BRITISH ECOLOGICAL SOCIETY

The Growth of Sphagnum: Some Effects of Environment
Author(s): R. S. Clymo
Reviewed work(s):
Source: *Journal of Ecology*, Vol. 61, No. 3 (Nov., 1973), pp. 849–869
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/2258654
Accessed: 20/07/2012 08:40

http://www.jstor.org

THE GROWTH OF SPHAGNUM: SOME EFFECTS OF ENVIRONMENT

By R. S. CLYMO

Westfield College, London NW3 7ST

INTRODUCTION

Some of the reasons for studying the growth of *Sphagnum* are summarized by Clymo (1970). Briefly, they are that the total mass of living plants is great, the physiology of *Sphagnum* is unusual, and the remains of *Sphagnum* form a large part of many peat deposits.

This paper is concerned with two problems. First is the distribution of the plants on a large scale in relation to H^+ and to Ca^{2+} concentration and supply. In the natural habitats of *Sphagnum* these factors are usually correlated, and both are correlated with shade, because the associated vascular plants grow larger (or are taxa with larger growth forms) where the water supply has high pH and Ca^{2+} concentration. For example, *S. squarrosum** and *S. fimbriatum* may often be found in the shade of *Betula* spp. and *Salix* spp. in fen carr, in flushed zones in woodland, or in the central zone of valley mires, in situations where the water may be of pH 6–7 and Ca^{2+} concentration 1 m-equiv./l. At the other extreme, *S. rubellum* and *S. fuscum* growing on hummocks on raised or blanket bog may be in contact with water of pH just over 3, and of Ca^{2+} concentration less than 0·01 m-equiv./l. In these situations there may be some shading by dwarf shrubs, for example *Calluna vulgaris*, or no shade at all. (There is nearly always self-shading, by *Sphagnum* of the same taxon, but in such cases the response is by the individual plant, rather than by the taxon.)

The second problem is the smaller scale distribution of the different species of *Sphagnum* in the microhabitats of pool, lawn and hummock. Some species appear to be rather closely restricted: *S. cuspidatum* to pools for example. Others are usually found in one habitat but occasionally in others: *S. fuscum* and *S. rubellum* in drier situations (often hummocks). Yet others are found in a wider range of habitats; *S. papillosum* and *S. imbricatum* are examples.

To throw light on these problems, experiments were made on the growth of several species of *Sphagnum* in relation to factorial combinations of H^+ and Ca^{2+} concentration, and to factorial combinations of water table and shading. Subsequent experiments were made on 'desiccation tolerance' and on rate of water loss in relation to water level.

METHODS AND EXPERIMENTS

There were four designed experiments and two sets of measurements from a natural (undesigned) experiment. These were to measure the following.

* Nomenclature follows Richards & Wallace (1950).

P

I. Growth in response to factorial combinations of:
   (a) water-table depth and shade;
   (b) pH and Ca^{2+} concentration.
II. Growth in response to:
   (a) factorial combinations of pH and Ca^{2+} concentration;
   (b) 'flushing'.
III. 'Desiccation tolerance'.
IV. Rate of water loss in response to variation in water supply.
V. Water content at various depths in natural conditions.
VI. Surface roughness of a bog in relation to water-table depth.

Experiment I

This experiment was made to survey the response of a wide range of species of *Sphagnum* to the major environmental factors: pH, Ca^{2+} concentration, water-table depth and shade, separately and in combination. A wide range of 'levels' of each factor was used (except for water-table depth for which a wide range was not practicable) as this was an exploratory experiment. Ideally all four factors would have been combined factorially, but this would have made the experiment unmanageably large. A further restriction was set by the difficulty in controlling chemical conditions, particularly cation concentrations around the apical meristem, due to the unusually high concentration of cation exchange sites in *Sphagnum* plants (Clymo 1963, 1966). Such control could have been effected by spraying solution over the plants continuously, but for a complex and long experiment this was impracticable. The alternative was to immerse the apices in solution, at least intermittently, but the chemical treatments could not then be combined with the water-table treatments. In consequence the experiment was made in two parts, with water-table depth and shade as factors in one part, and with pH and Ca^{2+} concentration as factors in the other part.

The twelve species used are listed in Table 3 (p. 856). They come from as wide a range of natural habitats as possible. The plants were cut initially to 50 mm length. To minimize changes in concentration of solution around the plants, and to reduce the effects of the previous history of the plant, they were then pretreated with five changes of solution containing 0·5 m-equiv./l Ca^{2+} and of pH 5·6, and then with five changes of the appropriate experimental solution. Each of these ten solutions was left in contact with the plants for about 30 min. The dose rate was about 1 ml of each solution per milligram dry weight of plant. The plants were then placed in groups on a 6-cm-deep bed of similarly pretreated homogenized dead *Sphagnum* in 1-litre Pyrex beakers, at a density approximating that found in natural conditions (Green 1968; Clymo 1970). The beakers were surrounded to capitulum level by black paper shields. All solutions contained the following concentrations (m-equiv./l) of the ions: 0·01, Na^+; 0·03, K^+; 0·03, Mg^{2+}; 0·10, SO_4^{2-}; 0·02, NO_3^-; and 0·01, 'orthophosphate'. These concentrations are about those found naturally in water squeezed from *Sphagnum* lawns and hummocks at Moor House National Nature Reserve (R. S. Clymo, unpublished), except perhaps for 'orthophosphate' for which reliable analyses were not obtained. The proportion of the various forms of 'orthophosphate' varied with pH. Solutions were kept at constant level below the plant apices using the 'chicken feeder' principle: a wide-mouthed glass container, painted black to minimize growth of algae, was filled with solution and inverted over a shallow dish from which siphons connected with the beakers. The solutions were siphoned off from each beaker three times each week, and pH and Ca^{2+} concentration measured. On

four occasions Na^+ and K^+ concentration were measured too. The position of the beakers was randomized anew at each solution change.

The experiment was made in a glasshouse, and lasted 57 days from 14 May 1965. At the end, growth in length and in dry weight of groups of fifteen plants were measured allowing for that part of the original capitulum carried up into the new growth by inter-node elongation, using the method described by Clymo (1970).

Details specific to one or other part of this experiment follow.

I(a). Three water-table levels (surface $= 0$ cm, -3 cm and -10 cm) were combined factorially with three degrees of shade (0, 0·45, 0·82). There were two replications.

The solution supplied had 0·05 m-equiv./l Ca^{2+} and pH 3·6, which approximates to that around most of the species in natural conditions. The Ca^{2+} and H^+ were added as chlorides.

The water-table levels must be considered as nominal. The beaker height (relative to the 'chicken feeder' mouth) was adjusted as the plants grew to keep the water table at the same level relative to the surface of the *Sphagnum* carpet. Because the plants grew in length at different rates, even in the same beaker, it became more difficult to define the surface as time passed. The difficulty was least in the -10 cm treatment. In the 0 cm treatment most of the plants had relatively weak stems, so that capitula tended to settle and float at the water surface, the stem bending below the surface. Though the largest differences in growth in length occurred in this treatment, the capitula of the shortest plants were never more than 2 cm below the surface. This might, of course, have reduced considerably the supply of carbon (as CO_2 or HCO_3^-) to these plants since diffusion rates in water are so much lower than in air. In the nominal -3 cm treatment the eventual range of growth in length was 4 cm so the real value for this water level was between -1 cm and -5 cm, depending upon the individual plant.

