

GROWTH FORM AND WATER RELATIONS OF MOSSES IN THE MARITIME ANTARCTIC

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ABSTRACT. Determinations of normal field water content and the approximate proportion held "externally" (e.g. between leaves and stem, among rhizoids, etc.) were made for a number of mosses on Signy Island. The effects of colony form (i.e. packing and arrangement of shoots) on water loss in desiccating atmospheres and on water uptake were determined experimentally.

Dense growth forms (cushions, turves, carpets) are predominant. Species of *Andreaea* and *Grimmia* (small cushions) exhibit the greatest effect of colony form upon evaporation rate and occupy the most exposed habitats. Their ability to take up water rapidly from an intermittent supply in contact with any part of the shoot is also marked. *Polytrichum alpinum*, belonging to similar habitats, exhibits resistance to evaporation from the shoots (perhaps a result of cuticularization) rather than any effect of colony form. This species occurs normally on particulate substrata and water uptake is largely from below. The peat-forming mosses *Polytrichum alpestre* and *Chorisodontium aciphyllum* both have a tomentum of rhizoids which facilitates the upward passage of water from the stem base, and the latter species also readily passes water downwards along the shoot from the apex. The water available to the growing regions of these dense turves may be derived both from the melting surface of the permafrost peat (c. 25 cm. depth) and from rain and snow on the surface. The carpet-forming species (e.g. *Calliergon* cf. *stramineum*) of swamp habitats and the large cushions of drainage channels (e.g. *Bryum algens*) are mosses, whose shoots when isolated lose water rapidly, and whose colony form is somewhat less effective in restricting the rate of loss. Most of these species from habitats having a permanent ground-water supply exhibit rapid uptake and effective ectohydric transport of water. *Drepanocladus uncinatus* ranges in growth form from a compact mat to a robust carpet type and shows a correspondingly wide ecological amplitude in relation to water supply.

THE vegetation of many areas within the Scotia Ridge–Antarctic Peninsula region has been described by several workers (Holdgate, 1964; Gimingham, 1967; Longton, 1967; Gimingham and Smith, 1970).

As Gimingham (1967) has pointed out, there are two approaches to determining the causes of species distribution and the association of certain species in distinct vegetational categories. Perhaps the most obvious and easiest approach is to investigate the response of species to various environmental factors under field conditions. Previous ecological studies of Antarctic vegetation have relied on this method; the occurrence and abundance of the predominantly cryptogamic flora, the ecological amplitude of individual species, and the distribution and composition of distinct communities have been attributed to such criteria as climate, origin, stability and chemical nature of the substratum, topography, biotic effects, etc. While most authors have stressed the importance of water availability during the growing season as the chief criterion limiting plant growth and the distribution and development of communities in the Antarctic, few observations or experimental studies have yet been attempted.

The second approach relies on experimental investigation. If the causal factors regarding the distribution of the principal species and the tendency for certain of these to associate are to be fully understood, it is essential that the moisture regime of the habitat should be considered in relation to "the systems by which it [water] is taken up by the plants, and their ability to conserve it against evaporation stress" (Gimingham, 1967). In the Bryophyta, ability to withstand desiccation has often been regarded as of greater significance than conservation of water, in determining ecological amplitude. However, particularly in the Antarctic, environmental oscillations during the summer are so great that periods favourable for growth are irregular in duration and often brief. Under these circumstances, conservation of water in the shoot system and rapidity of uptake are important in maintaining the plant in a hydrated condition suitable for growth whenever conditions permit. Therefore, "it is particularly important in mosses to take into account not only the properties of the individual shoots in respect of water uptake and loss, but also the effect of the way in which the shoots are grouped together in the colony: that is the growth-form of the moss" (Gimingham, 1967).

In regard to systems of uptake, transport and storage of water, bryophytes exhibit consider-

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able differences from vascular plants. In mosses, several mechanisms associated with each of these functions have been recognized and, perhaps as a result of this complexity, experimental investigations of water relations have been rather few. From the observations of generations of bryologists, the ecological amplitude of many species in respect of the water balance of the habitat can generally be stated with some accuracy, but explanations of the responses concerned often remain obscure.

Some difficulties arise in parts of the world supporting a complex vegetation of vascular plants. Here the ecological amplitude of bryophyte species may be determined to a considerable extent by the influence of vascular plants upon the environment, or by direct competition with them. Investigations of the influence of structural and morphological characteristics upon physiology and ecology are simplified if they can be conducted in a region comprising a relatively wide range of more or less purely bryophyte communities extending through a variety of habitats. A territory satisfying these conditions is the Scotia Ridge–Antarctic Peninsula region, where the oceanic climate (Pepper, 1954) permits a comparatively rich and well-developed cryptogamic flora.

In an attempt to interpret the ecological significance of the variety of growth-form types found in Antarctic mosses, the authors carried out an experimental investigation of the relationships between growth form and physiology in ecologically important species, with a view to relating their ecological amplitude to the structure and composition of the communities in which they associate and the habitats which they occupy. The work was undertaken at the British Antarctic Survey's biological station on Signy Island, South Orkney Islands, between January and July 1966.

METHODS

Investigations were concentrated on a number of the most prominent mosses contributing to the four major sub-formations occurring on Signy Island. These have been classified by Longton (1967) and Gimingham and Smith (1970) as:

- i. Fruticose lichen and moss cushion sub-formation.
- ii. Moss turf sub-formation.
- iii. Moss carpet sub-formation.
- iv. Moss hummock sub-formation.

These sub-formations occupy habitats which are distinct not only in regard to exposure to wind, low temperatures and duration of snow cover, but also with respect to type of substratum and the source and nature of the water supply. Of the mosses used in the experiments, 12 were studied in detail and some data were obtained on five others.

Growth form and shoot density

Drawings, photographs and descriptions were made of each species to record the size and form of the undisturbed colony, the arrangement of the shoots, type of branching, disposition of leaves, rhizoids, etc.

Measurement of field water content

To obtain an indication of the amounts of water normally held in the colony under field conditions, small cores of about 2 cm. depth and 1–1.5 cm. in diameter were cut and brought to the laboratory in specimen tubes. As a method for determining approximately the fraction of the total water which was held amongst stems and in the spaces between stems and leaves, rhizoids, etc., the samples were first weighed and then placed with their tips downwards on small gauze platforms in centrifuging tubes. Following slow centrifuging, i.e. at a little under 1,500 rev./min. (or *c.* 250 g) for 1 min. (plus the time taken to accelerate to and decelerate from this speed), they were weighed again and then oven dried. A number of preliminary tests showed that during this type of treatment a relatively large quantity of water comes off quickly (i.e. within the first 0.5 min.) after which, at least for a time, further loss is slight. On removal from the centrifuge, the shoots were still turgid but not visibly wet. For the present purpose, therefore, the quantity of water which is readily lost in this way is taken as an indication of the "externally held" water, while the quantity left after centrifuging gives some indication of the amount contained in the tissues of the shoots.

Assessment of water loss

Sample cores consisting of the upper 2 cm. of the colony were fully moistened either by standing for several hours with the basal 2 mm. in water or by entirely submerging the samples. Excess free water was then removed, in the first case by light application of blotting paper and in the second by centrifuging as described above. Experiments were carried out using single shoots extracted from the centre of the sample and suspended on fine fuse wire, and whole cores loosely held by a loop of wire so that shoot arrangement was disturbed as little as possible. These were then hung in small conical flasks in which the atmosphere was maintained at a constant relative humidity. Using saturated solutions of K_2CO_3 , $NaClO_3$ and $PbNO_3$, the following relative humidities were established: 45, 70 and 95 per cent,* all flasks being kept at a temperature of about 18–20° C.

The samples were suspended about 2 cm. above the solution which covered the base of the flask. The decline in weight of each sample was recorded by regular weighings, using a torsion balance in the case of the colony samples and an analytical balance for single shoots. The time interval in some experiments was 2–4 min. over a period of about 30 min., in others at less frequent intervals for periods of several hours.

In the absence of any stirring of the contained atmosphere, the rate of water loss from the sample will be modified by a resistance resulting from the gradient of concentration set up between the source and the sink. However, even though the control of external conditions was not sufficiently fine to assess this effect, it was taken as being equivalent in all cases and unlikely to affect comparisons. Any reduction in rate of water loss which was found during the experiments was therefore interpreted as being due to additional resistance arising from properties of the plant. Furthermore, the resistance contributed by the concentration gradient between source and sink was in fact reduced by periodic stirring consequent upon removing the sample for weighing.

It follows that the frequency of weighing was bound to affect the results, partly because this determined the extent of stirring, partly because temporary opening of the flask caused fluctuations of the conditions inside, and partly because the sample was exposed to unknown conditions when hanging on the balance hook. It was for this reason that experiments involving frequent weighings were compared with those requiring only infrequent disturbance. That no conflicting results were obtained lends confidence to the method, at least in so far as it was used for the identification of gross differences in the behaviour of the species tested. However, a more accurate interpretation could be achieved if isothermal conditions could be maintained within the flask, reducing the distance between source and sink, and eliminating the need to remove the samples for weighing.

