REPRODUCTIVE BEHAVIOUR OF MOSSES ON SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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ABSTRACT. A survey of the fruiting behaviour of bryophytes on Signy Island has shown that no liverworts and only 17 species of mosses are known to produce sporophytes. Some of these species are widespread and fruit regularly but others are very restricted in their distribution, although the latter are not necessarily rare in fruit. It has been confirmed that nine of the 17 species produce viable spores.

The gametangial and fruiting behaviour of two of the regularly fruiting species, *Dicranoweisia grimmiacea* and *Grimmia antarctici*, was examined in detail and it was found that both species produce two crops of gametangia per season only one of which regularly results in capsule production. The sporophytes in both species overwinter in a juvenile state so that the time from fertilization to spore dispersal is from 15 to 18 months. From the limited amount of data available, it appears that *D. grimmiacea* and *G. antarctici* are equally successful in producing fruit on other islands of the South Orkney Islands.

THE scarcity of fruiting in mosses in southern polar regions has been known since the early botanical studies of Brown (1906) and Cardot (1908). A recent investigation of the reproductive behaviour of the four species of *Polytrichum* and the two species of *Psilopilum* from the Falkland Islands, South Georgia, the South Orkney Islands and the Antarctic Peninsula has shown that, in general, reproductive success decreases with increase in altitude and latitude (Longton, 1972). Longton (1966) pointed out that, although many species of moss fruit on the sub-Antarctic island of South Georgia (lat. 54°21′ S., long. 36°40′ W.), only ten of the c. 50 species known from Signy Island (lat. 60°43′ S., long. 45°38′ W.) had been recorded with sporophytes. A few species appear to fruit on the Argentine Islands (lat. 65°15′ S., long. 64°17′ W.) but not farther north on Signy Island, suggesting that local climatic variation may override the effect of increasing latitude. These observations parallel those for the reproductive performance of the two Antarctic phanerogams, *Colobanthus quitensis* and *Deschampsia antarctica* (Holtom and Greene, 1967), and suggest that the South Orkney Islands, and in particular Signy Island, are climatically less favourable to reproductive success than areas at higher southern latitudes.

Signy Island, one of the smaller islands of the South Orkney Islands group which is situated on the Scotia Ridge, is c. 20 km.² in area with a maximum elevation of 280 m. It has an ice cap on its small central plateau and is bordered on the west and east coats by undulating lowlands which are ice-free in summer and abound with seasonal melt streams and small lakes. The bedrock of quartz-mica-schist, amphibolite and marble is covered with an extensive veneer of glacial drift and bears immature soils which are continually disturbed by cryoturbation. Thus, there are abundant habitats for the development of terrestrial vegetation which consists almost entirely of cryptogamic communities. The terrestrial flora is comparatively rich and forms a variety of plant communities which have been described in detail by Smith (1972), who has given a valuable summary and bibliography of knowledge of the island's topography, geology, climate and soils. In spite of the ameliorating effect of the surrounding ocean, the climate is severe with the mean monthly temperature ranging from $+0\cdot8°$ C in January to $-10\cdot3°$ C in July. There is a high mean annual cloud cover of 7 oktas and low mean annual sunshine of $1\cdot5$ hr./day. Total annual precipitation, as water equivalent, is low being c. 40 cm. and occurs mainly as snow.

The present paper gives a review of the reproductive biology of mosses on Signy Island and includes a detailed account of two widespread species which are often found in fruit, *Dicranoweisia grimmiacea* (C. Muell.) Broth. and *Grimmia antarctici* Card.

MATERIALS AND METHODS

The distribution and frequency of fruiting of the island's bryophytes were investigated by mapping, on a 1 km. grid basis, all collections from Signy Island in the British Antarctic

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Survey herbarium (AAS), the British Museum (Nat. Hist.) (BM), as well as material collected by the author which has been deposited in AAS. This gave a total of 250 moss specimens bearing fruit, the majority of which were collected during the last 10 years. Use was also made of fruiting information from field records in the British Antarctic Survey's herbarium data bank. Full collecting details of all these specimens and field records, together with the details of their reproductive behaviour, will be found in the data bank associated with the Survey's herbarium, which is currently housed in the Department of Botany, University of Birmingham.

The detailed study of *Dicranoweisia grimmiacea* and *Grimmia antarctici* was based on regular samples from a small number of special sites. Difficulty was experienced in finding sites with populations large enough to withstand regular sampling, and was partially overcome by scoring sporophyte development *in situ* and supplementing these results, and those for gametangia, by data from other areas.

The main fruiting site for *Dicranoweisia grimmiacea* was on a north-facing rock crevice on crags at the top of the slope behind the British Antarctic Survey station (GR 1041 0450; Fig. 1). A second site was located on a wide north-facing ledge on cliffs south of Factory Cove (GR 1038 0451; Fig. 1) where the moss was barren and received moisture only occasionally. A sheltered east-facing slope at the base of cliffs to the west of the slope behind the British Antarctic Survey station (GR 1041 0451; Fig. 1) was chosen as the third site and was dry and stony with small barren cushions.

Two main fruiting sites were sampled for *Grimmia antarctici*, one on a rock face with a northern aspect at the top of a large scree slope, *c*. 30 m. south-west of the British Antarctic Survey station (GR 1040 0451; Fig. 1), and the other on north-west-facing cliff ledges on crags overlooking a small valley below Knife Point (GR 1037 0453; Fig. 1). Two barren sites were also examined, the first being on a wide north-facing ledge which received occasional moisture, on cliffs south of Factory Cove (GR 1038 0451; Fig. 1) and the second on flat morainic debris between two marble knolls south-east of lake 6 in Three Lakes Valley (GR 1030 0459; Fig. 1).

The stages of development of gametangia and sporophytes were scored according to the maturation cycle described by Greene (1960) but the maturity indices were calculated by the method of Longton and Greene (1967). The terms sterile and fertile are applied, respectively, to the absence or presence of gametangia, while barren and fruiting refer to the absence or presence of sporophytes as defined by Longton and Greene (1969). The values of the fertility index cited in Table II were assessed by the method described by Longton (1966).

Sporophyte development for *D. grimmiacea* was scored using a 1 cm. by 1 cm. wire microquadrat fixed into the moss at the main site, the stages of development for all capsules within the quadrat being recorded once a month during the first 3 months of summer and twice a month during the last 3 months. These data were supplemented by collections from other fruiting sites for each of the six summer months. Winter samples were taken once a month from any cushion which was visible above the snow. *G. antarctici* was sampled from the two fruiting sites in the same way, i.e. by scoring sporophyte development in micro-quadrats three times a month during the summer and once a month during winter. These data for both species were supplemented by collections from other parts of Signy Island and the South Orkney Islands in 1971–72 and also by herbarium specimens collected in December and January of 1964, 1965 and 1966.

Samples for gametangial development were taken approximately twice a month from a single cushion in the case of *G. antarctici* but from either the study sites or other areas on Signy Island or other islands of the South Orkney Islands for *D. grimmiacea*. Development of the sex organs was studied by scoring the maturity of each organ within 15 inflorescences per sample for *D. grimmiacea* and 18 inflorescences per sample for *G. antarctici*.