Reduction of incident radiation flux was made with either two or six layers of black nylon gauze. Absorption of incident radiation by this material (measured in a spectro-photometer) was about 0·45 for two layers and 0·82 for six layers (close to additive absorbance of 0·13 layer^{-1}). Between 0·2 μm and 15 μm the absorption was almost independent of wavelength. Similar absorption values were measured with a solarimeter, in both sunny and overcast conditions.

Since natural light was used, these treatments are called 'shading' though the shading to which the plants are subject in natural conditions might also be selective for wave-length, having more energy in the green relative to the red and blue parts of the spectrum. The spectral distribution of energy below a *Calluna* canopy is, however, little different from that in natural light incident on the canopy (Grace 1970). The apices of plants in shaded beakers were sometimes hotter and sometimes cooler than those in unshaded containers. The differences measured were up to 4° C, and this temperature effect is con-founded with shading. Such differences exist in natural conditions too, but the correlation of natural and experimental effects is not known.

Some of the results of this experiment are shown in Fig. 1, and in Tables 2 and 3.

I(b). Three Ca^{2+} concentrations (5·0, 0·5 and 0·05 m-equiv./l) were combined factori-ally with three pH levels (3·6, 5·6 and 7·6). There were three replications. The water table was kept at the surface.

Monitoring of Ca^{2+} and Na^+ concentrations in the solution showed that there was (with two isolated exceptions) less than 20% change during the time which the plants were in contact with the solution. The pH changed markedly however, in all but pH 3·6 treatments (Table 1), mostly during the first 30 min after solution replacement, and

probably therefore due to cation exchange. The designed pH levels, excepting 3·6, are consequently only nominal and are described as 3·6, '4·8' and '5·7'. As with water level treatments these descriptions cover differing degrees of variation. Some of the results of this experiment are shown in Fig. 1 and Table 4 (see later).

Experiment II

Because of the reduction in actual pH range in the treatments in experiment I, so that the effects of the interaction of high pH and high Ca^{2+} level were only just apparent, it seemed worth repeating the essential features of experiment I but with improved pH control. This involved the use of flowing solutions. The effect of rate of presentation of ions ('flushing'), besides their concentration, was consequently examined separately. The experiment is again therefore in two parts.

Eight species of *Sphagnum* (listed in Table 6) were used. Their usual habitats span the range of chemical conditions in which *Sphagnum* is found. The plants were cut to 50 mm and arranged in 1-litre beakers on a bed of homogenized *Sphagnum*, as in the first experiment. The basic solution composition was the same as that in experiment I, but

Table 1. *Geometric mean pH of solutions removed from beakers in experiment Ib (each figure is based on forty-four measurements)*

Nominal pH	Nominal Ca^{2+} concentration (m-equiv./l)		
	5·0	0·5	0·05
7·6	5·6	5·5	6·0
5·6	4·6	4·8	5·0
3·6	3·6	3·6	3·6

the pretreatment solution was applied at a rate of 2·5 ml/mg dry weight, compared with 1 ml/mg in experiment I. Solution was supplied continuously at the base of the beaker, the rate of supply being controlled by short lengths of capillary tube. The standard rate was 2 litres per day.

Each beaker had a siphon, adjustable in height, set to empty when the solution had submerged the apices of the *Sphagnum* plants. Physical conditions thus fluctuated two to three times each day between those found in a pool and those on a low hummock. Control of pH was improved; the range of values found for solution siphoning out of all nominal pH 7·6 treatments was 6·5–8·2 (seventy-two measurements).

The beakers were kept outdoors protected from rain by an overlapping canopy of clear polythene held 1 m above the beakers. The experiment lasted 77 days from 26 May 1966. The beakers were randomized anew every 14 days.

Details specific to the two parts of this experiment follow.

II(a). Three Ca^{2+} concentrations (5·0, 0·5 and 0·05 m-equiv./l) were combined factorially with three pH levels (3·5, 5·5 and 7·5). There were two replicates.

Some of the results of this experiment are shown in Fig. 2 and Tables 5 and 6.

II(b). Six flushing rates were replicated twice. The flushing rates were obtained by adjusting the flow rate of the solution and/or by using distilled water with no added solutes. The standard solution had pH 3·5 and Ca^{2+} 0·5 m-equiv./l. The treatments were: (a) standard solution, full flow rate (about 2 litres/day); (b) standard solution, 1/5 full flow rate; (c) standard solution, 1/25 full flow rate; (d) standard solution, no flow, replaced every 14 days; (e) distilled water, no flow, replaced every 14 days; (f) distilled water, full flow rate.

Treatments (e) and (f) removed ions from the system and may be considered as leaching or 'negative flushing'. Some of the results of this experiment are shown in Fig. 3.

Experiment III

The results of experiment I(a) with variation of water level directed attention to the possibility that the natural habitat restrictions of different species of *Sphagnum* might be caused by differing abilities to survive desiccation. The following experiment was therefore made.

Constant air humidity was maintained over sulphuric acid solutions (Hodgman, Weast & Selby 1961), in cylindrical glass dishes, 30 cm diameter and 15 cm tall with glass covers. Capitula of *Sphagnum* were put on 2 mm mesh nylon screens 3 cm above the solutions. Each dish contained fifty capitula of each of seven species. The species are listed in Fig. 4, and were chosen to cover the range of habitat wetness usual for *Sphagnum*. There were two replicates of each humidity. The dishes were kept in a dimly lit room at $25° \pm 1°$ C. Samples of capitula were reweighed until the change in weight became erratically positive and negative (after 12 days). After 21 days the capitula were transferred to damp filter paper in Petri dishes, and put on a west-facing window sill. The proportion of capitula which showed new growth, and of those which were still green after 3 weeks were recorded.

The amount of water lost by the plants was in no case sufficient to produce a significant change in the sulphuric acid concentration.

Proportional humidities of 1·000 (distilled water), 0·998, 0·991 and 0·981 were used. At the three lower humidities and at 20° C circular glass capillaries of radii 0·55 μm, 0·12 μm and 0·06 μm respectively would just remain full of water. (The size of pores in hyaline cells of *Sphagnum* leaves is about 4–25 μm, depending on species.) The results are shown in Fig. 4.

Experiment IV

It seemed possible that besides differences in desiccation tolerance, there might be differences between species in the ability to transport water to the plant apices, or in the amount of water which can be kept in the capitulum if the water table is lowered. The following experiment was made to investigate differences in transport ability.

Sphagnum plants of three species, representing the range of micro-habitats, were cut to the length of a 600-ml beaker and carefully packed into the beaker, at natural density, with the capitula level with the surface of the beaker. The species were *S. rubellum* (hummock), *S. papillosum* (lawn) and *S. cuspidatum* (pool). This last was collected from the edge of a pool where it showed an upright growth habit. A fourth beaker contained no *Sphagnum*. For each 'species' (including the empty beakers) three water levels were used: −1 cm, −5 cm, and −10 cm. The water levels were altered from one level to another every day for 9 days, and the change in weight of beaker plus contents (assumed due to loss of water) measured each day. The order of alteration was determined by a Latin square design. There were two replicate blocks.

The beakers were stood close to each other, but not touching, on a glasshouse bench, with a double 'guard ring' of *Sphagnum*-filled beakers around. The positions of the treatment beakers were randomized each day. The glasshouse windows and doors were open. The experiment was carried out in June; all days but one were sunny. The results are shown in Fig. 5.

Experiment V

Independent of the transport abilities of different species it seemed likely, because of the

Growth of Sphagnum

differences in hyaline cell size, that there would be differences in the water content of capitula in natural conditions. This experiment was made to find out whether or not this was so.