The water content at each time of weighing was expressed as a percentage of the water contained in the sample at the start, so that the results are comparable irrespective of variations in the quantity of water contained at the outset. Tests were carried out to determine the difference made by blocking the cut ends of the shoots with wax. Although slight differences could be detected in the larger plants such as *Polytrichum alpinum*, these were not found to influence the findings discussed below. In the case of colony samples, attention is drawn to the fact that evaporation is permitted from the exposed sides and base of the core. The effect of colony form (i.e. packing and arrangement of shoots) in reducing the rate of water loss will therefore have been underestimated.

Assessment of water uptake

Investigations of behaviour in regard to water uptake were of limited scope but they contributed some further relevant information.

The results of experiments on water uptake in mosses will clearly depend to a considerable extent on the condition of the sample at the start. The aim, however, was to examine the characteristics of water uptake by shoots which had been deprived of most of their "externally held" water. Tests were therefore carried out first with samples which, after standing with their stem bases in water to permit full turgidity of all tissues, were centrifuged as described above

* This humidity was quoted by Gimingham (1967) as 93 per cent. As the humidity control ($PbNO_3$ solution) was accurate only within $\pm 2-3$ per cent, figures in this paper are given to the nearest 5 per cent.

to extract any superficial moisture, and secondly with samples which had been air dried, reducing their moisture content to about 10–20 per cent of oven-dry weight. Except where otherwise stated, the results in both cases led to the same interpretations, but were more consistent when air-dried samples were used. Accordingly, only experiments starting with air-dried shoots have been considered in the results.

As in the previous experiments, readings were obtained both for isolated shoots and for small cores from undisturbed colonies, lightly held together with short lengths of fine fuse wire. After weighing, shoots or colony samples were placed either with the basal 2 mm. in contact with water, or upside-down with the apical 2 mm. submerged. Before subsequent weighings at 1, 2 or 4 min. intervals, free water was removed from the portion which had been submerged, by light application of blotting paper for 10 sec. While it was necessary to prevent this "surplus" water contributing to the recorded weight, the blotting procedure introduced an unknown influence upon the uptake process which was difficult to standardize. Although the method cannot be expected to produce rates identical to those in undisturbed colonies in the field, it provided a means of comparing the several species. A test sample of a colony of *Andreaea gainii* reweighed at intervals of 5 sec. gave the same pattern of uptake as a similar sample weighed at 1 min. intervals. Thus it appeared that the frequency of blotting and weighing did not greatly modify the results.

Absorption of water vapour

Sample cores from moss colonies, prepared as in the foregoing experiment and subsequently air dried, were suspended about 2 cm. above the surface of water which half-filled a sealed container. These were kept at 18–20° C and reweighed daily for 10 days.

GROWTH FORM AND SHOOT DENSITY

The species examined were assigned to growth-form classes, largely following the scheme of

TABLE I. SHOOT DENSITY, SHOWING THE NUMBER OF SHOOT TIPS/cm.² AT THE SURFACE OF THE COLONY

Species	Mean shoot density	Number of counts	Range		Growth form of colony
			Minimum	Maximum	
<i>Andreaea regularis</i>	382	3	358	422	Small cushion
<i>Andreaea depressinervis</i>	130	3	111	140	Small cushion
<i>Grimmia antarctici</i>	106	3	92	126	Small cushion
<i>Tortula</i> cf. <i>fuscoviridis</i>	41	4	38	45	Small cushion
<i>Chorisodontium aciphyllum</i>	127	3	113	144	Turf
<i>Polytrichum alpestre</i>	27	3	26	28	Turf
<i>Polytrichum alpinum</i>	17	4	12	21	Turf
<i>Brachythecium</i> cf. <i>antarcticum</i> (short slender form)	1,445	1	—	—	Carpet
<i>Calliargon</i> cf. <i>stramineum</i>	122	3	108	134	Carpet
<i>Drepanocladus uncinatus</i> (robust form)	114	3	107	120	Carpet
<i>Brachythecium</i> cf. <i>antarcticum</i> (tall robust form)	48	3	43	55	Carpet
<i>Bryum algens</i> (tall form)	54	3	48	64	Large cushion
<i>Brachythecium</i> sp. (cushion form)	42	4	35	45	Large cushion

Gimingham and Birse (1957). Shoot density was estimated where possible by counting the number of shoot tips visible within squares of fine wire measuring 1 cm.², placed on the surface of the colony (Table I).

It will be noted that the range of growth-form types represented amongst these commonly occurring species is restricted. The compact colony forms, in particular the cushions (large and small), turves and carpets, are clearly the most prominent. The latter growth form takes on an importance seldom paralleled in temperate vegetation, and its characteristics are altogether more pronounced (see below).

Small cushions and related types

Species with this type of growth form belong mainly to the fruticose lichen and moss cushion sub-formation, e.g. species of *Andreaea* and *Dicranoweisia* occupying the quartz-mica-schists and soils, and species of *Grimmia* and *Tortula* on substrata of higher base status (marble and amphibolite). Colonies were found to consist of either isolated cushions (Fig. 1)

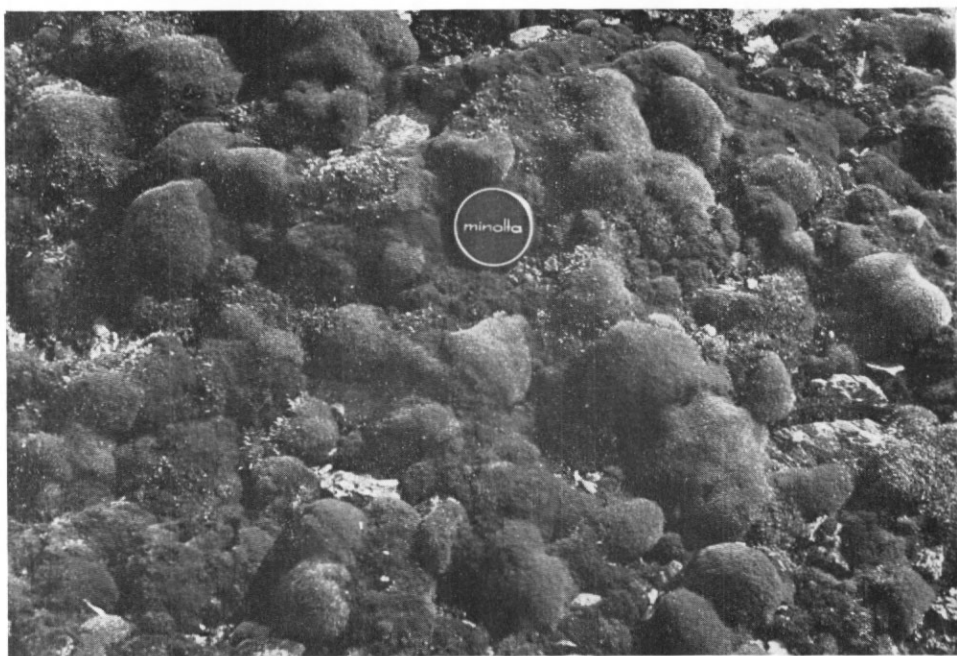


Fig. 1. The small cushion growth form, exemplified by *Tortula* cf. *grossiretis* (paler cushions), *T.* cf. *fuscoviridis* (darker cushions) and *Bryum algens* (flat cushions). The scattered whitish shoots belong to a species of *Brachythecium*. The scale object is 5 cm. in diameter. Reproduced from Gimingham and Smith (1970).

or of continuous stands with a more or less undulating surface, probably representing coalescence of numerous cushions. Evidence for the latter conclusion is found in the arrangement of the much branched shoots, which radiate from localized attachment areas, characteristic of this growth form. Consequently, although individual shoots may measure up to 8 cm., the depth of the colony seldom exceeds 3 cm. The shoots may be densely packed but are not coherent and tend to fall apart whenever the colony is disturbed. Those of *Grimmia antarctici* are somewhat larger and less densely packed than in species of *Andreaea*.

Turves

Stands of *Polytrichum alpinum* consist of erect shoots, about 3–4 cm. tall, occasionally exceeding 10 cm., and are rigid but not very dense (Fig. 2). Branching occurs near the tip but



Fig. 2. The tall turf growth form. Part of a colony of *Polytrichum alpinum* showing the loosely aggregated erect shoots which arise from the rhizome-like base. The total height of the section is about 5 cm.

production of new stems takes place from the rhizome-like system below the soil surface. This species is frequently associated with species of *Andreaea* but it also forms communities with *Drepanocladus uncinatus*, particularly where disturbance in the vicinity of bird colonies and seal wallows is evident.

Polytrichum alpestre and *Chorisodontium aciphyllum* are taller erect species which are the main agents of peat accumulation in the communities of the moss turf sub-formation (Fig. 3).



Fig. 3. Part of a peat bank formed by the moss turf sub-formation, chiefly *Chorisodontium aciphyllum* with some *Polytrichum alpestre*. The ski stick is 130 cm. long.

