pentastichum</u>	-	-	-	-	-	-	-	2/ 0.1	-
<u>Bartramia subsymmetricum</u>	-	-	-	-	-	44/ 3.4	-	-	-
<u>Barbilophozia sps.</u>	-	-	-	45/ 9.8	36/11.6	-	-	98/11.9	96/ 6.7
<u>Cephalozia sps.</u>	-	-	-	5/ +	-	96/ +	10/ 3.0	-	-
<u>Lophocolea sps.</u>	-	4/ 0.4	2/ +	10/ 2.5	12/ +	96/ +	-	4/ +	-
<u>Riccardia sps.</u>	-	-	-	-	-	-	2/ 0.4	-	-
<u>Fungi</u>	-	-	-	-	-	-	2/ +	-	-
<u>Lichens</u>	-	-	-	15/ +	12/ 0.6	100/27.6	-	100/21.0	44/ 1.2
<u>Bare ground</u>	38/ 9.0	-	14/ 2.0	45/ 6.4	8/ 1.2	100/24.0	-	2/ 1.0	1/ 0.3

Only 2 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 site at which the hybrid was recorded was Site VI, and this was also the only site at which no A.magellanica was found. A.tenera occurred at 5 out of the 9 sites but was an important constituent at only two, Sites IV and VI. A.magellanica on the other hand occurred in 8 sites and was more or less prominent at them all. The table shows very markedly the floristic poverty of well established A.magellanica swards (Sites I-III).

On the basis of these data some observations can be made on the performance and importance of each of the Acaena taxa in the various community types, dealing first with A.magellanica.

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. Observations suggest that colonisation of new areas occurs both by seed and by rhizome growth. Primary colonisation 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. The author's observations suggest that this is not generally true, other mosses and plant bases often providing a suitable microclimate 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 observation by R. E. Longton (pers. comm.)

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 have been found at a depth of 1.5 m. which were apparently undecomposed but it is impossible to say if 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 with very wet peat. This association can also develop on dry scree slopes and on flat outwash areas of morainic debris. Flowering appears to be influenced most markedly by site exposure, but is affected by water availability. Sites facing due south flower later than those facing due north in any given locality.

The association formed between A. magellanica and Festuca contracta (Sites VIII and IX) can have either species as the dominant on a cover basis, or even co-dominance. This is a widespread community type on the northern side of the island, especially in the areas around Cumberland Bay and Stromness Bay. Floristically it is classed as a grass heath by Greene (1964) and is quite a rich community, but this is largely due to its cryptogamic component. Generally this community contains a high proportion of Festuca contracta standing dead 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 sites, often with the development of a simple brown earth soil. A. magellanica does not flower as profusely in this community as in the Acaena-Tortula ones, and the scapes that are produced are usually shorter than in the Acaena swards.

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 not found in the Acaena sward can become major constituents. The lichens found are generally species of the genera Cladonia, Cetraria, Pseudocyphellaria and Stereocaulon.

There are two other community types in which A.magellanica can occur as an important constituent. One is the mire communities generally containing Rostkovia magellanica and/or Juncus scheuzerioides as the dominant phanerogam, whilst the other is the tussock grassland, dominated by Poa flabellata.

Only one wet community is shown in Table 26 and that is Site VII. The dominant phanerogamic species is Rostkovia magellanica, although a small amount of Juncus scheuzerioides is present. A.magellanica has a high frequency throughout the community but low overall cover. The leaves of plants in this type of wet community are normally small and more tightly clustered than in drier communities. Often the leaves are tinged a reddish colour. Flowering is infrequent and when it does occur the scapes and heads are both small. Rhizome or stem is only visible where it produces leaves, the remainder being hidden under the layer of moss. The particular community examined contained an overwhelming proportion of Tortula robusta but communities with a high content of Drepanocladus uncinatus and Chorisodontium aciphyllum are also common. Not surprisingly these mire communities are underlain by peat deposits often of considerable depth, especially where the community lies in a basin.

No example of the Poa flabellata tussock community is included in Table 26. A.magellanica is only an important constituent of this when the tussock is 'open', i.e. when the stools are far apart. It then forms a continuous sward between the stools, in some cases growing on to stools

damaged by seals. A. magellanica does not stand up very well to trampling being quickly affected by the establishment of penguin rookeries or seal populations. It is usually the only Acaena species occurring in this community and so the only one likely to suffer this kind of pressure. In Royal Bay an area was found in which A. tenera replaced A. magellanica in the area between the tussocks but this only occurred on steep slopes well away from the beach and is an unusual occurrence in this community. In the flat beach areas where standing water is found between tussocks A. magellanica does not occur. The growth form of the Acaena in this community is similar to that in the swards but flowering is limited to the most open areas, often seeming to follow drainage channels.

A type of community in which A. magellanica does not occur is the fellfield. Data for this community are given under Site VI. This is typified by a high cryptogam content and considerable bare ground. It is normally found in relatively high exposed situations and all its phanerogamic constituents are smaller and more compact than in their other habitats. A. tenera is an important constituent here together with Phleum alpinum and Festuca contracta. A wide variety of lichens, both foliose and ^scrustose, are present along with species of Polytrichum and, frequently, Rhacomitrium. A small amount of the Acaena hybrid can also be found here, but this does not grow very well. A. tenera is often found flowering 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 moss clumps at the base of boulders where they can gain adequate protection from the wind.

A.tenera is not normally found in dense swards. It is a rare constituent of most of the Acaena-Tortula communities and is not common in the Festuca grassland. It has only been found in the tussock association in the Royal Bay area as already mentioned, its most common habitat being bare scree in exposed situations. In almost all cases the plant will be found with a moss cushion, usually of Polytrichum spp. in the drier habitats and species of Chorisodontium or Brachythecium in the wet ones. However, young plants obviously derived from seed have been found growing at the base of stones and boulders without a moss base. Experiments reported earlier suggested that this species could germinate and establish itself in bare ground and this is borne out by field observation. It can tolerate a considerable degree of exposure having been found growing on the floor of Hodges Corrie with only two other phanerogams, Phleum alpinum and Deschampsia antarctica. All the species appeared somewhat dwarfed but the presence of old scapes showed that flowering did occur but was restricted to sites with a northern aspect.

The ecology of the Acaena hybrid has so far hardly been mentioned. It 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. The sites it is found in are usually well drained and may be floristically rich (Site V in Table 26). It appears to be unable to compete particularly well with either of its parents but to have rather better exposure tolerance than A.magellanica, being more frequent in fellfield communities and other exposed situations than that species.

On a transect up Mt. Duse from sea level to 550' the hybrid began to form an important part of the community at c. 300', the point at which A.magellanica began to become a less important constituent. What is not clear is whether the hybrid plants are restricted to the intermediate sites by the formation of the hybrids in areas of population overlap, or if this restriction is only the 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 are the reverse, normally eliminating most phanerogams quite quickly. Rats appear to have little effect but reindeer, the other introduced mammal, has a very marked effect on A.magellanica and the hybrid in two areas of the island (Lindsay, 1973). These species are grazed back to the rhizome and apparently have little opportunity to flower. A.tenera is the least 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. Normal seal activities tend to eliminate both A.magellanica and the hybrid whose rhizomes are very susceptible to trampling. A.magellanica is however an early coloniser on the bare areas of deserted wallows.

In many parts of the island A.magellanica becomes infected by a fungus, Ovularia sp., towards the end of summer. Yellow necrotic spots appear on the leaves, often affecting every leaf in a sward. It has not been determined if this fungus has any important effect on the growth of the plant.

Discussion:

Both species of Acaena range widely over the whole island, and records collected to date suggest that the hybrid is probably equally well distributed. They 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 recognised on South Georgia, with the hybrid appearing as an important constituent generally only in areas where competition from its parent species is low.

The 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 leaves much larger 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 abnormally 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, 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 in A.tenera. Germination and establishment of hybrid on bare earth in the shelter of a stone appears to be far more common in A.tenera than A.magellanica, which shows a distinct preference for germination in moss mats. The field establishment of 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 does best in pure stands with a moss under-storey. On Îles Crozet it appears to be limited to peaty soils, not being such an active coloniser of the scree slopes as on South Georgia, whilst on Îles Kerguelen its natural ecological position has been considerably changed by extensive rabbit grazing. In both Macquarie Island material and that from Kerguelen the red colouration in the leaves typical of plants growing in boggy areas of South Georgia was remarked upon. The situation on Heard Island where A. magellanica appears to be limited to a small number of localities may be due only to inadequate exploration of the island.

On Staten Island where the ranges of the diploid A. magellanica and A. tenera apparently overlap no specimens have been seen showing hybridisation. 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 1500'.

Both chromosome races of A. magellanica appear to have wide ecological tolerances throughout their respective ranges. A. tenera on the other hand apparently shows a much wider range on South Georgia than in Tierra del Fuego and this is probably due to the much greater species pressure and lack of fellfield habitats at sea level in the latter.

Microclimate Measurements:

Materials and methods:

During February and March 1971 the opportunity arose to use a Grants automatic microclimate monitoring station for a short period. These stations are battery powered and with suitable sensors can monitor temperature, wind run, humidity and radiation automatically. Only temperature probes (thermistors) and a Kipp and Zonen solarimeter were available so that no measurements of wind or humidity could be made. Recordings were made hourly of the following parameters:

air temperatures at 50, 25, 10, 5 and 0 cms. above ground level
soil temperatures at 5, 10, 20 and 40 cms. below ground level
incident radiation at ground level

The recorder was run from 17.2.71 until 9.3.71. The measurements were made in the A. magellanica sward at Site II, the air probes being fixed to an aluminium mast at the appropriate heights and shielded above from the direct sun by means of a white-painted perforated gauze. The height of the Acaena magellanica shoots around the mast was about 15-20 cms. 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 microclimate mast. They were set up at 50, 25 and 7.5 cms. above ground level and were read as frequently as possible.

Results:

Extracts from the data collected are shown in Fig. 33.

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 the period together with data from the evaporimeters are given in Table 27. The evaporimeters were read at c. 1400 hrs daily so rates of evaporation are placed between the meteorological data for individual days.

