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Quantitative Community Analysis and Bryophyte Ecology on Signy Island

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Quantitative community analysis and bryophyte ecology on Signy Island

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Introduction

Longton & Holdgate and Longton, in earlier papers of this Discussion (pp. 237, 213), have outlined the general features of the vegetation of Signy Island, drawing comparisons with other Antarctic island groups and with the Peninsula. Signy Island is characterized by a relatively extensive cover of bryophyte and lichen communities, which exhibit considerable diversity in composition.

This presents a situation well suited for the investigation of some of the principles of community construction and the causes of patterns of plant distribution, under the conditions of an Antarctic environment. This paper, the outcome of work carried out on Signy Island between 12 January and 7 March 1966, first describes an approach to the recognition of the main ecological categories within the vegetation, and secondly singles out for more detailed consideration the water relations of certain of the dominant species, as one of their attributes affecting distribution.

Community analysis

The division of vegetation into categories may be effected either on the basis of the judgement of the worker, or by statistical procedures. When a relatively large area is to be examined for the first time, the former is often the only quick method. Despite the element of subjectivity involved, schemes of value for further biological investigations may be produced in this way by experienced observers. A case in point is Holdgate's (unpublished) list of the principal physiognomic categories recognizable in the vegetation of Signy Island, the distribution of which was entered on a map. Subsequent phytosociological work on the bryophyte and lichen communities in progress by R. I. L. Smith has proved the value of this scheme, which has been slightly amended and elaborated to take account of further observations by Holdgate, Longton, Smith and Gimingham.

Formations and subformations are distinguished by means of physiognomic criteria and subdivided into 'associations' on the basis of floristic composition. Within associations smaller units are differentiated according to the dominance of particular species. With the addition of a few categories not represented on Signy Island, this system is adopted by Longton (this Discussion, p. 213) in his treatment of the vegetation of the Maritime Antarctic, and will not be repeated here.

However, even when carefully and critically constructed, such a classification remains a subjective assessment. For detailed correlations between aspects of the environment and community composition it is necessary to determine whether the categories recognized have objective reality. Therefore, as part of the programme of work, sets of data were obtained on the occurrence of species in small quadrats (400 cm^2). Three study areas, ranging in size from

960 to 1900 sq.yd., were chosen in different parts of the island, with the aim that each should incorporate as wide a variety as possible of the different aspects of the vegetation of the Island. Within each, either 70 or 100 of the small quadrats were systematically arranged at equidistant points on a grid, and the species contained and their cover recorded.

These data have been subjected to the 'normal association analysis' of Williams & Lambert (1959, 1960), using an Elliot 803 computer. The result of this calculation is a hierarchical division of the samples into groups which incorporate the strongest associations among the species. They are, therefore, likely to reflect distinct categories within the vegetation if these exist.

It is not possible to present here the detailed results of this analysis: these will be published later. However, it may be reported that the outcome gives substantial support to the classification system referred to above. For the present purposes, attention may be drawn to certain groups of samples which were most regularly established by analysis of the data:

(A) *Groups clearly referable to the 'open lichen and moss cushion subformation'.*

(1) Quadrats with *Andreaea* spp. well represented and one or both of *Usnea antarctica* and *U. fasciata*. On non-calcareous, exposed rocky ground.

(2) Quadrats containing both *Polytrichum alpinum* and *Andreaea* spp. in quantity. On soil amongst rocks; exposed ground.

(3) Quadrats with *Grimmia antarctici* well represented, usually associated with species of *Encalypta*. On rocks or debris derived from marble outcrops.

(4) Quadrats with *Tortula fusco-viridis* well represented, often associated with *Pohlia cruda*. Also on rocky or stony ground influenced by marble outcrops.

(B) *Groups clearly referable to the 'moss turf subformation'.*

These groups are composed entirely of quadrats with one or both of *Dicranum aciphyllum* and *Polytrichum alpestre* figuring prominently, often in association with various lichens. The samples are invariably from peat banks on more or less well-drained slopes not far from the sea.

(C) *Groups clearly referable to the 'moss carpet subformation'.*

Quadrats in these groups contain one or more of *Drepanocladus uncinatus*, *Acrocladium* sp., *Brachythecium* sp. These may be variously associated or in almost pure stands, forming extensive patches always on swampy ground.