The branching systems of fertile or fruiting samples were determined using an average of 38 shoots for *Dicranoweisia grimmiacea* and 50 shoots for *Grimmia antarctici* for each of the six summer months, while the annual extension growth and the mean number of leaves per shoot was estimated from an average of 55 shoots for each of the six summer months for *D. grimmiacea* and an average of 37 shoots for each of the six summer months and three winter months for *G. antarctici*. The branching system and annual extension growth of
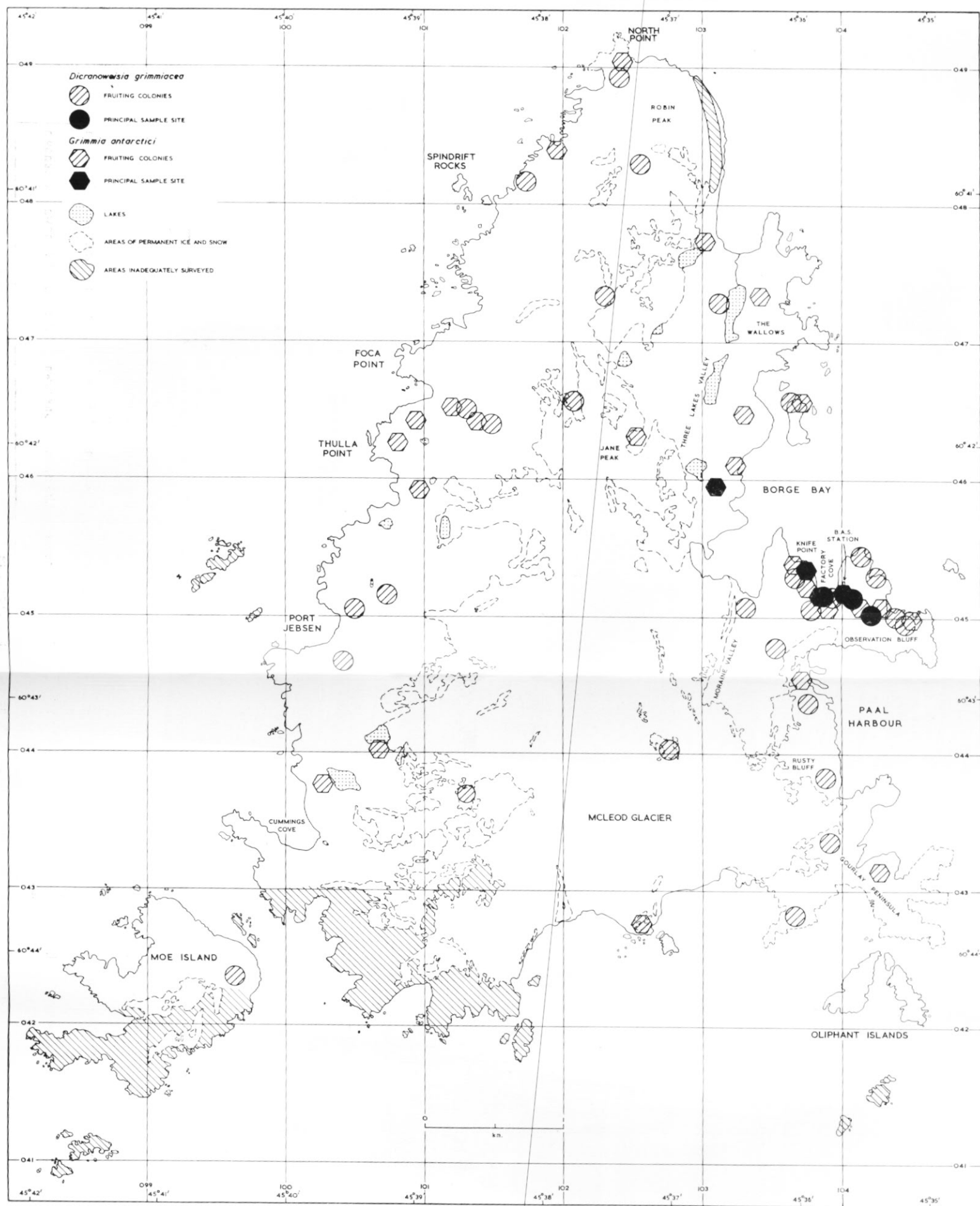
Fig. 1. The distribution of fruiting colonies of *Dicranoweisia grimmiacea* and *Grimmia antarctici* on Signy Island in relation to the 1 km. grid, together with the positions of the principal sample sites.

TABLE I. REPRODUCTIVE CHARACTERISTICS OF THE 17 SPECIES OF MOSS KNOWN TO FRUIT ON SIGNY ISLAND

Species	Distribution and frequency	Number of specimens with fruit	Number of seasons found in fruit between 1960–61 and 1971–72	Fertility index	Sexual habit	Period of gametangial maturation*	Main period of fertilization	Stage of sporophyte over-wintering	Period of spore dispersal	Length of sporophyte cycle (months)
Andreaea gainii Card.	Widespread and abundant	15	4	3	Autoecious	September to November	October	Unknown	January	14
Andreaea regularis C. Muell.	Widespread and abundant	20	6	4	Autoecious	Unknown	Late February	Unknown	December and March	Unknown
Bartramia patens Brid.	Widespread and occasional	13	5	3	A form of paroecious	March to November	Late November	ECI	April	16
Bryum algens Card.	Restricted and abundant	3	3	1	Dioecious	Unknown	Unknown	Unknown	March to April	Unknown
Dicranoweisia grimmiacea (C. Muell.) Broth.	Widespread and abundant	32	6	4	Autoecious	For details of the two cycles see text	November to December for both cycles	ECI	March	15
Dicranoweisia cf. *immersa* Broth.	Very restricted and rare	1	1	2	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Dicranoweisia mackayi (Broth. et Dix.) Broth.	Very restricted and rare	9	3	4	Autoecious	March to late January	Mid January	ECI	March to April	13
Encalypta cf. *patagonica* Broth.	Restricted and occasional	12	6	4	Autoecious	Late January to early November	Late October to early November	LCP	Early March	16
Encalypta cf. *peruviana* Broth.	Restricted and occasional	6	5	3	Autoecious	Unknown	Possibly late October	ECI	March	16
Grimmia cf. *alpicola* Sw. ex Hedw.	Very restricted and rare	1	1	2	Autoecious	Unknown	Unknown	Unknown	Unknown	Unknown
Grimmia antarctici Card.	Restricted and abundant	39	7	4	Autoecious	For details of the two cycles see text	For details of the two cycles see text	LCI	February to April	18
Orthotrichum crassifolium Hook. f. et Wils.	Restricted and occasional	3	1	1	Autoecious	Unknown	September to October	Unknown	April	15
Polytrichum alpinum Hedw.	Widespread and abundant	1	3	1	Dioecious	March to March	Early December to late January	ECI	Possibly late March	13
Pottia cf. *austro-georgica* Card.	Restricted and abundant	21	5	4	Autoecious	March to December	October, December, February	All abort	April to May	8–9
Stegonia latifolia (Schwaegr.) Vent. ex Broth.	Very restricted and rare	2	1	3	Autoecious	Unknown	September to October	Unknown	April	8
Tortula fuscoviridis Card.	Restricted and abundant	2	2	1	Synoecious	Unknown	Unknown	Unknown	Unknown	Unknown
Tortula cf. *grossiretis* Card.	Restricted and abundant	2	1	1	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown

* Taken as from the appearance of juvenile gametangia to the end of the mature stage.

sterile shoots of *D. grimmiacea* were assessed from 22 shoots of a collection made in April 1971 and 15 shoots from an earlier collection made in April 1965, while 24 shoots for each of the six summer months were used for *G. antarctici*.