The top of the leaf canopy between 15 and 20 cms. and the moss layer 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, the limit of the boundary layer. A similar situation exists for cold spots occurring during cloudless nights. 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 the hot days the mean wind speed was much lower on 17 February than on 19 February. This is reflected in the measurements of much higher temperatures, over 20°C., in the first hot spot than in the second (Fig. 33). During the intervening cloudy day the wind speed was very low and this, together with the lack of radiative heating, resulted

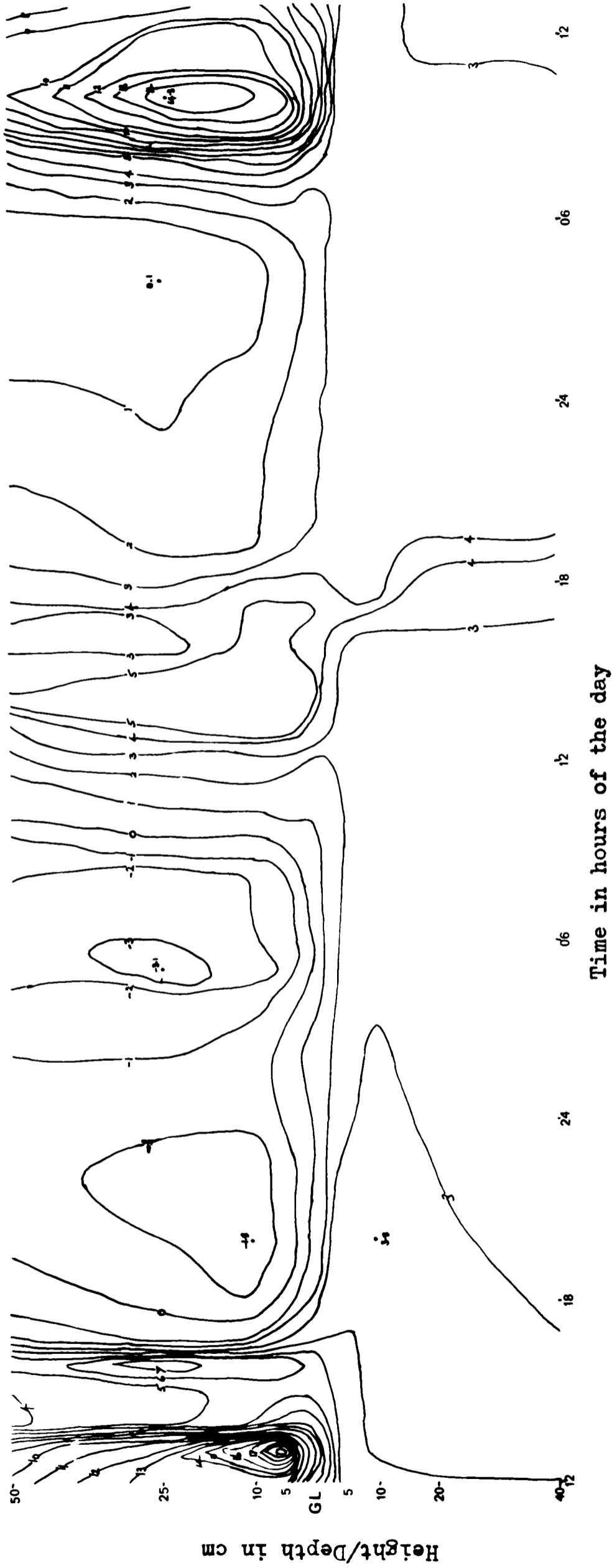


Figure 33. Isothermal diagram to illustrate the changing temperature patterns with time in a profile through an Acaena magellanica community on South Georgia

Table 27 Meteorological and evaporimeter data for February 1971

	Date						
	17	18	19	20	21	22	23
Max. screen (°C.)	7.9	6.4	10.2	5.4	5.8	10.6	11.1
Min. screen (°C.)	0.9	0.2	2.4	0.1	2.8	0.6	4.4
Mean screen (°C.)	3.8	3.6	5.4	2.9	7.3	6.0	7.6
Sunshine (hrs.)	8.3	0.1	8.5	0	1.0	7.8	0.4
Rain (mm.)	12.6	0.7	trace	0	11.7	3.3	17.5
Mean wind speed (kts)	3.9	2.0	8.3	8.7	4.0	9.0	10.3
Snow/sleet	-	+	-	-	-	-	-
Evaporimeter 50 cm.	0.2	3.0	3.15	3.6	1.55	6.5	
(loss in mm.) 25 cm.	0.2	2.55	2.5	1.5	1.5	5.45	
7.5 cm.	0.05	0.65	0.8	0.35	0.3	1.35	

in the persistence of sub-zero temperatures in the air profile until late morning. The moss mat acts as an insulator above the soil so that even the major daily temperature fluctuations do not usually penetrate very far into the soil, normally being contained within the top 5 cm. Indeed, it can be clearly seen in Fig. 33 that it is only when pronounced temperature foci develop within the canopy that any change can be seen in the soil temperature profile. However, long term seasonal changes in the overall soil temperatures do take place, though generally quite slowly.

It is quite clear that the upper parts of the Acaena sward can be subjected to temperatures several degrees below zero for short periods (several hours) without suffering any irreparable harm. It is also clear that the cover of moss which so frequently underlies the Acaena acts as a fairly efficient insulating layer which normally keeps the soil surface and subsoil temperatures relatively stable. The space between the top of the moss layer and the top of the canopy experiences far greater extremes of temperature than those shown by ambient air temperature above the sward. The 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 sward during December and January, whilst the frequency of frosts obviously increases as winter approaches. The accuracy of the Grant recorders is probably to about $\pm 0.5^{\circ}\text{C}$. but it is thought that this would be unlikely to alter the general shape of the figures very much.

The results from the evaporimeters show 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 sward was 100% and the rate of evaporation within the sward, even under quite warm conditions, suggests that air movement was very small at this height 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.

Within the tribe Sanguisorbae Juss. (= Poterieae) of the Rosaceae, Hutchinson (1964) lists 16 genera of which Acaena, Cliffortiana and Polylepis are the largest in the Southern Hemisphere, and Agrimonia, Poterium and Alchemilla the largest in the Northern Hemisphere. Within the genera largely restricted to the Southern Hemisphere the closest relatives of Acaena are Polylepis (Bitter, 1911) and Margyricarpus (Bitter, in Skottsberg, 1922). Its closest relative in the Northern Hemisphere is Sanguisorba sensu Nordborg (Nordborg, 1966). Van Steenis (1962) has made much of the occurrence of species/genus pairs in the two hemispheres - Fagus/Nothofagus, Acaena/Sanguisorba - deducing from this that their ancestors originated in the tropics and that the present close similarities between the groups are due to similar evolutionary trends in both hemispheres. Acaena and Sanguisorba for instance occupy similar habitats in both hemispheres and show very considerable overall morphological similarities. Axelrod (1952, 1959, 1972) and Thorne (1963), together with Florin (1963) have all supported the theory of a tropical origin. Axelrod (1959) has suggested a pre-Cretaceous origin for the angiosperms. This would mean that their initial development and speciation began at the same time as the initial breaking up of Gondwanaland (Dietz and Holden, 1970), and that the tropical areas of origin moved around as the rifting of the super-continent proceeded. These assumptions do not agree very well with those of Melville (1966), who suggested that present circum-Antarctic distributions such as that of Juncus scheuchzerioides came about during the Cretaceous over land bridges, some of which seem to be entirely hypothetical (e.g. 'Pacifica'). Thorne (1972) rejected any connection between the break up of

Gondwanaland and present circum-south temperate distributions, and called for long distance dispersal and migration over a much warmer and more extensive Antarctic archipelago to explain the dispersal.

It would seem most unlikely that any one explanation will ever be found to satisfy all cases. Reviewing all the opinions listed above the following hypothesis can be put forward for the distribution of Acaena.

If it is accepted that Acaena is the result of differentiation in the Southern Hemisphere of a tropical ancestral species, the disjunct species in California and Hawaii (A.californica and A.exigua) are likely to have resulted from long distance dispersal from South America. Solbrig (1972) has discussed the disjunctions between North and South America and given three possible explanations: 1. long distance dispersal, 2. relicts of a continuous distribution, 3. parallel evolution. Given the close similarities between the northern species and apparently related species in South America, the third explanation seems unlikely. If the original distribution was continuous one would expect to find a greater species representation in temperate North America. Thus, long distance dispersal seems the most likely explanation and this conclusion is supported for A.exigua by Carlquist (1967).

Turning now to the distribution of the genus in the Southern Hemisphere. Skottsberg (1936), treating Acaena as an Antarctic genus, stated that the present distribution could not be accounted for by rapid transport across oceans but only by the slow migration of a differentiating genus across land with subsequent isolation and dying out. Godley (1967), in discussing disjunction in Hebe (Scrophulariaceae), came to the firm conclusion that long distance dispersal between Australasia and South

America was the only answer, a contention supported by Hamlin (1959) in the case of Uncinia (Cyperaceae). In Chapter 5 the possible origin of the various Australasian taxa of Acaena was examined in some detail. The case for regarding the species as probably resulting from only three separate introductions is at least partly supported by Orchard (1969). He says "The affinity of the Australasian complex (of A.ovina) with South American species implies that it has its origin in Australia as an introduction into eastern Australia from South America. Furthermore, the obvious close relationship between the species within the complex supports the postulated introduction of a single taxon with subsequent diversification". On the basis of estimates by Crocker and Wood (1947) of the onset of the present arid conditions in South Australia he goes on to postulate that the original introduction was probably no more than 10,000 years ago, and may have been less. In the case of the Tasmanian endemic A.montana, the close similarities between it and A.antarctica, the inbreeding characteristic of this group in the genus and the apparently narrow climatic requirements of all the species within this group definitely point to a South American origin quite possibly of considerable antiquity.

The origin of the New Zealand species is certainly much earlier than 10,000 years since speciation has progressed much further than in Australia. Raven (1973) points out that Acaena and Uncinia are undoubtedly dispersed between continents and islands by birds but suggests that both these genera were probably present in New Zealand in Paleogene times. Since he points out that rapid evolution on isolated islands is common in some genera, there does not seem any reason to believe that speciation did not occur in Acaena as quickly as in Colobanthus and Celmisia and that a later date for introduction, say late Pliocene-early Pleistocene, cannot be used.

The spread of species from South America to these remote localities has been suggested by Andrews (1940) to be closely linked with the movement of the ocean currents. Tests with Acaena seeds have shown that they normally sink within 3 or 4 days of being put into salt water and will not germinate after prolonged immersion. Many species in the genus are however equipped with well developed hooked spines on each fruit. Hamlin (1959) has suggested that the hooked fruits of Uncinia are ideally suited to long distance dispersal by birds, this idea being fully supported by Falla (in Hamlin, 1959). Field observations in South Georgia have shown that many birds have Acaena magellanica fruits in their feathers from time to time, and some of them such as Giant Petrels (Macronectes) have a circum-polar range. Ridley (1930) and Croizat (1952) are both in no doubt about the dispersal of Acaena by birds.