The shoots of *P. alpestre* are more densely packed in the colony than those of *P. alpinum*, and differ also in that many bear abundant long rhizoids. Branching occurs rather sparsely from below the apices but frequent innovations are produced from lower parts of the stems. These young shoots are ensheathed in a dense tomentum even before the emergence of the scale leaves. In this way the density of the turf is maintained and increased, while the shoots are strongly coherent as a result of the interweaving of their tomenta.

A still denser but less compact turf is produced by *Chorisodontium aciphyllum* as a result of prolific branching below any apex which has ceased growth. Rhizoids are abundant below the zone of green leaves and the shoots cohere strongly in the colony.

Carpets

The growth form designated by this title (Fig. 4) is produced by certain pleurocarpous species whose shoots grow in a parallel, erect or ascending fashion from an intertwined matrix below.* This produces a deep carpet, the upper 4–8 cm. of which consist of a dense arrangement of erect shoots usually producing laterals which hold the colony together, so that if a small sample is cut out it will stand firmly without collapsing. The species mentioned below contribute, either mixed or in pure stands, to the moss carpet sub-formation.

In *Brachythecium* cf. *antarcticum* the shoots are rather robust and relatively little branched, the terminal 5–8 cm. being erect. *Calliergon* cf. *stramineum* has finer shoots with a density even greater than *B.* cf. *antarcticum* at the surface of the carpet. An extreme example of this growth form is found in another plant also designated as *Brachythecium* cf. *antarcticum* because of its structural and anatomical similarity to that species, but in which there is a high density of very slender, almost unbranched erect shoots in the upper 3 cm. of the carpet, the whole colony presenting a remarkably solid appearance in profile.

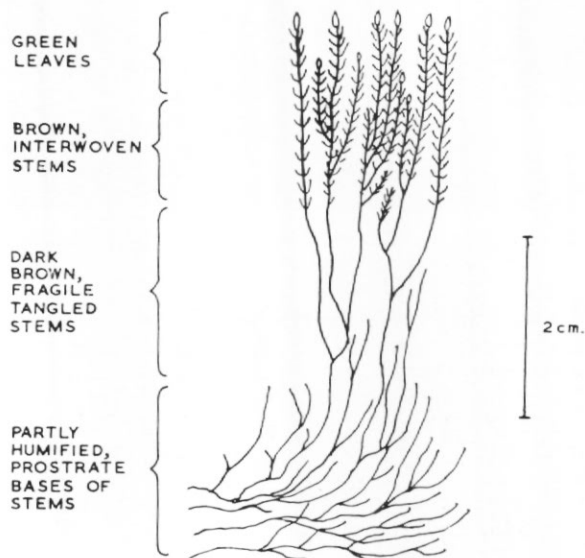


Fig. 4. The moss carpet growth form. Diagram of shoots, partially separated, from a colony of *Calliergon* cf. *stramineum*.

* In the scheme of Gimingham and Birse (1957) this type of growth form was described as "tall turfs, with divergent branches of limited growth". It is now regarded as warranting more distinctive treatment and a more concise descriptive title. The title "carpet" is intended to take account of the extensive uniform stands frequently developed by communities composed largely of this type of growth form. The "mat" form is distinguished by the thinner, more compact structure of prostrate interwoven shoots.

Mats

The mat form, in which prostrate, more or less pinnately branched shoots are interwoven, is not well represented. *Calliergon* cf. *sarmentosum* presents a somewhat intermediate pattern of growth form between the carpet and the compact mat. An interesting series of types is seen in *Drepanocladus uncinatus* which in size and growth habit is very variable. The smaller forms (Fig. 5) produce mats, about 1.5–2 cm. in thickness, in which the much branched shoots



Fig. 5. The mat growth form. Pure stand of *Drepanocladus uncinatus* (compact form) on moist stony ground. The diameter of the stone in the centre is about 5 cm.

adopt a spreading or ascending habit, intertwining densely. These colonies, which can be peeled intact from the substratum, occupy the drier habitats, often in association with species of *Andreaea* and *Polytrichum alpinum*, or in pure stands covering the ground between the larger stones. At the other extreme is a robust form, in which the arrangement of the shoots is parallel and erect in the upper 3 cm. or more, growth being mainly monopodial with lateral branches restricted in length. This form can be classified among the carpets and occurs in swampy habitats with species of *Calliergon* and *Brachythecium*. A complete series can be found of plants intermediate in size and form between these two extremes, tending to occupy habitats which are intermediate in wetness.

Large cushions

Mosses such as *Bryum algens*, *Tortula excelsa* and a species of *Brachythecium** form symmetrical deep cushions of up to 10–15 cm. radius, composed of branched shoots all radiating from a common point of attachment (Fig. 6). A feature of all the examples mentioned is that the cushion, when cut in half and viewed from the side, shows clear banding, indicative

* This species will be referred to as the cushion form to avoid confusion with the forms of *Brachythecium* cf. *antarcticum*.

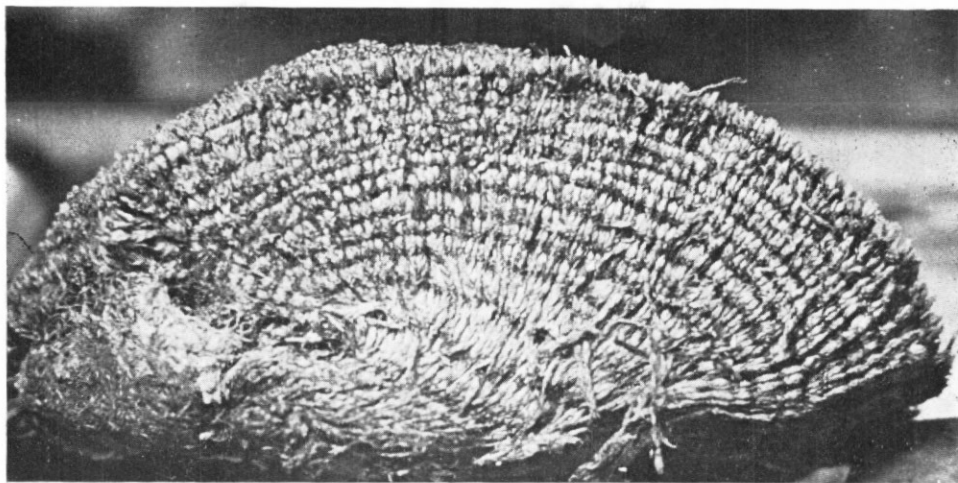


Fig. 6. The large cushion growth form. *Bryum algens* showing banding by rhizoids indicative of annual growth increments. The cushion is about 6 cm. tall. (Photograph by N. J. Collins.)

of annual growth increments. The shoots are usually robust, rather densely packed and readily separable one from another. The moss hummock sub-formation (Fig. 7) is composed largely of species of this form, although they extend to other communities as well.

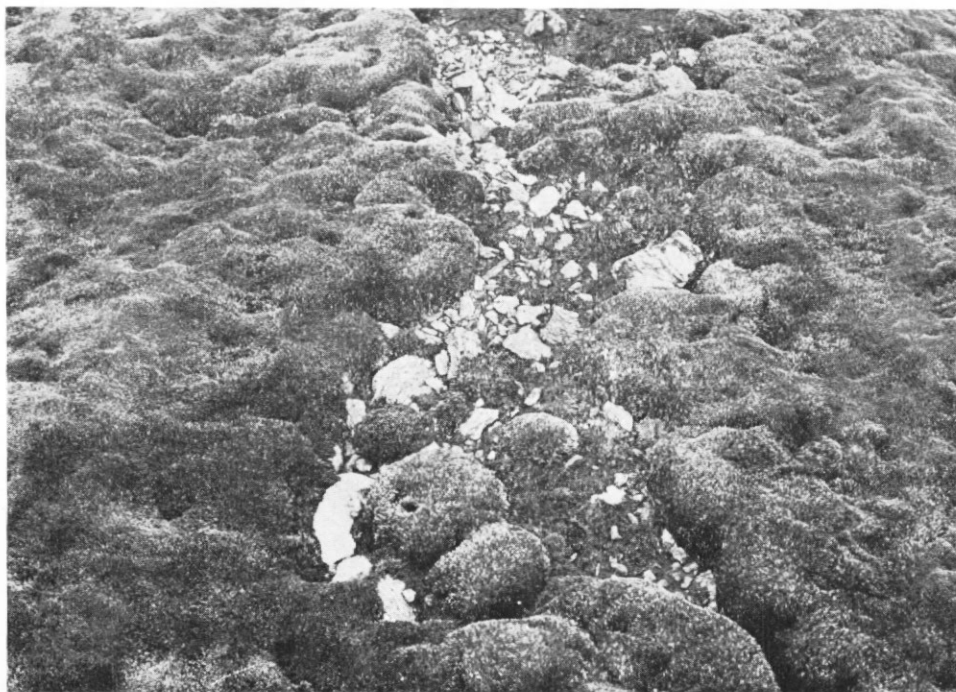


Fig. 7. Moss hummock sub-formation along a melt-water channel with *Brachythecium* (large cushion form) giving place on either side to *Drepanocladus uncinatus* (carpet). The large stone in the centre right of the channel measures approximately 16 cm. in length.