(D) *Groups clearly referable to the 'moss hummock subformation'.*

Quadrats contain species of *Bryum*, *Pohlia* and *Tortula* often with a large cushion-forming species of *Brachythecium* ('*subplicatum*'). Damp flushed areas, sides of drainage channels, etc., particularly where water has passed over basic rocks, e.g. marble.

The separation, as a result of association analysis, of these groups and a few other less clearly defined, closely parallels the 'associations' determined by phytosociological methods. It demonstrates further, that there are certain groups which, although differing in composition, show features in common. These prove to be groups which can be placed together in one subformation on physiognomic grounds (growth-form representation, etc.), although special environmental factors (ultra-basic substrata, for example) lead to largely distinctive assemblages of species. Furthermore, it is evident from the analysis that the occurrence of samples belonging to the several groups is markedly correlated with distinctive types of habitats.

This result poses the problem of determining the causes of the distinction and distribution of these vegetational categories.

Bryophyte ecology

One approach to this problem is to investigate the ecological relationships of the chief species in each category. Current investigations by R. I. L. Smith are being directed towards the response (in terms of occurrence and quantity) of certain species to aspects of the microenvironment, particularly temperature regime, exposure to wind, duration of snow cover, soil instability, and the 'base status' of the substratum.

However, from the community analysis it becomes evident that a further factor of importance is the quantity and source of origin of the water supply during the growing season. This must be related to the systems by which it is taken up by the plants, and their ability to conserve it against evaporation stress. In this regard 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. The range of growth-form in the Antarctic is considerably less than it is in Britain, and tends to be limited to the more compact cushions, turfs and mats (figure 26; see also Gimingham & Birse 1957).

Investigations of loss and uptake of water in selected species therefore centred on comparing the properties of isolated shoots with those of small samples of the intact colony, in which the arrangement of the shoots was undisturbed. Water loss from moist samples was followed in controlled conditions of relative humidity of 93, 70 and 45% at room temperature, to simulate mild and severe evaporation stress; water uptake or 'rehydration' was followed by using samples from which free water had been spun off by centrifuging (see below), standing them with either the base of the shoot or, in some experiments, the tips of the shoots in contact with water. In addition, measurements were made of the contained water in samples from the field and also that proportion of it which could be spun off by slow centrifuging at approximately 250 ***g***. This was because in mosses varying quantities of water may be held externally in the capillary spaces between the leaves and stem or among rhizoids, rather than in the tissues; and the amount removed by centrifuging was taken as an indication of this externally held water. These spaces also frequently serve as external pathways for water conduction, often effective in the rehydration referred to above.

These tests were carried out on fourteen species; full details will be published elsewhere, but a summary account follows of the results for 6 important species.

Acrocladium 'austrostramineum'[*]

As a first example, one of the species forming extensive carpets on swampy ground is taken. It occurs frequently in pure stands of densely packed shoots (*ca.* 125 shoot tips/cm^2).

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[*] Note. Since several of the taxa referred to have not yet been fully investigated taxonomically, names which have been applied to them are here cited in inverted commas.

These are somewhat intertwined below, but in the apical 2 to 3 cm are little branched, adopting a vertical or ascending habit (figure 26). This produces a colony some 7 to 8 cm deep which is so compact that a portion cut from the carpet will stand free without collapsing.