Examining the scope for early colonisation by plants on South Georgia explains the limited flora. In a review of the types of unglaciated areas likely to have persisted during the ice ages Dahl (1946) suggested that in coastal areas with high mountain ranges near the coast complete glaciation would never occur. The refugia left if the firn line reached sea level would however be unable to support more than a few mosses and lichens according to the parallels he draws with the present situation on the Antarctic continent. Under this hypothesis all the phanerogamic flora must have been introduced by long distance dispersal fairly recently, a conclusion also reached by Skottsberg (1915). Taylor (1955) came to this conclusion for Macquarie Island as did van Zinderen Bakker (1971) and Huntley (1971) for Marion and Prince Edward Islands. Valuable supporting evidence for Taylor's (1955) conclusion was provided by Bunt (1956) who, comparing fossil and present-day pollen floras, found no connection between the two. Comparative evidence such as this would be most useful for all the

other sub-Antarctic islands. The situation on Îles Kerguelen is rather different since the archipelago does not seem to have suffered from such major glacial action as the others and the presence of large numbers of fossils and endemic genera suggest that the origin of the flora may be partly relictual.

Moore (1972) has suggested that Acaena may have differentiated in the Cretaceous, its present distribution being largely due to later long distance dispersal. He has postulated that the diploid race of A.magellanica survived the last glaciation in ice-free refugia, either in southern South America or on partly unglaciated islands such as Îles Kerguelen, and then spread northwards with the retreat of the ice to occupy its present range as the tetraploid form. It is difficult to imagine the diploid moving back against the winds and currents from Îles Kerguelen to Tierra del Fuego and would seem much more likely that, as far as the South Georgian plants are concerned, the diploid has spread eastwards from its unglaciated refugia in Tierra del Fuego.

Although the oldest radio-carbon dates so far obtained for South Georgia are about 7000 B.P. (Fergusson and Libby, 1964) the samples did not constitute the bottom of the peat profile. Geomorphological evidence also suggests that some parts of the north-east coast have probably been ice-free for much longer than this (Clapperton, 1971), one suggestion being 20-25,000 years (Smith, 1960). It would however seem reasonable to assume that most of the area currently covered by phanerogamic vegetation has probably only become available during the last 10-12,000 years. It is during this period that multiple hybridisation has occurred between A.magellanica and A.tenera. The introduction of only the diploid race of A.magellanica suggests a direct dispersal from either the south-east of Isla Grande or Isla de los Estados, this connection being reinforced by the presence of A.tenera

and Phleum alpinum on South Georgia, both being species from roughly the same area as the diploid A. magellanica and neither species occurring in the Falkland Islands.

From the original introductions of A. magellanica and A. tenera, the species and their hybrid have spread to virtually all the vegetated areas of the island. The review of ecology in Chapter 9 has shown that the high degree of morphological variability shown by A. magellanica is apparently paralleled by wide habitat tolerances and a considerable amount of physiological flexibility. Likewise, the morphological stability of A. tenera is paralleled by its more rigorous habitat restriction, whilst the hybrid plants appear to be intermediate in most respects. The inter-relationships of these three taxa on South Georgia should provide an interesting study in the life strategies adopted by these dwarf shrubs which should, in turn, provide further material for the interpretation of their biogeography. In examining the life strategies of the species on South Georgia two of the most interesting problems are their success in establishing themselves and their production of a hybrid unknown anywhere else. It is the production of this hybrid taxon that connects the two Acaena species on the island and their inter-related breeding systems are illustrated diagrammatically in Fig. 34.

Pollen from A. magellanica flowers can have several possible destinations on this diagram. The likelihood of the F_1 cross being only in one direction has been reasonably established by the morphological measurements on scape elongation and floral development in the two species, further supplemented by the only F_1 hybrid plants to be raised from seed all coming from A. tenera seed. There must obviously remain some possibility of a cross in the reverse direction but this would seem to be of extremely low occurrence. The measurements of low pollen

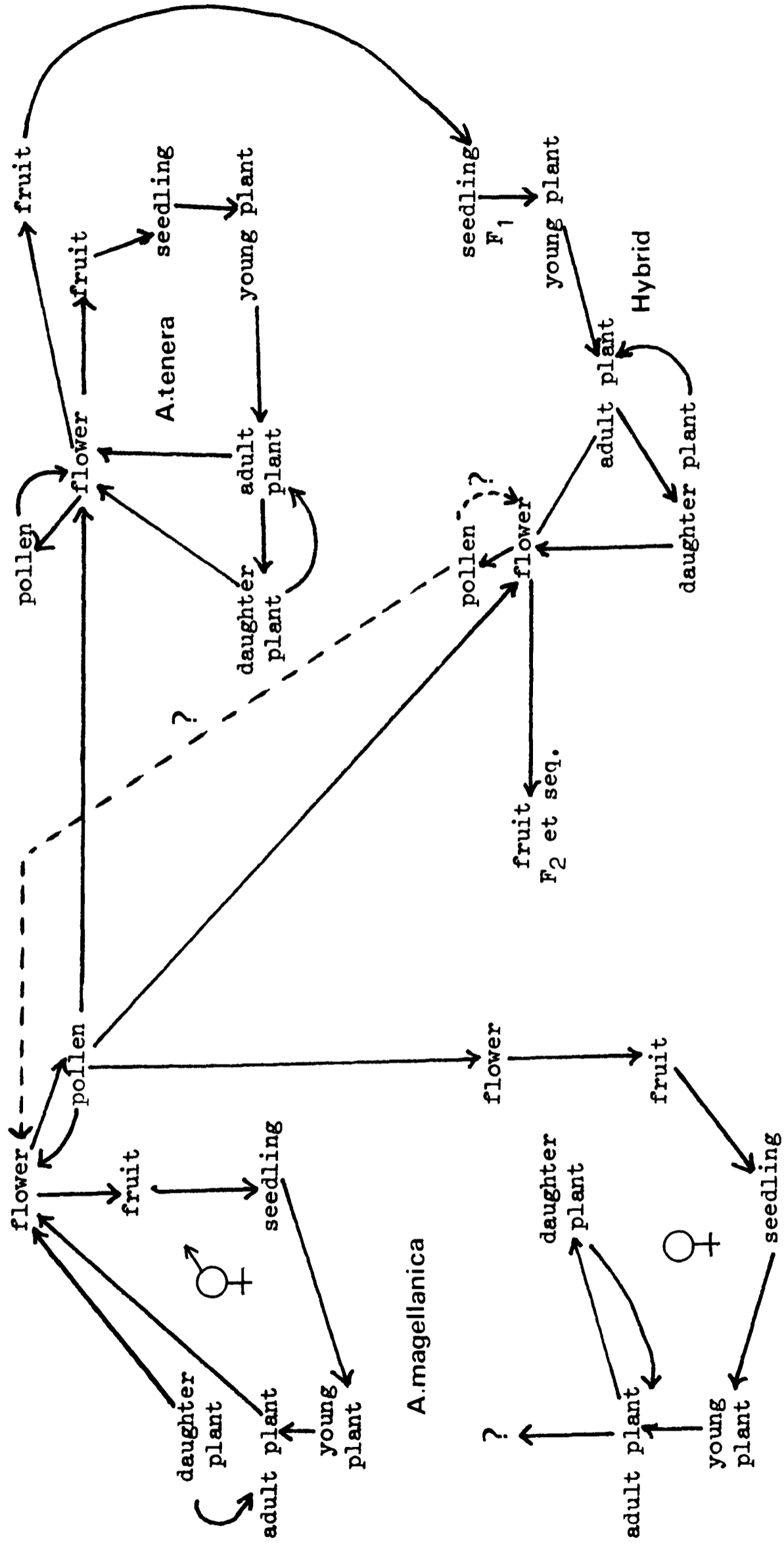


Figure 34. The probable inter-relationships between breeding systems in South Georgian Acaena

viability in the hybrid together with the observation that in some flowers the anthers do not dehisce normally makes it impossible to know if selfing is likely to produce any viable seed. Since the apparent morphological trend in hybrid populations is towards A. magellanica it must be presumed that, in the majority of cases at least (bearing in the mind the very low seed viability of the hybrid), the F₂ seed is formed from the backcross to A. magellanica. The possibility of fertilisation in either of the parents by viable hybrid pollen may well exist but nothing is known of its occurrence.

The position of the female populations of A. magellanica in the relationship has also not been finally elucidated. Clearly, since they produce viable seed, the pollen for fertilisation must be coming from the hermaphrodite flowers but, since no seed from female heads has been grown up to flowering stage, it is not known if the seed will produce only female plants or female:hermaphrodite in a fixed ratio. Because of the widespread distribution of the female populations, which show a similar degree of morphological variability to A. magellanica hermaphrodite plants, it seems likely that they may well have arisen independently. Although two ploidy levels have been established for hermaphrodite plants, the female ones await further cytological investigation. The occurrence of these female plants, should allow the establishment of a breeding programme in the future to investigate crossability and character inheritance.

Although it has been shown that it is only in South Georgia that the distributions of the diploid A. magellanica and A. tenera overlap, it still appears remarkable that these two species should hybridise, coming as they do from completely different sections of the genus. There can be no doubt that the hybrid is a successful plant on South Georgia but it does

not show the usual degree of hybrid vigour when compared with the parent species. Its position ecologically on the island tends to be in marginal areas. It cannot compete with A.magellanica in the favourable lowland habitats and will not grow in the extreme fellfield areas that A.tenera is often found in. Low seed viability will prevent any extensive colonisation of new areas, so that spread must be by further production of F_1 plants and by vegetative growth of established hybrid plants.

No controlled crossing experiments have been carried out so far but the analysis of hybrid material allows one to make certain general conclusions about the dominance and inheritability of various characters. Since all hybrid specimens seen have terminal inflorescences it must be assumed that this character is dominant over axillary. The inheritance of other characters is not as clearcut. Hybrid leaf colour is intermediate between those of the parents, as is stigma shape. Fruit type is very similar to A.magellanica but with frequent subsidiary spines. Both uniseriate and multicellular glandular hairs are found in the hybrid, but no "manna" hairs on the fruits.

The overall growth form and branching pattern of the F_1 plants is also more similar to A.magellanica than to A.tenera and this resemblance will be enhanced by any backcrossing to the former in the production of F_2 and subsequent generations.