FREQUENCY OF FRUITING AND GAMETANGIAL PRODUCTION

On Signy Island

Table I lists the 17 species of moss which have been found in fruit on Signy Island and shows the number of seasons in which fruit has been observed over an 11 year period, together with a summary of the salient features of their reproductive behaviour. Since virtually the whole of the snow- and ice-free areas of the island, apart from the extreme south-west corner and a few other small areas (Fig. 1), have been examined for bryophytes it is thought that Table I includes all species which produce fruit frequently to commonly on Signy Island. Of these species, *Andreaea gainii*, *A. regularis*, *Bartramia patens* (Fig. 2a), *Dicranoweisia grimmiacea* and *Polytrichum alpinum* are widespread on the island. *Bryum algens* (Fig. 2b), *Grimmia antarctici* and *Pottia* cf. *austro-georgica* are confined to calcareous habitats where they are abundant, while *Encalypta* cf. *patagonica* (Fig. 2c), *E.* cf. *peruviana*, *Tortula fusco-viridis* and *T.* cf. *grossiretis* show a restricted distribution in dry calcareous habitats. *Ortho-trichum crassifolium* is restricted to acidic rock in the coastal spray zone. The remaining species are very restricted, occurring in only one or two localities with *Dicranoweisia* cf. *immersa* on dry acidic habitats, *D. mackayi* on wet gravelly soil, *Grimmia* cf. *alpicola* on acid rock and *Stegonia latifolia* on base-rich disturbed soil (Smith, 1972).

Polytrichum alpinum (Fig. 2d), *Tortula fuscoviridis* and *T.* cf. *grossiretis* are rare in fruit, sporophytes being formed only in some years in *P. alpinum*; the same may also be true for the two species of *Tortula*. *Orthotrichum crassifolium* also fails to fruit every year and, although sporophytes were reasonably common in 1965–66, none was seen during 1971–72. *Dicrano-weisia* cf. *immersa* and *Grimmia* cf. *alpicola* have only been observed once in fruit and are so restricted in their distribution that it is impossible to assess how commonly sporophytes are produced. The remaining species all appear to fruit regularly (Table I) with sporophytes being uncommon in *Bryum algens*, common in *Andreaea gainii*, *Bartramia patens*, *Encalypta* cf. *peruviana* and *Stegonia latifolia*, and very common in *Andreaea regularis*, *Dicranoweisia grimmiacea* (Fig. 2e), *D. mackayi*, *Encalypta* cf. *patagonica*, *Grimmia antarctici* (Fig. 2f) and *Pottia* cf. *austro-georgica*.

All the fruiting species are acrocarpous, 15 being monoecious, mainly autoecious, and only two dioecious. In a number of cases there was insufficient material or too few dates of collection to determine the time of fertilization or spore dispersal, while for *Dicranoweisia grimmiacea* and *Grimmia antarctici* detailed gametangial and sporophyte cycles are presented below. In the remainder of the species, with two exceptions, fertilization appears to take place in spring or early summer with the spores being dispersed in the autumn of the following year, giving cycles varying in length from 14 to 18 months.

Pottia cf. *austro-georgica*, and possibly *Stegonia latifolia*, differ from the other species in the speed with which their sporophytes attain maturity. After fertilization in early spring, by gametes produced in gametangia which have overwintered, the ensuing sporophytes normally shed spores during the autumn of the same season. Gametangia form at intervals throughout the summer but the sporophytes resulting from these later fertilizations have insufficient time to shed their spores before winter and normally abort.

To obtain information on the viability of spores formed in fruiting mosses on Signy Island, samples were inoculated on to nutrient agar and germination was obtained in the following species: *Andreaea regularis*, *Bartramia patens*, *Dicranoweisia grimmiacea*, *D. mackayi*, *Encalypta* cf. *patagonica*, *Grimmia antarctici* and *Pottia* cf. *austro-georgica*. In all cases except *Andreaea regularis* the protonemata developed sufficiently to produce leafy buds. It is also of interest to note that spores of *Pottia* cf. *austro-georgica*, *Dicranoweisia mackayi* and *Grimmia antarctici* were germinated on a crushed and moistened quartz-mica-schist substrate using the method adopted by Keever (1957). Longton (1972) has reported successful germination of spores produced on Lynch Island by *Polytrichum alpinum*, while Smith (1972)
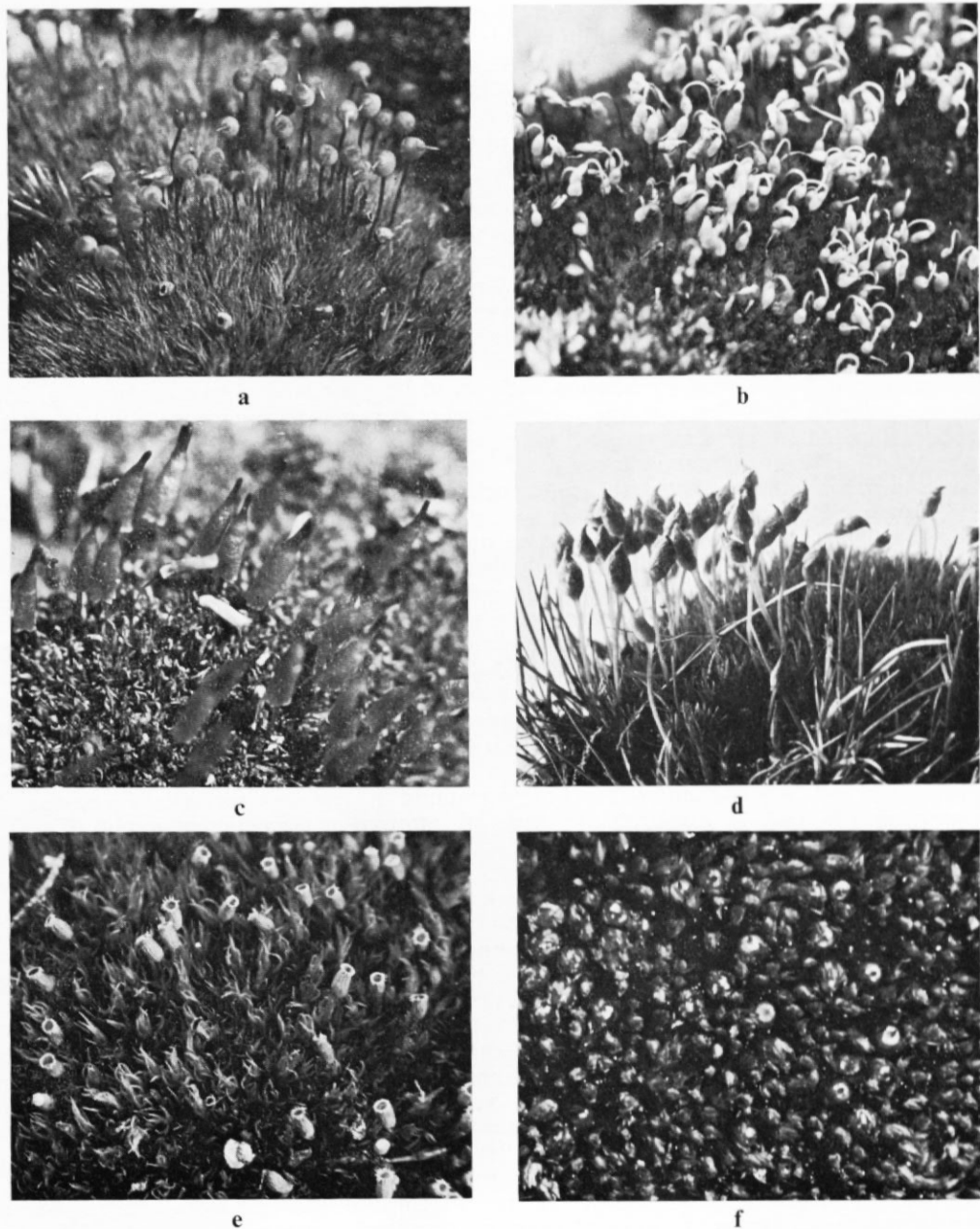
Fig. 2. Fruiting colonies of Signy Island mosses.
  a. *Bartramia patens* from cliffs south of Factory Cove, January 1972.
  b. *Bryum algens* from marble flush inland from Thulla Point, February 1972.
  c. *Encalypta* cf. *patagonica* from frost-heaved basic soil at Knife Point, January 1972.
  d. *Polytrichum alpinum* from a moist gravelly north-facing slope, Lynch Island, January 1966. (Photograph by R. I. L. Smith.)
  e. *Dicranoweisia grimmiacea* from morainic debris at snout of Orwell Glacier, March 1969. (Photograph by N. J. Collins.)
  f. *Grimmia antarctici* from basic cliffs, Knife Point, January 1972.