Plants of three species (*S. cuspidatum*, *S. papillosum* and *S. rubellum*) were collected during one period of 2 h from natural habitats. The plants were cut into 1- or 2-cm segments, put into tubes (sealed for transport), and the water content measured. Care was taken to make the minimum disturbance to the plant during removal, and the plant was kept vertical whilst being cut into sections. There were eight to twelve replicates, varying with depth.

One set of plants was taken from the middle parts of carpets dominated by the species. A set of *S. papillosum* plants was also taken from isolated plants amongst *S. rubellum*. The results are shown in Fig. 6.

Experiment VI

Consideration of the results of experiment I(a) (effects of shading and of different water tables on growth) led to the prediction that the surface roughness of a *Sphagnum* carpet would be negatively correlated with distance above the water table. Measurements on natural communities at Cranesmoor (Nat. Grid Ref. SU 1903) were therefore made to test this hypothesis. A measure of roughness was obtained using the variance of height (Harper, Williams & Sagar 1965) of twenty-five light pointers (culms of *Deschampsia cespitosa* (L.) Beauv.) held vertical in a frame. The points were 1 cm apart in two staggered rows. The whole set was photographed against graph paper background. Water table was measured in an open hole 5 h after digging. There was no rain in this time. One set of results is shown in Fig. 7.

RESULTS
Expression of results and statistical treatments

(1) Growth in weight (in experiments I and II) has been expressed as mg (mg cm^{-1} stem)$^{-1}$, because comparison between species is justifiable if the difference in apex size is taken into account. The base for comparison is the dry weight of a unit length of stem, which itself correlates with capitulum weight (Clymo 1970). The range of results using this unit was about 2·7, but using the simpler mg plant^{-1} the range was 35.

The variance of both growth in weight and growth in length is not independent of treatment effects. Because of this, and because the measurements involve growth, during which effects are likely to be combined geometrically, a transformation to logarithms was used before statistical analysis. Error bounds are thus 'times/divide' not 'plus/minus'. The mean values shown in tables and figures have been back-transformed, and the growth in weight results in tables have been further converted to units of mg plant^{-1}, as the main interest in these cases is comparison between treatments, and the unit mg plant^{-1} is easier to visualize. The logarithmic transformation was fairly satisfactory with the exception of those effects connected with water table. These are discussed later.

(2) The percentage survival data (experiment III) were transformed to the arcsin before statistical analysis. The mean values shown in Fig. 4 have been back-transformed.

Experiment I(a)

Some of the results are shown in Fig. 1 and Tables 2 and 3. The main effects (Table 2) are connected with species and shade treatment, but there are notable interactions between

water table and shade, and between water table and species. The first of these is shown in Fig. 1, and the second in Table 3. It is obvious in Fig. 1 that the two measures of growth vary in different ways. In general, if the plants were shaded and/or the water table was high growth in weight was less. Growth in length, however, was reduced only when the water table was low and the shade was dense. The combined effect was that the plants became more straggling in shade and/or high water table. Green (1968) reported that five species of *Sphagnum* showed greater extension growth in wetter conditions, and that *S. imbricatum* and *S. papillosum* both have a lower branch density in wetter conditions, though individual branches are longer. Presumably the increased length of branches in
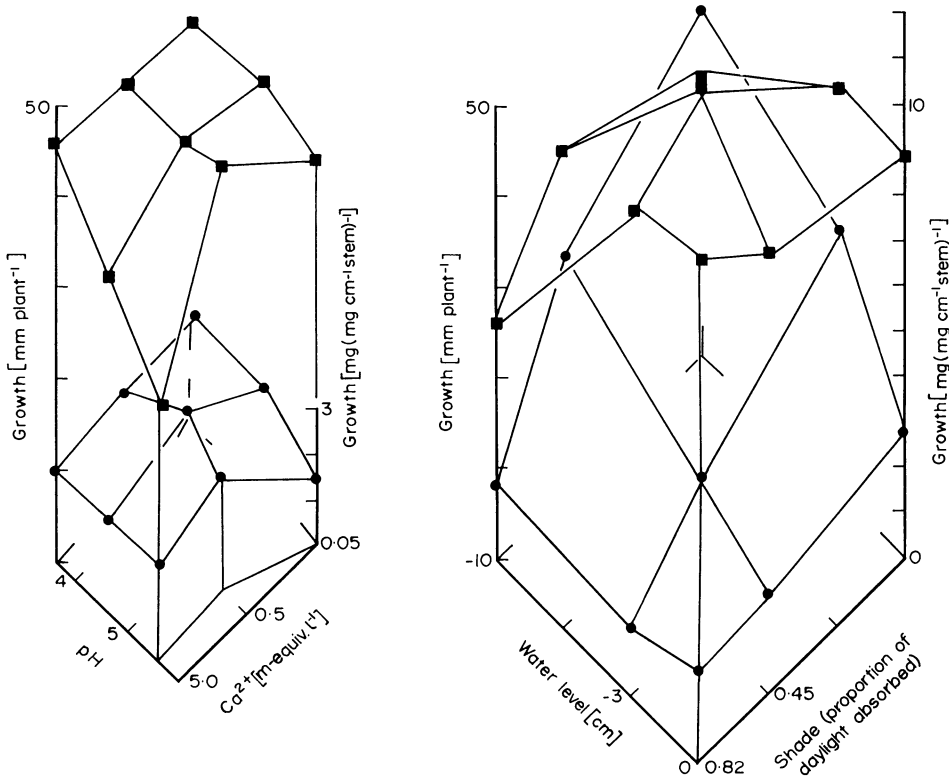

FIG. 1. Growth in length (■, and left-hand vertical axis), and growth in weight (●, and right-hand vertical axis) of *Sphagnum* in various chemical and physical conditions: experiment I. See text for details.

wetter conditions is not sufficient to counterbalance the decrease in density of branches as the weight per unit length of plant is less. The change in length might be described as etiolation where the plants are shaded, and where the water table is lower the effect may be partly due to lower water potential in the capitulum. The reduction in growth in weight may be due to the increased liquid diffusion path for CO_2 and to reduction in incident radiation flux.

In Table 3, showing the species/water table interaction, the first eight species are arranged in order of increasing depth of water table in the usual habitat; the last four are difficult to place in this series. No obvious pattern emerges though there is perhaps some indication that growth in length with a low water table is less reduced for the species which normally grow in drier habitats.

Experiments I(b) and II(a)

The noteworthy effects in experiment I(b) were confirmed and extended in II(a). The most important effects are associated with pH and Ca^{2+} concentration and their interaction (Tables 4 and 5). These are shown in Figs. 1 and 2. The interaction of species with pH and of species with Ca^{2+} concentration (Tables 4 and 5) are shown, for experiment II(a), in Table 6.

Table 2. *Analysis of variance of growth in length, and of growth in weight* (*bold figures*) *of* Sphagnum *in various physical conditions* (*experiment Ia*)

Treatment		Degrees of freedom	Mean square		F	
Water table	(A)	2	6·72	**5·48**		
Shade	(B)	2	0·39	**20·8**		
Species	(C)	11	6·49	**27·3**		
Interactions AB		4	0·38	**3·10**	6·27***	**5·96***
AC		22	0·39	**1·34**	6·32***	**2·56***
BC		22	0·11	**0·79**	1·82*	**1·51**
ABC		44	0·096	**0·80**	1·57	**1·52**
Error		108	0·061	**0·52**		

* $0·05 \geqslant P > 0·01$; ** $0·01 \geqslant P > 0.001$; *** $0·001 \geqslant P$.
Where interactions have $P < 0·01$ the main effect F values are omitted.