A.magellanica and A.tenera appear to have evolved rather different strategies in terms of colonisation and growth. Although the rate of production of fruits per flowering head is higher in A.magellanica the germination experiments showed that a similar number of seedlings per fruiting head would result for both species. This suggests that

A. magellanica regularly produces a considerable proportion of inviable seed. A similar degree of waste in terms of dry matter allotment is not seen in A. tenera, the much smaller and less leafy plants of this species being unlikely to have a production surplus. The much greater range of germination temperatures for A. tenera obviously allows seed germination under a wider range of conditions than is possible for A. magellanica. Germination at lower temperatures is likely to be of considerable significance in a cool climate since it will allow the seedling to have a long growing season: Taken together with the preference of A. tenera for open fellfield communities and the slow rate of growth of its seedlings, the experiment on seedling establishment only confirmed the expected result - that A. tenera would establish much more readily than A. magellanica in stony mineral soils.

In both species flowering is delayed until the plants are several years old and it seems reasonable to assume this will also be true for the hybrid. The position in which the inflorescence is produced has considerable bearing on the possible density in terms of heads per square metre. In theory a much higher density is possible for A. tenera with its axillary heads, several of which can be produced on a single stem. In practice it is normally A. magellanica which has the highest head densities per unit area due to its production of pure dominant communities. Features of the local habitat apparently influence both the rate of flowering and scape elongation. Flowering is never as prolific for A. magellanica in the bog communities as it is in the colonising communities or in the low altitude pure swards. A. tenera is not usually found in very wet communities and flowers best and most prolifically in the more fellfield communities. Although it does flower in the grass heath community much more of its dry matter production appears to go into leaf

and tiller production there, growing under much more sheltered conditions. For both species, and for the hybrid, the sites with the most favourable microclimate appear to stimulate vegetative growth rather than flowering. The aspect of the site can have an important influence on the rate of floral development, north-facing sites generally showing earlier and faster rates of development than south-facing sites. Initiation of the flowering heads will also be earlier in the north-facing sites as snow melt occurs earlier there. Wind exposure affects the final scape length in all three taxa, the longest scapes always being found in the most sheltered habitats and the shortest in the most exposed.

It seems rather strange that the hybrid should apparently have physiological reactions as well as morphological attributes that are intermediate between those of its parents. The fact that its floral development and scape growth rates appear to be a compromise between anthesis after scape elongation and flowering before elongation may be due to the development of the subsidiary heads so common in this taxon. To have more than one major organ requiring large amounts of elaborated photosynthate on a single scape probably slows down the overall rate of development by carbohydrate shortage. It was suggested earlier in this discussion that the position of the flowering head during anthesis was of great importance in determining the probable pathways for hybridisation. From a general examination of herbarium material it appears likely that in most if not all the species of Acaena with terminal capitulate heads the scape elongates to put the head above the leaf canopy before anthesis, whilst in those species with axillary capitulate heads anthesis always occurs whilst the head is still amongst the leaves. Following the same argument as has been advanced for the South Georgian species it might

be expected that greater morphological stability would be found in the inbreeding group of species which behave like A.tenera whilst those species behaving like A.magellanica should show much greater variability due to outcrossing. More than adequate confirmation of this is given by Bitter (1911) who described a plethora of species with terminal heads but very few with axillary heads.

Although no data are given for the hybrid and A.tenera, the standing crop data for the A.magellanica sward show that the greater part of dry matter production goes into vegetative growth and not into floral structures. The standing crop in this community is very high and a comparison with the values given by Wielgolaski (1972) shows that it is probably equal to the highest recorded at any I.B.P. site, including the Russian shrub tundra. Since it is a deciduous species a large part of the annual production is returned very quickly to the nutrient cycling system. Decay of leaves is very rapid (Walton, 1973) and for this reason nutrient turnover must be very high, unlike that in the South Georgia grassland (Greene, Walton and Callaghan, 1973). The decay of these leaves is undoubtedly assisted by the appearance in late summer of a fungal infection of the leaves (this is probably an undescribed species of Ovularia - Fungi Imperfecti, pers. comm. Dr. R. Watling), and by the moist and still microclimate maintained within the canopy which allows various other saprophytic fungi to flourish (Dennis, 1968).

Whilst it cannot be said with any certainty at the moment that physiological ecotypes exist in Acaena, it is obviously in the more wide-ranging species that they might be expected to occur. A.magellanica, as the only species known with two ploidy levels, and as the most wide-ranging species in the genus, is therefore the most likely candidate. The initial

measurements of photosynthesis have shown a clear difference between the South Georgian material and the two populations from Tierra del Fuego. The peak rates of photosynthesis for all except the low light A. magellanica, were around 10°C. and active photosynthesis was still occurring below 0°C. Whilst these observations fit well with the microclimatic measurements made in the A. magellanica community, the response of the plants at the lower light intensity is unexpected. It is not clear why the upper compensation point for the South Georgian material was 40°C. whilst for the two Tierra del Fuego populations it would probably have been c.20°C. Although there are differences in specific leaf area between the two groups it would be strange if this factor only affected the response at low light intensities. Clearly, further work is called for on this aspect of growth but the initial results at least show that there may well be quantifiable physiological differences between geographically isolated populations of this species. It may even prove possible to identify ecotypes on South Georgia as has been done for Phleum alpinum (Callaghan, 1972).

It was suggested in Chapter 8 that on the basis of the chlorophyll a:b ratios for the taxa of Acaena the island should be regarded rather as a sea-level alpine area than as a sub-arctic one. Further evidence to support this view has recently been put forward by Smith and Walton (1974) and Callaghan (in press). Under these alpine conditions, and the similar ones prevailing on the other sub-Antarctic islands and Tierra del Fuego, Acaena is a highly successful genus. The South Georgian taxa can survive for limited periods under the arctic conditions in the South Orkney Islands but do not thrive or set ripe seed (pers. comm. J. A. Edwards). The production of red pigmentation in exposed conditions, apparently a temperature controlled response, is a reaction shown by several South Georgian species beside the Acaena taxa and may well have some adaptive significance in the

more exposed habitats on the island. Certainly, it would seem unlikely that Caldwell's (1968) correlation of red pigmentation with ultra violet protection in alpine species is likely to be an adequate explanation for plants growing near sea level. A more likely possibility is that the red pigmentation may produce higher leaf temperatures than normal which would probably be of great advantage for development in the early spring period.

Despite the observations that taxa of Acaena can photosynthesise below 0°C. the transplant experiments conducted by J. A. Edwards (unpublished) to Signy Island, South Orkney Islands suggest very strongly that the genus has reached its southern distributional limit on the sub-Antarctic islands, the conditions on Heard Island probably being the most rigorous that A. magellanica can actively thrive in.

This study, based largely on the South Georgia taxa of Acaena, has attempted to illustrate two main points: the probable origin of some elements of the phanerogamic flora of South Georgia and the importance of the Acaena species occurring there in terms of the biogeography and evolution of the genus as a whole, and the life strategies of and inter-relationships between the three South Georgian taxa in terms of survival on South Georgia. Many questions are still left unanswered but it appears that some of the most fruitful lines of research that could be pursued would be those looking for correlations between physiological races and chemical or morphological groupings.

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Appendix 1 Complete synonymy of the species Acaena tenera, A.masafuerana and A.antarctica as recognised by the author.

No subspecific categories are recognised within these three species by the author. Although there are a few more literature citations than those listed below it was not deemed necessary to give them as has been done for A.magellanica in Appendix 3 since the degree of nomenclatural confusion for these species is by no means as great as for A.magellanica.

A.tenera Alboff. Rev.del Museo de La Plata VII,367,t.0,(1896).

Syntypes: N.Alboff 233,234, Tierra del Fuego, (Mt.) Pyramidis supra torrentem Ushuaia (SI!,LP).

ssp.epilis Bitt. Bibl.Bot.Stutt. 74,56-57,fig.8(1911).

Type:N.Alboff 233. Tierra del Fuego, in regione alpina montis Pyramidis (supra torrentem Ushuaia). (SI!SGO!,LP).

ssp.pilosella Bitt. Bibl.Bot.Stutt. 74,58,t.4(1911).

Holotype: C.Skottsberg,s.n. Tierra del Fuego, Azopardo Valley, nr.Lago Fagnano. (UPS!).

A.masafuerana Bitt. Bibl.Bot.Stutt. 74,45(1911).

Holotype: C. Skottsberg,s.n. Juan Fernandez,Masafuera. 1100-1300m. 27.7.1908. (UPS!).

A.antarctica Hook.f. Flora Antarctica, vol.2,269(1847).

Holotype: J.D.Hooker,s.n. Hermite Island,Cape Horn, on the mountains, rare, 1000 feet.(K!,BM!,E!).

var.argutidentata Bitt. Bibl.Bot.Stutt. 74,54,t.3(1911).

Holotype: C.Skottsberg.193. Tierra del Fuego,in valle fluminis Azopardo.250m. 29.2.1908. (UPS!).

var.laxiuscula Bitt. Bibl.Bot.Stutt. 74,54,t.3.(1911).

Type: C.Skottsberg,208. Tierra del Fuego, prope Rio Azopardo. 3.3.1908. (UPS!).

A.tenuifolia Bitt. Bibl.Bot.Stutt. 74,52,(1911).

Holotype: .F.W.Neger.Andes de Villarrica.1897. (M!).

A.valida Bitt. Bibl.Bot.Stutt. 74,51-52,t.1,(1911).

Type: C. Reiche,s.n. Chile, Cordillera del Rio Manso.1000m. (B - destroyed).

A1.2

A.pumila Phil. Linnaea XXXIII,67,(1864-65).non Vahl 1804.

A.pearcei Phil. Anal.Univ.Chile Santiago LXXXIV,626(1894)

Holotype: R.Pearce,s.n. In Los Andes de Ranco, a saber en un prado situado a unos, 1,350m.Herb.no.049890. (SGO!).

A.pearcei Phil. var.glabrinervis Bitt. Bibl.Bot.Stutt. 74,53,(1911).

Holotype: F.W.Neger,s.n. Chile, Andes, Villarrica.1897.(M!)

A.microcephala Schlect. Linnaea XXVIII,463(1856).

Isotype: Lechler 2951. Chile,in summis Cordiller. de Ranco. December 1854. (K!).

A.microcephala Schlect. var.minuta Bitt. Bibl.Bot.Stutt. 74,55 (1911).

Holotype: Dusen,s.n. Aysen Expd., South Chile.1300m.1896-97. (M!).