TABLE II. TOTAL WATER CONTENT AND "EXTERNALLY HELD" WATER IN SAMPLES FROM THE FIELD

Species	Mean total water content as a percentage of dry weight	Range		Mean percentage of total driven off in centrifuge	Range		Number of estimations
		Minimum	Maximum		Minimum	Maximum	
A. Species with low field water content and small proportion held "externally"							
<i>Grimmia antarctici</i>	176·9	141·5	205·4	7·1	4·9	9·0	4
<i>Polytrichum alpinum</i>	177·9	158·1	190·4	7·1	4·0	11·3	4
<i>Drepanocladus uncinatus</i> (small mat form)	188·6	151·6	220·0	8·1	5·2	11·0	6
<i>Tortula</i> cf. <i>fuscoviridis</i>	220·8	—	—	4·9	—	—	1
B. Species showing intermediate values							
<i>Andreaea regularis</i>	199·0	150·6	268·8	15·2	4·4	37·7	7
<i>Andreaea depressinervis</i>	220·1	174·5	266·7	36·2	34·7	37·7	2
<i>Polytrichum alpestre</i>	355·2	256·1	453·5	15·9	2·1	40·4	10
C. Species with high field water content and generally high proportion held "externally"							
<i>Chorisodontium aciphyllum</i>	402·7	307·2	606·2	34·7	6·3	62·8	7
<i>Tortula excelsa</i>	460·3	—	—	27·2	—	—	1
<i>Brachythecium</i> cf. <i>antarcticum</i> (tall robust form)	562·5	376·4	748·7	20·6	10·1	31·2	2
<i>Drepanocladus uncinatus</i> (large carpet form)	687·6	533·3	764·8	35·5	18·8	46·2	3
<i>Calliergon</i> cf. <i>sarmentosum</i>	806·0	757·9	875·0	61·8	55·5	65·0	5
<i>Brachythecium</i> sp. (cushion form)	876·6	525·0	1,091·5	53·7	21·9	62·3	7
<i>Brachythecium</i> cf. <i>antarcticum</i> (short slender form)	981·6	846·9	1,078·5	65·2	56·8	85·1	4
<i>Calliergon</i> cf. <i>stramineum</i>	1,170·7	931·5	1,616·7	63·1	55·9	67·4	7

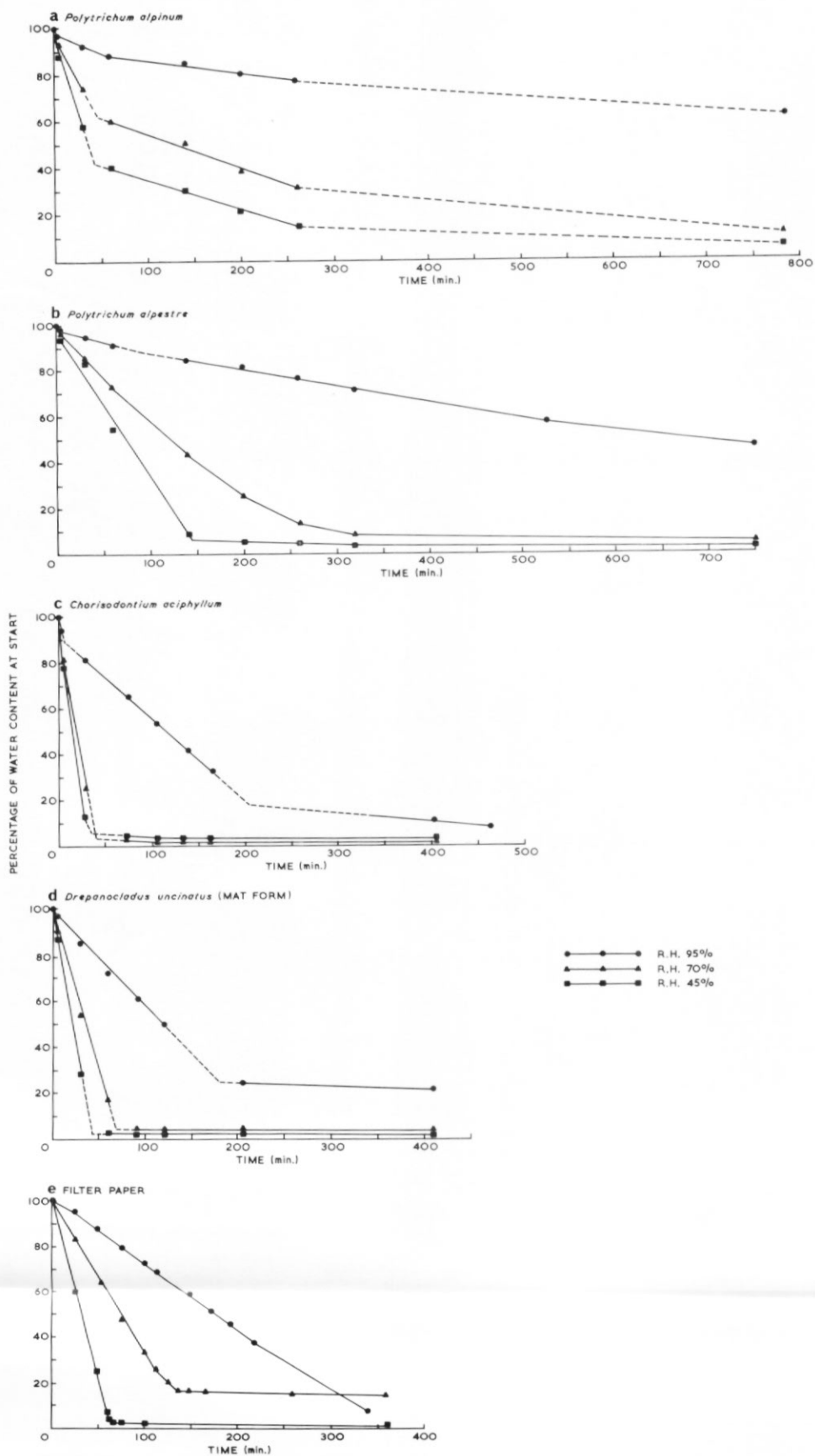


Fig. 8. Decline in water content of single shoots of four species, and similar samples of filter paper, at relative humidities of 95, 70 and 45 per cent at 18–20° C. Broken lines indicate periods over which the angle of slope is uncertain.

FIELD WATER CONTENT

The results of estimates of field water content in a number of species of different growth forms are given in Table II and may be summarized as follows:

- A. Several species show field water contents generally slightly below 200 per cent of dry weight, of which only a relatively small proportion (i.e. less than 10 per cent of the total) is driven off by the centrifuging treatment. These include two of the small cushion species, *Grimmia antarctici* and *Tortula* cf. *fuscoviridis*, as well as *Polytrichum alpinum* (turf) and the compact mat form of *Drepanocladus uncinatus*.
- B. A rather higher proportion of water is held externally in the small cushions of species of *Andreaea*, although the total content is of much the same order as in the species in category A. *Polytrichum alpestre*, a tall turf, shows a greater range of water content, perhaps associated with the presence of a well-developed tomentum.
- C. The remaining mosses examined all normally contain large quantities of water in the colony (always over 300 per cent of dry weight), of which 20 per cent or more is usually driven off by centrifuging. Amongst these are the large cushions of *Tortula excelsa* and a species of *Brachythecium* (cushion form), which commonly occur in drainage channels, etc. *Chorisodontium aciphyllum*, a regular associate of *Polytrichum alpestre* on the peat banks, also furnished with abundant rhizoids, has similar characteristics. The largest quantities of contained water are found, as is to be expected, in the carpet species of swampy areas particularly *Calliergon* cf. *stramineum* and *Brachythecium* cf. *antarcticum* (slender form), in which nearly two-thirds of all water present is readily released by the centrifuge. These figures are approached by *Calliergon* cf. *sarmentosum* which, although approaching a mat in growth form, occupies similar habitats. The robust form of *Drepanocladus uncinatus* is a frequent associate in these communities, and in terms of water content and "externally held" water resembles the foregoing plants more closely than the smaller and more compact form of its own species.

Although the species in groups A and B apparently hold only a small fraction of their water externally, the total water content is also low in relation to dry weight. These are mainly plants of dry habitats. In some, such as the species of *Polytrichum*, the stems have a relatively high dry weight per unit length, containing tissues with thickened cell walls; in others, such as *Grimmia* and species of *Andreaea*, the stems are thin and wiry with small leaves. By contrast, the tissues of species of group C, mainly plants of wet habitats, are largely unspecialized with some having thick stems and large leaves. While the proportion of the total water content held externally in these species is greater than in those of the other groups, they can also hold considerably more internally. Their total water content, whether expressed in relation to dry weight or to length of shoot, is therefore normally greater.