Table 3. *Mean values of growth in length, and of growth in weight* (*bold figures*) *of* Sphagnum *with various water tables* (*growth in weight is given as mg per plant; the outer columns are expressed as a percentage of the central ones* (*those in parentheses*); *experiment Ia*)

	Water table (cm)				
	−10	−3			0
Species	Percentage of −3 cm result	(100 =) (mm)	(mg per plant)		Percentage of −3 cm result
S. subsecundum (var. *inundatum*)	56* **107**	(64)	(5·3)		98 **36**
S. cuspidatum	36* **132**	(103)	(8·3)		109 **140**
S. recurvum	42* **104**	(73)	(2·4)		86 **71**
S. papillosum	51* **189**	(55)	(2·7)		73 **89**
S. magellanicum	41** **109**	(64)	(10·4)		66 **41**
S. rubellum	60 **159**	(58)	(2·2)		81 **86**
S. fuscum	126 **100**	(19)	(0·4)		110 **50**
S. compactum	128 **600**	(7)	(0·2)		186 **500**
S. fimbriatum	41* **73**	(88)	(9·4)		76 **47**
S. plumulosum	65 **73**	(57)	(2·2)		70 **18***
S. squarrosum	50* **125**	(94)	(9·1)		98 **76**
S. palustre	48* **50**	(96)	(18·0)		85 **74**

* $0·05 > P > 0·01$ for comparisons with −3 cm treatment.

The ranges of pH and Ca^{2+} concentration in these experiments were larger than those normally experienced by most species of *Sphagnum*, in contrast to the range of water table in experiment I(a) which was well within the range normally experienced by *Sphagnum* (Ratcliffe & Walker 1958). None the less, the effects on growth were, on the whole, smaller than those when water table or shade were varied. Growth in weight and
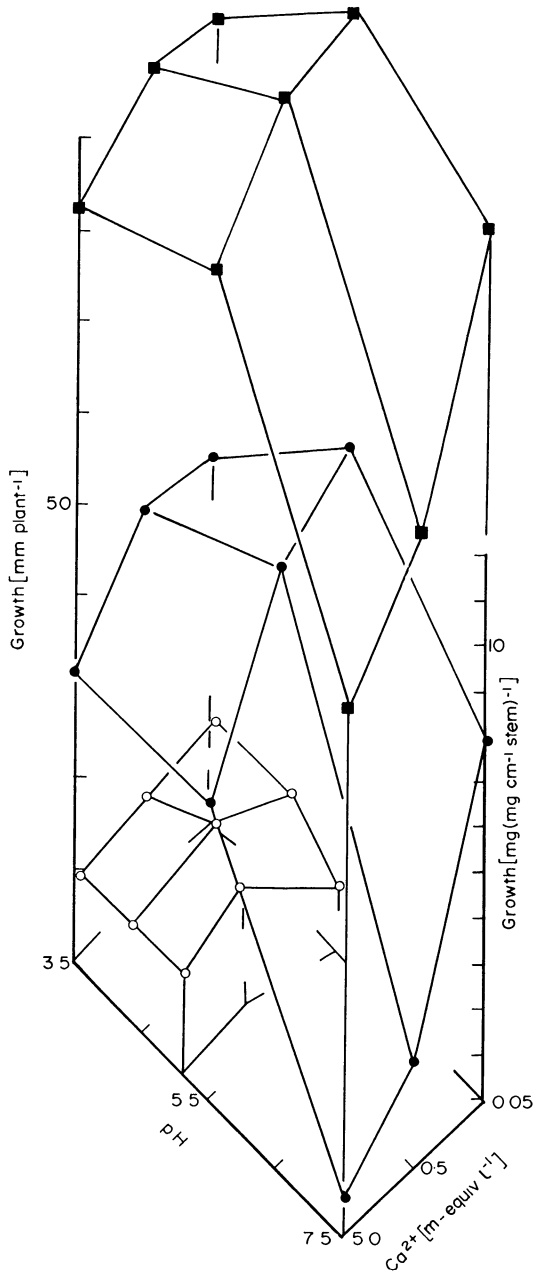
FIG. 2. Growth in length (■, and left-hand vertical axis) and growth in weight (●, and right-hand vertical axis) of *Sphagnum* in various chemical conditions. The smaller block of weight growth results (○) is repeated from Fig. 1; the rest are from experiment II(a). See text for details.

in length were affected about equally, so there were no obvious changes in plant morphology (as there were when water table or shade were varied). The most obvious feature (Fig. 2) is that raising the pH or the Ca^{2+} concentration separately to unnaturally high levels had little effect but raising both together was for some species lethal, and for most

caused much reduction in growth. The same tendency was clear even where the plants were not killed.

In Table 6 the order of species is of increasing susceptibility to high pH and high Ca^{2+} concentration in these experiments. This mirrors the order in which the species would be placed on the basis of field behaviour, with the exception of *S. magellanicum* which is perhaps more often a species of flushed areas (Newbould 1960; Chapman 1964).

Olsen (1923) also found *S. subsecundum* to be less affected by high pH than were *S. rubellum* and *S. magellanicum* in experiments during which the solution level was kept 2 cm below the capitulum. However, one is even more uncertain what the pH around the capitulum was in his experiments.

Table 4. *Analysis of variance of growth in length, and of growth in weight (bold figures) of* Sphagnum *in various chemical conditions (experiment Ib)*

Treatment	Degrees of freedom	Mean square				F
Ca^{2+} (A)	2	1·71	**1·87**			**2·20**
pH (B)	2	0·68	**1·43**			**1·69**
Species (C)	11	8·35	**42·8**			**50·5***
Interactions AB	4	0·754	**1·06**	28·9***	**1·24**	
AC	22	0·108	**1·57**	4·12***	**1·84***	
BC	22	0·050	**0·80**	1·90**	**0·94**	
ABC	44	0·037	**0·98**	1·43	**1·16**	
Error	216	0·026	**0·85**			

See Table 2 for conventions on significance levels.

Table 5. *Analysis of variance of growth in length and of growth in weight (bold figures) of* Sphagnum *in various conditions (experiment IIa)*

Treatment	Degrees of freedom	Mean square				F
Ca^{2+} (A)	2	0·66	**12·1**			
pH (B)	2	1·15	**22·7**			
Species (C)	7	0·21	**19·0**			
Interactions AB	4	0·23	**4·5**	43***	**15·5***	
AC	14	0·012	**0·91**	2·2*	**3·1***	
BC	14	0·029	**2·22**	5·3***	**7·7***	
ABC	28	0·0077	**0·76**	1·4	**2·6***	
Error	72	0·00540	**0·290**			

See Table 2 for conventions on significance levels.

Experiment II(b)

The statistical significance of the effect of variation in supply of solutes was not great (*P* about 0·06), but this analysis takes no account of the regression of growth on solute supply (Fig. 3). The treatment with flowing distilled water could not be quantified as too few analyses were available to allow reliable estimates of the amount of solutes removed. The chance of getting the growth ranked in the same order as supply is only 1 in 720. Differences between species were small.