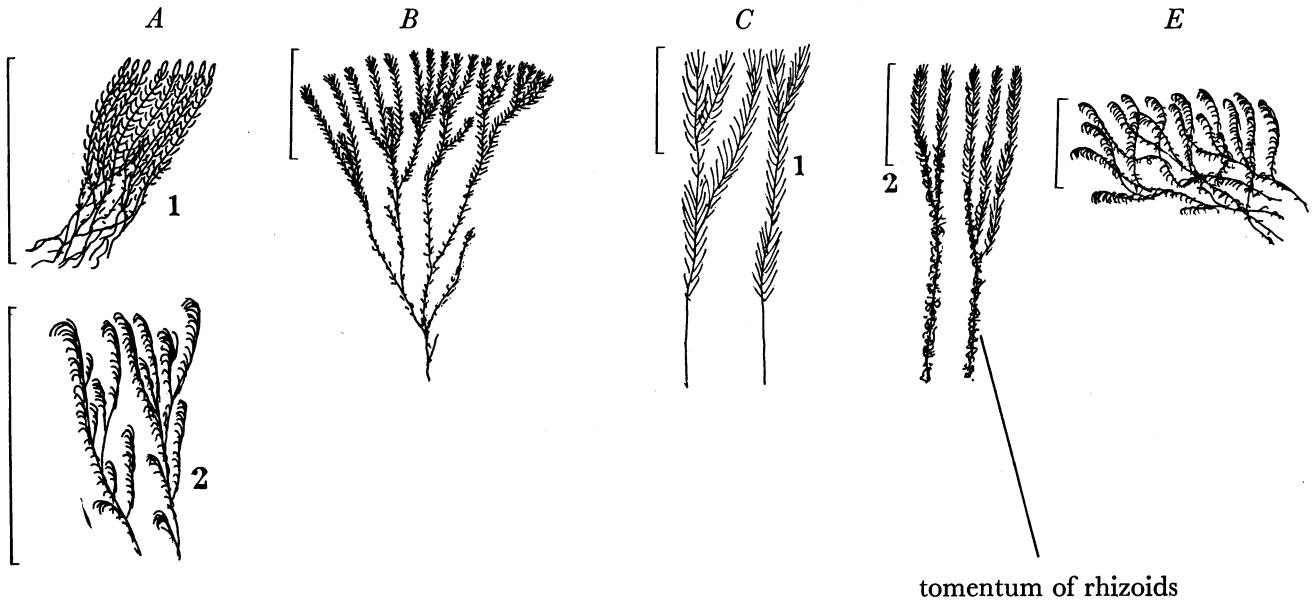

Figure 26. Diagrams of growth-form of species investigated (see text). *A*. Moss carpets from swampy ground: 1, *Acrocladium 'austrostramineum'*; 2, *Drepanocladus uncinatus* (large type). *B*. Small cushion: *Andreaea 'regularis'*. *C*. Tall turfs: 1, *Polytrichum alpinum*; 2, *Polytrichum alpestre*. *D*. Mat: *Drepanocladus uncinatus* (small type). Scales represent 1 cm.

The results of water-loss experiments from isolated shoots of this species are given in figure 27, the three main curves showing the decline in water content of shoots on exposure for increasing lengths of time to atmospheres of the three chosen humidities. An indication of the rate of water loss is given by the slope of the curves, while inset is a smaller graph to the same scale, for a sample of the intact colony subjected to the lowest relative humidity (45 %). The slope of the latter graph may be compared directly with that of the first part of the lowest of the three curves for isolated shoots.

As to be expected in a species with thin cell walls, slender and relatively undifferentiated stems, the rate of loss for isolated shoots in the lower humidities is very fast. The rather close packing of the shoots in the intact colony makes some difference, expressed in the slightly reduced rate of loss from the colony sample, but this difference is small. Samples of the colony taken direct from the field contain a quantity of water between 1000 and 1600 % of their dry weight, of which up to 60 % can be spun off in the slow centrifuge and may thus be regarded as held externally. Rehydration, or replacement of this proportion of the water content, will take place in most cases within about 4 min irrespective of whether water is supplied to the lower parts (the samples were cut at 2 cm below tips), or to the tips of the shoots. In view of the susceptibility to drying out of this species and yet the apparent demand for a large quantity of water to be contained among and around the leaves and shoots, its ecological limitation to areas with a ground-water supply, from which there is ready uptake by an external conduction pathway, is explicable.

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Very similar results were obtained for a robust species of *Brachythecium* (‘*antarcticum*’), which shows a highly significant positive association with *Acrocladium* ‘*austrostramineum*’ in the field surveys.