has noted that on Signy Island both *Pottia* cf. *austro-georgica* and *Stegonia latifolia* readily colonize open soils by means of spores which germinate after the ground has become snow-free in spring.

Although no attempt was made to investigate the reasons for the absence of fruit in the remaining species of moss on Signy Island, it is known that some of them produce gametangia. Longton (1972) has given information on gametangial development in *Polytrichum alpestre*, *Polytrichum juniperinum* and *Psilopilum antarcticum*, while Table II presents such information as is available for a further five species. Apart from *Racomitrium austro-georgicum*, only immature gametangia have been observed and so it is not possible to give any assessment of the period of fertilization.

Elsewhere in the South Orkney Islands

The remaining South Orkney Islands have not been surveyed adequately for bryophytes and such sites as have been examined have been visited only at infrequent intervals. Table III lists those moss species which have been found in fruit together with their localities. It will be seen that all the species which are widespread and frequent in fruit on Signy Island also fruit on the other South Orkney Islands, but in view of the inadequacy of botanical survey, no biological significance can be placed on the absence of fruit in the rarer or less frequently fruiting species. The case of *Orthotrichum crassifolium* is interesting as the records are for 2 years when it was not found fruiting on Signy Island and suggests that a more detailed survey may reveal other species with an enhanced performance or indeed species unknown in fruit on Signy Island. For example, Longton (1972) has provided information to show that *Polytrichum alpinum* is apparently reproducing more frequently on Lynch Island than on Signy Island.

REPRODUCTIVE CYCLE OF *Dicranoweisia grimmiacea*

Dicranoweisia grimmiacea is a monoecious acrocarpous moss, with exserted capsules and frequently branched shoots, which forms compact cushions. On Signy Island, the species grows in a range of habitats from ledges and crevices to fine soil between boulders and at the base of cliffs (Smith, 1972), being most abundant where there is a regular supply of water throughout the year. The species is commonest on the amphibolite outcrops in the cliffs south of Factory Cove where cushions up to 6 cm. in diameter are found, but smaller cushions, only 4 cm. in diameter, grow on south-facing ledges, in shaded crevices and under overhanging rocks which often receive little moisture. Cushions in south-facing habitats are often barren but fruit is common on north-facing moist rock ledges and crevices.

Branching system

The presence or absence of sex organs or sporophytes exerts a distinct influence on the form of the branching system in cushions of *D. grimmiacea*. In sterile specimens the form of the branching system is governed by the presence or absence of a viable shoot apex at the end of the winter. When the apex is undamaged, apical growth continues in the spring and a long unbranched shoot is formed with the season's growth marked by variations in leaf size. The larger leaves, *c.* 2·0 mm. long and which grow close together, occur at the end of season, while those formed earlier are 1·0–1·5 mm. long and are spaced farther apart. The two sterile cushions examined in detail showed a mean annual extension growth of 3·1 mm. with 25 leaves and 3·3 mm. with 32 leaves, respectively. If the shoot apex is damaged during the winter, then secondary shoots, frequently as many as six, arise just below it and as each grows at more or less the same rate, they form a profusely branched shoot system. At times, whole cushions may exhibit this form of branching and they are further characterized by a more vigorous growth of rhizoids than is found in fruiting populations.

The pattern of branching in fertile cushions was found to be more regular and appears to be determined by the presence or absence of a developing sporophyte. As the winter snow melts, one or two branches are formed at the same time as and immediately below the developing apical sex organs, one branch being situated one or two leaves below the other. These branches continue extension growth until late December or early January and in the absence of a

TABLE II. GAMETANGIAL INFORMATION FOR SOME MOSSES WHICH ARE UNKNOWN IN FRUIT ON SIGNY ISLAND

Species	Distribution and frequency	Number of fertile specimens	Number of seasons with gametangia	Sexual habit	Notes
Conostomum magellanicum Sull.	Restricted and rare	1	1	Unknown	Only perigonia seen
Conostomum pentastichum (Brid.) Lindb.	Restricted and rare	3	1	Dioecious and autoecious	Immature males and females abort without achieving fertilization by passing from an immature to a withered brown stage without dehiscence. Fertile on Coronation Island
Pohlia cruda (Hedw.) Lindb. var. imbricata (Card.) Bartr.	Widespread and occasional	4	3	Dioecious	Only immature gametangia seen
Pohlia nutans (Hedw.) Lindb.	Widespread and abundant	3	2	Paroecious	Only immature gametangia seen
Pohlia wahlenbergii (Web. et Mohr) Andrews var. glacialis (Schleich. ex Brid.) E. F. Warburg	Very restricted and rare	1	1	Dioecious	Only immature antheridia seen
Racomitrium austro-georgicum Par.	Restricted and occasional	2	1	Unknown	Immature, mature and dehisced stages of both sexes present

TABLE III. LOCALITIES FROM WHICH FRUITING MOSSES HAVE BEEN OBTAINED THROUGHOUT THE SOUTH ORKNEY ISLANDS (EXCLUDING SIGNY ISLAND)

Species	Locality	Season fruiting	Collection number
Andreaea gainii Card.	Laurie Island		
var. *gainii*	Cape Geddes	1946–47	FIDS C8/1003/1
	Powell Island		
	East side	1964–65	R. Smith 225a
	Matthews Island		
	West side	1964–65	R. Smith 159
	Coronation Island		
	Saunders Point	1964–65	R. Smith 23
	Olivine Point	1964–65	R. Smith 115
	East side of Sunshine Glacier	1971–72	Webb 49, 55, 152
	Promontory opposite Lynch Island	1971–72	Webb 112
var. *parallela* (C. Muell.)	Powell Island		
S. W. Greene	John Peaks	1964–65	R. Smith 271a
Andreaea regularis C. Muell.	Powell Island		
	East side	1964–65	R. Smith 197c
	West side	1964–65	R. Smith 230
	Matthews Island		
	North-west coast	1963-64	Field record 5351
	Coronation Island		
	Olivine Point	1964–65 1970–71	R. Smith 116, 117, 118 McManmon 200
	East side of Sunshine Glacier	1971–72	Webb 153, 168
Bartramia patens Brid.	Matthews Island		
	North-west coast	1964–65	Field record 5349
	Coronation Island		
	Olivine Point	1964–65	Field record 5346, 5347
	East side of Sunshine Glacier	1971–72	Webb 156, 162
Dicranoweisia grimmiacea	Laurie Island		
(C. Muell.) Broth.	Cape Geddes	1970-71	Webb 7
	Powell Island North-west coast	1964–65	R. Smith 233

