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PLANT AND INVERTEBRATE PHYSIOLOGY

The growth and reproduction of *Polytrichum alpestre* Hoppe on South Georgia

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Introduction

It has long been realized that bryophytes are one of the most important groups in the flora of the Antarctic Peninsula–Scotia Ridge sector of Antarctica, being well represented both in number of species and in the contribution they make to the vegetation (Longton 1967, this Discussion, p. 213). Cardot (1908) pointed out that the bryophyte flora was made up of a number of phytogeographical elements, one being a group of bipolar species some of which are known from many localities throughout the area. Cardot also drew attention to the rarity of fruit on most specimens he had seen from Antarctica. As many bryophytes are known to show a marked decline in reproductive success towards the limit of their ranges, and as there was evidence that species of the bipolar group appeared to be behaving in this way, an investigation was started to determine the reproductive behaviour of selected species throughout the Antarctic Peninsula–Scotia Ridge area.

Field studies were initiated in the 1960–61 season on South Georgia (Greene 1964*a*) and were extended in the 1963–64 and 1964–65 seasons when further observations were made on South Georgia and in a range of localities from the Falkland Islands south to Marguerite Bay (Longton 1966). The work in the field had two principal objectives, the first relating to the behaviour of the mosses and the second to the nature of the environment. Observations and collections were made extensively in as many localities as possible to provide an assessment of reproductive behaviour throughout the region, while intensive sampling was carried out in a small number of localities over an extended period to provide information on possible differences between seasons. Studies on the environment were confined to the sites of intensive sampling on South Georgia, Signy Island (South Orkney Islands) and Galindez Island (Argentine Islands).

Polytrichum alpestre Hoppe (= *P. strictum* Banks) was one of the first species to be investigated. It is widespread in north polar regions and throughout the temperate zone of both hemispheres, and is abundant on many islands of the Scotia ridge and at sites along the west coast of the Antarctic Peninsula as far south as Neny Island. The present paper gives an account of the reproductive behaviour of this species on South Georgia, a mountainous, heavily glacierized, Sub-Antarctic island. A description of the vegetation, together with an examination of the principal features of topography and climate of this island, will be found in Greene (1964*b*).

Methods

The most intensive observations on the reproductive behaviour of *P. alpestre* on South Georgia were made on the north-east coast between Fortuna Bay and Hound Bay, but specimens collected in this and other areas during the present investigation and by previous collectors have been examined so as to provide as full an account as possible of its behaviour on South Georgia.

With the assistance of the resident meteorologists, samples were obtained at approximately fortnightly intervals during the summer from a study site on a large bank of *P. alpestre* on King Edward Point, Cumberland Bay (figure 43), between February 1961 and March 1962 and again between December 1963 and February 1965. The environmental records for South Georgia also apply to this site.

P. alpestre is a robust, turf-forming, dioecious moss with its stems tightly compacted by the development of an extensive tomentum. Inflorescences are formed at the apices of the stems and branches, but with later growth they may become buried in the turf. Male stems bear prominent discoid perigonia, and are readily recognizable, but owing to the similarity between perichaetial bracts and comal leaves, it is impossible without dissection to distinguish between female and sterile stems, in the absence of sporophytes.

The annual maturation cycles of gametangia and sporophytes were determined from scorings of developmental stages present in specimens collected at different times throughout the growing season. The developmental stages recognized were similar to those described for other mosses (Greene 1960, 1964*a*), but the sporophyte *operculum intact* stage was not subdivided as many capsules of *P. alpestre* were found to dehisce while yellow or greenish in colour. An index scale of 1 to 4 was assigned to the stages passed through by developing gametangia, while the scale for sporophytes extended from 1 to 8, in both cases increase in maturity corresponding to an increased rating. By scoring a sample of five male stems, five female stems and at least fifteen capsules per specimen and calculating a mean, separate index values for the development of male and female gametangia and sporophytes were obtained. The scoring of *swollen venter* and *capsule in perichaetium* stages involved dissecting inflorescences, and a maturity index for these stages was normally based on five sporophytes per specimen. Where sporophytes representing two distinct cycles were present, they were scored separately, but withered gametangia or battered capsules persisting from earlier years were ignored. A graphic representation of the maturation cycle was obtained by plotting the indices of specimens against date of collection, detailed indices of this sort being calculated for the 1961–62 series from King Edward Point and for all sporophyte scorings. The remainder of the gametangial material was assessed using the majority state method, i.e. the state of the development of a gathering was scored as the stage reached by the majority of the sex organs, the presence of any other stages being recorded separately (Greene 1960).

REPRODUCTIVE BEHAVIOUR

Distribution and fertility

On South Georgia, *P. alpestre* is common and often abundant, particularly among coastal grassland dominated by *Poa flabellata*, where, with *Dicranum aciphyllum*, it often forms extensive banks, often over deep peat: it also occurs as small discrete turfs. *P. alpestre* is less abundant in inland vegetation, but it is occasionally encountered in bogs and, less frequently, in grass heath communities. It has been noted from sea level up to about 250 m, and may extend considerably higher among tussock on steep coastal cliffs.

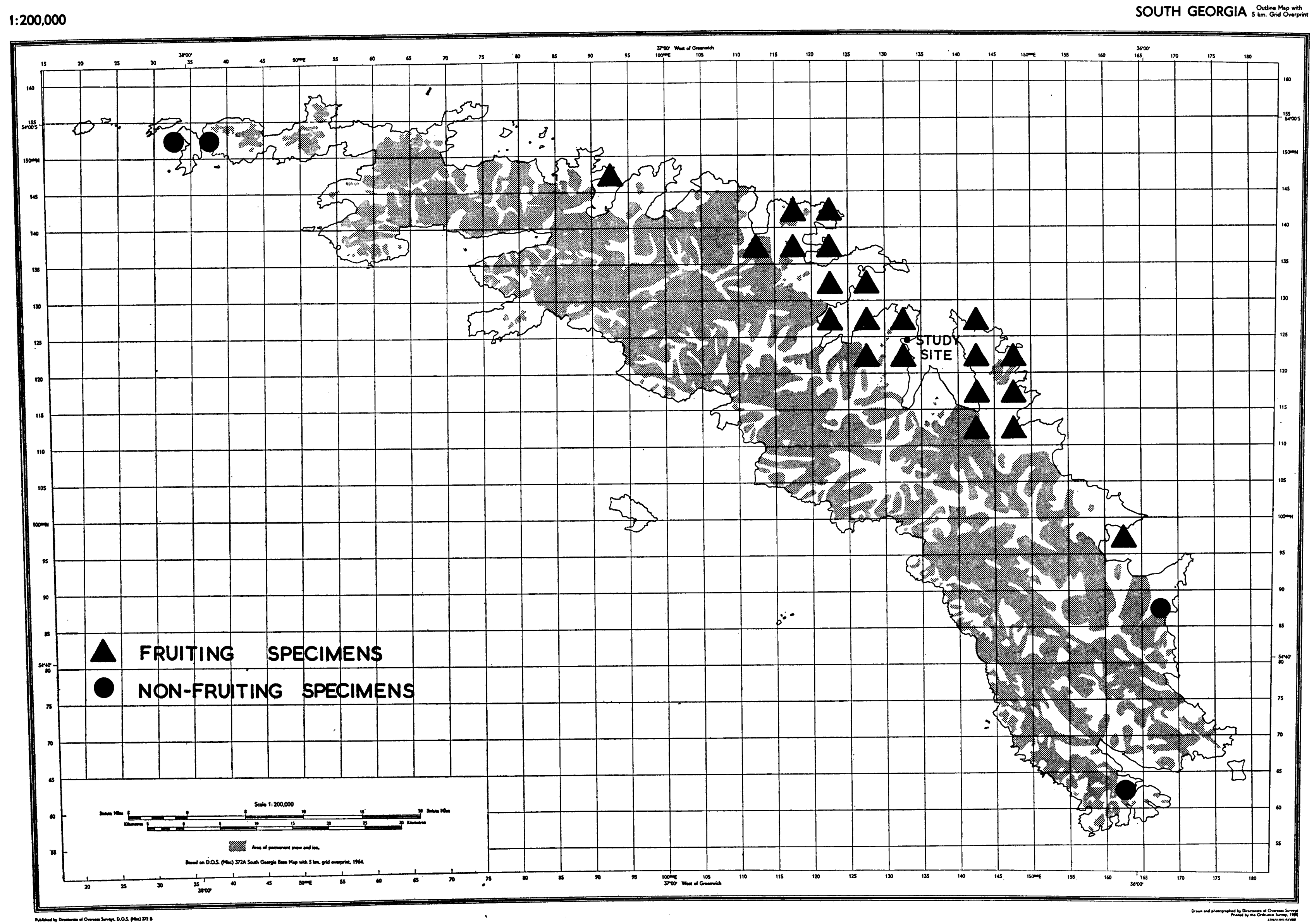

FIGURE 43. Known distribution of *Polytrichum alpestre* Hoppe on South Georgia, based on presence or absence in 5 km grid squares. The position of the study site on King Edward Point is also shown.

It can be seen from figure 43 that the species is widespread on the north-east coast and that fruit is produced in almost all areas. Owing to the relatively small amount of field work that has been carried out on the south-west coast and towards the north-west and south-east extremities of South Georgia, it is uncertain whether the available records are representative of the species distribution or behaviour in these areas.

From an examination of the substantial number of specimens collected over the last 50 years and from direct observations in the areas intensively worked on the north-east coast, it is quite clear that *P. alpestre* produces fruit regularly and often abundantly in this part of South Georgia. The occurrence of gametangia and fruit was examined in detail in twenty-nine widely spaced localities, individual sites covering a range of habitats on level and sloping ground of different aspects at varying altitudes up to 220 m. Male and female inflorescences and sporophytes were recorded at every site, and in most, at least a proportion of the populations could be said to be fruiting freely, i.e. capsules were so numerous that many were touching.

However, in addition to the fruiting colonies, non-fruiting turfs were present at most sites. Since dioecious species are known to form both unisexual and bisexual populations, the sex distribution of fifteen of these non-fruiting turfs of *P. alpestre* was examined further by analysing microscopically a 20-stem sample of non-male plants from each. The results showed that five turfs were unisexual female, seven were unisexual male and only three were bisexual. Thus, none of the turfs were sterile, i.e. completely lacking in inflorescences, but only three of the non-fruiting turfs were bisexual, and these alone could have borne fruit. The gametangia in these three turfs appeared healthy, and as male and female plants were in close proximity it is not known why sporophyte production failed. Inspection of a range of populations confirmed that unisexual turfs were widespread but bisexual turfs with sporophytes were equally common.

In addition to these discrete turfs of varying size, *P. alpestre* also forms extensive, more or less continuous banks, such as occur behind the disused whaling station at Husvik, where their origin has been attributed to spread following the destruction of *Poa flabellata* tussock by grazing (Greene 1964*b*). To determine the distribution pattern of male and female plants within these banks detailed mapping of gametangia and sporophytes was carried out in five quadrats of 1 m^2 placed at 5 m intervals along a 25 m transect line: thus the quadrats were selected without bias in respect of sex distribution.* The types of turf recognized in the field, and their fruiting condition, are indicated in figure 44. The results of analysing two samples of twenty female or sterile stems from each type showed that the samples included material from unisexual male, unisexual female and bisexual turf. As female and sterile stems could not be distinguished in the field, it is not certain that the samples were identical in every area of turf within a quadrat; but the uniformity noted within each pair of samples suggested that they were adequate, even if not a complete expression of the composition of the various types of turf. On this basis it can be seen that of the four quadrats illustrated in figure 45, *a* was predominantly female, while *b* was

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* The bank sampled was immediately north of Husvik whaling station (Grid Reference 119137), and the quadrats were left marked to enable mapping to be repeated at intervals. Precise details of their location are held among the British Antarctic Survey records at the Department of Botany, University of Birmingham.

predominantly male. Male, female and small bisexual areas were represented in *c*, and *d* consisted of more extensive bisexual turf.