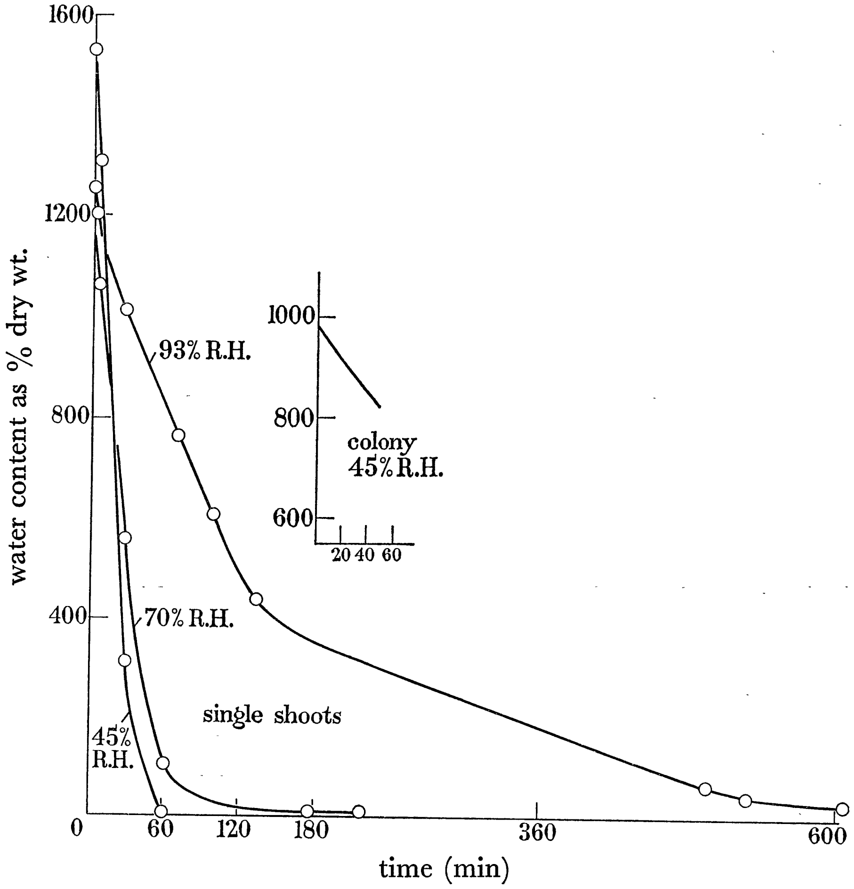

Figure 27. *Acrocladium* ‘*austrostramineum*’. Graphs of decline of water content with time: single shoots exposed to atmospheres of controlled relative humidity (at room temp.) as shown; inset, sample of colony with shoots undisturbed, exposed to 45 % r.h.

Andreaea ‘*regularis*’

This species, from exposed rock surfaces or rock debris, occupies a markedly contrasting habitat to that of *Acrocladium*. It has the form of a small dense cushion (figure 26), with shoots radiating from a centre, only about 2·5 cm high. The form of the curves for decline of water content in isolated shoots (figure 28), is not unlike that in *Acrocladium*: the rate of loss in the lower humidities is fast. However, two important differences emerge. First, less water is contained in samples from the field (*ca.* 250 % of dry weight), only about 20 % of which is removed in the centrifuge; and, secondly, the rate of loss to a drying atmosphere from samples of the cushion is considerably slower than from the isolated shoots. This is presumably due, in part at least, to the close packing and overlying of the shoots in the dense cushion, at the periphery of which there are about 365 shoot tips/cm^2. Rehydration in this species involves the uptake of less water in proportion than in *Acrocladium*, but is again nearly complete in 4 min when water is supplied either at the base of the colony sample or to the tips of the shoots.

This then, is a moss which, despite again having shoots susceptible to rapid drying, demands and holds less water externally than *Acrocladium*. However, probably as a result of its colony structure, this moisture is conserved more effectively within the cushion. The source of water is not from a permanent supply at ground level, but from an intermittent supply in contact with any part of the shoot following thaw, rain, or melting snow flakes on the surface of the cushion. From these sources, the necessary water may be taken very rapidly into the cushion. Alternate drying out and rehydration of this species is frequently observed in the field.