5

TABLE III—*continued*

Species	Locality	Season fruiting	Collection number
	John Peaks	1964–65	R. Smith 264
	Matthews Island		
	Promontory on north-east coast	1963–64	Field record 5348
	Coronation Island		
	Promontory between Devils Corrie and Avalanche Corrie	1950–51	Sladen H613/2, H613/3
	Cape Vik	1965–66	Field record 5353
	Saunders Point	1964–65	Field record 5352
	Olivine Point	1970–71	Webb 6
	Promontory opposite Lynch Island	1971–72	Webb 134
	Lynch Island	1965–66	Lindsay 950, 966
		1970–71	Webb 8
		1971–72	Webb 109
Grimmia antarctici Card.	Laurie Island	1952–53	Kühnemann 1953/102
	Powell Island		
	Falkland Harbour	1964–65	R. Smith 273
	South-east coast	1964–65	R. Smith 207
	John Peaks	1964–65	R. Smith 268
	Matthews Island		
	North-west coast	1963–64	Field record 5350
	Coronation Island		
	Saunders Point	1964–65	R. Smith 36
	Olivine Point	1964–65	R. Smith 114
	Meier Point	1965–66 1970–71	R. Smith 579 McManmon 26
	Cape Vik	1965–66	R. Smith 558
	Shingle Cove	1966–67	R. Smith 450
	East side of Sunshine Glacier	1971–72	Webb 48, 171
Orthotrichum crassifolium Hook. f. et Wils.	Powell Island		
	John Peaks	1964–65	R. Smith 255

TABLE III—*continued opposite*

TABLE III—*continued*.

Species	Locality	Season fruiting	Collection number
	Coronation Island		
	Saunders Point	1964–65	R. Smith 37
	Shingle Cove	1966–67	R. Smith 451
	Lynch Island	1965–66	R. Smith 506
Polytrichum alpinum Hedw.	Coronation Island		
	Promontory opposite Lynch Island	1971–72	Webb 111
	Lynch Island	1965–66	R. Smith 514
		1966–67	Field record 5354
Pottia cf. *austro-georgica* Card.	Powell Island		
	South-east coast	1964–65	R. Smith 216
	Matthews Island		
	North-west coast	1964–65	R. Smith 161, 170
	Coronation Island		
	Olivine Point	1964–65	R. Smith 127
	Meier Point	1965–66	R. Smith 586
	Cape Vik	1965–66	R. Smith 566
	Shingle Cove	1966–67	R. Smith 453
	East side of Sunshine Glacier	1971–72	Webb 159
	Lynch Island	1965–66	R. Smith 526

developing sporophyte one or both produce new branches and gametangia. When a sporophyte develops in the apical inflorescence, the adjacent branches increase in length throughout the summer but do not branch until the following spring when sex organs and new branches are formed on the lower of the two. Thus the presence of a developing sporophyte appears to inhibit branching and sex-organ initiation in the shoot immediately adjacent to it.

The mean annual extension growth of branches on shoots with or without sporophytes was found to be *c.* 3·0 mm. with about 30 leaves. The initial spring growth is rapid but in mid summer there is no significant increase in leaf number between December and February or in branch length between January and February. Growth then resumes until April when it ceases at the onset of winter.

Thus growth is confined to the summer months with branches arising when the apical cell is damaged or used in the production of gametangia. Damage to the apex results in irregular branching patterns but the development of gametangia or sporophytes gives a regular branching sequence.

Gametangial cycle

The start of gametangial production varies from year to year as it is correlated with the beginning of the spring melt which, on Signy Island, is usually in September or October. Gametangia are formed at this time on the lower of the two shoots adjacent to a developing

sporophyte in a terminal inflorescence group which is surrounded by bracts and encloses a discrete terminal perigonium and one or two lateral perichaetia borne immediately below. Up to ten antheridia develop per perigonium with normally two archegonia per perichaetium. Development within the group as a whole is protandrous so that juvenile males are already present before archegonia begin to differentiate. During the remainder of the cycle, gametangia of the same sex are all at about the same stage of maturity within an inflorescence but archegonia continue to lag slightly behind the antheridia. A high degree of synchrony was noted between inflorescences in the same cushion.

The maturity indices for each summer month for the seasons 1970–71 and 1971–72 (Fig. 3) indicate that the gametangia of both sexes passed from the juvenile phase in October to the dehisced stage in January with the mature phase in December. Mature archegonia are easily recognized but antheridia are rarely seen in this stage, suggesting that it is passed through quickly. Normally only one ovum per perichaetium is fertilized although one case of polysety was observed. Fertility, as expressed on a per shoot basis, seems to be rather low since in the December samples only 36 per cent of the inflorescences bore swollen venters.

Failure of fertilization in these "spring-cycle" gametangia results in another crop of gametangia being formed in December or early January at the apices of adjacent shoots. Maturation of these "summer-cycle" gametangia is slower than those produced in the spring, the sex organs only reaching the juvenile or immature stage by April so that overwintering takes place in these stages. The following spring the antheridia develop rapidly, many having dehisced by November when the overwintering archegonia are still immature. Subsequent development of these archegonia is rapid and all are dehisced by December. Many sex organs are damaged during the winter, and of those inflorescences which survive in a viable condition, only 6·2 per cent were found to produce swollen venters.

The development of the spring-cycle gametangia from the juvenile to the dehisced stage takes *c.* 3 months, while the summer-cycle gametangia take about 12 months, so that gametes from both cycles are fertilized at approximately the same time. The spring-cycle gametangia appear more successful in producing capsules not only because very few of them are damaged but also because there is a greater synchrony during the mature phase of both sexes. Both spring- and summer-cycle gametangia were found together in fertile cushions, the behaviour of an individual shoot depending on the presence or absence of a developing sporophyte. By way of contrast, only summer-cycle gametangia have been observed in barren colonies and with their consequent low success rate sporophytes are very unlikely to be formed.

Sporophyte cycle

Fig. 4 shows the maturity indices for individual samples and the monthly means for sporophytes formed by spring-cycle gametangia of *D. grimmiacea.* Only one sporophyte per perichaetium has been observed. Swollen venters (SV) present in late November reach the early calyptra intact (ECI) stage by March or April, i.e. before the onset of winter. About 7 months are spent in this stage during the winter when a number of capsules abort. For example, in the case of a sample collected on 7 December 1971, 29·9 per cent of the capsules were scored as aborted in the late capsule in perichaetium (LCP) and ECI stages. Development continues after the snow melts the following spring and the late calyptra intact (LCI) stage is reached about 8 weeks later. The stages from LCI to the late operculum intact (LOI) stage are passed through rapidly, taking only 19 days at one site, so that the majority of the capsules are in the LOI stage by late January. The operculum intact (OI) stage lasts for nearly 2 months, during which time the spores are maturing. The operculum fallen (OF) stage, when the spores are being dispersed, on average lasts for a few weeks in March and early April but with one closely observed capsule the process only took 3 days to complete. The EF capsules of the 1969–70 cycle were not scored after September 1971, but such capsules persist for at least a winter during which their numbers gradually decrease but, by the middle of the following summer, most have disappeared. Thus, in early summer capsules representing three different cycles may be found in a fertile cushion of *D. grimmiacea.*