Appendix 2 Notes on the identification of type collections

In the case of taxa where the only identifiable type material has been lost or destroyed there has obviously been only the author's original description to go on. In other cases however type material not seen by Grondona has been examined, and in all cases the present author is in agreement with him about the reduction of these taxa to synonymy with A. magellanica.

A few notes are however pertinent on some of these specimens. Yeo's (1973) detailed examination of nomenclatural problems and the difficulties of correct attribution of the earliest type material uncovered the loss of all Vahl's type specimens in transit from Copenhagen to Argentina in 1957. As the original types were examined by Bitter and were included in his monograph (Bitter, 1911) under species now reduced to synonymy with A. magellanica there does not appear to be any need to proceed any further with this line of enquiry. It seems quite reasonable to accept the lectotype designated by Yeo for A. magellanica ssp. magellanica as the type for the species A. magellanica (Lam.) Vahl sensu Grondona. The type material of Ancistrum magellanicum Lam. var. B Lam. listed by Yeo (1973) as a synonym of A. magellanica ssp. laevigata (Aiton) Bitt. also appears to come within the present concept of the species.

Material designated as type material of A. coxi Phil. was seen at SGO and identified as A. magellanica by the author. Difficulties arose with the collections of Hooker designated by Bitter as types. Hooker's collections bear no numbers or other distinguishing marks for the most part so that it is impossible to designate accurately isotype material at other herbaria of the collections from Berlin used by Bitter. In these instances, e.g. A. adscendens (Lam.) Vahl var. semperpilosa Bitt., reliance has had to be placed on the original descriptions again.

Bitter (1911) described a number of species within the section Ancistrum for which the designated holotypes were in the Berlin herbarium. Unfortunately, during World War II the herbarium was bombed and all the Acaena material was destroyed. Type material of the following species was destroyed:

A.acutifida, A.adscendens var. semperpilosa, A.adscendens var. utrinqueglabrescens, A.chamacaena, A.colchaguensis, A.frondosibracteata, A.ischnostemon, A.longiscapa, A.longisepala, A.molliuscula, A.novemdentata, A.purpureistigma, A.subtussericascens, A.tasmanica, A.triglochin, A.tomentella, A.valida, A.venulosa.

In some cases isotype material at other herbaria was listed by Bitter, but for several species only the collection at Berlin was given. It has been possible to find isotype material for certain species in herbaria which were not listed by Bitter. However, a few species whose only designated type material was destroyed have insufficient collecting details given for any certain identification of possible isotype material.

Other type material that is now missing includes:

A.distichophylla(BREM), A.calvivagina and A.parvifoliata(HBG), A.glaucella, A.magellanica, ssp. grandiscapa, A.neglecta, A.subflaccida and A.tenuipila (all from UPS).

The designation of some collections as type material also seems doubtful in certain cases, the greatest number of these cases occurring at SGO in the Philippi herbarium.

The following species have been determined by the author as further additions to the list of synonyms for A.magellanica published by Grondona (1964). In each case type material has been examined when it could be found and this is cited with ! after the herbarium. Otherwise the original descriptions have been used. A small group of species are included at the end under nomina dubia. They include species with no type material in which the original description is too vague or lacking in the essential characters for an accurate attribution to be made and species in which although the material examined appears to be related to A.magellanica it does not correspond clearly to that of any single taxon. The critical characters used included leaflet shape, inflorescence position and type, fruit shape and type of hairs on fruit, number of spines on fruit, shape and colour of stigma, number and colour of stamens. All references to Bitter without date citation refer to Bitter (1911). All herbarium abbreviations are taken from Lanjouw and Stafleu (1964). In Appendix 3 will be found a complete synonymy of all the taxa falling within A.magellanica sensu Grondona as determined from these studies.

ACUTIFIDA Bitter - Bitter (1911): "Cordillera de Curico, Chile. Leg. C. Reiche." B. Type material lost.

Material originally identified as A. laevigata Ait. was used by Bitter as the type material for A. acutifida. He described it as being very close to A. macrostemon, being distinguished from that species by the size of the anthers, smaller leaves and more acutely pointed leaflets, and a very short pedicel to the cupule. In all respects it is included within the description of A. magellanica. An early phototype of the type material was seen at SGO and confirmed this.

ADSCENDENS ssp. GEORGIAE-AUSTRALIS Bitter - Bitter (1911): "Umgebung der Station, grosse, trocknere Flächen bedeckend. Ist neben Dactylis die für das vegetationsbild charakteristischste Pflanze. Busche von 30cm Höhe bildend. Leg. Will, nr. 13." M.Z!

This subspecies was distinguished by Bitter from the other ssp. by its having a short thickened scape often ribbed in the middle, and thin pale green leaflets. Two varieties were distinguished on the basis of leaf size, in this single collection. Examination of the syntype material at Z showed that it was clearly referable to A. magellanica. Philcox (1962) used this subspecies and the varietal names but misinterpreted them, using var. majuscula for all A. magellanica material and var. minuscula for all A. tenera material from South Georgia.

ADSCENDENS var. GLABRISCAPA Bitter - Bitter (1911): "Oberer guter Standort, oberhalb der ertsten Kuppenreihe. Leg. W. Schimper, nr. 42. Gazellehafen, bester Standort oberhalb des Strandes Kerguelen. Leg. W. Schimper. Sumpfform, Kerguelen. Leg. W. Schimper, nr. 39." No herbarium given.

According to Bitter this variety is distinguished from other forms of A. adscendens by the pilosity of the scape, a very variable character. It is therefore reduced to a synonym of A. magellanica.

A2.4

ADSCENDENS var. PILOSISCAPA Bitter - Bitter (1911): "Im Sande des Strandes, Kerguelen. Leg.W.Schimper, nr.43. Observatory-Bai, Kerguelen. Leg.Vanhoffen. Ahlefeld-Halbinsel, in Sumpf, Kerguelen. Leg.W.Schimper, nr.41." No herbarium given.

This variety is only distinguished by Bitter from other forms of A.adscendens on the pilosity of the scape. All its principal characters fall within the description of A.magellanica.

AFFINIS Hook.f. - Hooker (1847): "Kerguelen's Land, marshy places near the sea, abundant. Leg.Anderson. Kerguelen's Land, in Cook's third voyage. Leg. J.D.Hooker and Dr.Lyall." K! E!

From the type description it seemed quite clear that this species should be included within A.magellanica, since the characters of fruit and flower used by Hooker to characterise it correspond closely to those typical of female populations of A.magellanica. An examination of type material from K and E confirmed this viewpoint.

BRACHYGLOCHIN Bitter - Bitter (1911): "Cordillera at 3500'. Martio. Leg.R.A. Philippi, PL.Chilenses nr.129." BREM!

Examination of the holotype material confirmed that this species should be treated as a synonym of A.magellanica. Bitter's description of the floral and fruiting parts was based on 3 incomplete fruits, and it is presumably for that reason he placed it in his section "Species incertae sedis".

COLCHAGUENSIS Bitter - Bitter (1911): "Cordillera de Colchagua. Leg.Da Mazzei, Nov.1883." FI!

Type material for this species also existed at B but has been destroyed. This syntype, on two sheets, was originally determined as A.canescens Ph. by Philippi, a species which has now been reduced to synonymy with A.magellanica. by Grondona. The material has both female and hermaphrodite flowering heads with 4 spined fruits, purple anthers and plumose stigmas.

DENUDATA Reiche - Reiche (1896): No type specimen or collecting information beyond "Rejion del Rio Corcovado" is given. No herbarium.

The description of this species is incomplete for some characters. However, although it was described as having only 2 stamens and a hairy fruit, it was also said to have 4 spines and was placed between A.magellanica and A.krausei by Reiche. Since A.krausei has been reduced to a synonym of A.magellanica it seems likely that this species is more correctly referred to A.magellanica than to A.ovalifolia.

DEPAUPERATA Bitter - Bitter (1911): "Cordilieres de Maule, Chile. Leg. Germain, Oct. 1858." FI!

Examination of the holotype showed this material to be A.magellanica, Bitter only distinguishing it from A.humilis and A.grandistipula on such variable characters as stipule size, stigma size and leaflet dentation.

DISTICHOPHYLLA Bitter - Bitter (1911): "From living material grown in Bremen Botanic Garden." No type material has been found.

This species was described by Bitter as having 4 stamens with purple anthers, a plumose purple stigma, 4 spined fruits, glaucous leaves and a red stem. This description is thought sufficient to reduce the species to a synonym of A.magellanica.

EXALTATA Bitter - Bitter (1911): "Punta Arenas, Rio de las Minas. Leg.C. Skottsberg, exped.suec.1907-09. 20.2.1908." UPS!

Bitter described this species as differing from A.rubescens and A.purpureistigma in having only 3 sepals and 3 spined fruits. Examination of the holotype material showed that this was not the case for all fruits and that the material was clearly referable to A.magellanica.

FRONDOSIBRACTEATA Bitter - Bitter (1911): "Damp meadow, Punta Arenas.

Leg.Naumann." B.Type material destroyed.

The type material of this species had been originally under the name of A.ovalifolia, and was on the same sheet as the type of A.oligoglochis var.dolichoglochis Bitter. The material was obviously not A.ovalifolia since Bitter described it as having 4 spined fruits, purple anthers and a fruits without stiff white or yellow ascending hairs. Bitter's description referred to its differences from A.glaucella, which itself fits the description of A.magellanica, none of the differences being sufficient to warrant keeping this species separate from A.magellanica.

GLANDULIFERA Bitter - Bitter (1911): "In valley Rio Aysen,Patagonia.

Leg.P.Dusen. 14.1.1897." S! UPS!

This collection was originally named A.adscendens by Dusen before Bitter used it as the type material for A.glandulifera. Examination of the type material showed it to have globose heads borne on slightly pilose scapes. The flowers had unusually small purple anthers and purple plumose stigmas, with 3 or 4 spines on the sparsely pilose fruits. The leaflet shape is typical of A.magellanica with which this species is deemed conspecific.

GLAUCELLA Bitter - Bitter (1911):"Punta Arenas, Chile. Leg.Dusen, nr.188.

16.12.1895." S. UPS!

An examination of the syntype at UPS confirmed that this species had flowers with 4 purple anthers and purple plumose stigma, and that the fruits were 4 spined. This species is therefore deemed conspecific with A.magellanica.

GRANDISTIPULA Bitter - Bitter (1911): "In Cordilieres de Maule. Leg.Ph.

Germain, nr.88(b)." FI!

Examination of the holotype showed this species to be conspecific with A.magellanica, the characters used by Bitter to distinguish it, e.g. size of stipules, length of filaments, being insufficient to warrant specific recognition.