Table 6. *Mean values of growth in length and of growth in weight (bold figures) of Sphagnum grown in various chemical conditions (the outer columns are expressed as a percentage of the central ones (those in parentheses); experiment IIa)*

Species	3·5 Percentage of pH 5·5 result	pH 5·5 (100 =) (mm)	(mg plant⁻¹)	7·5 Percentage of pH 5·5 result	Ca²⁺ m-equiv./l 0·05 Percentage of Ca²⁺ 0·5 result	0·5 (100 =) (mm)	(mg plant⁻¹)	5·0 Percentage of Ca²⁺ 0·5 result
S. subsecundum (var. inundatum)	87	(100)		*82	107	(94)		*81
	90		(11·6)	**88**	**110**		(12·0)	**65**
S. squarrosum	88	(113)		85	106	(102)		96
	65		(34·0)	**87**	**105**		(27·1)	**93**
S. plumulosum	85	(98)		*73	115	(83)		88
	84		(6·2)	**60**	**93**		(5·8)	**67**
S. recurvum	89	(112)		*73	100	(104)		*81
	95		(18·0)	**48**	**102**		(17·7)	**47**
S. papillosum	88	(92)		*75	115	(80)		87
	65		(12·6)	**27**	**150**		(8·8)	**34**
S. rubellum	86	(87)		*72	114	(73)		95
	110		(2·9)	***10**	***308**		(1·2)	**58**
S. magellanicum	91	(91)		*70	118	(78)		86
	86		(4·3)	***9**	***477**		(1·3)	**69**
S. cuspidatum	92	(104)		*60	117	(83)		93
	81		(6·9)	***7**	**128**		(3·2)	**41**

* 0·05 ⩾ P > 0·01
** 0·01 ⩾ P > 0·001 } for comparison with pH 5·5 or Ca²⁺ 0·5 m-equiv./l result.

Experiment III

The 'desiccation tolerance' experiments gave the results shown in Fig. 4. The species are arranged in order of decreasing tolerance in this test.

Results for survival over distilled water have been excluded because all but 8 (out of 700) of the capitula in this treatment became covered by fungi, and disintegrated when touched. Conditions in these containers were very favourable for fungal growth. It is almost certain that the plants in the other humidities had fungi on them too, so one of the effects of lowering humidity might be to change the balance between fungus and *Sphagnum.* However, this would be in the wrong sense to account for the reduction of survival at lower humidities and, since the results for proportional humidity 1·00 caused serious statistical problems, they have been omitted.

The tolerance measures used were, first, ability to restart growth and second, retention of green colour in some branches. The two measures of tolerance gave similar results, though the proportion remaining green was always greater than that showing renewed
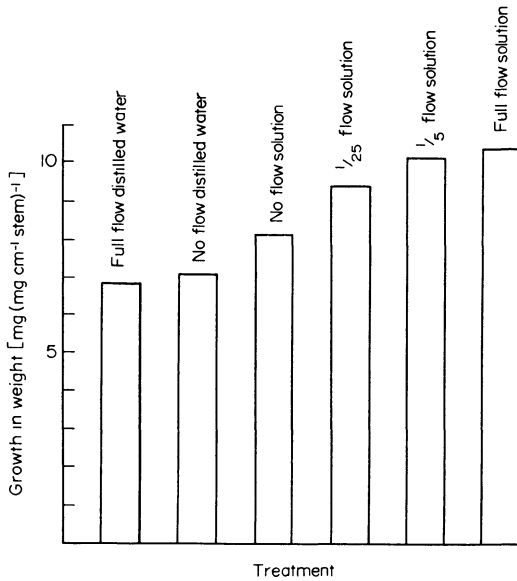

FIG. 3. Growth in weight of *Sphagnum* in various rates of solution supply and type: experiment II(b). See text for details.

growth. This agreement is important, since it might be argued that the difference between species is due to differences in the degree of protection of the apical cell. If this cell were covered by many overarching leaves and branches, it is possible that, though the change in weight had become erratically positive and negative, the water potential around the cell was still much higher than the average for the whole capitulum: that equilibrium had not been reached. (Even if this were so, the results would provide a useful comparison of species.) The cells which were assessed for the measure of greenness were, however, on the outside of the capitulum and might be expected to be. much nearer equilibrium. The humidities were such that the hyaline cells, which have pores more than 1 μm radius (Fig. 4) would be expected to be empty, and the whitish, papery appearance of the branch leaves showed that this was indeed so. The 'live' or 'enclosed' cells do not appear to have apertures 0·05 μm or larger in their walls and should have remained full of water, though

under tension, even at 0·981 humidity. If the plants had not reached equilibrium, one might expect too that the survival of larger capitula would be greater than that of smaller ones (though the tightness of packing of branches would be important too). There was though no obvious connection between tolerance and dry weight of capitulum (Fig. 4).

There seems to be no correlation between desiccation tolerance in this experiment and the wetness of the natural habitat of the species concerned. *S. subsecundum*, the most tolerant, normally grows in wet conditions, whilst one of the less tolerant species, *S. rubellum*, usually grows in drier habitats.
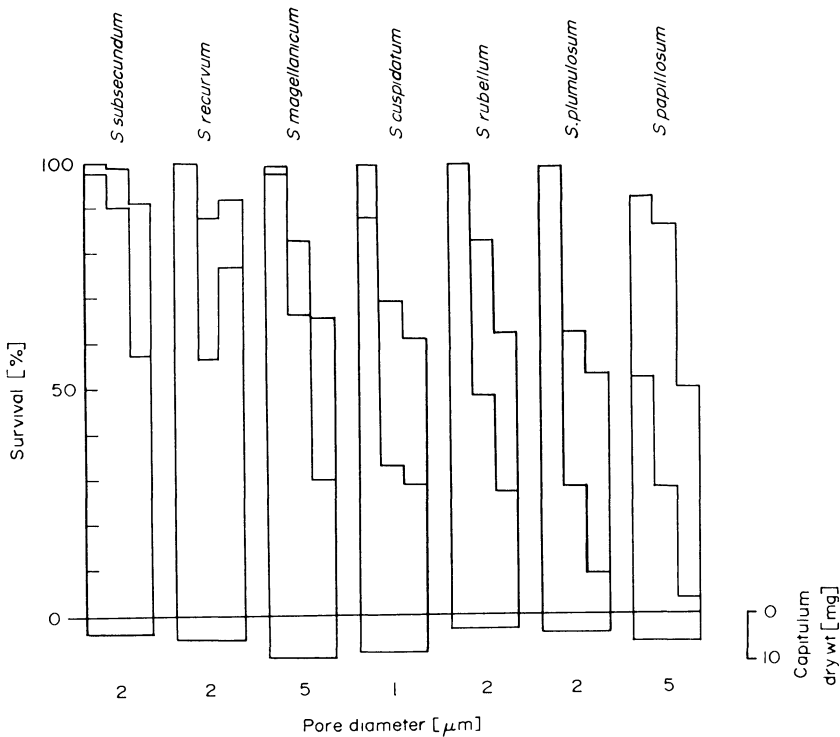

FIG. 4. Survival of *Sphagnum* in various relative humidities (experiment III). The upper blocks are of branches remaining green. The lower ones are of capitula able to resume growth. Below are inverted blocks showing capitulum dry weight, and numerical values of mean pore diameter (μm). The three upper pairs of blocks for each species refer to proportional humidities of 0·998, 0·991 and 0·981 (reading from left to right).

Experiment IV

As might be expected, the rate of water loss (Fig. 5) is reduced if the water table is lowered, but the effect is smaller for the *Sphagnum*-filled beakers than for the empty ones.

The rate of loss for a given water table was most for *S. rubellum*, less for *S. papillosum* and least for *S. cuspidatum*. The proportional effect of lowering the water table was also least for *S. rubellum* and greatest for *S. cuspidatum*.

An analysis of variance showed significant ($P < 0.001$) effects related to 'species' (including the empty beakers), water level, and day, with an interaction between 'species' and water level.