The foregoing determinations of water content of samples gathered from the field can give only general comparisons because of variations due to weather conditions, local habitat differences, etc., as indicated by the variation in the range of values presented in Table II.

WATER LOSS

For each species, a series of graphs was drawn showing the decline in water content of the shoot or colony sample with time in each of the three atmospheres (Fig. 8). While differences between species were evident, the relationships between the curves for different humidities in any one species were in general similar. Hence, for the majority of species, attention is confined to the results for a relative humidity of 45 per cent, as representing an evaporation stress which is quite high but not unusual in the natural environment. Each line in the graphs represents the results for an individual shoot or colony sample but replicated experiments produced closely similar results.

By single shoots

The actual rate of water loss from an isolated shoot depends upon the area of evaporating surface in relation to the volume of the shoot, as well as resistance within the plant to the movement of water towards that surface. It may also be affected by progressive changes of the evaporating surface produced by contraction of the leaves towards the stem, etc. In mosses,

calculation of the area of the evaporating surface of a part of the shoot is difficult and, in the absence of data for all the species concerned, detailed comparisons of the results for different species are not justifiable. However, certain general differences in the patterns of water loss are evident from the results.

Considering first the sequence of water loss from isolated shoots, Fig. 8 illustrates the patterns for *Polytrichum alpinum* (a) and *P. alpestre* (b) in the three test humidities. These species stand apart from all the others investigated, two examples of the latter being given in Fig. 8, namely *Chorisodontium aciphyllum* (c) and *Drepanocladus uncinatus* (mat form) (d). The pattern in the latter two species displays a marked resemblance to that of moist non-living absorbent material in identical conditions (filter paper; Fig. 8e). A rapid and steady rate of loss (depending upon the saturation deficit of the atmosphere) is maintained until a low water content is reached, when considerable resistance to further loss develops. The evidence suggests that in the shoots of these species there is very little resistance to the passage of contained water to the surface, from which it evaporates, until most of it has been lost. A similar result was obtained by Tallis (1959), working with British material of *Racomitrium lanuginosum*. Some species, however, show slight reductions in rate, often within the first 10 min., before such low levels of water content have been reached, e.g. *Andreaea regularis*, *Brachythecium* cf. *antarcticum* (robust form), *Brachythecium* sp. (cushion form), *Calliergon* cf. *sarmentosum*, *Calliergon* cf. *stramineum*, *Drepanocladus uncinatus*, *Grimmia antarctici* (Fig. 9). This may be due, as suggested above, to reductions in the effective evaporating surface by movement (including twisting) of the leaves towards the stems.

In *Polytrichum alpinum* (Figs. 8a, 9a and b) the loss of water from isolated shoots is slower from the outset and, after reduction of water content to about 50–60 per cent of the initial amount, there is a marked diminution of rate of loss indicating some resistance operating in the shoot which prolongs for about 5 hr. the period before the 10 per cent level is reached. This behaviour is not so marked in *P. alpestre* (Figs. 8b, 9c) but over 2 hr. exposure to a relative humidity of 45 per cent is required before the water content is reduced to less than 10 per cent.

The swiftest reduction, to less than 10 per cent of the original water content, is shown by the very slender shoots of the second form designated *Brachythecium* cf. *antarcticum* (slender form; Fig. 9x). In the space of 6 min. the water content of these shoots was reduced to a level beyond which no further measurable quantity of water was driven off even by oven drying. Other species displaying particularly rapid initial rates of water loss include *Chorisodontium aciphyllum*, *Drepanocladus uncinatus* (carpet form), *Brachythecium* cf. *antarcticum* (robust form), *Brachythecium* sp. (cushion form), *Bryum algens* and *Calliergon* cf. *stramineum* (Fig. 9).

By colony

When water loss from the colony samples is compared with that of the isolated shoots as in Fig. 9, it is, as expected, invariably slower. The difference is least in *Polytrichum alpinum* (Fig. 9a and b), which is to say that the colony form in this species modifies the evaporation rate from the individual shoots less than in any of the others. The remainder may be divided into two groups: those species (Fig. 9c–m) in which the rate of loss is relatively slow and even after about 9 hr. between 25 and 35 per cent of the original water is conserved in the colony sample, e.g. *Polytrichum alpestre* and *Chorisodontium aciphyllum* (turves), species of *Andreaea*, *Tortula* and *Grimmia antarctici* (small cushions), *Bryum algens* (large cushion), and those (Fig. 9n–w) in which a moderately fast rate of loss is maintained from the colony at least until the water content is reduced to 10–20 per cent in 8–9 hr., e.g. a species of *Brachythecium* (large cushion form), *Calliergon* cf. *sarmentosum* (mat), *Brachythecium* cf. *antarcticum* (robust form) and *Drepanocladus uncinatus* (carpets).

A limited series of measurements of decline in the water content of colony samples was made under field conditions (Fig. 10). The initial water content was in these cases simply the amount contained in the samples as gathered. On exposure to the surrounding air and weighing at intervals, the rates of water loss were of a similar order to those produced experimentally, although the environmental conditions were not such as to permit direct comparisons. Under the prevailing conditions, the rate was least in *Polytrichum alpinum*, followed by *P. alpestre*, *Andreaea regularis*, *Chorisodontium aciphyllum* and *Drepanocladus uncinatus* (compact mat form).

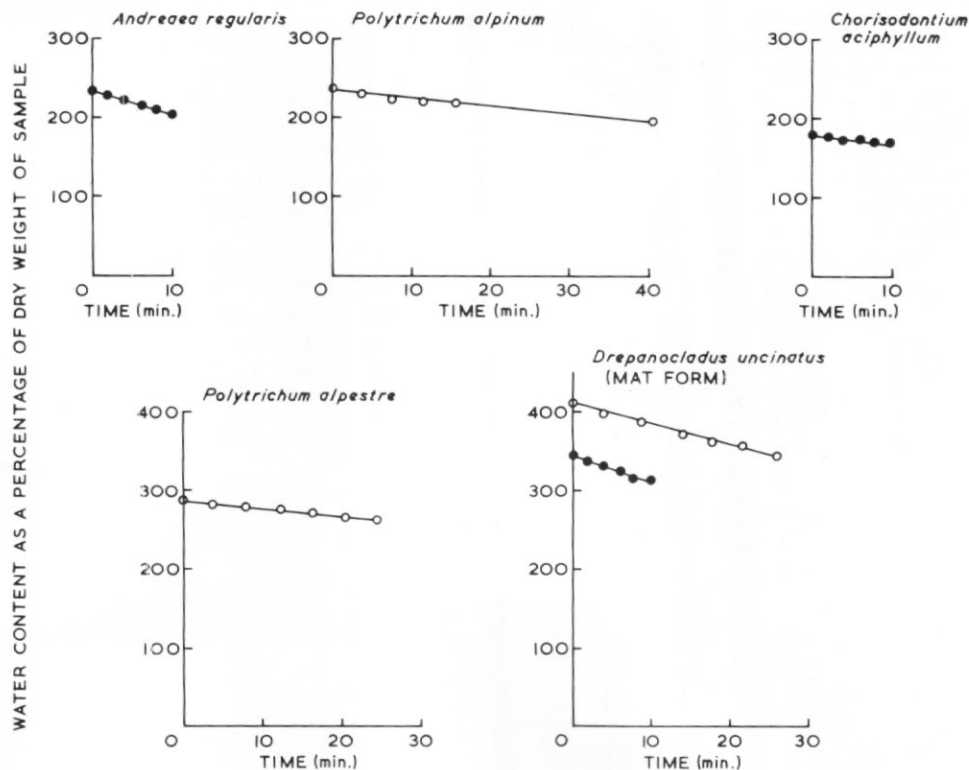


Fig. 10. Decline in water content of detached colony samples of five species under field conditions.

Solid circles: 22 January 1966; R.H. 73-85 per cent; dry-bulb temperature 3.6-4.4° C; wind velocity at moss level 1.01-1.26 m./sec.

Open circles: 27 January 1966; R.H. c. 86 per cent; dry bulb temperature -1.9° C; wind velocity at moss level 1.41 m./sec.

WATER UPTAKE

The results of an assessment of water uptake in various species are presented in Fig. 11, in which the water contained in the shoot or sample at the successive times of weighing is expressed as a percentage of the dry weight.

The experimental procedure was such as to test primarily the capacity of a species to replace rapidly the externally held water. Under the conditions imposed, the smallest increase was shown by *Polytrichum alpinum* (Fig. 11c). Uptake was slow, and little difference was evident between the behaviour of shoots in isolation and those associated in a sample of the rather loose turf. In this species, the proportion of water held externally is normally low (Table II), but even in comparison with others having similarly low proportions of externally held water, e.g. *Grimmia antarctici* and *Tortula* cf. *fuscoviridis*, both small cushions, the uptake in *P. alpinum* is restricted. The available evidence also suggests that only very slow uptake occurs when the water supply is in contact with the stem apices.

