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THE GROWTH OF *SPHAGNUM*: EXPERIMENTS ON, AND SIMULATION OF, SOME EFFECTS OF LIGHT FLUX AND WATER-TABLE DEPTH

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SUMMARY

(1) Experiments were made to determine the effects of both shading and of water-table depth on the growth of three species of *Sphagnum*. The species (and their usual habitats) were: *S. capillifolium* (hummocks); *S. papillosum* (lawns); and *S. recurvum* (pools and flushed lawns).

(2) Water-table depth had little effect on growth measured as increase of dry matter; shading reduced growth and there were specific differences associated with plant size. There were no significant interactions between water-table depth and shading.

(3) For growth measured as growth in length, there were highly significant interactions, individual species behaving differently in response to shade and, to a lesser extent, in response to water-table depth.

(4) In *Sphagnum* lawns in two natural habitats there was a negative correlation between depth of the water-table and surface-roughness. In experimental conditions surface-roughness increased both as the water-table was raised and as shade increased.

(5) A computer simulation of growth of *Sphagnum* in a lawn was able to reproduce the observed variations in surface roughness. In mixed lawns of two species, the one in its 'natural' habitat out-grew the other.

INTRODUCTION

Most attempts to measure the growth of *Sphagnum* have been concerned with obtaining values of productivity (e.g. Leisman 1953; Overbeck & Happach 1956; Pearsall & Gorham 1956; Bellamy & Rieley 1967; Clymo & Reddaway 1974; Ilomets 1974; Pakarinen 1978). Relatively few attempts have been made to measure growth in relation to the environment. Some of these (Chapman 1965; Clymo & Reddaway 1971; Boatman 1977) have entailed transplanting *Sphagnum* from one position to another in the field. Other studies, by Green (1968) and Clymo (1970, 1973) have included laboratory or garden experiments in which the environment was more precisely controlled, but only in a limited way.

The aim of the work presented here was to obtain more precise details about the growth of *Sphagnum* in relation to its environment. From this information, a quantitative model of the growth of a *Sphagnum* carpet was developed.

The earlier work indicated that two environmental variables—light flux and water supply—have an overriding influence on growth. Total light flux is important, but so is the variation of incident flux on a small scale, between one individual *Sphagnum* plant and another in a single lawn. These effects may be due to 'external' shading by larger, vascular plants or to 'self-shading' by neighbouring *Sphagnum* plants.

Water supply to the capitulum (the apical tuft of expanding branches) has been shown to depend, in a complex way, on the structure of the *Sphagnum* plant (which differs among

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species) and on water-table depth (Hayward & Clymo 1982). In general, however, water supply is inversely related to the depth of the water-table and, for a given water content in the capitula, the water-table will be at a greater depth below hummock species than it will be below lawn species. Thus, water-table depth can be used as a convenient, and easily measurable way, of expressing water supply.

Bogs have a water-table which is, compared with most terrestrial habitats, relatively close to the surface. The distribution of species appears to be related to the depth of the water-table (e.g. Ratcliffe & Walker 1958; Clymo & Hayward 1982). This implies that changes in the depth of the water-table will affect plants of different species in different ways, complicated by the fact that the water-table is not a plane surface beneath the hummocks, lawns and pools of the microtopography (Popp 1962; Goode 1970; Boatman, Goode & Hulme 1981). Because the water-table is close to the surface, small changes in its depth have a proportionally greater effect on bog plants than they would if the water-table were at a greater depth.

Both light flux and water-table depth were therefore controlled in these experiments and were included in the model of *Sphagnum* growth. The model had several quantitative consequences. Of these, the one which can most easily be measured in the field is the surface roughness of a *Sphagnum* carpet. There is some indication (Clymo 1973) that this is negatively correlated with depth of the water-table. Here we report measurements of surface roughness both in the field and in experiments.

THE SPECIES USED IN EXPERIMENTS

Plants of three species, *S. capillifolium**, *S. papillosum* and *S. recurvum*, were used in experiments. These species are typically associated with different bog microhabitats. *Sphagnum capillifolium* is naturally a species of drier areas such as hummocks, *S. papillosum* forms lawns at a height intermediate between bog pool and hummock, at or just above the water-table, and *S. recurvum* is found in pools and wet flushed lawns.

METHODS

Growth in relation to light flux and water-table depth

An experiment was made with plants of the above three species collected from Moor House N.N.R., Cumbria, from the areas around Burnt Hill and Bog End (National Grid references NY 753329 and NY 765329 respectively) growing in pots in a garden in London. It included treatments, for each species, of factorial combinations of five depths to the water-table (0, 3, 6, 10 and 14 cm below the surface) and five degrees of shade (absorbance of 0, 0.54, 0.80, 0.91 and 0.96 of incident light). We chose to use shade, with the consequent fluctuations in irradiance, rather than constant artificial light partly for convenience, and partly because we wanted to be able to relate the results to field behaviour.