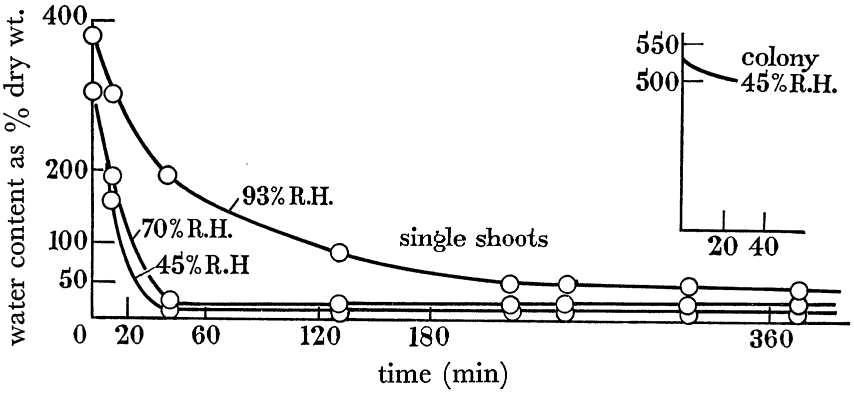

Figure 28. *Andreaea* '*regularis*'. Graphs of decline of water content with time. Details as for figure 27.

Polytrichum alpinum

This species frequently accompanies *Andreaea* when the latter occurs on soil or deposits of fine particles, or it may occur alone on bare or disturbed ground. It is widely distributed in exposed situations, although excluded from rock surfaces. In growth-form it is taller, more rigid with erect stems, somewhat branched near the tips (figure 26). The shoot density is only about 17 tips/cm^2, and the stems are less densely packed than in the preceding species. Figure 29 shows that isolated shoots lose their water much more slowly, and the difference in rate of loss between isolated shoots and portions of the colony, exposed to the same evaporation stress, is minimized. The total water content in the field is usually limited to about 180% of dry weight, and less than 10% of this can be removed by slow centrifuging. Water uptake will take place from the base of the shoots only, and is limited in amount.

The ability of this species to thrive in conditions similar to those occupied by *Andreaea* therefore depends upon a different system. Presumably the greater part of the required water is absorbed from the moisture contained in the particulate substratum, perhaps to a large extent through rhizoids. Conduction to the aerial parts of the stem and the leaves may be mainly internal: an internal conduction pathway can be demonstrated using eosin. Loss from the stems and leaves is controlled, presumably by mechanisms permitting the restriction of air-access to the photosynthetic lamellae, coupled with a form of cuticularization of other exposed surfaces. This, in turn, would largely restrict water uptake to the lower parts of the shoots, as is found to be the case.

Polytrichum alpestre

This related species can colonize in habitats similar to those occupied by *P. alpinum*, but is most characteristic as a very dense turf in which the shoots, although not particularly numerous (*ca.* 27 tips/cm^2), cohere firmly as a result of the intertwining of a tomentum of rhizoids which reaches to within 1 cm of the apex (figure 26). In this type of colony, it is frequently associated with *Dicranum aciphyllum* as an agent of peat formation.

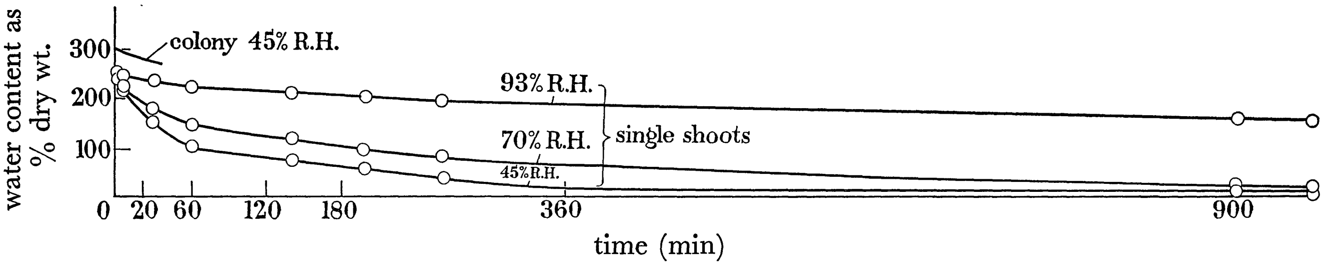

FIGURE 29. *Polytrichum alpinum*. Graphs of decline of water content with time: lower three curves, single shoots exposed to atmospheres of controlled relative humidity as shown; upper curve, sample of colony exposed to 45 % R.H.