GROSSIFOLIA Bitter - Bitter (1911): "Cape Fairweather (Buentiempo),
Patagonia. Leg.Capt.King, nr.10." G!

This species was described by Bitter as being very similar to A.distichophylla, a species already reduced to synonymy with A.magellanica. It was distinguished only on leaf characters, all of which are very variable. Examination of the holotype has confirmed that it is conspecific with A.magellanica.

HUMILIS Bitter - Bitter (1911): "Santiago, Andes. Leg.Neger.1895." M!

The type description of this species suggested that its affinities were more with A.magellanica than A.ovalifolia. Examination of the holotype confirmed this, the material having purple anthers, leaflets of typical A.magellanica shape and no stiff yellow or white ascending hairs on the fruits.

KRAUSEI Philippi - Philippi (1872): "Comun en la provincia de Valdivia,
senaladamente cerca del Corral." No
herbarium given. SGO!

In SGO there are 2 sheets in the type collection of this species with a total of 6 labels on them. Sheet 49935 seemed the more likely type since its label stated "Rosaceae.Acaena Krausei, spec. nov.1859" in Philippi's writing. Although the sheets obviously comprised at least three gatherings all the material on them was referable to A.magellanica. Reference to the type description supported this view since the species was described as having purple anthers and fruits with 4 spines.

LONGISCAPA Bitter - Bitter (1911): "Bolivia, loco speciali non indicato."

B. Type material destroyed.

In Bitter's description this species was said to have 4 spined fruits, flowers with 4 purple anthers and no stiff ascending hairs on the fruits. The characters used to distinguish it from the other species in the section were its long scape, large stipules, narrower stigma and 11-13 leaflets. All the characteristics described fall within those of A.magellanica. This is the only specimen referable to A.magellanica that has been found recorded from Bolivia.

LONGISEPALA Bitter - Bitter (1911): "Cordillera de Curico. Leg.C.Reiche."

B. Type material destroyed.

The type material of this species had been originally identified as A.laevigata, the collection being split by Bitter and described as two new species - A.longisepala and A.acutifida. Since the latter species has been referred already to A.magellanica it seems reasonable to treat this species as conspecific also, since it is described as having a 4 spined fruit and purple anthers and stigmas.

LONGISTIPULA Bitter - Bitter (1911): "Cordillera Linares. Leg.Philippe Germain. Enero 56." S!

The holotype of this species consisted of a single shoot with a single female flowering head. The head was globose, borne on a very pilose scape with a bract and an axillary flower. The female flowers have purple stigmas and staminodes. The material is definitely referable to A.magellanica.

MACROPODA Bitter - Bitter (1911): "Cerro Toro, Patagonia austral. Leg.O. Borge, nr.214. 18.3.1899." S!

This material was originally under the name A.laevigata before being used as type material for A.macropoda. The holotype of A.macropoda has been examined and was definitely referable to A.magellanica on the basis of its purple anthers and stigmas, 4 stamens and characteristic leaf shape.

MACROSTEMON ssp.PACHYSTIGMA Bitter - Bitter (1911): "Grown in Bremen Botanic Garden for three years from seed from Kew labelled A.macrostemon.
"No type material at BREM.

All of the other 6 subspecies described by Bitter for this species have been reduced to synonyms of A.magellanica by Grondona (1964). The type description does not show any characters incompatible with A.magellanica and it is therefore determined as conspecific with that species.

MAGELLANICA ssp. PYGMAEA Bitter - Bitter (1911): "1. Cordillera de Linares.
Leg. R.A. Philippi. (Under name A. laevigata).
2. Cord. de Maule. Leg. Ph. Germain.
(Under name A. laevigata)." Vienna.

This is the only subspecies of A. magellanica that Grondona (1964) did not consider. It was distinguished from the other subspecies by Bitter on the length of the fruiting scape and details of leaflet size, number and dentation. These characters are variable within single populations and are inadequate for delimitation of a subspecies. The type material has not been located as no herbarium is listed in Vienna in Index Herbariorum.

MOLLIUSCULA Bitter - Bitter (1911): "Ad ped. Mont., Rio Maipu, Chile. Leg. Meyen." B. Type material destroyed.

A. stellaris Meyen is given as a synonym for this species by Bitter. The material was described by him as having 4 spined fruits, 4 stamens with purple anthers and a long narrow stigma. The cupule was glabrous below and densely pilose between the spines and sepals. This species appears to be conspecific with A. magellanica.

NEGLECTA Bitter - Bitter (1911): "Terra magellanica. Leg. Andersson, nr. 280. 1852." S! UPS specimen lost.

Examination of the Stockholm syntype, which has 3 female fruiting heads, showed purple anthers on the staminodes, fairly small purple stigmas and 4 spined fruits. The species is reduced to a synonym of A. magellanica.

NOVEMENTATA Bitter - Bitter (1911): "Ad ped. Mont., Rio Maipu, Chile. Leg. Meyen." B. Type material destroyed.

This collection was on the same sheet as A. molliuscula, Bitter giving A. stellaris as a synonym again. This species differed from A. molliuscula only in the length of the filaments, the leaflets numbering only 11 and being 8-9 dentate, and in the stipules being simple. The description falls within that of A. magellanica with which it is deemed conspecific.

OBTUSILOBA Bitter - Bitter (1911): "Cape Gregory Bay, Straits of Magellan.
Leg. Capt. King, nr.16." G!

From Bitter's description, which listed the species as possessing 4 spined fruits, 4 stamens with purple anthers and a plumose purple stigma it would seem that this species is conspecific with A.magellanica. Examination of the holotype has confirmed this.

PARVIFOLIATA Bitter - Bitter (1911): "Cord. de Santiago. Burmeister's Herbarium." H. Type material missing, probably lost.

This species is described by Bitter as having 4 stamens with purple anthers, a long narrow stigma, 4 spined fruits, densely pilose cupule and small pilose leaves. The hairs on the cupule are apparently not the stiff ascending type. This species appears to be conspecific with A.magellanica.

PETIOLULATA Philippi - Philippi (1894): "Valle de Yeso, prov.Santiago. Jan.1866. Leg.Philippi, nr.599." SG0!

There are 2 sheets of type material for this species, both under one label. The species is clearly referable to A.magellanica on the grounds of leaf shape, 4 spined fruits without stiff ascending hairs and purple anthers and stigmas.

PURPUREISTIGMA Bitter - Bitter (1911): "Sandy Point, Port Famine. Leg. Dr.R.O.Cunningham, Survey of H.M.S.Nassau."
B. Type material destroyed.

The type material of this species had been previously identified as A.adscendens. Bitter described it as having red or purple anthers, 3-4 stamens and cupules with 3-4 spines. A possible isotype has been seen at Kew and this confirmed that this species is conspecific with A.magellanica.

SUBFLACCIDA Bitter - Bitter (1911): "Punta Arenas, Chile. Leg.P.Dusen,
nr.190." UPS!

The type material of this species was originally identified as A.adscendens. Bitter's description of A.subflaccida stated that the flowers had 3 red anthers, a red plumose stigma and glabrous cupules with 4 spines. An examination of the holotype has confirmed that this species is conspecific with A.magellanica.

Nomina dubia

BASIBULLATA Bitter - Bitter (1911)

CADILLA Hook.f. - Hooker (1847)

OLIGOGLOCHIN Bitter - Bitter (1911)

Appendix 3 Complete synonymy of the taxa recognised by the author
within A. magellanica (Lam.) Vahl including literature citations

- Ancistrum adscendens* (Vahl) Poir. Lamark, (1810)p.347; Gaudichaud, (1825)
p.106; D'Urville, (1825)p.54; Dusen, (1900)p.165; Duse, (1905)
p.352.
- decumbens* Gaertn. Gaertner, (1788)p.163; Hooker, (1847)p.9;
Walton & Greene, (1970)p.30; Yeo, (1973)p.199
- laevigatum* Lagasca. Lagasca, (1876)p.7; Duse, (1905)p.355
- magellanicum* Lam. Lamarck, (1791)p.76; Vahl, (1805)p.297;
Gray, (1854)p.495; Duse, (1905)p.352; Grondona, (1964)p.240;
Moore, (1968)p.78; Yeo, (1973)p.196
- magellanicum* var. B Lam. Lamarck, (1791)p.76; Vahl, (1805)p.297;
Aiton, (1810)p.68; Gay, (1847)p.299; Hooker, (1847)p.268;
Reiche, (1898)p.233; Grondona, (1964)p.240
- (*magellanicum* var. B) *humile* Pers. Persoon, (1805)p.30;
Hooker, (1847)p.10 & 268; Gray, (1854)p.496; Dusen, (1900)p.165;
Yeo, (1973)p.199
- Acaena acroglochin* Bitt. Bitter, (1911)p.163; Kalela, (1940)p.47;
Grondona, (1964)p.242
- acutifida* Bitt. Bitter, (1911)p.186
- adscendens* (Lam.) Vahl Vahl, (1805)p.297; Hooker, (1833)p.308;
Walpers, (1843)p.325; Gay, (1847)p.299; Hooker, (1847)p.267;
Presl, (1849)p.56; Hooker, (1867)p.56 & 268; Moseley, (1874)
p.387; Spegazzini, (1896)p.54; Citerne, (1897)p.41; Kuntze,
(1898)p.74; Reiche, (1898)p.233; Spegazzini, (1899)p.287;
Dusen, (1900)p.165; Melville, (1903)p.5; Duse, (1905)p.352;
Skottsberg, (1905)p.7; Macloskie, (1905)p.477; Schenk, (1906)
p.102 & 115; Bitter, (1911)p.175; Wright, (1911)p.317;
Skottsberg, (1913)p.38; Skottsberg, (1916)p.244; Hauman,
(1918)p.268; Vallentin & Cotton, (1921)p.18; Kalela, (1940)
p.47; Grondona, (1964)p.240; Greene, (1964)p.43; Moore,
(1968)p.78; Yeo, (1973)p.198