The whole cycle of sporophyte development from fertilization to spore discharge takes an average of 16 months and appears to show reasonable uniformity between seasons, as demon-
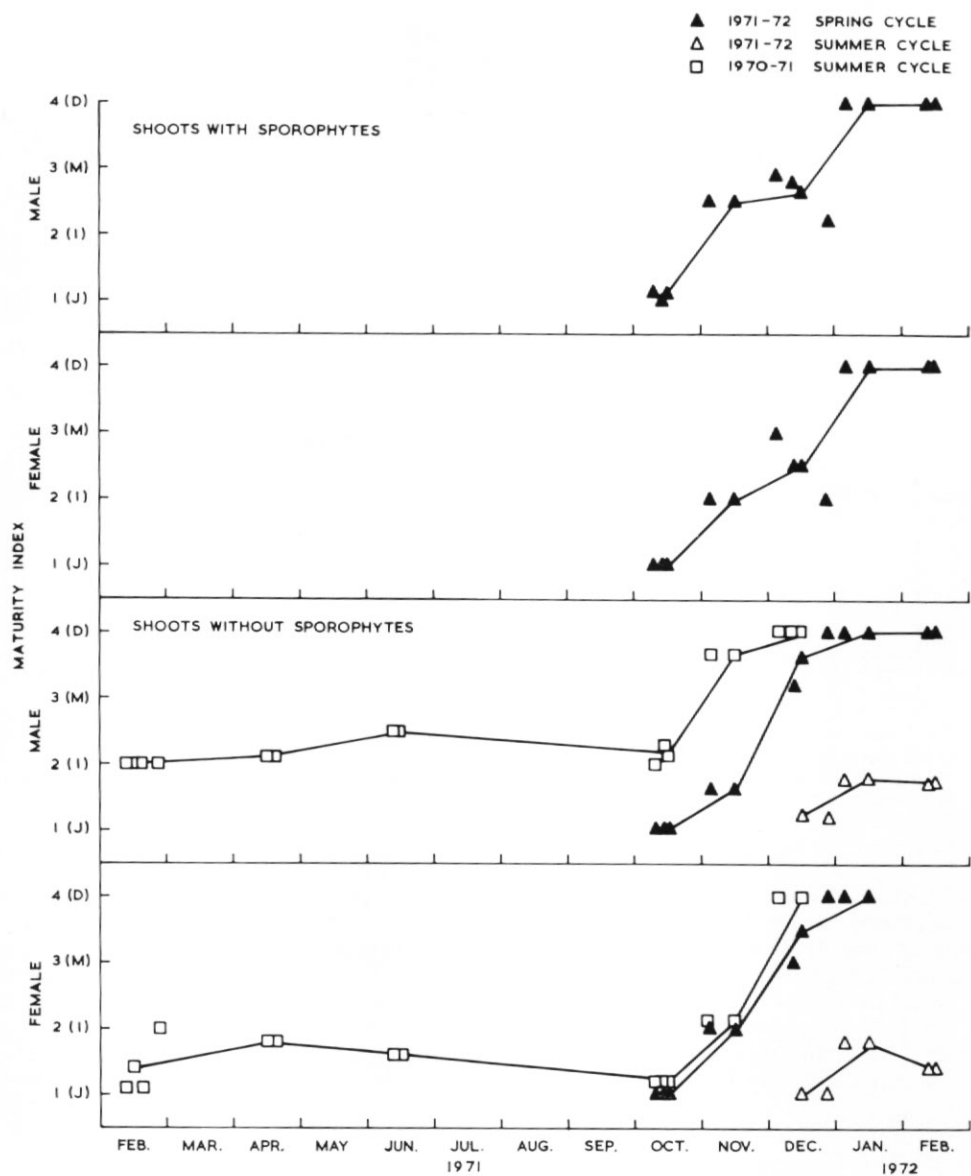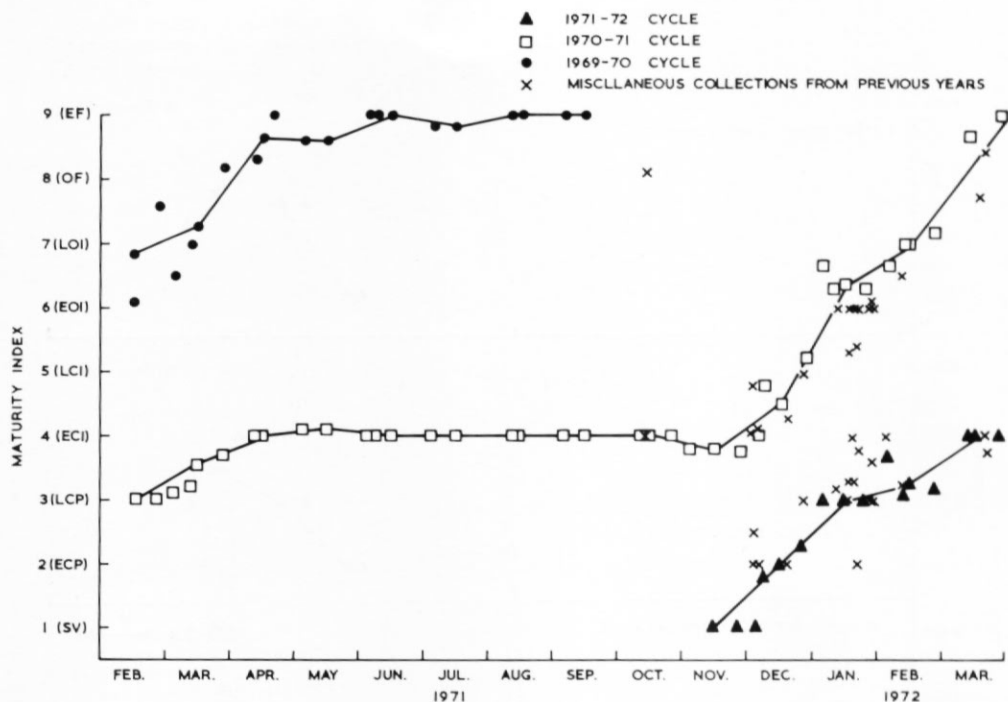
Fig. 3. The relationship between the maturity index of individual gametangial samples and their date of collection in *Dicranoweisia grimmiacea*. The lines connect symbols indicating the mean value for each month and have been calculated independently for each season.

strated by the degree of synchrony of maturation stages with time represented by the three seasons and older individual records in Fig. 4.

Only a small number of the summer-cycle gametangia result in the production of SV stage sporophytes during February and March but as development of the zygote appears to be very slow they are still in the SV stage in April and all apparently abort during the winter.

Fig. 4. The relationship between the maturity index of individual sporophyte samples and their date of collection in *Dicranoweisia grimmiacea*. The lines connect symbols indicating the mean value for each month and have been calculated independently for each season, the miscellaneous collections having been ignored.

REPRODUCTIVE CYCLE OF *Grimmia antarctici*

G. antarctici is a monoecious acrocarpous moss, with immersed capsules and frequently branched stems, which forms cushions. On Signy Island the species occurs where there is an abundant supply of water such as below late snowbanks and occupies two main habitats, one on rock faces and ledges of basic outcrops where it forms compact cushions and the other on morainic debris, where the loose cushions coalesce to form low turves which are often broken by cryoturbation (Smith, 1972). The cushions on outcrops can attain 20 cm. in diameter but above this size they break up, while the coalesced cushions on morainic debris can form pure stands up to 10 m.². Sporophytes are common at sites on north-facing moist cliffs.