It thus appears that the banks consist of a mosaic of unisexual male, unisexual female and bisexual areas, each of which may be likened to the discrete turfs considered earlier; indeed, it is likely that the banks developed through coalescence of such turfs, as *Poa flabellata* was progressively eliminated. Furthermore, the development of the banks has almost certainly led to an increase in the reproductive success of the species compared to that achieved in the discrete turfs. Isolated bisexual turfs are known to fruit freely, but discrete unisexual colonies must, of necessity, remain reproductively ineffective if they are separated by more than the fertilization range of the antherizoids; indeed the widespread occurrence of such non-fruiting colonies has already been demonstrated. In the larger banks, however, the two sexes are brought into constant contact, at least round the edges of the unisexual areas. Thus, it is not surprising that, in the quadrats, sporophytes were recorded over large areas of female as well as bisexual turf, much of both types being found to fruit freely. Nevertheless, sporophytes were absent from several small areas of female turf in situations adjacent to male plants, e.g. in quadrats *c* and *d*, a situation comparable to that in the three isolated, bisexual non-fruiting turfs discussed earlier. Again the archegonia appeared normal, and it is clear that failure in sporophyte production in these female areas was not due to excessive distance from male plants as sporophytes were widespread

fruiting	symbol	field designation of turf type	sex of samples
absent	▦	predominantly ♂, with ♀ or sterile <20%	♂
	▤	both ♂, and ♀ or sterile >20%	♂
		predominantly ♀ or sterile with ♂ <20%	♀
sparingly	∵▤	both ♂ and ♀ or sterile >20%	♂+♀
	∵	predominantly ♀ or sterile, with ♂ <20%	♀
freely	⁙▤	both ♂ and ♀ or sterile >20%	♂+♀
	⁙	predominantly ♀ or sterile with ♂ <20%	♀
	■	dead *Polytrichum*	
	F	a grass, *Festuca erecta*	
	P	a grass, *Poa flabellata*	

FIGURE 44. Relationship of fruiting behaviour to turf type in sample quadrats from a bank of *Polytrichum alpestre* Hoppe near Husvik.

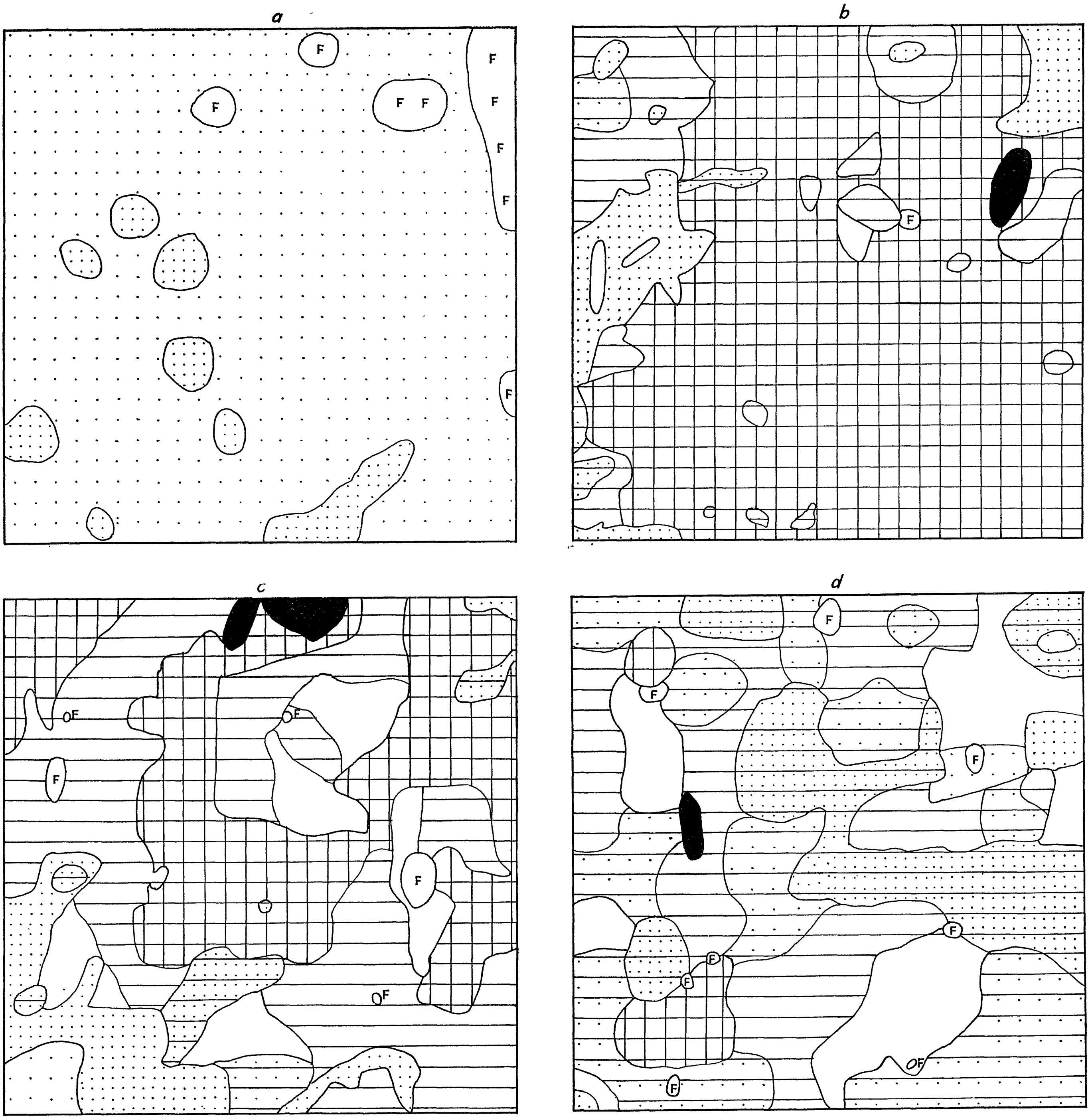

Figure 45. Distribution of turf types in four quadrats from the bank of *Polytrichum alpestre* Hoppe near Husvik. Symbols as in figure 44.

and locally abundant in quadrat *a* although no male plants were present. Moreover, measurements of the distance from some of the small freely fruiting areas in this quadrat to the nearest male inflorescences indicated an unusually long fertilization range up to 75 cm.

Inspection of additional banks at Husvik and at other localities along the north-east coast, confirmed the widespread repetition of this mosaic pattern of sex distribution, which may thus be regarded as characteristic of the larger banks of *P. alpestre* in this part of South Georgia.

Gametangial development

As in many other mosses with discoid perigonia, *P. alpestre* shows a marked contrast between the number of gametangia in male and female inflorescences. On South Georgia, perigonia normally contain 50 to 100 antheridia, the latter reaching a length of 1·0 to 1·2 mm, but six was the maximum number of archegonia recorded in a perichaetium. Individual archegonia reached 1·2 to 1·5 mm long and have exceptionally long and slender necks which normally become detached at the apex of the venter within a few weeks of dehiscence.

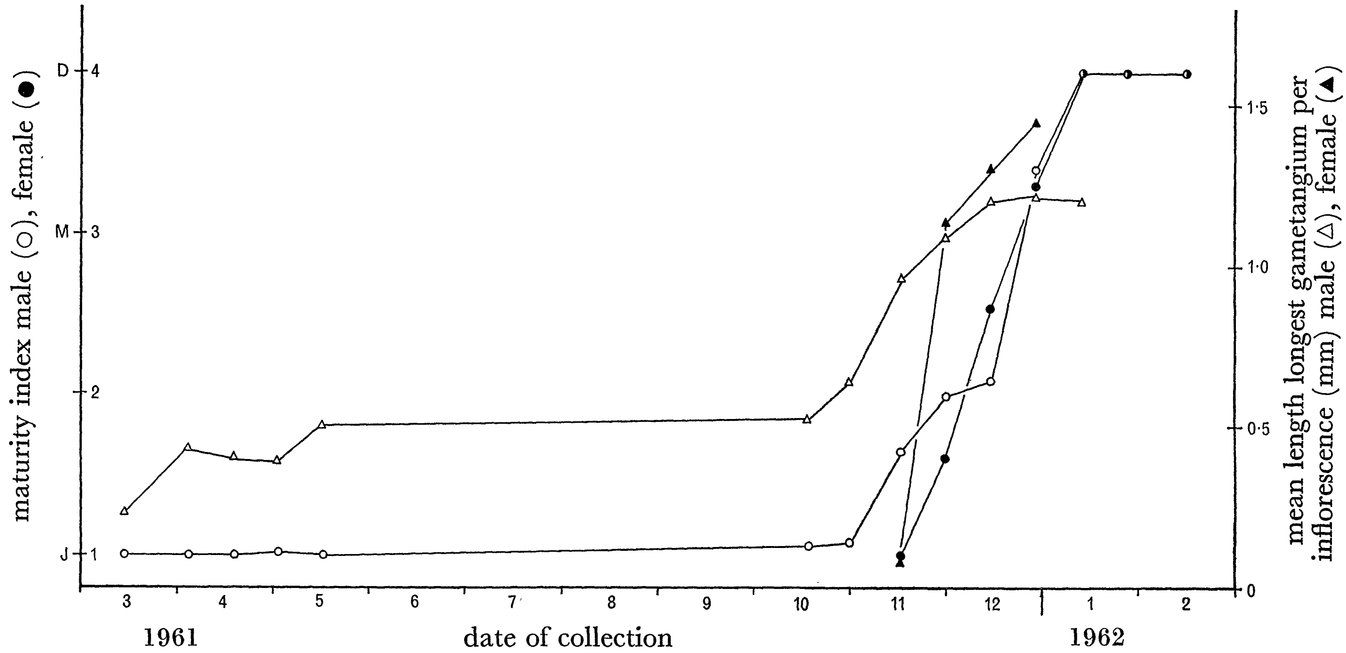

FIGURE 46. *Polytrichum alpestre* Hoppe gametangial cycle, based on maturity indices, for the 1961–62 King Edward Point study site series. The mean length in mm of the longest gametangium per inflorescence is also shown.

The cycle of gametangial development on South Georgia was first worked out in the earliest series of collections from the study site on King Edward Point (figure 46): it will be seen that measurements of sex organs were also obtained, the figures representing the mean length of the longest gametangium in each of five inflorescences per specimen.

The youngest antheridia were recorded in March and although some increased in size from then until the end of May, when the last summer sample was taken, the majority in each inflorescence remained in the *juvenile* state throughout this period. The first sample taken in early October, as the last of the winter snows were melting from the site, showed antheridia still in the same state, indicating that maturation and growth had been suppressed over winter. From October to early January when the first inflorescences were recorded with the majority of the antheridia in the *dehisced* stage, there was a rapid and steady increase in maturity, although the majority of antheridia had attained their maximum size by early December. Although some variations was noted, the majority of antheridia in each inflorescence were clearly at one stage of development. The data for the present series thus indicate that December and early January was the period over which antherozoids were liberated.

In contrast to antheridia, *juvenile* archegonia were not observed until near the end of November, undergoing immediate and very rapid growth and development. In spite of the approximate 8-month delay in their appearance, *mature* archegonia, i.e. those in a state receptive to antherozoids were present over the same period as *mature* antheridia; indeed, for the remainder of the cycle the development of male and female gametangia was identical.

In figure 47 the results obtained by a maturity state assessment of both the 1961–62 and the 1963–65 series are compared with the remainder of the available South Georgian material. It is clear that a similar cycle was followed during both seasons on King Edward Point, and at other localities on the north-east coast of the island. Antheridial development begins as early as February in some sites, a few antheridia reaching the *immature* stage during March, but no *juvenile* archegonia were seen in samples from the study area or in eight specimens collected elsewhere between February and May. They were seen in one specimen collected from the study site in late October 1964, and were present in one of five other specimens collected in October, but they were not common in the samples collected before November. Thus, it seems clear that on the north-east coast of South Georgia, most antheridia appear in late summer or early autumn and overwinter in the *juvenile* stage, but the youngest archegonia are not seen until 3 or 4 weeks after the snow has melted in the spring.

It is also clear from figure 47 that most gametangia of both sexes pass through the *mature* stage in December and early January, which may thus be regarded as the period of fertilization for *P. alpestre* on this part of the island. It will be noticed, however, that a low proportion of *juvenile* gametangia of both sexes were recorded in late December and January. These are considered to represent retarded gametangia in inflorescences where most of the sex organs had developed further, and were never in the majority within an inflorescence.