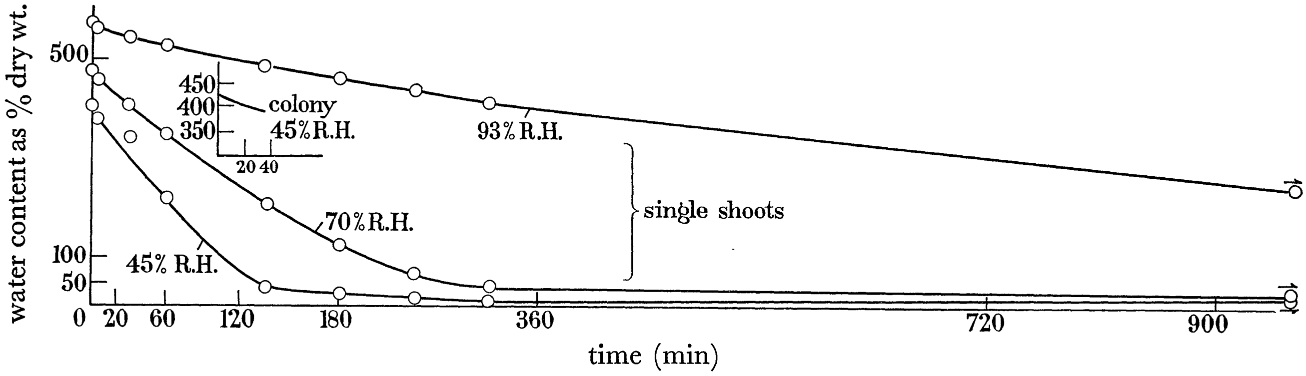

FIGURE 30. *Polytrichum alpestre*. Graphs of decline of water content with time. Details as for figure 27.

The results of experiments on this species in some respects stand intermediate between those for *P. alpinum* and those for *Dicranum aciphyllum* (see below). The decline in water content of isolated shoots in the test atmospheres follows a similar pattern to that in *P. alpinum*, though the rate of loss is slightly faster (figure 30). However, this is offset by the fact that the compaction of the shoots in the colony leads to a reduction in the rate when the colony structure is undisturbed. More water is contained in samples from the field (between 250 and 450 % of dry weight), and rather more of this (up to 40 %) appears to be held externally, some of it presumably in the tomentum. Like *P. alpinum*, uptake of water is confined to the lower parts of the shoots, but more is taken up than in *P. alpinum*. This may be related to the possession of an external conduction pathway among the rhizoids, acting as a wick, as well as an internal one, the operation of which can again be demonstrated with eosin.

These results suggest that the capacity of this plant to continue growth above its brown and frozen remains on peat banks depends to a considerable degree on its ability to pass water upwards from a source below, and to conserve it in the dense colony of growing shoots. The water source might be the summer melt-surface in the peat, which may lie between about 10 and 30 cm below the level of the turf.

Dicranum aciphyllum

This species will not be considered in detail, but in view of its regular association with *P. alpestre*, a brief comparison is useful. Like *P. alpestre*, it has abundant rhizoids extending nearly to the apical part of the stem, and the shoot density is greater, at *ca.* 125 tips/cm^2. One important difference, however, is that rehydration takes place readily from the shoot tips, as well as from below. It is evident that the combination of these two species in the community is particularly effective, in that while both can conduct water from below, *Dicranum aciphyllum* can also draw it into the turf from rain or melting snow on the surface.