Branching system

As with *D. grimmiacea*, the branching pattern is influenced by the presence or absence of sex organs and sporophytes. In sterile specimens of *G. antarctici* the pattern of branching is governed by the presence or absence of a viable shoot apex at the end of winter. When the apex is undamaged, apical growth continues in the spring and a long unbranched shoot is formed with the season's growth marked by variations in leaf size. The larger leaves, up to 1·5 mm. long, are formed at the end of season while those formed earlier are only up to 1·0 mm. long. When the apex is damaged during the winter, up to four secondary shoots arise just below it, any number of which may grow at more or less the same rate; the remainder fail to develop.

In fertile cushions, the pattern of branching is modified by the formation of gametangia, one or two branches developing at the same time immediately below the apical sex organs

which are formed during mid summer and late autumn. Branches formed in mid summer grow until the onset of winter, growth resuming in the spring and continuing until gametangia and new branches are produced either in late December or early January or, if no sex organs are formed, they remain unbranched until the autumn. Autumn-formed branches behave similarly but overwinter in a bud-like form.

Unlike *D. grimmiacea*, the presence of a developing sporophyte does not inhibit branching in the adjacent shoot and, since autumn-formed gametangia are rarely successful in producing sporophytes, branching systems may bear fruit every year, be barren every year or bear fruit every alternate year.

The annual extension growth of shoots, measured from their point of branching in both fertile and barren cushions, was found to be *c*. 3–4 mm. with 30–40 leaves formed. Branches formed in mid summer in fertile cushions reach 1–5 mm. by the beginning of winter during which there is no significant growth. The following spring growth is resumed and by mid summer the shoots are *c*. 3 mm. long.

Gametangial cycle

In *G. antarctici*, the apical inflorescence group consists of a single terminal perigonium with up to 18 antheridia while, one or two leaves below, there are up to four very short lateral branches each bearing up to five archegonia per apical perichaetium. In its early stages of growth the whole inflorescence group is surrounded by bracts but during later stages of development the perichaetial branches elongate so that the perichaetia project above the level of the surrounding bracts.

Gametangia of the autumn cycle are formed just before the onset of winter (Fig. 5) and are protandrous, the males reaching the juvenile stage while the females are still undifferentiated. Both sexes overwinter in the juvenile stage and in early spring development continues slowly until all are dehisced by March. Throughout this period of maturation there is a marked lack of synchrony between and within perigonia and perichaetia, the latter sometimes having all
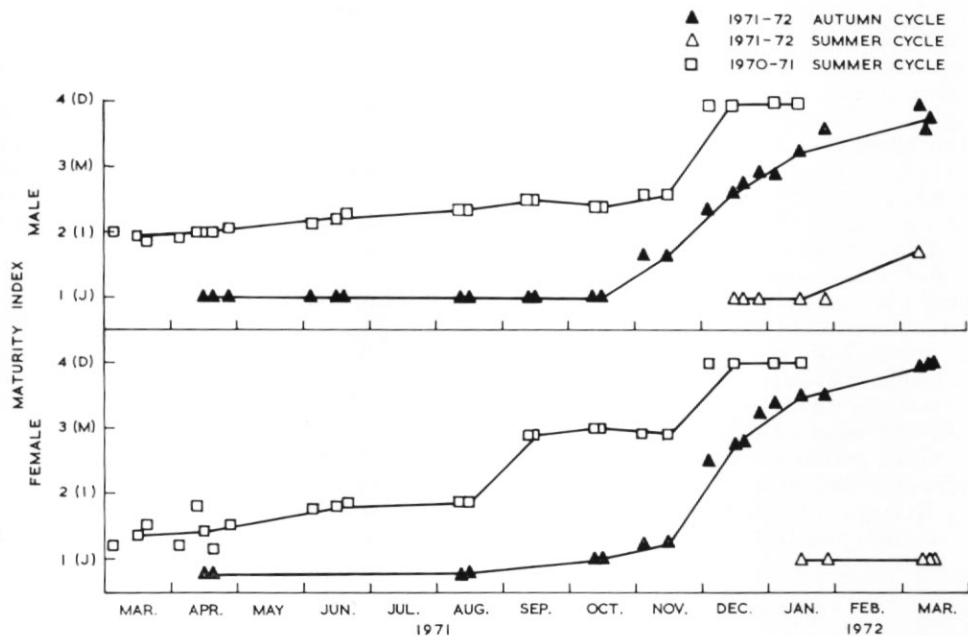

Fig. 5. The relationship between the maturity index of individual gametangial samples and their date of collection in *Grimmia antarctici*. The lines connect symbols indicating the mean value for each month and have been calculated independently for each season.

stages from juvenile to swollen venter within the same inflorescence. Some mature organs of both sexes may be found at any time between November and March but the main period for fertilization is probably December and January, the time when the maturity indices (Fig. 5) approximate to the mature stage.

During late December or early January another crop of gametangia is produced at the apices of shoots formed either in the previous summer or autumn. Antheridia in the juvenile stage were found to occur in late December and reach the immature stage by April, while juvenile archegonia did not appear until a month later, i.e. late January and were juvenile to immature in April (Fig. 5). Organs of both sexes remain in these stages over winter but maturation continues in early spring and mature organs of both sexes were found in samples from September to November. There is again a marked lack of synchrony between and within inflorescences with mature organs of both sexes being normally present from September to late November. All the gametangia had dehisced by early December.

An examination of 30 inflorescences from an October specimen showed 36 per cent of them to be no longer viable due to complete dehiscence, abortion during winter or the failure of female gametangia to develop. Nevertheless, fertility is slightly higher than with the autumn-cycle gametangia since 40 per cent of the inflorescences examined in early December contained sporophytes representing $30 \cdot 9$ per cent of the perichaetia examined.

Thus mature gametangia of the summer cycle are present throughout the season and inflorescences of this cycle take *c.* 12 months to pass from the juvenile to the dehisced stage, while the autumn-cycle inflorescences pass through the same stages in 11 months although they remain in the juvenile stage for 6 months over winter. There is no overlap in the periods of fertilization between the cycles and both summer- and autumn-cycle gametangia are found in fruiting colonies.

Sporophyte cycle

The maturity indices for individual specimens and the monthly means for sporophytes from both gametangial cycles are shown in Fig. 6. Although the autumn-cycle gametangia produce sporophytes in January, their development is slow and the majority of them are only in the early calyptra in perichaetium (ECP) stage by April. All these sporophytes abort during the winter, the only sporophytes which mature being those produced by the summer-cycle gametangia.

Only one sporophyte per perichaetium has been observed. Swollen venters from the summer cycle are present in September and October, most capsules developing to the late calyptra intact (LCI) stage by April. Further maturation does not take place until the following spring, spores being shed any time between February and April or, in a small number of cases, late operculum intact (LOI) capsules persist over winter and shed their spores early the following spring. The very long period during which spores are shed is a result of fertilizations taking place over a considerable time since each capsule requires approximately the same length of time to mature from swollen venter (SV) to operculum fallen (OF). The calculation of maturity indices, even for individual specimens, while clearly indicating the stage of maturity for the majority of capsules, masks the degree of spread during the middle part of the cycle. For example, SV and ECI sporophytes can be found in separate perichaetia in the same inflorescence group, 14 sporophytes from a June sample being scored as 28 per cent ECI stage, 65 per cent LCI stage and 7 per cent EOI stage.