Sporophyte development

The results of the investigation into sporophyte development at King Edward Point, based on the 1961–62 series, are shown in figure 48. The earliest specimens, collected in February 1961, already contained young sporophytes in the *early capsule in perichaetium* stage, while *late capsule in perichaetium* stages were recorded in mid-April. The slight reduction in the maturity index value between mid-April and mid-May appears to represent sample error between specimens and suggests that development may vary slightly over the bank. Most sporophytes remained in the same stage until mid-October, but there was rapid setal elongation and capsule development during November and December. Most capsules stayed in the *operculum intact* stage during January and February and no dehisced capsules were recorded until mid-March 1962, although the earliest stages of the next sporophyte cycle were already visible in mid-January. These results for early 1962 are paralleled by those for February to April 1961, when the oldest sporophytes were completing

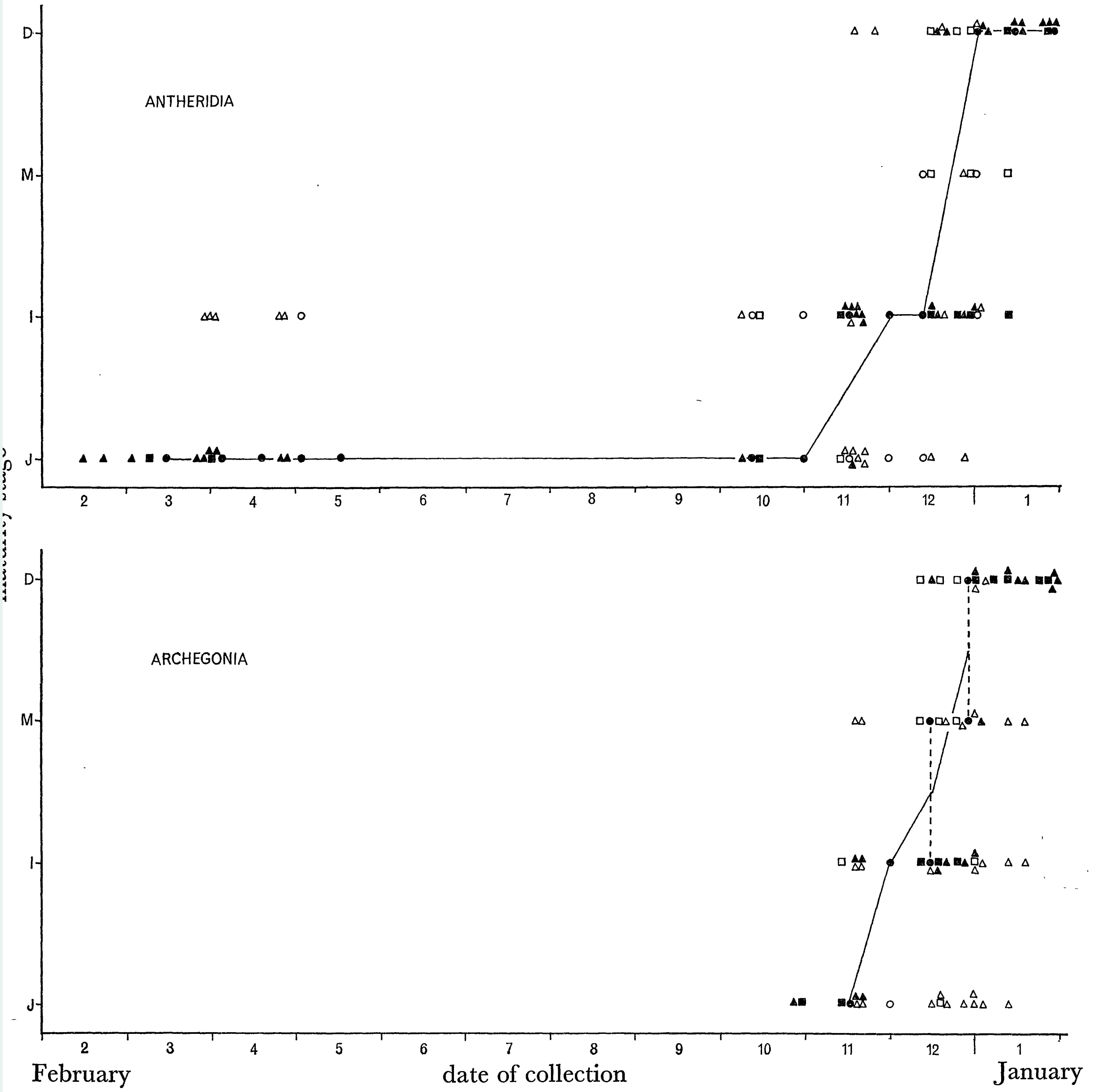

Figure 47. *Polytrichum alpestre* Hoppe gametangial cycles, based on majority state assessment for the two King Edward Point series and other localities on the north-east coast of South Georgia.

Key.	majority stage	other stages	
	●	○	King Edward Point, 1961–62
	■	□	King Edward Point, 1963–65
	▲	△	other localities

dotted lines indicate equal numbers of two stages recorded.

their maturation and dehiscing while young capsules of the new cycle were at the *early capsule in perichaetium* stages during February and March.

When these and the remaining South Georgian data are compared (figure 49) it is seen that development elsewhere on the north-east coast is very similar to that outlined for King Edward Point. Sporophytes in the *swollen venter* stage were first recorded in December

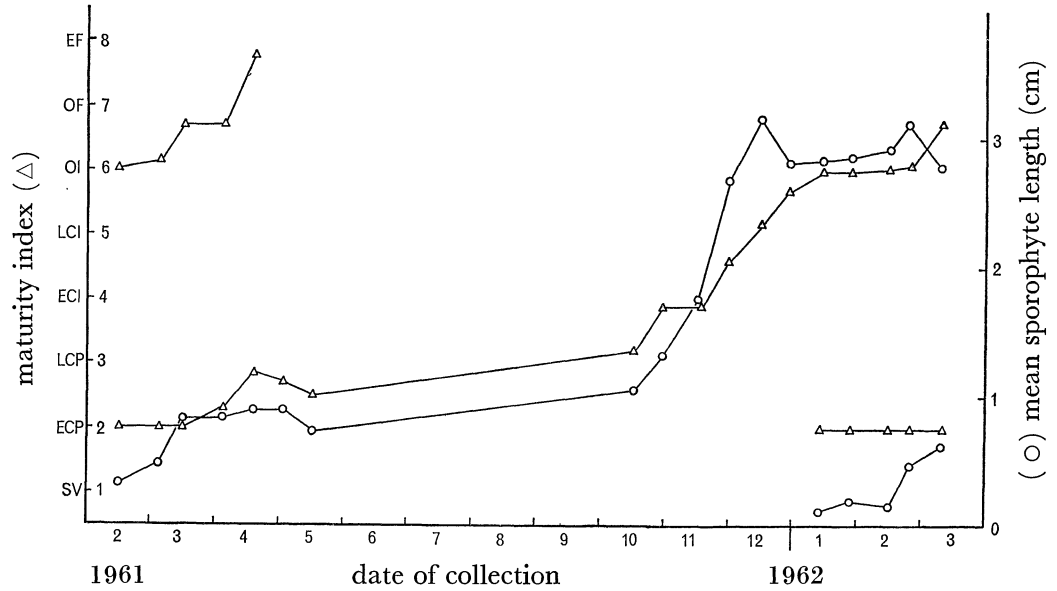

Figure 48. *Polytrichum alpestre* Hoppe sporophyte cycle, based on maturity indices, for the 1961–62 King Edward Point study site series. The mean sporophyte length in cm is also given.

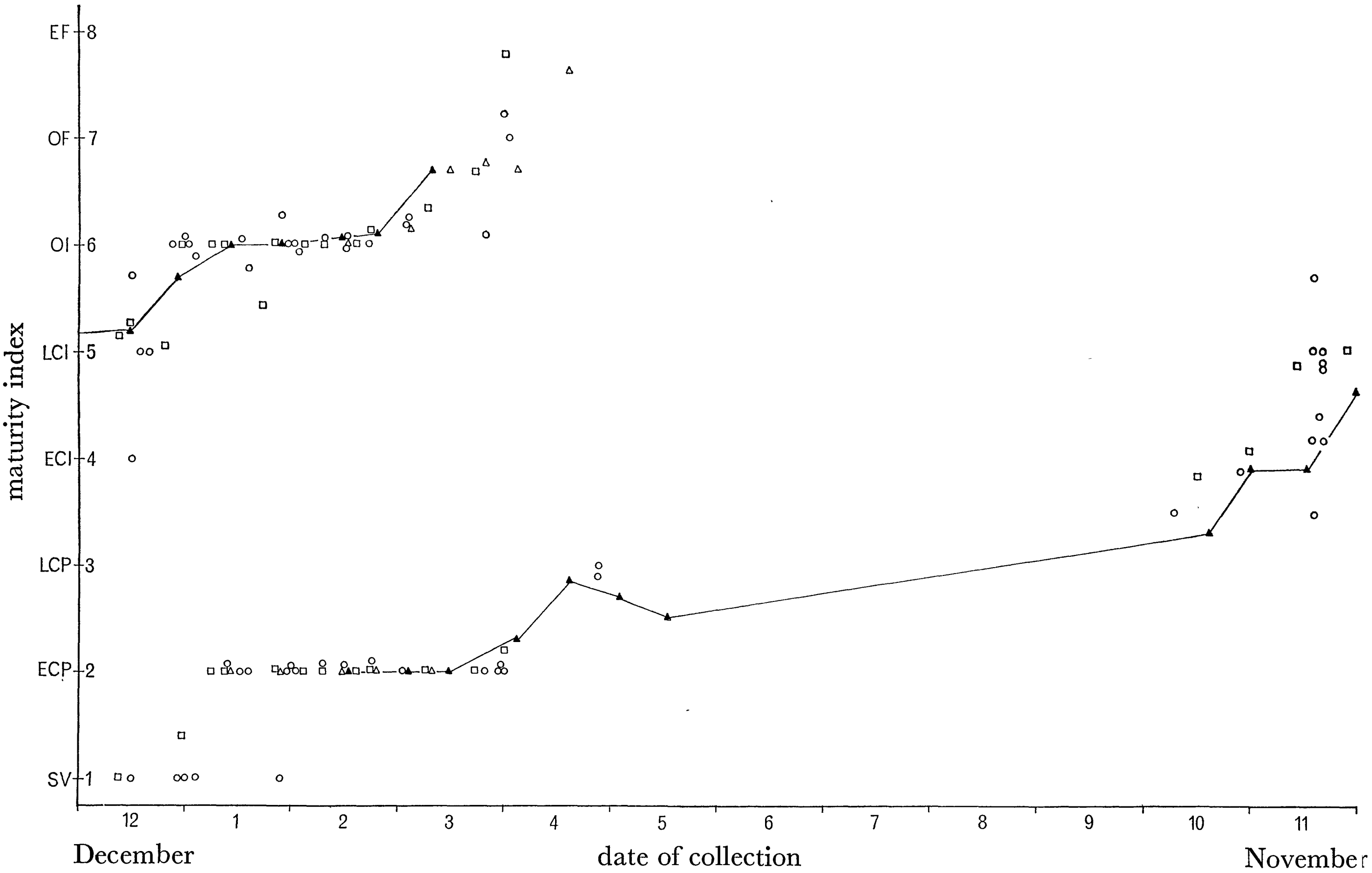

Figure 49. *Polytrichum alpestre* Hoppe sporophyte cycles, based on maturity indices, for the two King Edward Point series and other localities on the north-east coast of South Georgia.

Key ▲ King Edward Point, 1961–62 series, 1961–62 cycle
△ King Edward Point, 1961–62 series, other cycles
□ King Edward Point, 1963–65 series, all cycles
○ collections from other localities

and, as the gametangial data indicate that December and January were the principal months for fertilization, the occurrence of the youngest sporophytes during this period suggests immediate development of the zygote. However, the amount of development is not initially very great as sporophytes stay partially or completely immersed in the perichaetial bracts for the remainder of the season, maturation to the later stages not starting until the beginning of the following spring.