A similar behaviour was displayed by shoots of *Polytrichum alpestre* lacking a tomentum (Fig. 11b). In those furnished with a dense tomentum (Fig. 11a) uptake is both faster and greater. Since colonies normally contain both types of shoot, i.e. those with and without tomentum, the curves for uptake in colony samples containing both resemble those for the tomentose shoots. However, as the tomentum does not reach as far as the shoot apex, uptake was found to be delayed or restricted if only that part of the shoot tip devoid of rhizoids is placed in contact with water, or if the colony sample is composed entirely of shoots lacking the tomentum.

In all other species tested, water uptake will occur if shoot apices or bases are placed in contact with the water. In most cases, application of water to the apices or bases of the samples produced substantially the same results but in some, notably colonies of *Chorisodontium aciphyllum* (Fig. 11d) and the species of *Brachythecium* (cushion form; Fig. 11k), repeated experiments confirmed that uptake via the apices was superior both in quantity and rate. There is a suggestion that this may apply also to some other species (Fig. 11e, f, g, j, l and m).

With the exception of *Polytrichum alpinum* (Fig. 11c), all species display considerably faster uptake and gain larger quantities of water when their shoots are aggregated in the colony than when they are isolated.

Those species showing the most uniformly rapid and effective uptake, particularly in the colony samples, belong to the cushion form, e.g. *Grimmia antarctici* (Fig. 11f), *Tortula cf. fuscoviridis* (Fig. 11h) and *T. cf. grossiretis* (Fig. 11i). Other species with dense growth forms such as species of *Andreaea* (Fig. 5e), *Racomitrium cf. crispulum* (Fig. 11g), *Tortula excelsa* (cushions; Fig. 11j), *Chorisodontium aciphyllum* (turf; Fig. 11d), *Drepanocladus uncinatus* (Fig. 11l) and *Calliergon cf. sarmentosum* (mats; Fig. 11m) are also similar, and only slightly

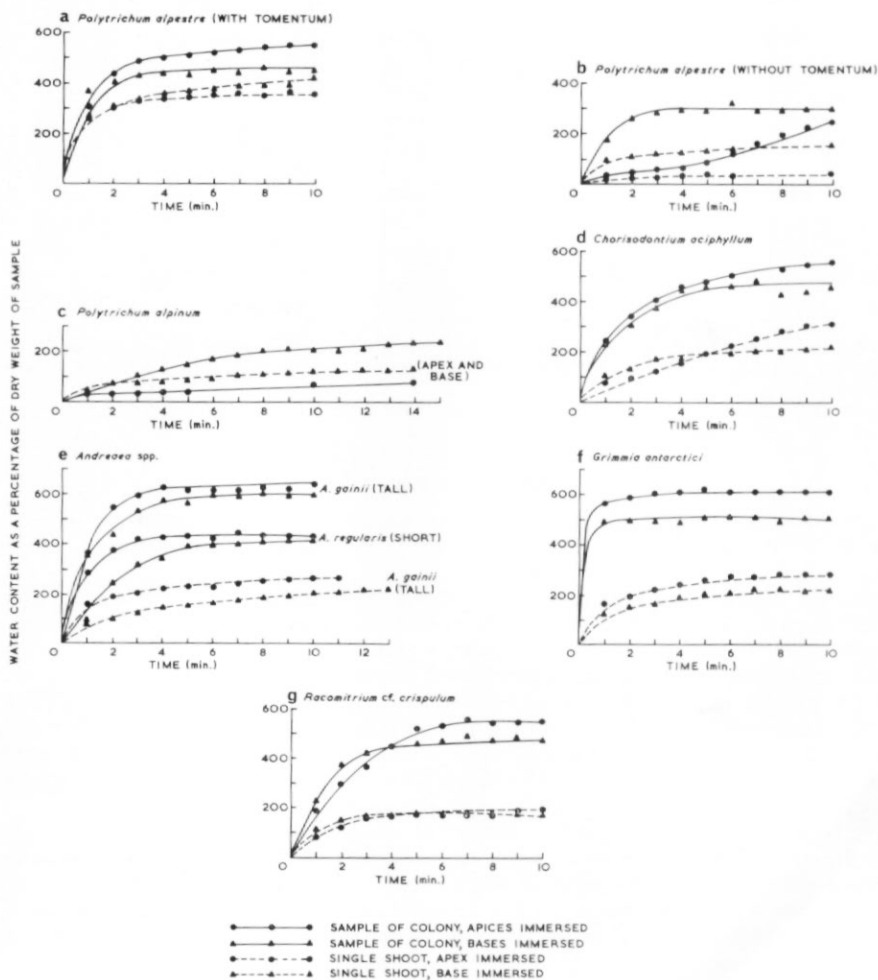


Fig. 11 and caption continued on facing page

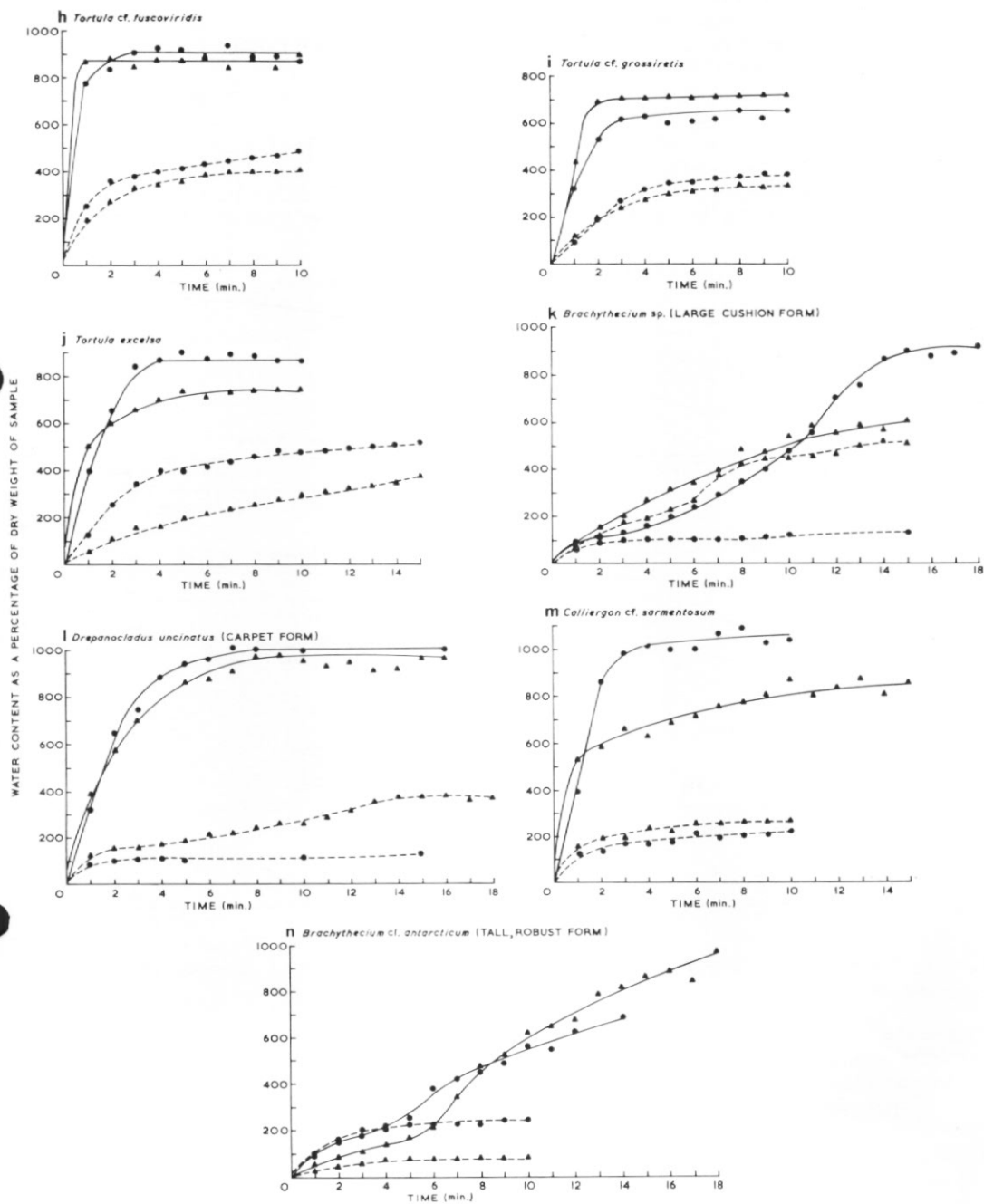


Fig. 11. Water uptake via apices and bases by single shoots and colony samples of 13 species, after air drying.

slower in achieving full hydration. In all these species the uptake is normally largely complete within 5 min. Species with looser aggregations of shoots such as the species of *Brachythecium* (large cushion form; Fig. 11k) and *B. cf. antarcticum* (robust form carpet; Fig. 5n) show a slower and more prolonged pattern of uptake, although ultimately large quantities of water are incorporated. However, in the latter species uptake was much faster when the shoots had been centrifuged rather than air dried.