Experiment V

   The water content, in natural conditions, of *S. cuspidatum* and *S. papillosum* growing in pure stands was similar to a depth of 8 cm (Fig. 6). The water content of *S. rubellum* at 8 cm was lower, but declined less rapidly as the apex was approached. The capitulum was
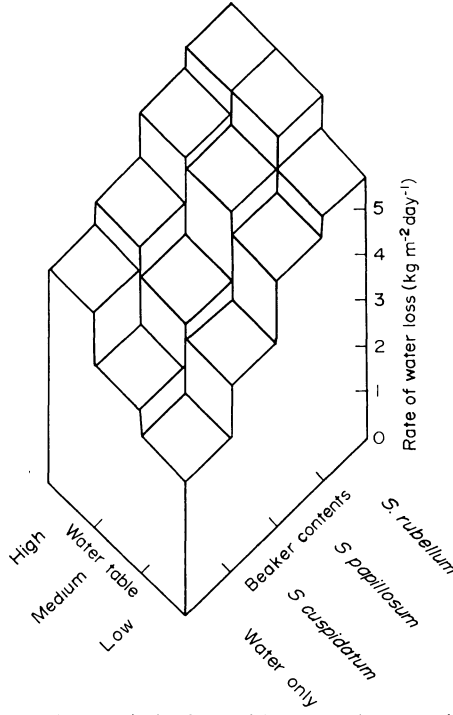

FIG. 5. Water loss from *Sphagnum* in beakers with water table at various levels (experiment IV). See text for details
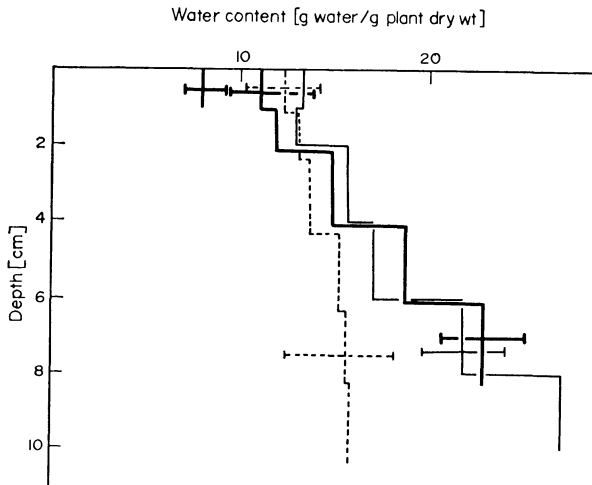

FIG 6. Water content of *Sphagnum* at various depths below the surface (experiment V). Thick lines, *S. papillosum*; thin lines, *S. cuspidatum*; broken lines, *S. rubellum*. Bars show the 95% confidence intervals. The left-most (0–2 cm) *S. papillosum* result is for isolated plants amongst *S. rubellum*.

of similar water content to that of the other species. Isolated *S. papillosum* plants amid *S. rubellum* had a lower capitulum water content.

Experiment VI

One set of measurements of surface roughness is shown in Fig. 7. They are for *S. papillosum* at Cranesmoor. Eight other sets showed similar features. The results shown are of residual variance after fitting (by least squares) a straight line and a cubic to the twenty-five data points. This was done to allow for a general slope or hummock and hollow (on the scale of about 10 cm), since the interest here is in roughness on a smaller scale: about 1 to 10 mm. In this set of results the only site showing much reduced variance after fitting a cubic was the −28 cm one, which did indeed span a hollow and hummock.
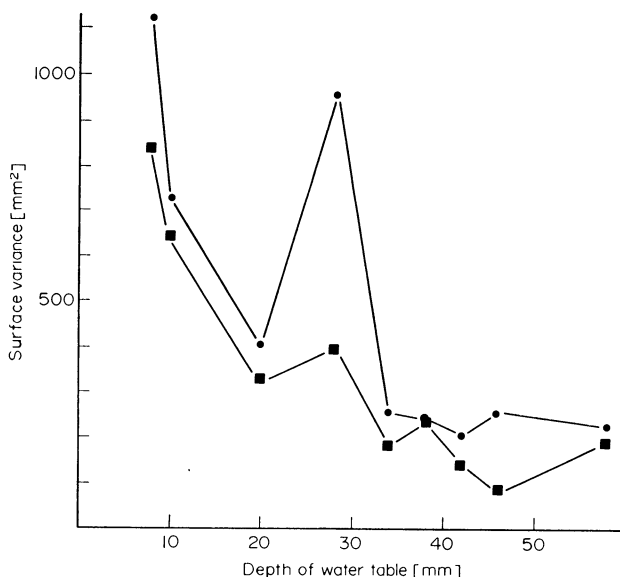

FIG. 7. Surface variance of *Sphagnum papillosum* relative to water-table depth (experiment VI). Each point is based on twenty-five samples. Polynomials of degree 1 (●) and 3 (■) were fitted, and the residual variance is plotted. The site with water table 28 cm below the surface showed an S-shaped profile, as it spanned a small hummock and hollow. Fitting a cubic equation reduces the residual variance considerably. For the other sites this effect is less marked.

DISCUSSION

The conditions in these experiments were neither completely controlled nor entirely natural. The shade treatment, for example, had little effect on the spectral composition of the transmitted radiation, and the shade differences were confounded with temperature differences (positive or negative at different times). There is, however, no such thing as a completely unconfounded treatment, and it is assumed here that the shade and water-level effects are similar in broad outline to the effects which would be produced in natural conditions. The chemical treatments (pH, Ca^{2+} and flushing) were more different from natural conditions because of the difficulties caused by cation exchange. The rate of supply of solution in the second set of experiments was much greater than in natural ombrotrophic conditions but the results of the flushing experiment indicate that the effects of this difference are relatively small. The fluctuation of the water table, and consequently of capitulum water supply, in this experiment was also unnatural, as it was too in the flushing experiment. The results of the first experiment (with variation of pH and Ca^{2+}

concentration and more natural conditions) are not, however, contradictory of the results of the second more unnatural though better controlled experiment.

The results of the chemical treatments are in accord, too, with expectation based on field observation. In the field, high pH is almost always associated with high Ca^{2+} concentration, and where this combination of conditions occurs *Sphagnum* is absent. These conditions caused some death of *Sphagnum* in the experiments too. *S. squarrosum*, which survived and grew well in these conditions, is one of the first species to appear when immersion by calcareous water of high pH becomes rarer as a fen increases in height. The ability to tolerate occasional immersion in such conditions, coupled with the ability to make acid (by cation exchange) the small amount of water left around the plants when the flood subsides, could account for the natural distribution of this species. *S. subsecundum*, which was fairly tolerant of high pH and Ca^{2+} concentration in the experiments, is often found in slow-flowing streams and ditches. Here the ability to grow immersed in continually renewed solutions of moderate pH and Ca^{2+} concentration may be more important than that of surviving occasional short immersion in high levels.

The general correspondence of field distribution and experimental results may seem trivial, but such correspondence is certainly not universal (Lloyd & Pigott 1967). One may conclude that the obvious chemical factors could indeed account for the large-scale field distribution.

The second clear conclusion to be drawn is that high pH and high Ca^{2+} concentration are not individually very injurious, though the sharpness of such distinctions must depend very much on the length of the experiment and on the general stress to which the plants are subjected; once plants have died, differences between treatments can be accentuated simply by running the experiment for longer.

It might be thought that the differences between species were related to the cation exchange properties of the cell walls. This seems unlikely, however, since the wall is simply a cation exchange box surrounding the cytoplasm, and would (if the cytoplasm were inert) reach equilibrium with the surrounding solution within a few minutes at most (Clymo 1963). The most the wall could do would be to affect the rate of movement of ions in and out of the cell. Too little is known about the physiology of these plants to make further speculation useful.