Plants were cut initially to (known) length, sufficient to allow all cut ends to be at least 1 cm under water at the start of the experiment (Table 2). The lowest 1 cm of each plant was stained with a cationic dye (crystal violet) so that any loss during the experiment could be detected. There were no losses. All plants of the same size and taxon were well mixed

* Nomenclature of *Sphagnum* follows that of M. O. Hill (1978); that of vascular plants follows Clapham, Tutin & Warburg (1981).

before being allocated, forty plants to each treatment. The forty plants were tied into loose bundles, so that they could be recovered easily, surrounded by other cut but unmarked plants (to reduce edge effects) and packed at natural density into pots made from square section 2-litre plastic bottles by cutting off the top part leaving a 10-cm square, 20-cm tall container with straight sides. The shorter plants were placed on an underlying bed of chopped *Sphagnum* to bring the capitula of the plants in all treatments to the same level in the pot. The apparatus shown at the top of Fig. 1 was used to pack the plants in the pots. The left container was a sliding fit inside the right one. The plants were packed as shown and the left container plus plants slid into the right container. The left container was then withdrawn with the string while the piston held the plants in position in the right container. The filled pots were close packed on a flat level surface and were surrounded by a 'guard ring' of other pots filled with *Sphagnum* on which no measurements were made. The experiment lasted for 77 days from 17 June. During this time the orientation and position of the pots was changed randomly each week according to a Latin square arrangement.

The water level in each pot was maintained through a tube inserted into its base (Fig. 1). The tube was attached to a device which kept the water level constant either by allowing excess rain to run away or by adding distilled water. With this arrangement there was no obvious accumulation of evaporites at the surface of the plants. As the plants grew, the pots were lowered to maintain the water-table at a constant depth below the surface of the *Sphagnum* lawn in each pot.

The pots were individually shaded by covering them with 0, 1, 2, 3 or 4 layers of black polyester gauze. The absorbance of light by this material was measured on a recording

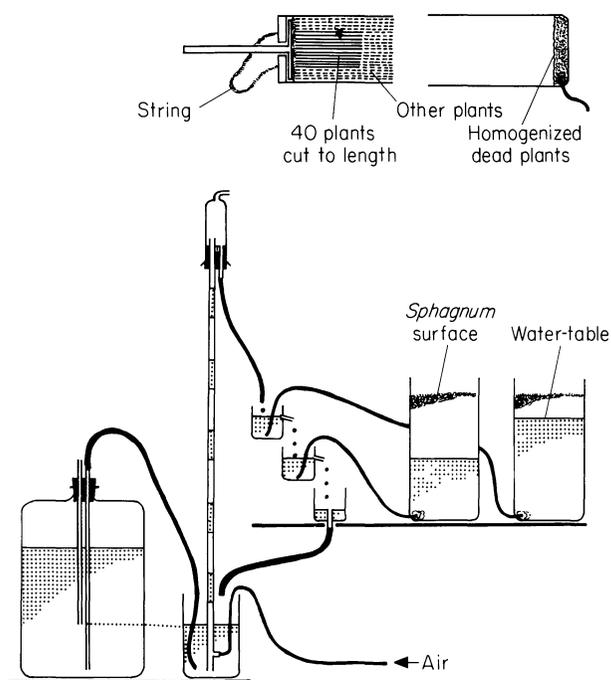


FIG. 1. Method used to maintain a constant water level in pots during the growth experiment. Only two of the five levels are shown. Water was cycled by raising it on a stream of air bubbles in a vertical glass tube. The 25-litre Mariotte bottle was refilled with distilled water as required. The upper diagram shows the apparatus used to pack plants in containers.

spectrophotometer. Between wavelengths of 350 nm and 1000 nm it was nearly independent of wavelength with an average value, between 400 nm and 700 nm, of 0.337. The absorbance of multiple layers was close to additive. The gauze did affect the rate of evaporation of water; the rate with gauze was about 20% below that without gauze. But the rate at which water moves up *Sphagnum* is high (Clymo & Hayward 1982) so it seems unlikely that the water supply to the capitula was much affected.

The size of the experiment (seventy five pots, 20 000 plants of which 3000 were cut accurately to size) precluded replication, so second order interactions were used as an estimate of error. If anything, they should tend to over-estimate error. However, in order to obtain more information about the types of error involved, a further fifteen pots were set up. All these contained *S. capillifolium*, all had a water-table 3 cm below the surface and all had one layer of gauze shading. Three harvests were made; after 5, 36 and 45 weeks.

At harvest, two types of measurement of growth were made: length and mass. Increase in length was measured directly with a ruler. Increase in dry mass was measured using the 'capitulum correction method' of Clymo (1970). The new growth was cut off together with an extra 1 cm to include all the original capitulum. From the dry mass of this material was subtracted an estimate of the mass of the original capitulum based on a linear regression between capitulum mass and the mass of a unit length of stem immediately below it. This method allows for changes in the size of the capitulum during the experiment and for material carried upwards by internode extension within the original capitulum.

The results of growth in mass were expressed in two ways: as growth per plant and as growth per mass of unit length of fully elongated stem (the section from 1–4 cm below the apex when the experiment began). The latter was used as a means of comparing plants, particularly those of different species, with different sized apices; stem mass is correlated with capitulum mass and hence with apex size (Clymo 1973). This procedure also reduced variability between individuals. During the experiments a few plants forked. The proportion doing so was about 0.01, and the two axes of such plants were treated as a single individual.