ABSORPTION OF WATER VAPOUR

Under the experimental conditions, some absorption occurred in all species, weight increases being generally negligible after 5–8 days. In several species, particularly those with a cushion growth form, equilibrium is almost achieved within 24 hr. The results for six species are presented in Fig. 12. The increase of weight was much in excess of what could be attributed to

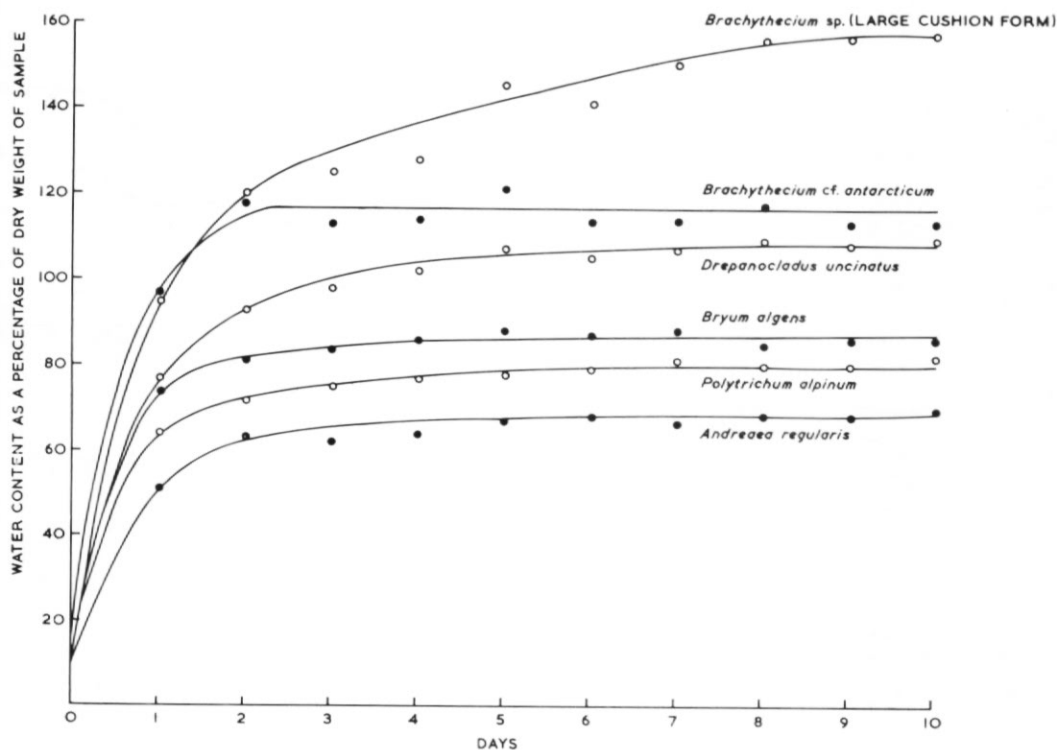


Fig. 12. Uptake of moisture from a saturated atmosphere by colony samples of six species over a period of 10 days.

increases in dry weight due to assimilation. Species such as *Brachythecium* cf. *antarcticum* (robust form), *Brachythecium* sp. (cushion form), *Calliargon* cf. *sarmentosum* and *Drepanocladus uncinatus* absorbed water up to 100–150 per cent of their dry weight, these being species forming carpets, large cushions and mats from the wetter habitats. Others, such as *Polytrichum alpinum*, *P. alpestre*, *Grimmia antarctici*, *Racomitrium* cf. *crispulum* and species of *Andreaea* and *Tortula*, i.e. mostly cushions and turves from somewhat drier habitats, showed increases of up to 70–85 per cent of their dry weight. The data obtained from 15 species are given in Table III. However, in these species absorption represented a greater proportion of their normal field water content than in the first group. Tallis (1959), working with British material, found that *Racomitrium lanuginosum* absorbed water from a saturated atmosphere only up to

with free water along most of their length, as in mosses growing by waterfalls or creeping over moist substrata, conduction along the stem will be minimal. But in species of drier habitats, particularly those with an erect habit of growth, some degree of conduction occurs. This may take place either internally (endohydric) or externally (ectohydric), i.e. in the capillary spaces between leaves and paraphyllia or between rhizoids and the stem. According to Mägdefrau (1935), both pathways are probably operative together. In cases where the water supply is chiefly from below, conduction is mainly upward, but where it arrives at any point on the stem, in the form of droplets, conduction may take place in either direction. In addition, ectohydric conduction may be influenced by the pattern of branching of the shoot, and particularly by shoot density as well as by the ways in which shoots and branches are associated in a colony. In *Sphagnum*, for example, upward conduction results from the disposition of the pendulous branches which together act as a wick. In other examples, the dense packing of vertical or ascending shoots, sometimes locked together by laterals, could provide additional spaces of capillary dimensions between parts of adjacent shoots.

In these ways, the growth form of the moss and the structure of its colony play a considerable part in the mechanisms of water uptake and transport. Furthermore, potential water loss to a desiccating atmosphere must be reduced by the density of stems and branches where the colony takes the form of a cushion, dense turf or mat (Gimingham and Robertson, 1950; Gimingham and Birse, 1957; Hosokawa and Kubota, 1957).

Investigations of the structure of bryophyte communities and the distribution of mosses of different growth forms in various parts of the world have demonstrated correlations between growth-form representation and habitat type (Birse, 1957, 1958*a, b*; Gimingham and Birse, 1957). Growth form, as Watson (1964) has pointed out, is a purely morphological character and hence is only one among numerous properties of a species affecting its relations with the environment. In some species it is a relatively constant character but in others it shows considerable plastic variation in response to habitat differences. Nonetheless, growth form may be associated with physiological and other biological features which have a bearing on the ecology of a species, and may be at least partly responsible for correlations between distribution and aspects of the habitat.

The most striking feature of growth form among the prominent species of mosses on Signy Island is the preponderance of dense types of colony, notably the cushions, turves and carpets, and the virtual absence of the open or loose colony forms, e.g. the weft. That dense growth forms play a part in restricting evaporation is evident and it has been clearly demonstrated, for example, in the small cushions and compact mats which are shown to be the most effective of the colony types in this respect. It is not suggested that strong saturation deficits occur frequently in an oceanic climate such as that of Signy Island, but the vegetation is regularly subjected to high winds. Apart from those species which occupy habitats in which a permanent supply of ground water is present, many are dependent upon a water reserve held externally among the shoots or between stems and leaves, etc., and conservation of this reserve against evaporation may be significant in the occupancy of the more exposed habitats (Fig. 13). Since the Antarctic growing season is very short, desiccation, which has the effect of further reducing the time during which growth can proceed, may become a limiting factor.

The most abundant of the mosses examined which occupy stone and rock surfaces in exposed conditions are generally species of *Andreaea*, *Grimmia* and *Tortula*. These are plants whose isolated shoots lose water freely and rapidly under desiccating conditions, whereas the rate of loss is very greatly reduced by the normal aggregation of shoots in the small cushions and short turves. Furthermore, these species are not among those in which the field water content is normally high, and their habitat is not furnished with any regular water supply (Fig. 13). It may therefore be significant that *Andreaea* and the smaller cushion species have the ability to take up water rapidly from any part of the shoot, being thus in a position to make up deficits quickly when water from rain or melting snow is available. Indeed, the speedy expansion of dry cushions after moistening by rain is frequently observed in the field. Species of these groups can regain, after air drying, a significant proportion of their normal water content directly from a moist atmosphere.

The above suggestion of a relationship between uptake efficiency and occupancy of habitats subject to periodic lack of water is borne out by an interesting gradation in the three species

60 per cent of its dry weight. Willis (1964), however, found that *Tortula ruraliformis* increased to around 100 per cent of its dry weight when subjected to a saturated atmosphere over a period of 10 days, but to only a little over 40 per cent of its dry weight in a relative humidity of 95 per cent.

TABLE III. UPTAKE OF WATER FROM A SATURATED ATMOSPHERE
BY 15 SPECIES OF MOSSES

Species and growth form	Maximum daily value of water content as percentage dry weight over a 10 day period	Final water content as percentage dry weight after 7 days
Cushions		
<i>Andreaea gainii</i> (tall)	86.3	59.2
<i>Andreaea regularis</i> (short)	69.8	71.3
<i>Grimmia antarctici</i>	76.5	64.5
<i>Racomitrium</i> cf. <i>crispulum</i>	74.7	78.1
<i>Tortula excelsa</i>	77.8	88.0
<i>Tortula</i> cf. <i>fuscoviridis</i>	83.4	61.4
<i>Tortula</i> cf. <i>grossiretis</i>	83.9	81.2
Turves		
<i>Chorisodontium aciphyllum</i>	72.2	70.0
<i>Polytrichum alpestre</i>	86.6	78.5
<i>Polytrichum alpinum</i>	82.4	78.2
Large cushions		
<i>Brachythecium</i> sp.	157.3	154.1
<i>Bryum algens</i>	88.1	74.2
Carpets		
<i>Brachythecium</i> cf. <i>antarcticum</i>	121.4	116.2
<i>Calliergon</i> cf. <i>sarmentosum</i>	115.3	137.4
<i>Drepanocladus</i> cf. <i>plicatus</i>	102.5	88.0
<i>Drepanocladus uncinatus</i>	109.4	97.0

DISCUSSION

In relatively few species of moss is there effective limitation of evaporation from the aerial parts of the plant by means of cell cuticles. Where, however, some form of cuticularization occurs, as, for example, in species of *Polytrichum*, *Mnium*, etc. (Büch, 1947*a, b*), the surfaces over which evaporation is thereby restricted are also unavailable for water absorption. When, as a result, the chief absorptive surfaces are those of the rhizoids or other lower parts of the shoot, it is usual to find evidence of an internal conduction pathway with some degree of anatomical specialization.