The occurrence of sporophytes in both the *late capsule in perichaetium* and *early calyptra intact* stages in most October specimens raises the possibility that slight development takes place under winter snow. In October material, however, setal elongation was far from complete, the base of the calyptra not, or only barely clearing the bracts, so these sporophytes were very little advanced compared with the *late capsule in perichaetium* stages present in April. For example, in the 1961–62 series from King Edward Point (figure 48) the mean length of five sporophytes in the mid-October collection was only 2 mm greater than the mean length recorded in the mid-April and early May collections. Although it is not clear whether this difference represents error involved in sampling from different parts of the study site, or indicates slight elongation during the winter, it is safe to conclude that if any development took place under the snow it was very slight. This conclusion is reinforced by observations which showed that capsules near late-lying snow banks were retarded in development compared with specimens in exposed sites in the same locality. Thus a specimen of *P. alpestre* collected near Grytviken, approximately 0·5 m from a snow bank on 18 November 1964, had a maturity index of 3·5 and contained sporophytes in the *late capsule in perichaetium* and *early calyptra intact* stages, while other specimens collected on the same day, farther from the snow banks, and so exposed for longer, had maturity indices up to 5·7. From early spring onwards, capsules develop steadily, attaining the *operculum intact* stage during January, with dehiscence taking place in March, i.e. approximately 15 months after fertilization.

VEGETATIVE GROWTH

Relationship to inflorescence production

An examination of a range of South Georgian material of *P. alpestre* showed that its stems are simple or bear a few erect branches, and that both stems and branches are capable of indeterminate growth. The development of an inflorescence, however, may arrest extension, which is normally not resumed in an axis bearing a developing sporophyte. Hence sporophytes are normally terminal, and it may be noted that only once has the exception been seen of a stem with a lateral sporophyte.

Owing to the high reproductive success of *P. alpestre*, the continued growth of the shoot through the inflorescence is less common in female than male plants, but withered archegonial bases in lateral positions on stems may frequently be observed. Extension growth through a male inflorescence is well known in many species of *Polytrichum*, and in the South Georgian material of *P. alpestre* it is common to find a series of perigonia arranged one below the other on a single axis. Indeed male stems are often found with short, slender shoots, consisting entirely of young growth, projecting vertically from the centre of the perigonium, the youngest noted being from a December collection where the inflorescence had the majority of the antheridia still immature.

When growth ceases, due to inflorescence production or other causes, the stems of *P. alpestre* produce young shoots either just below the apex or more frequently at a distance of several centimetres below. The initial growth of shoots arising deep in the turf is presumed to be rapid, since only distantly spaced juvenile leaves, consisting of sheathing bases and short, extremely slender limbs, are formed: however, once the apex of the shoot approaches the surface of the turf, leaves of normal form and density develop.

Estimation of growth

The rates of vegetative growth in mosses can be determined directly by measuring marked stems or indirectly by recording the length of successive growth segments provided the species shows seasonal variation in leaf morphology. Both techniques were applied to *P. alpestre* on South Georgia.

In February 1964, fifty male stems and fifty female stems in the study site on King Edward Point were marked by tying cotton around the stems 5 mm below the apex. The material was collected 12 months later, and direct measurements of increase in length were made (table 20). In a few cases no extension was recorded, and dissection of the stem apices usually showed that the latter were brown and dead possibly due to damage sustained when marking the plants. A few other stems had developed terminal inflorescences and so it was not surprising that these showed little increase. The remaining stems had each elongated between 1 and 6 mm with a mean of approximately 3 mm for the year.

Table 20. Annual growth of *Polytrichum alpestre* Hoppe estimated by direct measurement

				stems with 1964–65 inflorescences		stems without 1964–65 inflorescences	
	number of stems marked	number of stems recovered	stems showing no extension	number	mean extension (mm)	number	mean extension (mm)
male	50	41	5	4	1·5	32	3·1
female	50	33	6	1	1·0	26	2·9

Before attempting to use the indirect method of assessing growth, it was necessary to define the nature and frequency of development of the successive segments characteristically shown by shoots of *P. alpestre* (figure 50). Microscopic examination showed that all the leaves consist of an oblong sheathing base with a spreading, slender limb and that they are arranged on the stem in alternating zones of narrow areas with short, distantly spaced leaves and broader regions of longer, more tightly packed leaves. Measurements were made of the dimensions of successive leaves along a 2 cm portion of stem comprising four segments, the results being presented as a leaf spectrum (figure 51). It will be noticed that the length and breadth of the sheathing portion remained constant throughout, approximately 1·5 mm by 1·0 mm respectively, but the length of the limb varied from approximately 0·5 to 2·2 mm, with four distinct peaks corresponding to the broad region of each growth segment. The two complete central segments each contained between thirty and forty leaves. Thus it is possible to define the growth segments in terms of limb length of the leaves.

To determine the duration of the growth period represented by each segment, limb lengths of the upper leaves were measured for a series of typical male and female stems from the 1961–62 series. The resulting leaf limb spectra, in each case representing leaves from approximately the centre of the uppermost segment present in March 1961 to the stem apex, showed a gradual decrease in limb length towards the apex in all samples from mid-March to mid-November 1961 (figure 52). In the sample for 30 November 1961, the first with new leaves visible above those of the previous segment, limb length of leaves in the stem apex showed a slight increase. This increase was maintained in samples from mid-December to mid-February 1962 but in the late-February sample, limb length of the apical leaves once more showed a decline. Therefore, the most active period of leaf growth was from late November to mid-February, with the annual production bounded by leaves with shorter limbs.

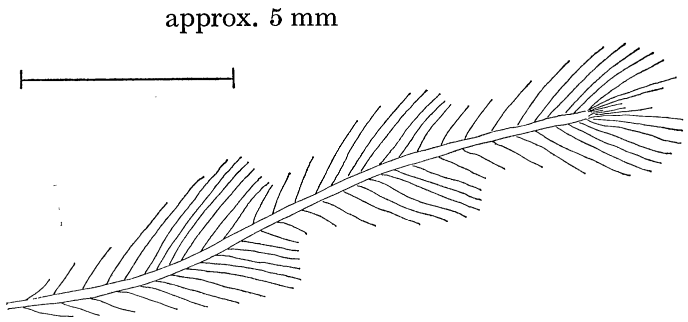

FIGURE 50. Diagrammatic representation of the stem segments in *Polytrichum alpestre* Hoppe.

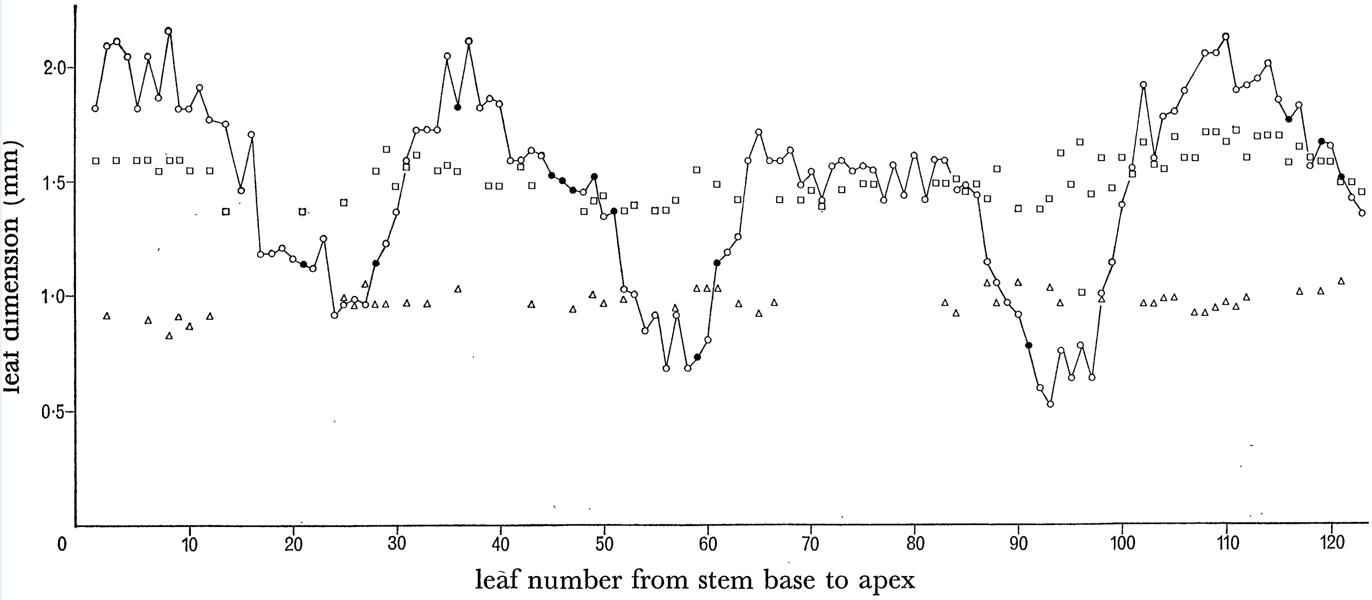

FIGURE 51. Leaf spectra showing limb length, base length and base width in mm for all leaves for four successive segments of a stem of *Polytrichum alpestre* Hoppe.

Key ○ limb length
● limb length adjusted by 0·2 mm for absence of apex
□ base length
△ base width

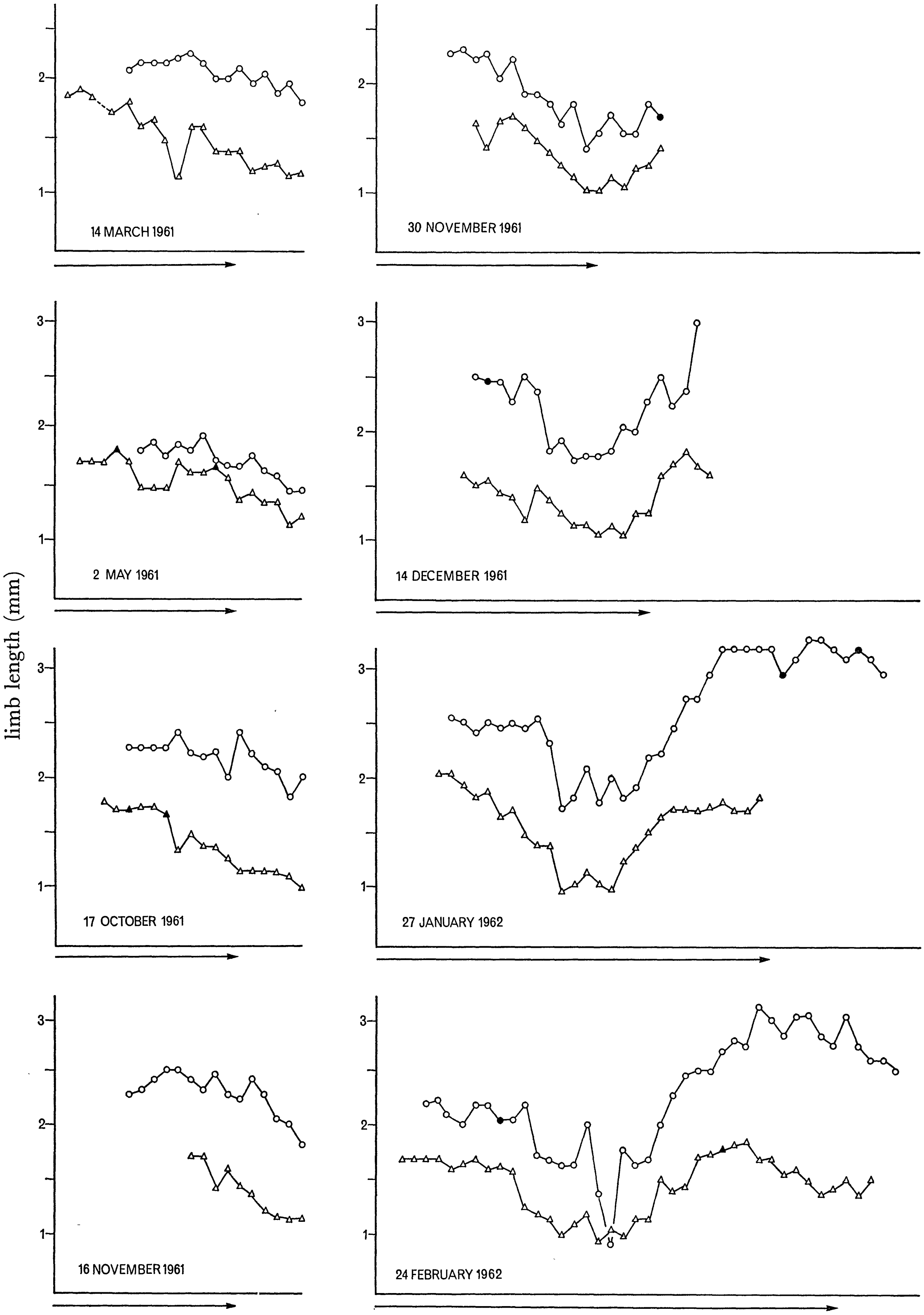

Figure 52. Seasonal variation of limb length spectra of all leaves from apical region of male and female stems of *Polytrichum alpestre* Hoppe.