Whilst the effects of chemical factors were similar in experiments and in field conditions, the responses to differences in water level were dissimilar. Most species grew better in the drier conditions of these experiments (Table 3). Transplants in fluctuating field conditions may show a different pattern (Clymo 1970; Clymo & Reddaway 1971, and unpublished) with generally greater growth in the wetter habitats but each species growing better than competitors in the habitat which it normally occupies. The range of water level in the beaker experiments (a range determined by practical limitations) was but 10 cm, which is only about one-third of the average range in the field experiments and perhaps a quarter of the natural range (Ratcliffe & Walker 1958). One might expect differences to be accentuated with the larger range.

It is not obvious from these results therefore how the rather clear habitat restriction of the different species in the field is caused. The importance of rare extremes in climate (an 8-week drought occurring perhaps five times a century for example) as determinant of the habitat preference of different *Sphagnum* species is not known at all. 'Desiccation tolerance' is a complicated concept. Green (1968) allowed 5-cm-long groups of *Sphagnum* to dry out at humidity 0·7–0·8 for various times, and then rewatered the plants and recorded the proportion which remained green in the 'apical meristematic regions'. In these

conditions the results would depend not only on the inherent resistance of the cells to low water potentials, but also on the water storage capacity of the plants and on the rate of transport about the plant. No indication is given of the ability to resume growth, which may be an important property too. In the experiments described here an attempt was made to separate the inherent properties of the cells, particularly the apical cell, from the transport properties. (In natural conditions the exact state of the apical cell will probably depend too on the interacting present and past effects of water-table position, rainfall, air humidity, windspeed and the effects of surrounding species. The effects of large diurnal changes of radiation climate, temperature and dew formation will further complicate the problem.) There seems to be no connection between the inherent resistance to desiccation (at least as measured in these unnatural conditions) and the conditions of the habitat in which the species is normally found (Fig. 4).

The ability to transport water to the capitulum in times of rapid evaporation might be of some importance in desiccation resistance. One might expect the evaporation rate to be related to the wetness of the capitula, though making valid measurements of evaporation rate is notoriously difficult. The method used here may, however, be used for comparison between species. The experiments (Fig. 5) indicate that the rate of water loss is related to the normal habitat: least for the pool species and most for the hummock species. Lowering the water table accentuates the differences, as Overbeck & Happach (1956) found too. It is surprising though that there are differences when the water table was only 1 cm below the surface, and Overbeck & Happach report that in such conditions the rate of loss from a pool species of *Sphagnum* was greater than from lawn or hummock species. The containers in their experiments were not randomized at intervals, however, and they had no 'guard rings'.

It is therefore valuable to find that direct measurements (Fig. 6) show that there is some connection between the usual habitat conditions and the rate of change of water content with height above the water table.

The water content of the hummock species *S. rubellum* declines more slowly with height above the water table than does that of the lawn and pool species *S. papillosum* and *S. cuspidatum*. All three have nearly the same capitulum water content, about 12 g g^{-1}, when in their own normal habitat. *S. papillosum* growing amongst *S. rubellum* has a lower water content. These results must be treated with some caution, since the harvesting procedure may have affected the water content; a non-destructive method would be preferable. It is interesting, however, that the optimum water content for net photosynthetic rate of *S. rubellum* (Grace 1970) is about 10–14; below this the rate decreases sharply, above it decreases more slowly (presumably due to limitation by CO_2 diffusion).

The explanation of these differences lies (probably) in differences in the proportion and distribution of capillary spaces in the range 10 μm to 1 mm. The cells and leaves of *S. rubellum* are small and the stem has an investing sheath of pendant branches. In *S. papillosum* the pendant branches are well developed too, and differ markedly in stiffness from the spreading branches. Cell and leaf sizes are larger than in *S. rubellum*, however. *S. cuspidatum* has a relatively poorly developed pendant branch system. These structural differences may be one of the main factors affecting the distribution of the species of *Sphagnum* on a small scale.

Because the rate of water loss is high (about 6 kg m^{-2} day^{-1} corresponding to a depth of 6 mm day^{-1}) it seems likely that in conditions of rapid evaporation movement of water occurs through the capillary spaces among the pendant branches around the stem. If it is

Q

assumed that the cross-sectional area of this path is 0·01 of the total carpet area (which is probably an over-estimate), the average flow velocity would be about 0·4 mm min^{-1}. During the middle of the day the rate might be much greater. If a rate of four times the average is assumed, then from Stokes' law, spheres of density 1·5 g cm^{-2} (that of carbohydrate) and of radius 5 μm could be kept in suspension. Smaller spheres would move upwards. This might then produce differential sorting by 'upwash' of pollen and spores. The necessary climatic conditions are not common in peatlands though.
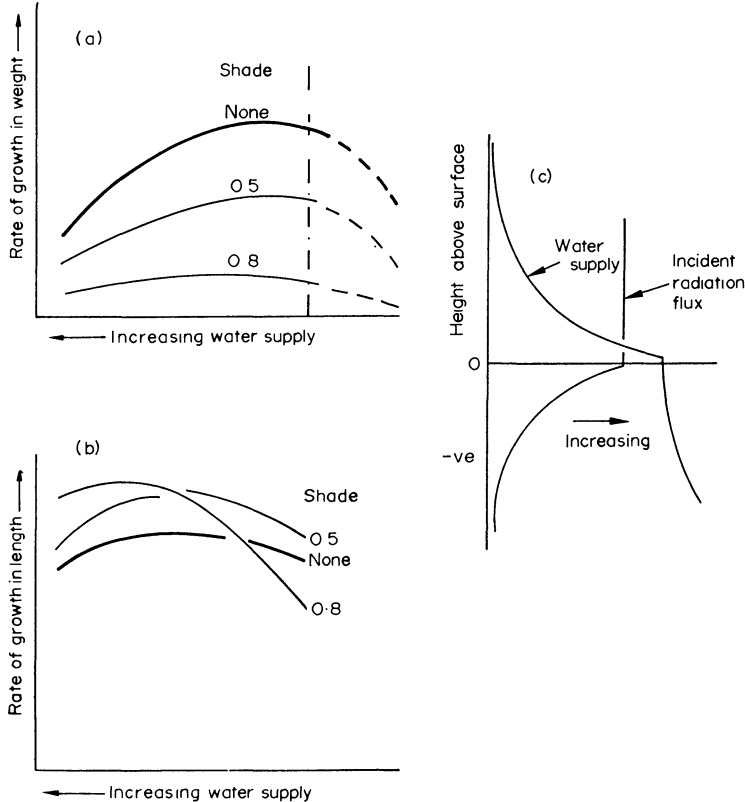

FIG. 8. Idealized diagram, based on results for *Sphagnum papillosum* and *S. magellanicum* in experiment I, to show responses of *Sphagnum* growth in weight (a) and growth in length (b) to change in incident radiation flux and water supply. The variation of incident radiation flux and water supply relative to the surface of the *Sphagnum* carpet is shown in (c).

One predictable consequence of the results of the experiment with variation of water table and shade is that the surface roughness of a *Sphagnum* carpet should be smaller the higher it is above the water table.

Consider a level lawn of *Sphagnum*. The growth responses as a function of position relative to the carpet surface are shown (idealized) in Fig. 8. Responses on the left have been shown in these experiments. Reduction of net photosynthesis by *Sphagnum* in dry conditions has been shown by Stålfelt (1938) (and for *Rhacomitrium lanuginosum* by Tallis (1959)) and the complete curve has been shown by Grace (1970).