The whole period of sporophyte development from fertilization to spore discharge takes *c.* 18 months, although a small number of capsules formed by late fertilizations takes 25 months to pass through their maturation cycle. The empty capsules persist for many years and in a section through a cushion, old capsules marking horizons of previous years growth can be clearly seen.

DISCUSSION

All the 17 mosses which fruit on Signy Island are acrocarpous and all but two of them are monoecious. Holmen (1960) found a comparable situation in the high Arctic in Peary Land, north Greenland, where $95 \cdot 1$ per cent of fruiting species were acrocarpous, the majority
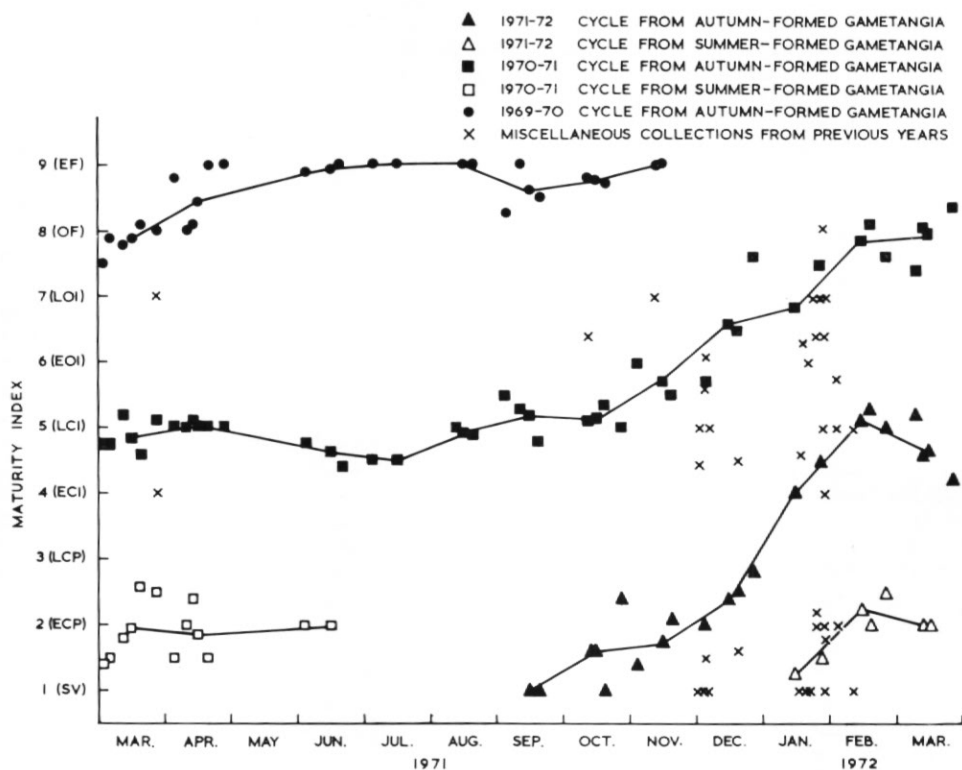
Fig. 6. The relationship between the maturity index of individual sporophyte samples and their date of collection in *Grimmia antarctici*. The lines connect symbols indicating the mean value for each month and have been calculated independently for each season, the miscellaneous collections having been ignored.

being monoecious. As yet, no hepatics have been seen in fruit on Signy Island or elsewhere in the South Orkney Islands. Although acrocarpous species outnumber pleurocarpous species in the Signy Island flora, the species found fruiting are not always the most widespread or abundant; in fact some species are very rare, for example *Dicranoweisia mackayi*. There is no clear indication that some areas of the island are more favourable for reproductive success than others or that particular ecological niches are especially good but a species can show a better performance at sites where the winter snow melts early, thus increasing the length of the growing season, or where the water supply remains adequate throughout the season. Benson-Evans and Brough (1966) pointed out that drought can retard reproductive development and certainly the barren and sterile sites of *Grimmia antarctici* and *Dicranoweisia grimmiacea* received very little moisture during the summer, and it was noticed that sporophytes on cushions which had dried out for long periods, failed to resume growth on rehydration.

Information systematically collected over a number of years is not available on the fruiting behaviour of the Signy Island mosses, but the available data suggest that the majority of the species which fruit do so fairly regularly, although *Polytrichum alpinum* and *Orthotrichum crassifolium* clearly show an intermittent performance. This suggests that the reproductive cycles for most of the species are suited to the prevailing climate but, as adequate information on the reproductive performance of these species throughout the rest of their geographical ranges is not available, it is impossible to say whether they show any special adaptations to Signy Island conditions. This is particularly unfortunate in the case of *Dicranoweisia grimmiacea* and *Grimmia antarctici*, the two species studied in detail, as their reproductive cycles

show some interesting features. For example, both produce two crops of gametangia per season which in turn results in two crops of sporophytes, only one of which normally reaches maturity. In *D. grimmiacea* the second crop of gametangia is not formed until after the first crop has matured and they are limited to those branching systems which are not bearing a developing sporophyte from the first crop. A similar inhibitory effect from developing sporophytes has been noted in British material of *Mnium hornum* where basal branches which bear gametangia rarely occur on shoots bearing sporophytes (Newton, 1972). By contrast, the presence or absence of a sporophyte does not influence gametangial initiation in *G. antarctici.*

It is of interest to note that in both species the two crops of gametangia do not mature at the same rate. In *D. grimmiacea* the gametangia formed in the spring all dehisce in *c.* 3 months, whereas those formed in mid-summer take *c.* 12 months to dehisce. Spring-formed gametangia mature under conditions of increasing day length and temperature, whereas mid-summer gametangia experience the reverse conditions and mature very slowly only reaching the juvenile or immature stage in the 4 months before their development is completely arrested by the onset of winter. Both mid-summer and autumn-cycle gametangia overwinter in *G. antarctici* but those formed in autumn take 11 months to become dehisced, most of their development taking place in the spring, whereas those formed in mid-summer take *c.* 12 months to reach the same stage, part of their development taking place in late summer and autumn. Clarke and Greene (1971) have demonstrated that both day length and temperature can influence the rate of gametangial maturation in polar mosses but, in view of their findings of differential environmental response in *Pohlia nutans* of British and South Georgian origin, it would be unwise to speculate on which factors exert the greatest influence in the present species. *Pottia* cf. *austro-georgica* is interesting as the only fruiting species on Signy Island with two or more crops of gametangia maturing within the one season and it is only those gametangia which are immature at the onset of winter which exhibit arrested development. There is obviously a great need for experiment under controlled conditions to determine which factors exercise the greatest influence and what features, if any, of the different cycles are due to inherent rhythms.

One cycle of sporophytes, in both *D. grimmiacea* and *G. antarctici*, is successful in producing viable spores, whereas from the other cycle no mature capsules are formed. This lack of success in one cycle is due to the abortion of sporophytes during winter probably because of immaturity. Observations have shown that capsules younger than ECI abort and in *D. grimmiacea* the majority are in the SV stage at the beginning of winter, and the LCP stage in *G. antarctici.*

The other cycle sporophytes which complete their development are older at the onset of winter, being in the ECI stage in *D. grimmiacea* and in the LCI stage in *G. antarctici* and spores shed in the following autumn are known to be viable although their success under natural conditions is unknown.

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