Key △, male; ○, female. Solid symbols indicate measurement adjusted by 0·2 mm for lack of apex. Arrow indicates direction of stem apex.

From the evidence it appears that individual segments on a stem correspond to annual growth increments, and consequently measurements of the distance from the tips of the apical leaves to the tips of the upper leaves of the previous segment should indicate the amount of growth that has taken place. Measurements of the distance were made on samples of ten male and ten female stems from the two series of collections from King Edward Point. After measuring, the bases of the lowest leaves of the apical segment were exposed by removal of the older leaves below, and the segment length, i.e. from the base of the oldest leaves to the uppermost leaf apices, was measured. Finally the apical segments were cut from the plants and dried to constant weight, the results of these measurements for male plants in the 1961–62 series being summarized in figure 53.

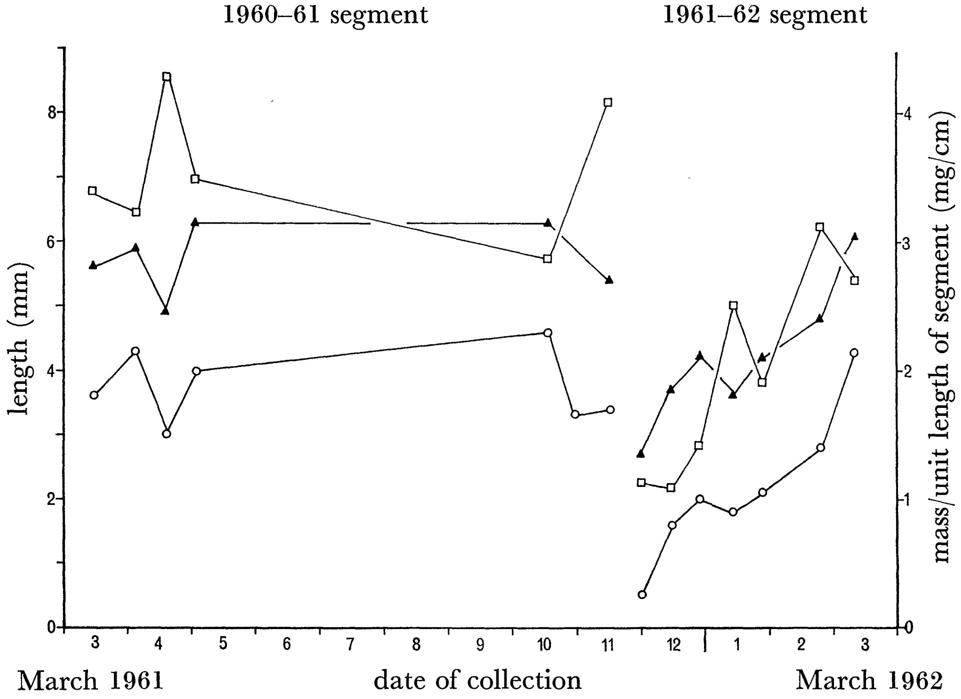

FIGURE 53. Seasonal variation of upper segment length (mm) for male plants of *Polytrichum alpestre* Hoppe, together with stem extension (mm), and mass per unit length (mg/cm).

Key ▲, segment length; ○, stem extension; □ mass/unit length of segment.

It is clear that neither the length of the upper segment nor the stem extension varied greatly from mid-March to mid-November 1961 (figure 53). At the end of November, however, the first leaves of a new segment were visible above the upper leaves of the older one, and the new upper segment showed a gradual increase in length during the summer. By mid-March, the length of the new upper segment was comparable with that of the older segment below, i.e. the segment of the previous year. The gradual increase in the robustness of the new segment during the summer is reflected in the rise in its mass per unit length. Towards the end of the season the segments attained a mass of approximately 3 mg/cm, and by mid-March 1962, when the new segments averaged 6·1 mm in length the mean mass of each was 1·7 mg. However, the graph shows some fluctuations in mass per unit length, no doubt reflecting variation between the robustness of plants in different fortnightly samples. The pattern shown by the male plants was paralleled by the female plants in the 1961–62 series and by both sexes in the 1963–65 series, although the new segment appeared earlier in November 1964 than in November 1961.

These results, together with those obtained from an analysis of limb length variation, indicate that one growth segment is formed each year. Stem elongation appears to take place over most of the season, i.e. from November to March with the development of the longest leaves corresponding to the period of high summer, i.e. mid-December to late February: spring and autumn growth is characterized by shorter leaves. No evidence was found of growth under winter snow cover. When estimates of growth obtained by direct measurement of the marked plants from the 1963–65 series were compared with assessments of the same plants using the indirect method a very close correlation was obtained, reinforcing the belief that the measurement of growth segments can be used as an adequate estimate of extension growth of *P. alpestre*, at least on South Georgia.

Estimates of annual growth based on five stem samples from ten localities on the north-east coast of South Georgia varied from 2 to 8 mm and were most frequently between 3 and 5 mm thus corresponding to the 3 to 5 mm annual increase estimated from the study site on King Edward Point, although it was noted that for 1961–62 many female plants there grew as much as 9 to 10 mm.

Environmental measurements

Methods

The second part of the present investigation involved measuring certain microclimatic factors at the study site on King Edward Point, as climatic and edaphic factors are among the most important environmental influences affecting the growth and reproduction of plants. Daylength and temperature are thought to be the climatic factors of greatest importance, but an adequate relative humidity is also essential for bryophytes owing to the limited development of mechanisms for controlling water loss in this group of plants. Edaphic factors were not studied, although it may be noted that one of the most important, water availability, is unlikely to have been limiting at the study site owing to the frequent and heavy summer precipitation.

The study site on King Edward Point is situated at an altitude of a few metres above sea-level, approximately 400 m NNE of the meteorological office, and thus records of daylength, duration of sunshine and precipitation measured as part of the synoptic observations can be applied directly to the study site. As air temperatures and relative humidity are subject to dramatic fluctuations over short distances, both these factors were measured at plant level.

A Casella 7-day hygrograph, placed on the surface of the *P. alpestre* bank so that the sensitive hair was 3 cm above the surface of the turf, was used to obtain a continuous record of relative humidity between 13 January and 2 April 1961.

The temperature at plant level was recorded daily from 13 January to 22 March 1962. Measurements were made at 3-hourly intervals, at the times of the synoptic observations, by means of a Wheatstone bridge circuit in the meteorological office connected to two platinum resistance thermometers, or probes, at the study site. The probes were accurate to 0·25 degC over a range from −25 to 35 °C, and had a highly polished, protective surface thus absorbing very little radiation. Both were unshaded, the lower being placed between the stems at the level of the comal leaves, while the upper was supported 3 cm vertically above the surface of the turf. Thus the lower probe measured air temperature at the level of the stem apices and developing gametangia, i.e. in the upper 5 mm of the turf, while the upper recorded similar data at capsule level. During winter an estimate was kept of snow cover over the study site.

Temperature

From a comparison of the mean daily, mean daily maximum and mean daily minimum temperatures, for successive fortnights from 13 January 1961 to 11 January 1962 (figure 54) it can be seen that although the mean daily temperatures at plant level followed the same general trend as air temperature there were often striking differences. Thus, the mean daily screen temperatures varied from approximately 7 °C in summer to −6 °C in winter, but showed relatively little fluctuation throughout the year. The probes, however, recorded mean temperatures of up to 10 °C in summer, but in winter the mean remained within 1 degC of zero, being above freezing for most of the time.

In summer, fluctuation at plant level, as shown by the mean daily maximum and minimum, was greater than at the screen, the readings at the study site being usually higher with the lower probe usually slightly higher than the upper probe. Thus, the mean daily maximum temperatures at plant level (lower probe) rose to *ca.* 21 °C but the mean daily minimum rarely fell below 2 °C. During the winter there was continuous snow cover over the study site from mid-May to mid-October, the depth of snow varying from 30 to 100 cm. Under the snow cover the temperature variation was negligible, the screen air temperature now showing a greater fluctuation. Indeed the lowest temperatures at the surface of the moss were recorded, not in winter, but during autumn and spring when the site was clear of snow. Figure 55 shows the foregoing data rearranged to present a clear picture of the amplitude of variation recorded at the screen and at the study site. The striking difference between summer and winter temperatures at plant level is once more apparent, the maximum amplitude shown being 17 °C during high summer. Moreover it is clear that temperature change is rapid, the data suggesting a large diurnal fluctuation in summer.

The extent of this fluctuation may be assessed from the graphs of the actual 3-hourly readings over a 7-day period in summer and in winter (figure 56). The summer data were recorded between 28 January and 4 February 1961 and so represent a period when the maximum fluctuations are experienced. It can be seen that the temperature at leaf level (lower probe) is usually a little higher than that by the capsules (upper probe,) but that both were substantially higher by day and lower by night than air temperature in the screen. The maximum diurnal fluctuation was 31 degC recorded during 28–29 January.

The winter week 15 to 22 June 1961 (figure 56) covered mid-winter's day, when the site was under approximately 37 cm of snow. During most of this time, the two probes recorded almost identical temperatures slightly above freezing with no diurnal amplitude, although air temperatures fluctuated some 7 to 8 degC falling to −2 or −3 °C at night. Indeed it was only when the air temperature reached −10 °C on the night of the 14–15 June that a slight fall was noticeable in the temperature recorded by the probes.