In a large number of species, however, absorption and loss of water may take place at almost any part of the plant's surface. For example, where shoots are continuously in touch

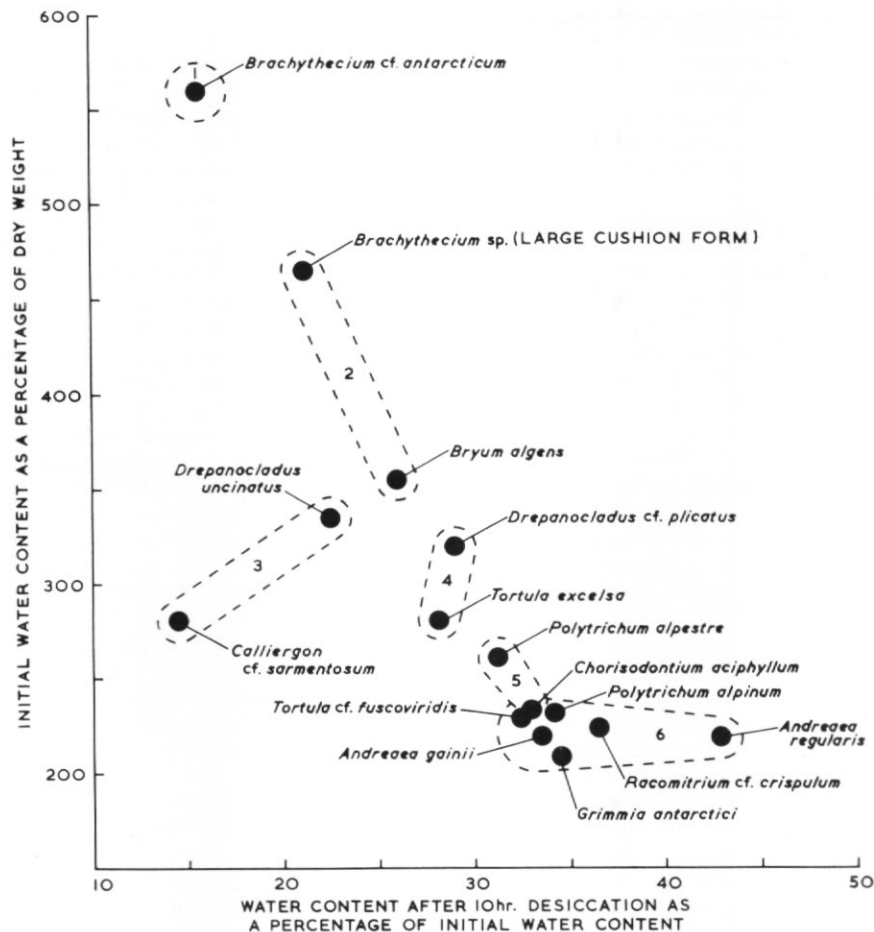


Fig. 13. Summary diagram illustrating relationships between initial water content, water content after a period of drying, and habitat occupied, in 15 species.

Types of habitat occupied by mosses: 1. Permanently wet areas of swamps. 2. Melt-water channels and wet rocks. 3. Temporarily wet ground at margin of swamps. 4. Moist flushed ground. 5. Peat banks. 6. Dry, stony exposed ground.

of *Tortula* which were tested. Of these, *T. cf. fuscoviridis* displayed the most rapid uptake, both in isolated shoots and colony samples, followed in order by *T. cf. grossiretis* and *T. excelsa*. The first of these is characteristic of dry soils, the second often accompanies it but also extends on to damp flushed soils, whereas the third ranges from moist flushes to permanently wet, swampy areas.

At first sight, the above interpretation of the ability of *Andraea* to occupy exposed habitats might be questioned in the light of the frequent occurrence of *Polytrichum alpinum*, a moss of very different physiology and morphology, in the same habitats. In this case, the colony (a turf) is not particularly dense and its form has relatively little influence upon water conservation; the normal externally held water content is low. But other mechanisms are evidently operative in restricting water loss and control is probably as effective in exposed situations as in *Andraea*.

In the first place, a considerable proportion of the normal water content is contained internally within the tissues of the shoot, and a degree of cuticularization establishes a resistance

to evaporation (Büch, 1947a, b; personal communication from N. G. Bayfield). Thus, after what may be a brief period of free water loss, the rate is soon slower than in the other species, while after some reduction in water content additional resistances come into play. It has been suggested that since the main evaporating surface in *Polytrichum alpinum* is provided by the photosynthetic lamellae, gradual imbrication of the leaves as the plant dries up, accompanied by folding along the mid-rib and shrinkage of the lamellae until the cap cells seal them off from the outside air, probably contribute to this additional resistance (personal communication from N. G. Bayfield). There is a marked difference, moreover, between *P. alpinum* and species of *Andreaea* in uptake behaviour, for in the former it is not rapid and is apparently limited to the lower parts of the shoots. Indeed if, as is probable, the control of water loss by evaporation results from surface cuticularization, absorption may be largely restricted to rhizoids. Thus a particulate substratum would be required and would normally retain a somewhat more lasting supply of water than a rock surface. This is borne out by the distribution of *Polytrichum alpinum*, which does not accompany *Andreaea* on to the rock surfaces but extends on to the finer, freely drained soils. It is noteworthy that *P. alpinum* is the least efficient of all species in absorbing water from a moist atmosphere.

The significant association of the two peat-forming tall turf species, *Polytrichum alpestre* and *Chorisodontium aciphyllum*, is also of interest in regard to their water balance. The former stands in an intermediate position between *P. alpinum* and the other species tested in regard to density of colony, normal water content and restriction of evaporation from the isolated shoots. *Chorisodontium aciphyllum* has a much greater shoot density, but at least some shoots in both species produce a tomentum of rhizoids and the resulting turf is extremely coherent and presumably effective in conserving its water content. Furthermore, the tomentum is an effective wick (as shown by the use of dyes) and, since the peat banks thaw out only to a depth of about 25 cm. in summer, it will probably serve to supply water to the surface of the turf from a relatively permanent source just above the permafrost. The ability to pass water along the shoot from its apex is particularly well developed by *Chorisodontium aciphyllum*, which will thus be able to incorporate into the turf water arriving at the surface in the form of rain drops or snow flakes. In partnership these two species seem well adapted to maintain adequate moisture in the growing region during the summer.

Those species with shoots which, when isolated, lose water rapidly and whose colony forms are not quite so effective in restricting this rate of loss, appear to be limited to habitats which, during the growing season, are provided with a permanent ground-water supply (Fig. 7). These mosses include the carpet-forming species of the swampy areas and the larger cushions of the flushes and channels. The high field water content of samples of the colonies of these species may simply reflect the nature of their habitats. It is likely that in the swamps any part of the shoot of a moss may be in contact with water. Some of the carpet species show rapid external passage of water along the stem, particularly when it is supplied at the apex, but on the whole their rates of water uptake are rather slower than those of species with other growth forms. This is perhaps not surprising, since they will normally be excluded from areas where they would be liable to desiccation. On the other hand, among the large cushion species, which constitute the moss hummock sub-formation of melt runnels, etc., uptake is more effective and this, together with the rather greater influence of colony form in restricting water loss, may be in line with the more intermittent nature of the water supply.

It remains to refer briefly to mosses which are described as mats. One of these, *Calliergon* cf. *sarmentosum*, occupies swampy habitats and shares many of the characteristics of the carpet-forming species. The other is *Drepanocladus uncinatus*, to which considerable interest is attached because of its variability in growth form. The properties of the smaller, more compact version of this plant, properly described as a mat, are akin to those of *Andreaea* in terms of field water content, proportion of water held externally and water loss from isolated shoots, although the reduction in rate associated with colony form is not so great, while, in regard to uptake, the response to a supply of water to the shoot is slower. It is not surprising, therefore, to find this form associated with *Andreaea* and *Polytrichum alpinum* in exposed and freely drained situations. At the other extreme, the robust forms are similar both morphologically and as regards most aspects of water relations to the carpet-forming species, freely associating with them in swampy habitats. Intermediate forms occur also in most of the other communities described.

In this species it appears that morphological plasticity is associated with a wide ecological amplitude.

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