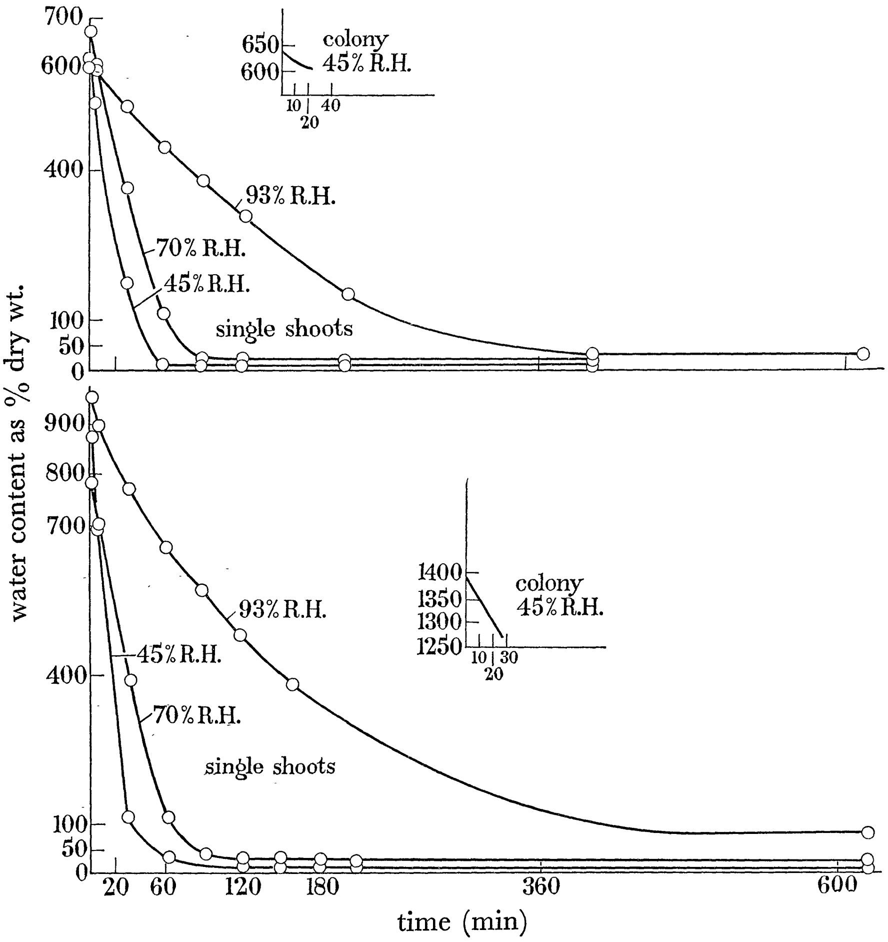

FIGURE 31. *Drepanocladus uncinatus*. Graphs of decline of water content with time. Details as for figure 27. Upper series—small type from drier habitats; lower series, large type from swampy ground.

Drepanocladus uncinatus

This species provides an important final example, ranging, in rather pure stands, from habitats where it is strongly associated with *Polytrichum alpinum* to much wetter situations in which there is significant association with *Acrocladium*. Correlated with this wide ecological range is considerable variation in growth form. This grades from a relatively compact mat in the drier habitats, about 3 to 4 cm deep, consisting of intertwined, much branched shoots, to a deeper (9 to 10 cm) carpet on swampy ground, in which the upper parts of the shoots are less branched and more parallel and ascending, somewhat similar in growth form to the associated *Acrocladium* (figure 26).

Treating the extremes separately, different results are obtained in the experiments (figure 31). Isolated shoots from specimens belonging to the drier habitats show a slower rate of water loss compared to the more robust type from the wetter situations, while the compact mat-form of the colony in the former further reduces the rate of loss when colony samples are compared, under similar conditions, with the isolated shoots. The pattern of the graphs for the larger, looser form from swampy habitats resembles that for *Acrocladium* (figure 27).

In regard to its water relations, *D. uncinatus* is evidently a species which occupies a position intermediate between species of freely drained or exposed situations, and those of swampy ground. Furthermore, the considerable diversity exhibited in its growth-form may be linked to the variations detectable in water loss and uptake properties, and both may contribute to the ability of the species to extend throughout an unusually wide range of habitats.

Conclusions

The results of experiments on the five selected species are sufficient to indicate the way in which such investigations will contribute to the explanation of the composition and distribution of some of the vegetational categories recognized on Signy Island. In each case, the particular type of water relations may enable a species to participate in the community most effectively in habitats where certain specific conditions of water supply operate. The water relations of the moss are themselves an expression of a combination of anatomical, morphological and physiological characteristics, each of which may be capable of a greater or lesser degree of variation. Many other factors of the environment interact with water supply in determining the local distribution of species and communities, but it is evident that in the short Antarctic growing season the provision of water is of great importance.

I am most grateful to the British Antarctic Survey for the opportunity to visit Signy Island. The field work on which the community analysis were based was carried out in collaboration with Mr R. I. L. Smith, whose detailed knowledge of the bryophyte flora was of inestimable value throughout. Thanks are also due to Miss A. M. Slater for undertaking the association analysis and other calculations.

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