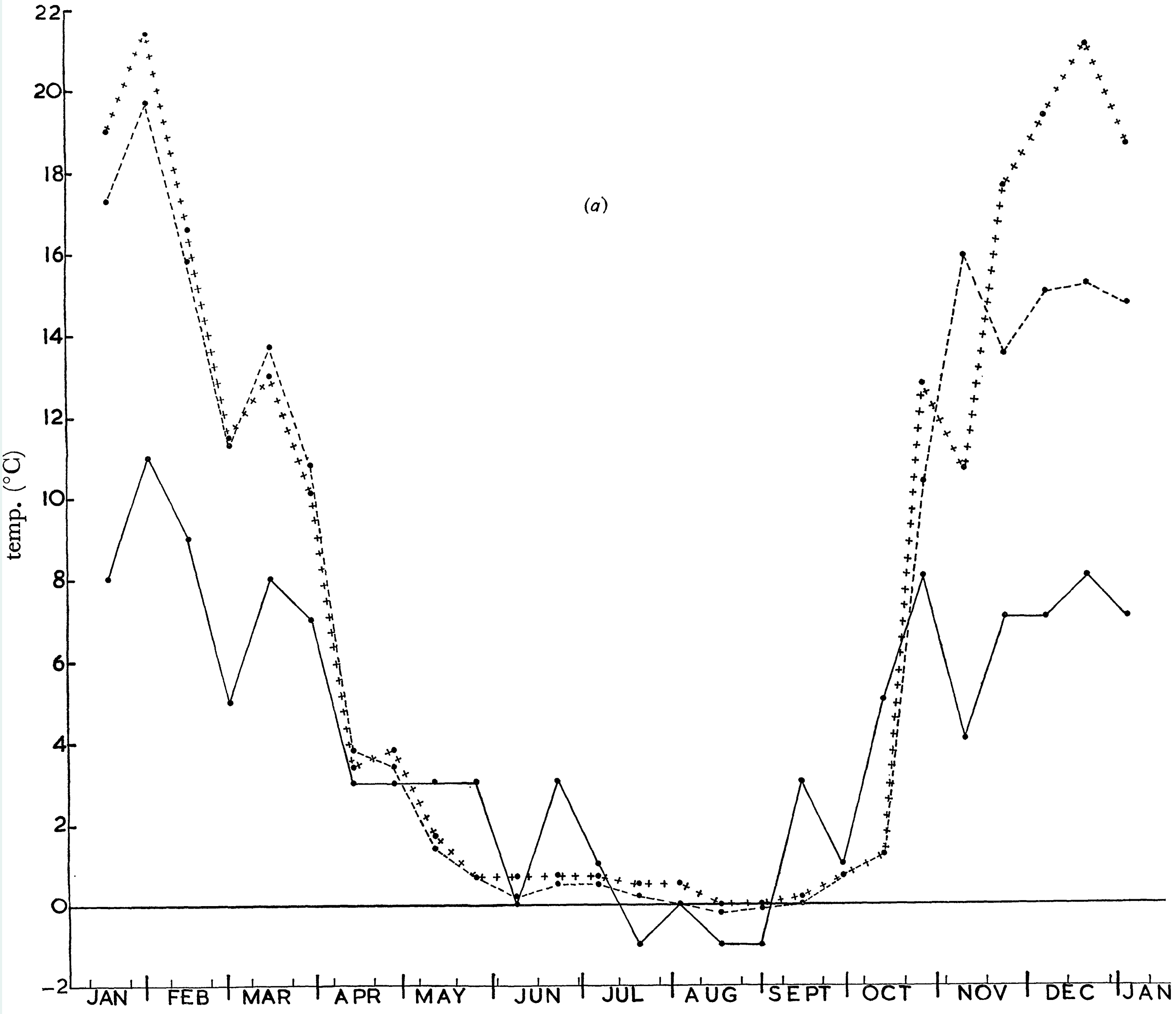

FIGURE 54. Comparison of (*a*) the mean daily maximum, (*b*) mean daily, and (*c*) mean daily minimum temperatures from screen and probe readings, for successive fortnights from January 1961 to January 1962. (*b*) and (*c*) on facing page.

Key – – – Upper probe; + + + lower probe; —— screen.

These data emphasize the insulating effect of snow, which by protecting the plant surface in winter, prevents excessive heat loss. It is clear, however, that in the summer rapid heating of the moss bank takes place by day with much of the heat being lost by night so that the plants experience a range of rapidly altering conditions resulting from the temperature fluctuations. An assessment of the period over which the various temperatures are maintained is given in table 21 which shows the frequency with which temperatures in 5 degC blocks were recorded by the lower probe, expressed as a percentage of the total for each fortnightly period. It is striking that, for each fortnight, the greatest frequency of records fell between 0·5 and 5 °C throughout the year except for 4 weeks in January and

February 1961 when it rose to between 5 and 10 °C. However, over 60 % of the records were above 5 °C in mid-summer, from early November to near the end of February, while in winter temperatures were mostly above freezing, in fact between 0·1 and 1 °C.

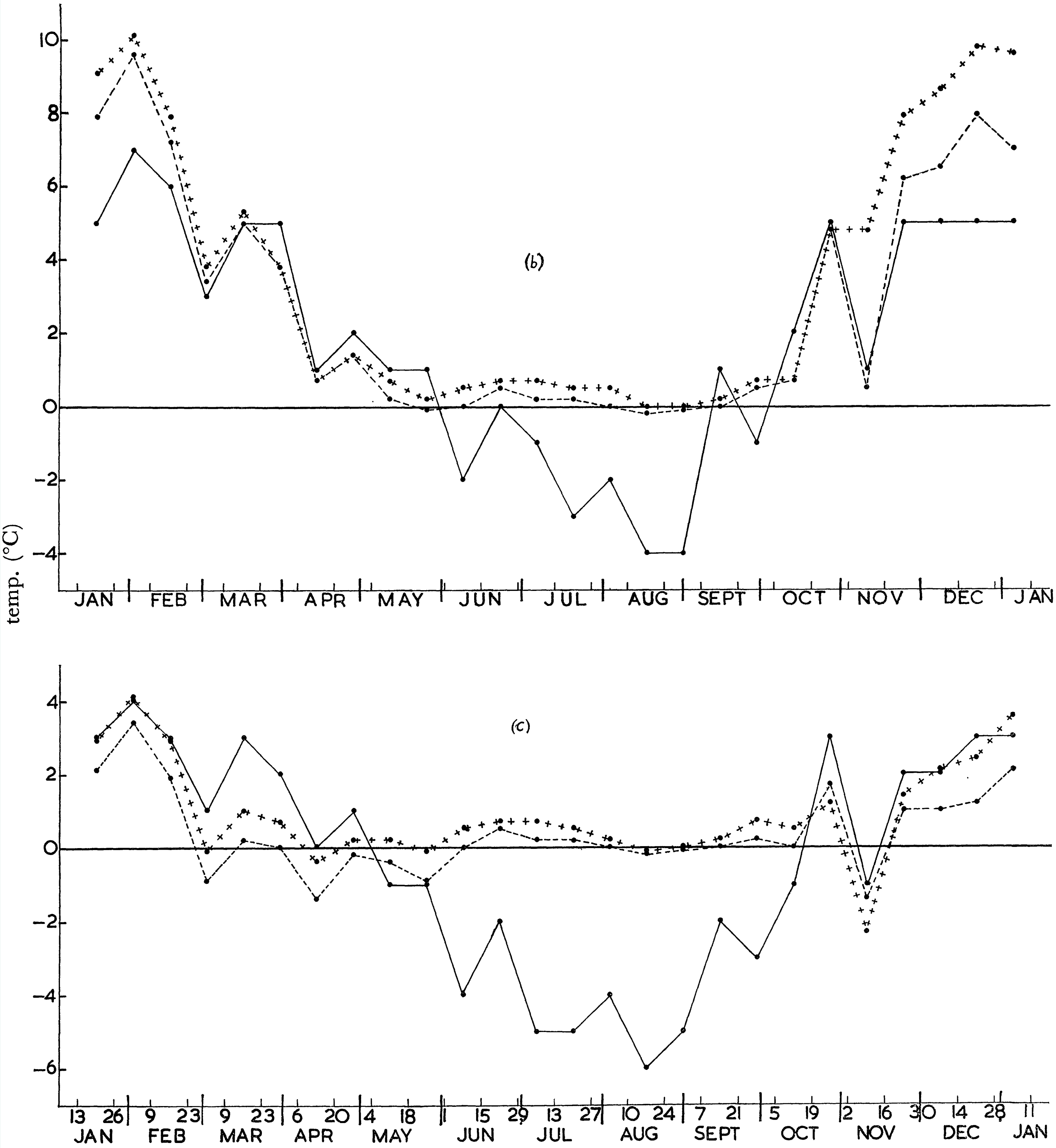

FIGURE 54 *b*, *c*. For legend see facing page.

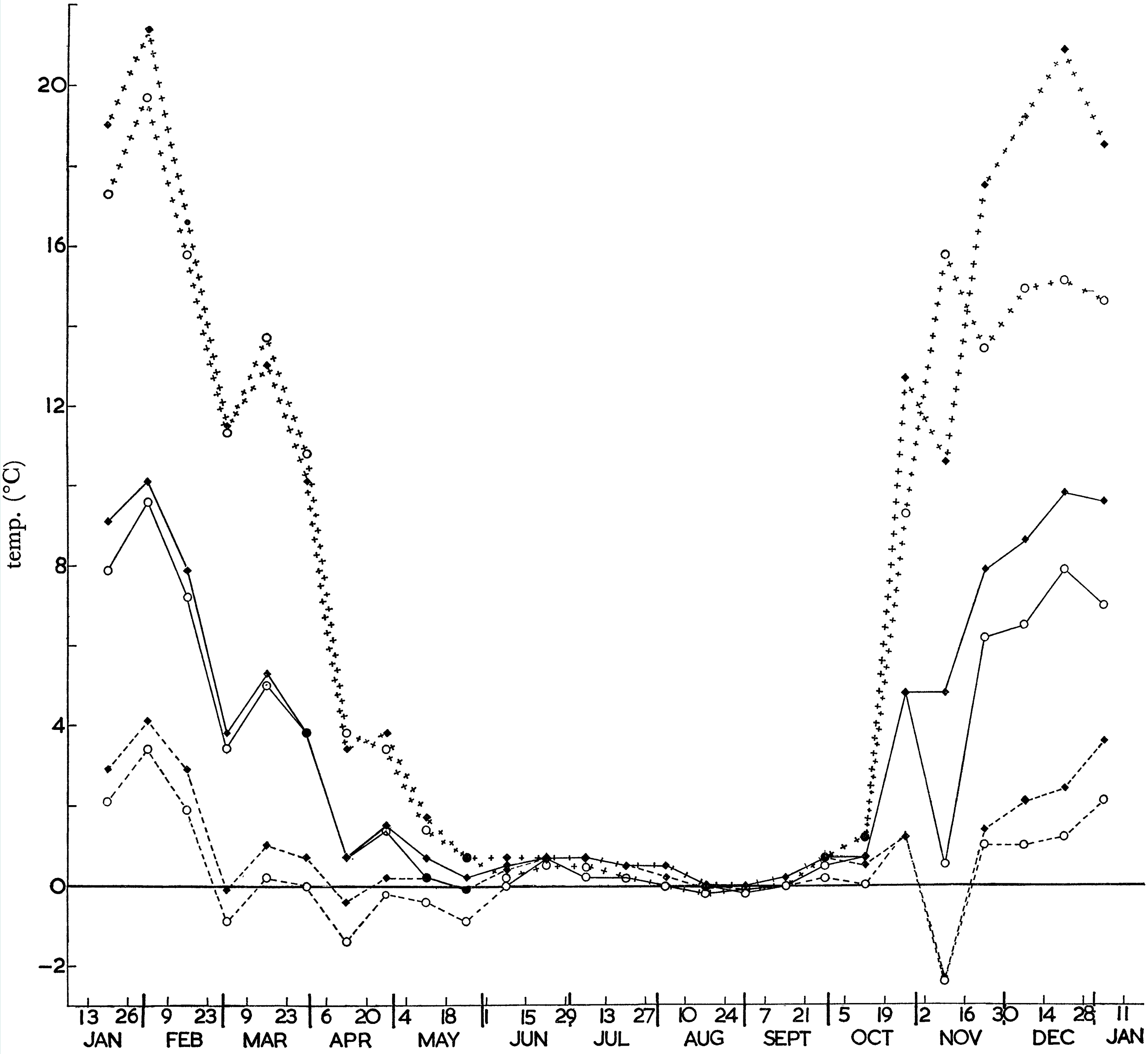

FIGURE 55. Amplitude of the mean daily, mean daily maximum and mean daily minimum temperatures from probe readings for successive fortnights from January 1961 to January 1962.

Key	upper probe	lower probe
max.	+ + + ○	+ + + ◆
mean	—— ○	—— ◆
min.	- - - ○	- - - ◆

Other factors

Of the remaining climatic factors to be considered, the values for relative humidity were the only ones measured at the study site. A continuous record was obtained from mid-January to early April 1961 but the data have been abstracted by using the values recorded every 3 h, i.e. at times corresponding to the temperature readings, the results being presented in a comparable fashion.