A3.2

- ssp. georgiae-australis* Bitt. Bitter, (1911)p.180; Philcox, (1962)p.244; Greene, (1964)p.43
var. majuscula Bitt. Bitter, (1911)p.181; Philcox, (1962)p.244
var. minuscula Bitt. Bitter, (1911)p.181; Philcox, (1962)p.245
var. incisa Bitt. Bitter, (1911)p.177; Grondona, (1964)p.242
var. glabriscapa Bitt. Bitter, (1911)p.178
var. luxurians Bitt. Bitter, (1911)p.178; Grondona, (1964)p.242
var. macrochaeta Franchet. Franchet, (1889)p.332; Alboff, (1896)p.366; Citerne, (1897)p.41; Reiche, (1898) p.233; Macloskie, (1905)p.477; Bitter, (1911)p.212; Grondona, (1964)p.242
var. semperpilosa Bitt. Bitter, (1911)p.177; Grondona, (1964) p.242
var. utrinqueglabrescens Bitt. Bitter, (1911)p.177; Grondona, (1964)p.242
var. pilosiscapa Bitt. Bitter, (1911)p.179

affinis Hook. f. Hooker, (1847)p.268; Duse, (1905)p.352; Yeo, (1973)p.203

alboffii Macloskie Macloskie, (1905)p.477; Grondona, (1964)p.241

brachyglochin Bitt. Bitter, (1911)p.291

calvivagina Bitt. Bitter, (1911)p.203; Grondona, (1964)p.243

canescens Phil. Philippi, (1860)p.192; Grisebach, (1874)p.139; Reiche, (1898)p.232; Hauman, (1918)p.270; Grondona, (1964)p.241

chamacaena Bitt. Bitter, (1911)p.198; Grondona, (1964)p.243

closiana C. Gay Gay, (1846)p.298; Weddell, (1857)p.242; Citerne, (1897)p.41; Reiche, (1898)p.233; Bitter, (1911)p.193; Grondona, (1964)p.240

colchaguensis Bitt. Bitter, (1911)p.205

A3.3

- compacta* Hauman Hauman,(1918)p.268; Grondona,(1964)p.243
- coxi* Phil. Philippi,(1864)p.63; Bitter,(1911)p.292; Grondona,(1964)
p.241
- craspedotricha* Bitt. Bitter,(1911)p.202; Grondona,(1964)p.243
- decumbens*(Gaertn.)D.W.H.Walton Walton & Greene,(1970)p.30; Yeo,(1973)
p.203
- denudata* Reiche Reiche,(1898)p.232; Bitter,(1911)p.295; Bitter,(1911a)p.493
- depauperata* Bitt. Bitter,(1911)p.206
- deserticola* Phil. Reiche,(1898)p.232
- dimorphoglochin* Bitt. Bitter,(1911)p.165; Grondona,(1964)p.242
- distichophylla* Bitt. Bitter,(1911)p.208; Yeo,(1973)p.203
- exaltata* Bitt. Bitter,(1911)p.229; Skottsberg,(1916)p.245
- floribunda* Bitt. Bitter,(1911)p.160; Grondona,(1964)p.242
- frondosibracteata* Bitt. Bitter,(1911)p.158
- glandulifera* Bitt. Bitter,(1911)p.223; Kalela,(1940)p.48; Grondona,
(1964)p.340
ssp.*Nordenskjoeldii* Bitt. Bitter,(1922)p.127
- glaucella* Bitt. Bitter,(1911)p.157; Kalela,(1940)p.46
- glaucophylla* Bitt. Bitter,(1911)p.155; Grondona,(1964)p.241; Yeo,(1973)
p.196
- grandistipula* Bitt. Bitter,(1911)p.206

A3.4

grossifolia Bitt. Bitter,(1911)p.211

humilis Bitt. Bitter,(1911)p.206

hystrix Chodat & Wilczek Chodat & Wilczek,(1902)p.295; Bitter,(1911)
p.197; Grondona,(1964)p.241; Bocher,Hjerting & Rahn,(1968)
p.158

var.*foliosior* Bitt. Bitter,(1911)p.197; Grondona
(1964)p.243

ischnostemon Bitt. Bitter,(1911)p.210

krausei Phil. Philippi,(1872)p.711; Reiche,(1898)p,231; Dusen,(1905)p.355;
Macloskie,(1905)p.479; Bitter,(1911)p.222; Kalela,(1940)p.48;
Grondona,(1964)p.340

var.*massonandra* Bitt. Bitter,(1911)p.223

var.*meionandra* Bitt. Bitter,(1911)p.223

subvar. *glabratula* Bitt. Bitter,(1911)p.223

subvar. *pilosior* Bitt. Bitter,(1911)p.223

laevigata (Lam.)Aiton Aiton,(1810)p.68; De Candolle,(1825)p.593; Gay,
(1847)p.300; Hooker,(1847)p.266; Spegazzini,(1896)p.54;
Spegazzini,(1899)p.287; Citerne,(1897)p.44; Reiche,(1898)
p.232; Dusen,(1900)p.165; Duse,(1905)p.355; Macloskie,(1905)
p.480; Bitter,(1911)p.170; Wright,(1911)p.317; Hauman,(1918)
p.270; Grondona,(1964)p.240; Moore,(1968)p.78; Yeo,(1973)
p.199

laevigata Aiton var. *venulosa* Reiche Reiche,(1898)p.233; Bitter,(1911)
p.168

laevigata Reiche Reiche,(1898)p.232

latifrons Bitt. Bitter,(1911)p.199; Grondona,(1964)p.243

laxa Bitt. Bitter,(1911)p.164; Grondona,(1964)p.242

- longiaristata* Ross Ross,(1907)p.449; Bitter,(1911)p.192; Grondona,
(1964)p.241
- longiscapa* Bitt. Bitter,(1911)p.195
- longisepala* Bitt. Bitter,(1911)p.195
- longistigma* Bitt. Bitter,(1911)p.200; Grondona, (1964)p.243
- longistipula* Bitt. Bitter,(1911)p.204
- macrophytes* (Franch.)Bitt. Bitter,(1911)p.212; Grondona,(1964)p.243
(as macrophytes)
- macropoda* Bitt. Bitter,(1911)p.159; Kalela,(1940)p.47
- macrostemon* Hook.f. Hooker,(1847)p.269; Gay,(1847)p.301; Weddell,(1857)
p.243; Reiche,(1898)p.233; Macloskie,(1905)p.480; Bitter,
(1911)p.187; Bitter,(1911a)p.491; Grondona,(1964)p.240;
Bocher,Hjerting & Rahn,(1968)p.158; Yeo,(1973)p.205
 ssp.barbaticupula Bitt. Bitter,(1911)p.190; Grondona
 (1964)p.242
 ssp.closiana(C.Gay)Bitt. Bitter(1911)p.193; Grondona
 (1964)p.242
 ssp.latisepala Bitt. Bitter,(1911)p.188; Grondona(1964)
 p.242
 ssp.longiaristata (Ross)Bitt. Bitter,(1911)p.192;
 Grondona,(1964)p.242
 var.basipilosa Bitt. Bitter,(1911)p.193
 var.supraconica Bitt. Bitter,(1911)p.193
 ssp.longiplumosa Bitt. Bitter(1911)p.189; Grondona
 (1964)p.242
 ssp.pachystigma Bitt. Bitter,(1911)p.190
 ssp.spectabilis Bitt. Bitter,(1911)p.188; Grondona,
 (1964)p.242

A3.6

- magellanica* (Lam.) Vahl ssp. *grandiscapa* Bitt. Bitter, (1911)p.172; Bitter, (1911a)p.491; Grondona, (1964)p.242
 ssp. *laevigata* (Aiton) Bitt. Bitter, (1911)p.170;
 Grondona, (1964)p.242; Yeo, (1973)p.198
 ssp. *pygmaea* Bitt. Bitter, (1911)p.169
 ssp. *venulosa* (Griseb.) Bitt. Bitter, (1911)p.168;
 Grondona, (1964)p.242; Yeo, (1973)p.196
 var. *pubescens* Bitt. Bitter (1911)p.168;
 Grondona, (1964)p.251
 var. *glabrescens* Bitt. Bitter, (1911)p.168
 var. *laevigata* Cit. Citerne, (1897)p.44
 var. *venulosa* Cit. Citerne (1897)p.44; Bitter, (1911)p.168
- molliuscula* Bitt. Bitter, (1911)p.196
- neglecta* Bitt. Bitter, (1911)p.183
- novemdentata* Bitt. Bitter, (1911)p.196
- nudicaulis* Alboff Alboff, (1896)p.367; Macloskie, (1905)p.481; Bitter, (1911)p.292; Grondona, (1964)p.241
- obtusiloba* Bitt. Bitter, (1911)p.182
- oligodonta* Bitt. Bitter, (1911)p.160; Skottsberg, (1916)p.245; Kalela, (1940)p.47; Grondona, (1964)p.241
- oligomera* Skottsberg Skottsberg, (1937)p.393; Grondona, (1964)p.243
- parvifoliata* Bitt. Bitter, (1911)p.203
- petiolulata* Phil. Philippi, (1894)p.624; Reiche, (1898)p.232; Bitter, (1911)p.294
- philippi* Gdgr. Gandoger, (1912)p.707

A3.7

pluribullata Bitt. Bitter,(1911)p.161; Grondona,(1964)p.242

purpureistigma Bitt. Bitter,(1911)p.226; Kalela,(1940)p.48

rubescens Bitt. Bitter,(1911)p.225; Bitter,(1911a)p.493; Skottsberg,
(1916)p.246; Grondona,(1964)p.340

sericascens Bitt. Bitter,(1911)p.201; Grondona,(1964)p.243

var.*novemjuga* Bitt. Bitter,(1911)p.201; Grondona,(1964)p.243

var.*sexjuga* Bitt. Bitter,(1911)p.202; Grondona,(1964)p.243

var.*tenuibracteolata* Bitt. Bitter,(1911)p.202; Grondona
(1964)p.243

stellaris Meyen Meyen(1834)p.348; Walpers,(1843)p.325; Reiche,(1898)
p.235; Bitter,(1911)p.175

subflaccida Bitt. Bitter,(1911)p.225

subnitens Kalela Kalela,(1940)p.44; Grondona,(1964)p.243

subtussericascens Bitt. Bitter,(1911)p.232

subtusvillosula Bitt. Bitter,(1911)p.231; Grondona,(1964)p.243

tomentella Bitt. Bitter,(1911)p.198; Grondona,(1964)p.243

triglochis Bitt. Bitter,(1911)p.194; Grondona,(1964)p.242

transitoria Bitt. Bitter,(1911)p.200; Skottsberg,(1916)p.247;
Grondona,(1964)p.243

venulosa Griseb. Grisebach,(1854)p.118; Hariot,(1884)p.151; Philippi,
(1894)p.625; Macloskie,(1905)p.485; Bitter,(1911)p.167;
Grondona,(1964)p.241; Yeo,(1973)p.196

Manuscript names used for specimens of A. magellanica (Lam.) Vahl

Sphaerula Anderson

Ancistrum inerme Banks

Acaena Grahamiana Gillies

Nomina incertae sedis

A. basibullata Bitt.

A. cadilla Hook. f.

A. oligoglochin Bitt.

APPENDIX 4

South Georgian Site Descriptions

Site I (Point Site)

This site on King Edward Point was on beach shingle with very little soil. The Customs House gave protection from the North and a small outhouse gave some shelter from the East. The site was completely flat except for very small surface irregularities. It comprised mainly an A. magellanica sward with Deschampsia antarctica and Poa annua as important constituents. The Acaena was usually prostrate with cover up to 100%. It was not continuous with any other vegetation in the vicinity although surrounded by scattered clumps of Deschampsia; flowering was very prolific.