For small distances (about 0·01 m) below the surface, water supply may be considered to be nearly constant, but incident radiation flux declines (Fig. 8c). For small distances

above the surface the reverse is true, incident radiation flux is constant, but 'water supply' decreases rapidly. This last point is supported by two observations. In glasshouse conditions when evaporation is rapid, emergent *Sphagnum* capitula often dry out (becoming white and papery) whilst the lawn around remains damp. If the lawn is watered only from below, then the tips of the exposed branches gradually accumulate a brown tarry deposit. This can be redissolved in water and has an absorption curve from 0.29 μm to 15 μm which is very similar to that of peat water from below the plants. The tarry deposit forms probably because the rate of supply of these brown compounds in the mass flow of liquid upwards considerably exceeds the rate of their diffusion downwards. Calculation of the magnitude of this effect is not simple (Briggs 1967). These deposits may sometimes be seen in natural conditions after long periods without rain. In experiments, the deposits are greatest on the emergent plants and on isolated emergent branches, indicating a more rapid rate of evaporation from these plants.

If, in a level lawn, a *Sphagnum* plant grows faster than its neighbours, it will move into a different water supply environment. If the water supply to the main lawn is high, movement above the lawn will result at first in a small increase in length growth rate, and a larger one in dry matter growth rate. Either or both the area occupied and the density

Table 7. *Variance of growth in length of* Sphagnum *in various water-table and shade treatments (experiment Ia)*

(A) Water table (cm)	−10	−3	0
(B) Shade (percentage of day-light absorbed)			
0	0·28	1·11	1·26
0·45	0·43	1·28	1·85
0·82	0·77	1·58	4·42

of branches must increase. The increase in length growth will accentuate the difference between the plant and its neighbours. Because the water supply profile is telescoped above the surface, the emergent plant will soon enter the region of declining length growth rate, and will eventually be growing in length at the same rate as the level carpet, but a few millimetres above it. Whether or not the area occupied by the plant (or the branch density) increases will depend on the relative position and shape of the curves in Fig. 8(a, b).

If the water supply to the lawn is already low, the emergent plant immediately enters the region where length growth rate is lower, although again dry matter growth rate may be greater, leading to larger individuals. The effect of this would be that surface roughness would be less as water supply decreases, but individual plants cover a larger area, or fill a partly occupied area more densely. Both these expectations were fulfilled in the laboratory experiments (Fig. 1 and Table 7) and in field conditions (Fig. 8). There is an inverse relationship between surface roughness and height above water table.

A second mechanism may reinforce this reduction of surface variance. If a plant grows in length more slowly than its neighbours, it moves into a different radiation climate (Fig. 8c), though water supply is not much altered. (This contrasts with the situation when a plant grows faster than its neighbours.) If water supply is high, the rate of growth in length increases and the plant therefore tends to return to the general level of the lawn, though it it falls behind its neighbours, dry matter growth rate declines, so the area occupied, or branch density, tends to decrease.

If the water supply is low, then the same mechanism operates, but there is an additional feature; length growth becomes reduced at low incident radiation flux, so the plant would then fall behind its neighbours irrevocably.

In summary, rate of growth in length is controlled by two feedback mechanisms, one on each side of the central point. The feedback is negative in most circumstances, but positive at low water supply (below an incident radiation flux limit dependent on water supply) and positive too, but decreasingly so, at high water supply.

This model could be made quantitative, but more detailed information on plant responses is necessary before this would be useful.

ACKNOWLEDGMENTS

SUMMARY

The growth of up to twelve species of *Sphagnum* was measured in experiments with factorial combinations of pH (3·5–7·5) with Ca^{2+} (0·05–5·0 m-equiv./l), and of water table (surface to -10 cm) with shading (none to 0·82). Most plants grew well at low pH and low Ca^{2+}, and nearly as well at high pH or high Ca^{2+}, but the combination of high pH with high Ca^{2+} was lethal to most species. *S. squarrosum* was notably more tolerant than the other species tested. Growth in weight and in length were highly correlated in most of these treatments, except when water supply and shade were the variables. In unshaded conditions growth in weight was greater at lower water-table levels, but water table had little effect if the plants were shaded. By contrast, growth in length was less in low water-table conditions, particularly if the plants were shaded too. The pattern of response of different species to water table and shade was not clearly correlated with field distribution.

There was a positive correlation between growth and supply of inorganic ions (varied concentration and flow rate).

Desiccation tolerance, in an artificial test, showed no correlation with field behaviour, but evaporation rate (used as a measure of supply) and ability to maintain a high capitulum water content did.

The surface irregularity of a *Sphagnum* carpet decreases as the water table falls, and a mechanism to explain this is proposed.

REFERENCES

Briggs, G. E. (1967). *Movement of Water in Plants.* Blackwell Scientific Publications, Oxford.
Chapman, S. B. (1964). The ecology of Coom Rigg Moss, Northumberland. I. Stratigraphy and present vegetation. *J. Ecol.* **52**, 299–313.
Clymo, R. S. (1963). Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot.* N.S. **27**, 309–24.
Clymo, R. S. (1966). Control of cation concentrations, and in particular of pH, in *Sphagnum* dominated communities. *Chemical Environment in the Aquatic Habitat* (Ed. by H. L. Golterman & R. S. Clymo), pp. 273–84. North Holland, Amsterdam.
Clymo, R. S. (1970). The growth of *Sphagnum*: methods of measurement. *J. Ecol.* **58**, 13–49.
Clymo, R. S. & Reddaway, E. J. F. (1971). Productivity of *Sphagnum* (bog-moss) and peat accumulation. *Hidrobiologia*, **12**, 181–92. (Available as Moor House Occasional Paper no. 3).

Grace, J. (1970). *The growth-physiology of moorland plants in relation to their aerial environment.* Ph.D. thesis, University of Sheffield.

Green, B.H. (1968). Factors influencing the spatial and temporal distribution of *Sphagnum imbricatum* Hornsch. ex Russ. in the British Isles. *J. Ecol.* **56**, 47–58.

Harper, J. L., Williams, J. T. & Sagar, G. R. (1965). The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *J. Ecol.* **53**, 273–86.

Hodgman, C. D., Weast, R. C. & Selby, S. M. (1961). *Handbook of Chemistry and Physics*, 43rd edn. Chemical Rubber Co., Cleveland.

Lloyd, P. S. & Pigott, C. D. (1967). The influence of soil conditions on the course of succession on the chalk of southern England. *J. Ecol.* **55**, 137–46.

Newbould, P. J. (1960). The ecology of Cranesmoor, a New Forest valley bog. I. The present vegetation. *J. Ecol.* **48**, 361–83.

Olsen, C. (1923). Studies on the hydrogen ion concentration of the soil and its significance to the vegetation especially to the natural distribution of plants. *C. r. Trav. Lab. Carlsberg*, **15**, 1–166.

Overbeck, F. & Happach, H. (1956). Über das Wachstum und den Wasserhaushalt einiger Hochmoorsphagnen. *Flora, Jena*, **144**, 335–402.

Ratcliffe, D. A. & Walker, D. (1958). The Silver Flowe, Galloway, Scotland. *J. Ecol.* **46**, 407–45.

Richards, P. W. & Wallace, E. C. (1950). An annotated list of British mosses. *Trans. Br. bryol. Soc.* **1**, Suppl. i–xxxi.

Stålfelt, M. G. (1938). Der Gasaustausch der Moose. *Planta*, **27**, 30–60.

Tallis, J. H. (1959). Studies in the biology and ecology of *Rhacomitrium lanuginosum* Brid. II. Growth, reproduction and physiology. *J. Ecol.* **47**, 325–50.