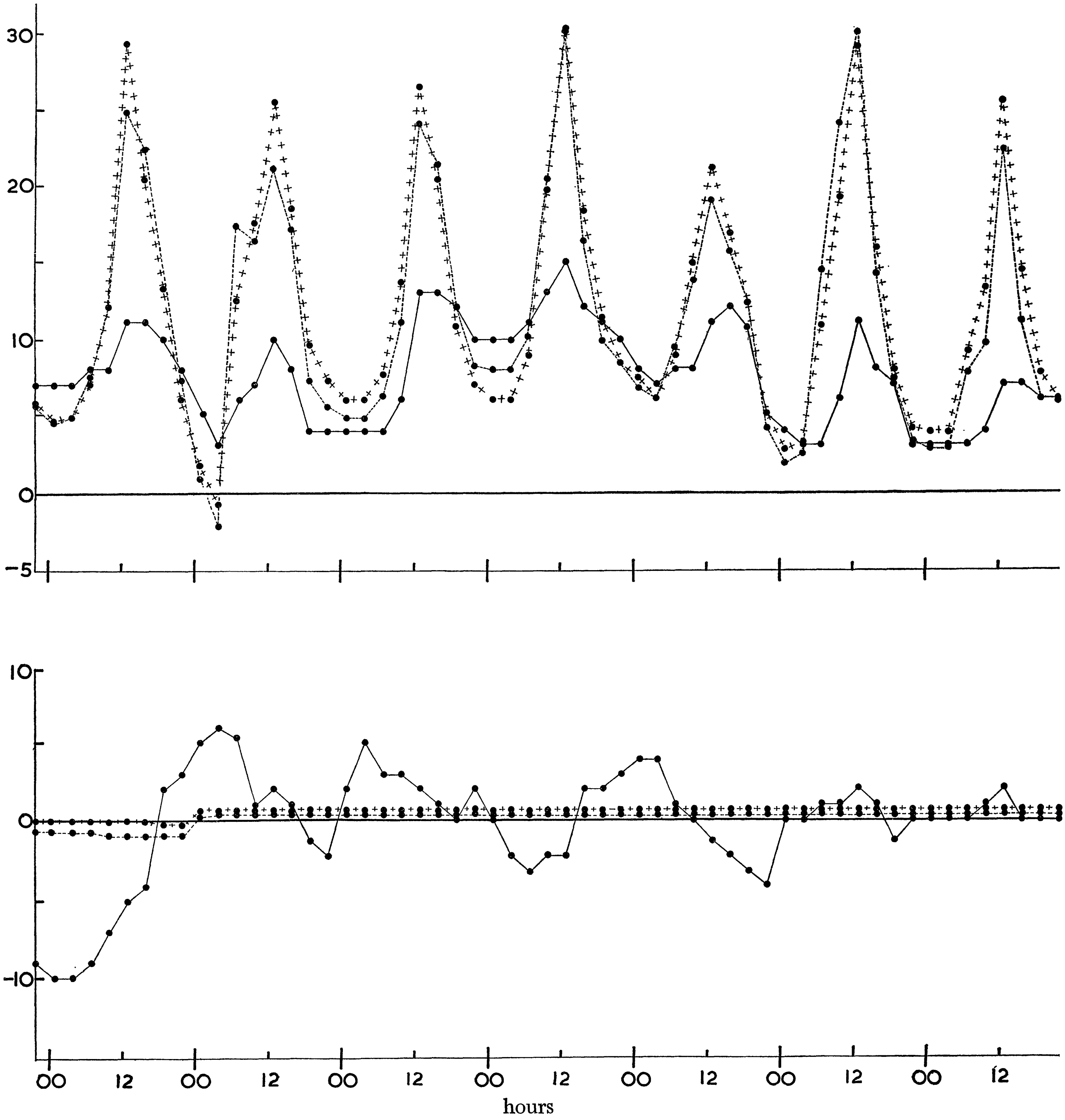

FIGURE 56. Actual 3-hourly temperature readings recorded at screen and by probes for a 7-day period in summer (upper) and winter (lower). Summer data from 28 January to 4 February 1961: winter data from 15 to 22 June 1961.

Key - - - Upper probe; + + + lower probe; —— screen.

The mean daily values for relative humidity, together with the mean daily maxima and mean daily minima for successive fortnights are given in figure 57. The mean daily values were between 72 and 81% and so correspond to the mean daily values obtained from the screen reading (table 23) for the same period. However, the mean maxima reached 92% while the mean minima were between 59 and 67%, except for the period 26 January to 9 February, when the figure fell to 53%. By comparing figure 57 with figure 45, it can be seen that this exceptionally low value corresponds to a period when the mean daily maximum temperatures, at plant level were at their highest, suggesting that for short periods, at least, the surface of the bank is liable to become unusually dry. Figure 58, which covers the same period as the summer temperature data in figure 56, shows the extent of the diurnal fluctuation, and as is to be suspected, there is a regular daily drying out of the air just above the surface of the moss bank, usually during the afternoons. By night the relative humidity builds up once more, the low values for the night of 31 Jan./1 Feb., being related to the unusual absence of rain during the 31 January.

Table 21. Fortnightly percentage frequencies of temperature readings at plant level (lower probe) (see text pp. 312–3)

date	−5·0–0·9 °C	0·0–4·9 °C	5·0–9·9 °C	10·0–14·9 °C	15·0–19·9 °C	20·0–24·9 °C	25·0–29·9 °C	30·0–34·9 °C
13–26 Jan.	2·7	29·1	36·4	11·8	7·3	9·1	2·7	0·9
27 Jan.–9 Feb.	0·9	21·5	39·3	19·6	9·4	2·8	5·6	0·9
10–23 Feb.	—	37·3	34·6	12·7	12·7	1·8	0·9	—
24 Feb.–9 Mar.	14·3	58·9	14·3	9·8	1·8	0·9	—	—
10–23 Mar.	6·3	50·5	28·8	9·9	3·6	0·9	—	—
24 Mar.–6 Apr.	16·8	54·9	19·5	7·9	0·9	—	—	—
7–20 Apr.	16·1	81·2	2·7	—	—	—	—	—
21 Apr.–4 May	11·7	82·0	6·3	—	—	—	—	—
5–18 May	19·8	76·6	3·6	—	—	—	—	—
19 May–1 June	21·8	78·2	—	—	—	—	—	—
2–15 June	—	100·0	—	—	—	—	—	—
16–29 June	—	100·0	—	—	—	—	—	—
30 June–13 July	—	100·0	—	—	—	—	—	—
14–27 July	—	100·0	—	—	—	—	—	—
28 July–10 Aug.	—	100·0	—	—	—	—	—	—
11–24 Aug.	43·8	56·2	—	—	—	—	—	—
25 Aug.–7 Sept.	23·1	76·9	—	—	—	—	—	—
8–21 Sept.	17·0	83·0	—	—	—	—	—	—
22 Sept.–5 Oct.	—	100·0	—	—	—	—	—	—
6–19 Oct.	1·8	97·3	0·9	—	—	—	—	—
20 Oct.–2 Nov.	—	69·6	12·5	8·9	4·5	3·6	0·9	—
3–16 Nov.	24·6	39·1	13·6	11·8	6·4	3·6	0·9	—
17–30 Nov.	2·7	38·4	29·5	15·1	8·9	3·6	1·8	—
1–14 Dec.	0·9	38·5	25·9	17·3	8·7	3·9	3·9	0·9
15–28 Dec.	0·9	30·3	23·8	23·8	10·1	8·3	2·8	—
29 Dec.–11 Jan.	—	23·7	34·5	22·7	10·9	6·4	1·8	—

The amplitude of the fluctuation shown by the relative humidity values is further emphasized by table 22, which shows the frequency with which the readings fall in 5% blocks, the results being expressed as a percentage of the total for each fortnight. Throughout the period covered by the records about 50% of the 3-hourly values were above 80% and although there is a wide spread of values below this figure, it is clear that a relative humidity lower than 60% was seldom sustained for any length of time.

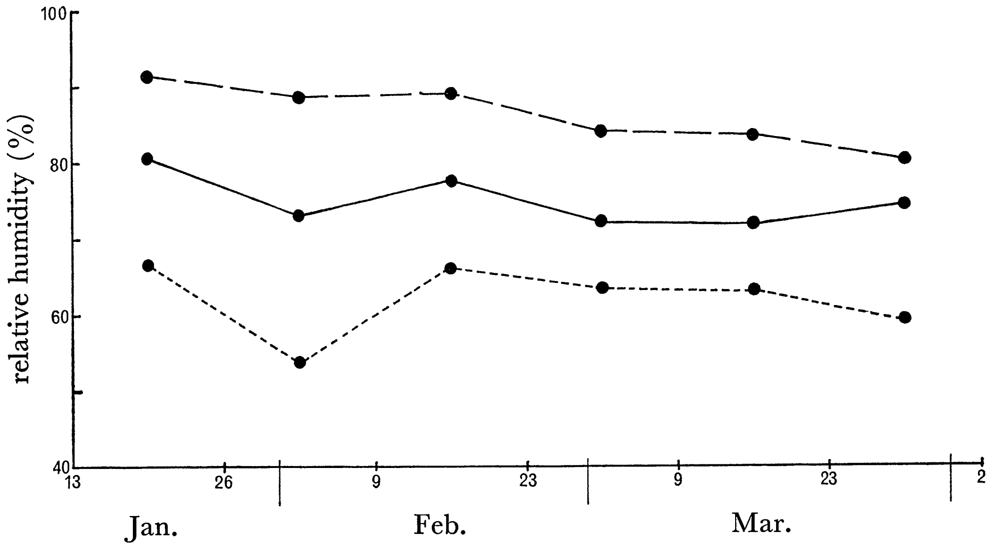

FIGURE 57. Amplitude of (—) the mean daily, (– –) mean daily maximum and mean (- - -) daily minimum values for relative humidity for successive fortnights from January to April 1961.

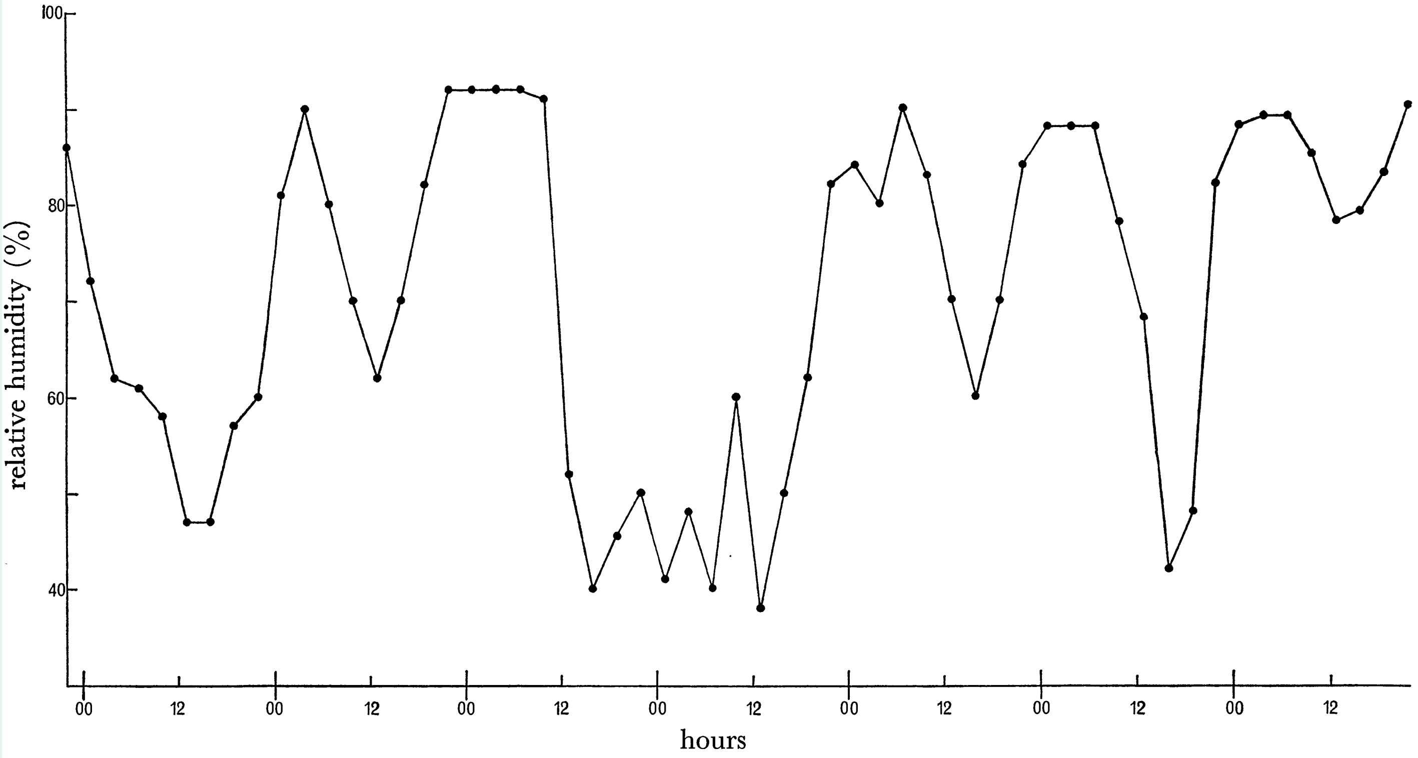

FIGURE 58. Actual 3-hourly values for relative humidity recorded over a 7-day period in summer (28 January to 4 February 1961) at the study site.