Site II (Sward Site)

The site was located on the South side of King Edward Cove, just above the Grytviken whaling station's old radio hut. The sward was in a depression in the hillside, facing North, with protection from a small ridge on the West. The situation was moist enough to allow small marshy areas to form after rain but the surface irregularities of the site were completely hidden by the sward. The general slope of the site was 20°. The centre part of the site was A. magellanica sward with a Tortula robusta understorey. Although Festuca contracta was common at the edges of the sward on the drier hillocks it was almost absent from the moister areas. Where the sward reached the drier ridges on each side a band of Acaena hybrid occurred. The sward height varied with the surface but could be more than 25 cm. Flowering was abundant throughout the sward but especially so in the moist lower part. The soil was very black

and peaty and usually rather wet. Soil analyses in Table 28.

Site III (Shackleton Site)

This site was located on King Edward Point, at the back of Shackleton House. The sward was on a steep scree slope of 44° on the side of Mt. Duse at an altitude of 50' facing S.W. The sward was fairly dense but flowering was restricted to the lower half and was not very common even there. Due to its aspect the snow lie was longer at this site than at the other Acaena magellanica sites and it received considerably less sunlight. The only other phanerogams occurring in the sward of A. magellanica were Poa flabellata and Phleum alpinum, both of which were very rare. The only bryophyte occurring in the quadrats was Tortula robusta but Chorisodontium aciphyllum and Grimmia sps. were also found on the site. Soil was restricted to pockets between the boulders and was usually rather humic.

Site IV (Dam Site)

This site was again on the side of Mt. Duse but further West than Site III, lying near a small dam at an altitude of 50'. It was composed of a low ridge of Poa flabellata bordered on each side by Acaena communities. The west side of the ridge was rather barer than the East, where the A. tenera grew in large clumps on the edge of a flush. A large bank of hybrid had formed between the A. tenera at the outer edges of the ridge and the A. magellanica that grew amongst the tussock above it. The floristic survey was carried out only on the area at each side that contained marked scapes. The data in Table 26 show this site to be much richer bryologically than most of the others. Polytrichum alpinum and P. alpestre were also abundant on the site amongst the tussock grass but did not occur in any of the quadrats.

Site V (Hope Site)

This site was used for studies on the hybrid Acaena and was situated at the foot of a West facing bank, slope around 20°, of Poa flabellata on Hope Point, King Edward Cove. At the base of the bank was a Rostkovia magellanica community and the community studied occupied the intermediate zone between this and the tussock. The overall cover was dense and composed mainly of phanerogams. This community contained more phanerogams than any of the others studied. The site was well protected on the North and East and the soil was damp but not boggy. The hybrid grew only on the drier sloping parts and did not extend into the Rostkovia to any extent.

Site VI (Acaena Fellfield)

The site was chosen as an example of the more rigorous habitat type that excludes Acaena magellanica. The site was situated on a N.E. facing slope at an altitude of around 230'. The total vegetation cover was much lower than at any of the other sites with a significant proportion of bare ground. The vegetation was very low except for clumps of Phleum alpinum and Festuca contracta. The soil had two very clear horizons - the upper one was covered with stones, loam coloured and about 5 cm. deep; the lower one was sand coloured and full of large stones. Soil analyses in Table 28. The overall slope of the site was about 13° with good drainage.

Site VII (Acaena Rostkovia)

The site chosen was at the back of King Edward Point. It was slightly sloping from 20' in the East to near sea level in the West and was

fed by several small streams from the side of Mt. Duse. Protection from Mt. Duse to the North tended also to shadow the site for part of the year. The community was uniform in the centre but tended to become deficient in Acaena magellanica towards the edges. Total cover was always in excess of 100%. The soil was black, peaty and very wet. This was the only site on which fungi were found.

Site VIII (IBP Festuca)

This site was on a fairly level piece of ground by Gull Lake, King Edward Cove, at an altitude of about 260'. A small degree of protection to the South was given some small hillocks, but other than this the site was rather open. The community was composed of an open association of Festuca contracta and Acaena magellanica with Drepanocladus uncinatus and various lichen species as the other important constituents. Flowering was found to be rather sparse. The soil profile showed 1-2 cms. of black humus above 3 cm. of chocolate-brown humic soil. Below this was a light brown clay. The soil was not very wet. Soil analyses are given in Table 28.

Site IX (IBP Primary)

This site was the main one used for all the I.B.P. productivity assessments. It was chosen because its cover of a closed Festuca/Acaena association was judged to be the best developed Grass Heath association in King Edward Cove. The site faced North at an altitude of 170' and had an overall slope of 25°. The soil profile showed a top horizon of black humus to a depth of 15 cm. Between this and the light brown clay subsoil was a thin ash-grey layer about 2 cm. thick. Soil analyses are given in Table 28. The site was well drained but had little protection in any direction.

Table 28 Soil Data

Location	Horizon	Mean pH	Mean water content as % dry weight	Clay % dry weight	Stone % dry weight	% ignition loss	% total N	Extractable Na	mg./100 gm. K	Ca	Mg	P
Site II	upper	5.67	299.5	98.1	1.9	44	1.8	12.1	14.3	542	35.5	3.3
	lower	5.15	7.4	51.1	48.9	4.5	0.09	1.0	0.4	2.8	0.6	0.6
Site VI	upper	4.83	23.8	88.5	11.5	11	0.35	2.0	6.8	11.4	7.0	1.8
Site VIII	upper	4.70	37.9	69.8	30.2	10.2	0.36	1.3	2.3	8.1	2.9	1.0
Site IX	upper	4.46	65.7	90.9	9.1	20.5	0.87	1.6	3.1	8.7	2.6	1.7
	lower	4.64	28.3	65.2	34.8	8.4	0.25	0.56	2.1	11.2	2.9	2.7

Notes:

Site II - sample taken from light brown peat below a top layer of 3-5 cms. of black undecomposed material.

Site VI - upper horizon 5 cms. deep, very humic and black; lower horizon yellow clay with stones.

Site VIII - soil brownish and rather clayey.

Site IX - upper horizon crumbly brown humic loam, lower horizon yellow clay with stones.

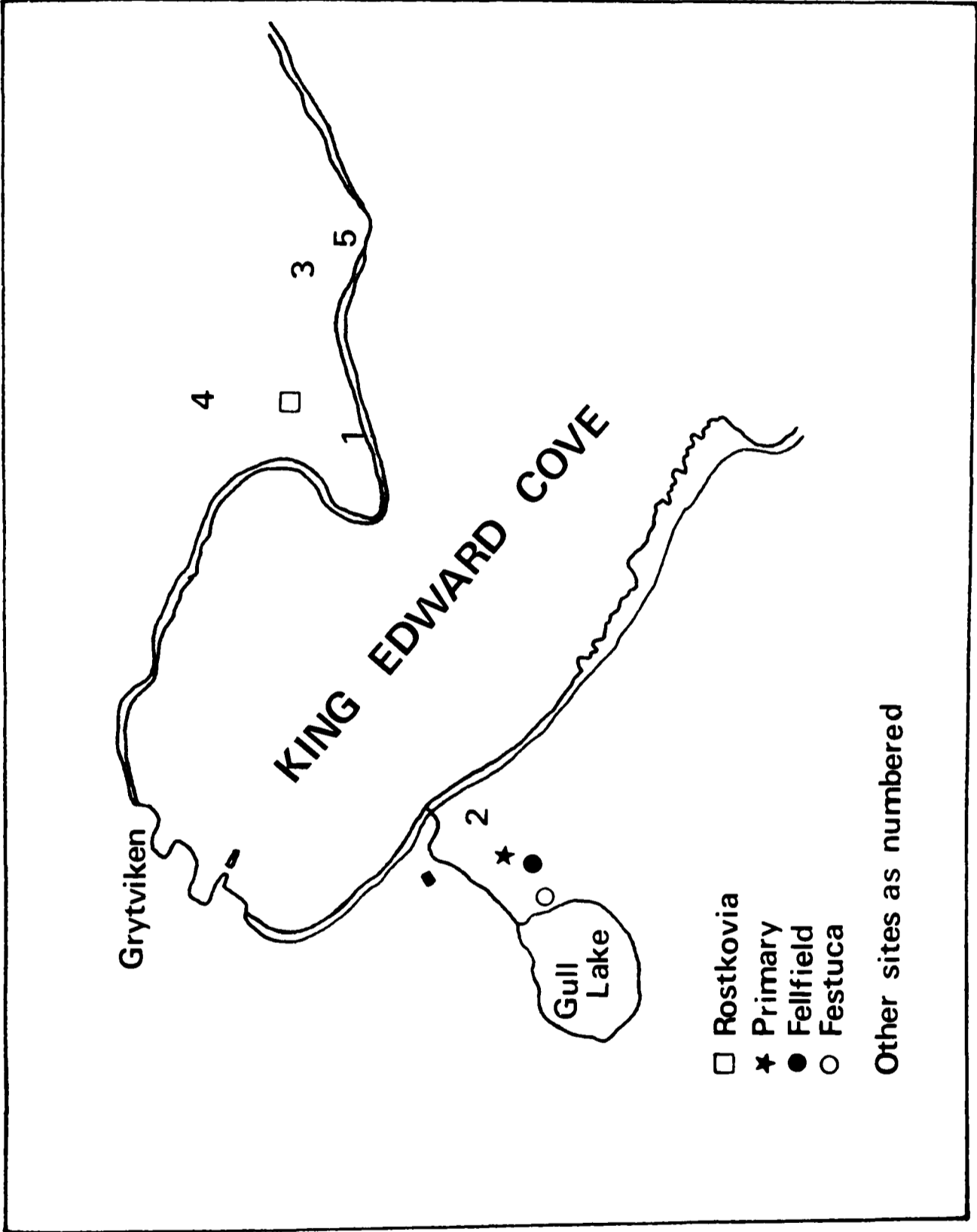


Figure 35. Location of experimental sites used on South Georgia