Table 23 presents the remainder of the relevant environmental data, which has been compiled from the *British Antarctic Meteorological Service Annual Meteorological Tables*: comparable data for the period 1944–50 will be found in Pepper (1954). It is clear that South Georgia experiences long days in summer, although frequent cloud cover restricts the amount of sunshine during the summer months to approximately one-third of the possible maximum. Under these cloudy conditions, precipitation is generally high, although there is a wide fluctuation in the amount of precipitation falling at King Edward Point each month. The annual total for 1961 was 161·7 cm, in fact rather higher than 139·6 cm the mean annual total for the ten years 1951–60. The precipitation falls mainly as snow in winter, and as rain in summer, but even at sea level, snow may fall and lie for short periods throughout the summer.

Table 22. Fortnightly percentage frequencies of relative humidity values at plant level (see text p. 316)

relative humidity	13–26 Jan.	27 Jan.–9 Feb.	10–23 Feb.	24 Feb.–9 Mar.	10–23 Mar.	13 Jan.–23 Mar. mean
95–99	0·9	0·9	2·7	—	1·8	1·3
90–94	32·7	17·8	22·3	0·9	0·9	14·9
85–89	11·5	14·3	13·4	11·6	18·7	13·9
80–84	20·2	20·5	16·1	24·1	14·3	19·6
75–79	4·8	4·5	9·8	14·3	12·5	9·2
70–74	10·6	8·9	10·7	11·6	17·8	11·9
65–69	7·7	0·9	7·1	6·3	9·8	4·4
60–64	7·7	8·9	7·1	14·3	5·4	8·7
55–59	1·9	3·6	5·4	7·1	5·4	4·7
50–54	0·9	4·5	0·9	7·1	7·1	4·1
45–49	—	5·4	1·8	1·8	0·9	2·0
40–44	—	6·2	2·7	0·9	2·7	2·5
35–39	0·9	1·8	—	—	2·7	1·1
30–34	—	0·9	—	—	—	0·9
25–29	—	0·9	—	—	—	0·9

Table 23. Summary of synoptic meteorological data from South Georgia from 1951–61

month	daylength ($\bar{x}$ h/day)	sunshine ($\bar{x}$ h/day)		cloud cover ($\bar{x}$ okts/day)		precipitation (Σ mm/month)		relative humidity ($\bar{x}$ daily)	
		1961	1951/60	1961	1951/60	1961	1951/60	1961	1951/60
Jan.	16·5	5·3	4·8	5·9	6·3	198·5	118·0	77	74
Feb.	14·7	5·5	5·1	5·8	5·8	59·0	114·7	72	73
Mar.	12·6	4·6	4·3	5·5	5·5	150·3	138·8	72	73
Apr.	10·4	1·8	2·2	6·1	5·8	192·4	126·4	83	77
May	8·4	0·6	1·2	5·9	5·3	278·0	173·6	74	79
June	7·4	0·0	0·5	5·5	5·1	259·0	123·4	75	78
July	7·9	0·6	0·8	4·7	5·2	80·6	113·4	74	77
Aug.	9·5	2·3	2·5	4·7	5·0	25·4	121·2	71	76
Sept.	11·6	3·2	4·2	5·2	5·1	90·1	102·2	72	75
Oct.	13·8	6·5	5·4	5·1	5·5	120·5	89·3	67	75
Nov.	15·8	6·5	5·8	5·5	5·7	40·2	92·2	65	71
Dec.	17·0	5·3	5·0	6·3	6·3	122·5	83·0	69	73

Discussion and summary

The present investigation into the behaviour and distribution of *Polytrichum alpestre* on South Georgia has shown that the species is widespread along the north-east coast and that it reproduces successfully over almost the whole of this area: unfortunately shortage of material has prevented an assessment of performance over the remainder of the island. Individual plants of *P. alpestre* from dense turfs which remain as discrete populations or coalesce to produce large hummocky banks and, while fruit is normally abundant in all localities, non-fruiting turfs or areas of banks are quite common. Gametangia were abundant in all the specimens examined, and from a detailed assessment of both types of non-fruiting situations it appears that the absence of fruit in some populations is due primarily to sex distribution and not to sterility. Unisexual populations will remain reproductively ineffective so long as they are outside the fertilization range of antherozoids, but in the larger banks, some female as well as bisexual areas contribute to sporophyte production.

The pattern of the growth and reproductive cycles for *P. alpestre* was established by an analysis of two extended series of fortnightly samples from a study site on King Edward Point, and a comparison of these cycles with results from other sites on the north-east coast allow the following deductions to be drawn:

(1) New growth begins some 3 to 4 weeks after the last of the winter's snow has melted from the plants, by continued extension growth from a vegetative apex or by the production of lateral shoots. If a reproductive phase does not intervene, growth will continue until the end of March, i.e. ceasing some 4 to 6 weeks before the winter snow cover is re-established.

(2) Extension growth of an axis is only temporarily interrupted by the development of gametangia, except in stems bearing sporophytes, where it normally ceases entirely. The appearance of new growth through an inflorescence begins earlier in male than female stems, i.e. during December and January respectively, and where no gametangia are formed, growth continues until March.

(3) Male gametangia are already present at the beginning of a season and mature steadily to liberate antherozoids during December and January. Female gametangia appear about the time new growth starts in November, and rapid development results in their being mature over the same period as antheridia. Withered gametangia of both sexes may persist for one or more seasons. The beginning of a new reproductive phase is marked by the appearance of *juvenile* antheridia in February or March, the majority remaining in this stage until the beginning of the following season, which, as already noted, is the time when the first *immature* archegonia are seen.

(4) Immature sporophytes are already present at the beginning of a season, growth beginning immediately the snow melts and continuing steadily until spores are shed the following March or April. Empty capsules may persist for one or more seaons. The *swollen venter* stage, the first evidence of the next sporophyte cycle is seen in December, i.e. during the period when male gametangia are liberating antherozoids. Initial growth is rapid, reaching the *capsule in perichaetium* stage in January, but is slow from then till the end of the season, sporophytes normally overwintering in this stage.

Table 24 summarizes the growth and reproductive cycles for *P. alpestre* on the north-east coast of South Georgia.

In spite of the full records available for the conditions under which growth and reproduction takes place on South Georgia, no detailed correlation of performance with particular environmental factors can be undertaken until the results of experimental studies are available. It seems clear, however, that conditions at plant level, particularly in winter, are far less stringent than is often supposed from the position of South Georgia in Antarctic waters well south of the Antarctic Convergence. Indeed the greatest threat to the survival of individual plants is more likely to arise from the effects of a too rapid or too wide diurnal fluctuation in temperature during summer, particularly when night temperatures fall below freezing, than from excessively cold conditions resulting from prolonged subzero winter temperatures: in fact, under snow, the temperature was slightly above freezing most of the time. Under the prevailing conditions, stems of *P. alpestre* have been shown to have a growth rate of between 3 and 5 mm per annum, but in the case of female plants, growth reaching as much as 9 to 10 mm per annum was recorded. It has been shown that gametangia and sporophytes have definite periods of formation and maturation and from the regular successful completion of the life cycle it appears that *P. alpestre* is well adapted to grow and reproduce under the climatic conditions prevailing over much of the north-east coast of South Georgia.

Since very few detailed reports of this type of study on other bryophytes are available for comparison, little evaluation can as yet be made of the present results. A similar pattern of sex distribution to that shown by *P. alpestre* is known in other dioecious mosses, e.g. in British populations of *Climacium dendroides* (Bedford 1938) and *Pleurozium schreberi* (Longton & Greene, unpublished), where unisexual populations outnumber those that are bisexual, with fruit appearing regularly in the latter. Gametangia and sporophytes of many mosses show clearly defined seasonal cycles of development (Greene 1960) and the sporophyte cycle of *P. alpestre* on South Georgia appears to parallel that of *Plagiothecium sylvaticum* in Britain. Moreover, the production of antheridia in autumn with their maturation delayed until spring, the time when the archegonia appear and develop, has been reported by Van der Wijk (1960) for several mosses in Holland.

The most comparable data, however, are from the preliminary results of a similar study on *Polytrichum alpinum* in Antarctic regions (Longton 1966). On South Georgia, *P. alpinum* has a sporophyte cycle almost identical to that of *P. alpestre* but no details for the gametangial cycle are yet available. In view of the fact that it too is a dioecious species, a comparison of gametangial maturation and sex distribution within populations will be of particular interest. South of South Georgia, fruit production in both species is extremely rare, capsules having been collected in only one or two localities. It is not yet clear if this failure to form sporophytes results from regular absence of gametangia or a too great spatial separation due to the sex distribution in the populations. It has been established, however, that antheridia and archegonia of both species can develop, at least in some seasons, at a number of localities near the Antarctic Peninsula, and for *P. alpinum*, the presence of non-fruiting, bisexual populations, on Signy Island, has been confirmed. A further possibility is that failure of capsule production could result from abortion of young sporophytes, but so far, no evidence exists to show that this is an important factor contributing to absence of fruit in mosses.

It appears, therefore, that conditions on the north-east coast of South Georgia approach those which are optimal for the regular completion of the annual growth and reproductive cycle of *Polytrichum alpestre*. When similar detailed results of this species's performance farther south, and under a range of experimentally controlled conditions, are available for comparison, a reasonable basis from which to investigate the growth and reproduction of bryophytes throughout the Scotia Ridge–Antarctic Peninsula should be available.

Table 24. Summary of the annual growth and reproductive cycle of *Polytrichum alpestre* Hoppe on South Georgia

month	vegetative stems	male stems	female stems	sporophytes: new cycle	sporophytes: old cycle
Oct.	no evidence of growth	most antheridia still in J stage	some J archegonia formed	—	LCP and ECI stages
Nov.	stem elongation begins. Short leaves formed	most antheridia reach I stage	juvenile archegonia formed, in some cases after short elongation of stem. Many reach I stage	—	LCI stage reached by setal elongation and swelling of capsule
Dec.	stem elongation continues. Increase in length of successive new leaves in early part of month	most antheridia reach D state. Vegetative growth resumed in centre of inflorescence	most archegonia reach D state, fertilization occurs	first SV stages	OI stage reached
Jan.	stem elongation continues. Longest leaves formed	antheridia persist in D stage. Vegetative growth continues	archegonia persist in D stage. Vegetative growth past inflorescence begins where fertilization failed	ECP stage reached	persist in OI stage
Feb.	stem elongation continues. Decrease in length of new leaves formed near end of month	vegetative growth ceases where J antheridia formed	vegetative growth continues	persist in ECP stage. Elongation occurs	persist in OI stage
Mar.	stem elongation ceases. Short leaves formed	most antheridia persist in J stage, a few reach I stage	vegetative growth continues	persist in ECP stage. Elongation occurs	OF stage reached. Spore liberation starts
Apr.	no evidence of growth	no evidence of growth	no evidence of growth	LCP stage reached	EF stage reached. Spore liberation completed
May to Sept.	no evidence of growth	no evidence of growth	no evidence of growth	? slight elongation	—

It is a pleasure to record our best thanks to D. Borland and his staff of meteorologists at King Edward Point, particularly D. O'Regan, for their help in taking the microclimatic readings and most of the samples at the study site. We would also like to thank many of our colleagues in the Department of Botany for helpful discussion of the results. Finally we are greatly indebted to Mrs D. M. Greene for untiring assistance with the preparation of the manuscript.

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