Fitting surfaces to results

Where required, multi-dimensional surfaces described by polynomial equations (detailed in the relevant places) were fitted to experimental results by minimizing a badness of fit function, g . The function was the sum of squared deviations from the measured values. Arbitrary values of the polynomial coefficients are chosen and the value of g calculated. New values of the coefficients are then chosen in such a way as to reduce the value of g . The process continues until no further reduction of g can be obtained. A more detailed description is given by Clymo (1978). The SIMPLEX option (Nelder & Mead 1965) of the CERN program MINUITS (library D506, D516) was used to locate minima and the MIGRAD option (using Davidon's 1968 method), which is extremely fast near a minimum, to refine the estimate.

Surface roughness in the field

Surface roughness was estimated by the point frame ('shoe-box') technique, as the variance of height (Harper, Williams & Sagar 1965; Boorman & Woodell 1966) after removal of larger scale (5–10 cm) topographic surfaces (Clymo 1973). A set of thirty-two light-weight 10 cm long pointers (culms of *Deschampsia cespitosa*) were supported vertically and parallel in holes in two horizontal pieces of stainless steel gauze. The pointers were arranged 8 mm apart in each direction in a 4 × 8 rectangular grid. Measurements of

surface height were made by photographing the tops of the pointers against a graph paper background. Pointers and camera were mounted on an aluminium frame incorporating a mirror at 45° angle which allowed the camera to be pointed downwards to record horizontal views of the pointers.

The results given are of residual variance in height after fitting a surface, with 25 degrees of freedom, of the general form $z = a + bx + dx^2 + ey^2 + fxy$ to the heights of the pointers (x and y are the two axes of the rectangular grid; z is the height above an arbitrary zero; a to f are parameters). A surface of this nature was fitted for two reasons: the frame holding the pointers did not have to be horizontal, and topographic features on a scale of about 10 cm were ignored whilst keeping the small scale (1 cm) roughness (Clymo 1973). Each frame thus gave a single value of roughness.

Field measurements were made at random points within an area chosen because it was occupied by a carpet of the required species of *Sphagnum* at about the required height above the water-table. Garden measurements were made on the centre of experimental cores.

Surface roughness in experiments

Cores, 30 cm in diameter, of *S. capillifolium*, *S. papillosum* and *S. recurvum* were collected with a stainless steel cutter from Coom Rigg Moss N.N.R., Northumberland and Brishie Bog on the Silver Flowe N.N.R., Galloway (National Grid references NY 690796 and NX 447833, respectively). Care was taken to disturb the cores as little as possible, and surface disturbance was negligible. The cores were maintained outdoors, as described for the growth experiment, with factorial combinations of two depths of water-table (3 cm and 15 cm below the surface) and two degrees of shade (absorbance of 0 and 0.80, from 0 and 2 layers of gauze respectively). Two cores (one in the case of *S. recurvum*) were allocated randomly to each treatment, one core from each site. No subsequent differences in surface roughness attributable to origin were observed. Vascular plants growing above the level of the *Sphagnum* capitula (mainly *Calluna vulgaris*, *Eriophorum angustifolium* and *E. vaginatum*) were cut off periodically and measurements of surface roughness made, with the apparatus already described, at intervals for a year.

RESULTS

Growth in mass and length in response to shade and water-table

The growth of plants in the extra fifteen *Sphagnum rubellum* pots is shown in Table 1. Variability in measurements of growth in both length and mass was related to the amount of growth. For these pots and all the others in the experiments (ninety in all) there was an

TABLE 1. Growth of *S. capillifolium* plants in pots (see text). The experiment began in September. Harvests were made in October (after 5 weeks), May (after 36 weeks) and July (after 45 weeks). Values are the mean for five pots except those for growth in length which are the mean for all individual plants in five pots (about 200 in all). Values in brackets are standard errors of the mean.

	Harvest after (weeks)		
	5	36	45
Growth in length (cm)	1.30 [0.04]	3.48 [0.06]	6.53 [0.21]
Growth in dry mass (mg)	1.62 [0.38]	4.10 [0.50]	8.17 [1.47]
Etiolation (cm mg ⁻¹)	0.97 [0.25]	0.91 [0.15]	0.97 [0.15]

approximately linear relationship ($r = 0.81$) between standard deviation and mean growth in length of plants. A log transformation was therefore applied to all the results before statistical analysis. This transformation had the incidental effect of reducing the coefficient of variation from a mean of 35% to 17%.

A second important result from the extra pots was that the morphology of the plants, measured as etiolation (quantified as growth in length divided by growth in mass), did not change between harvests. This implies that the time scale of the main experiment was not critical; the same relative results would have been obtained with experiments of different length.

Dry matter increase in the main experiment is shown in Table 2. Water-table depth had little effect, shading reduced growth and there were specific differences (associated with plant size). None of these effects are surprising as they agree in general with the results of other less detailed experiments (Clymo 1973). There were no very significant interactions.

Growth in length showed highly significant interactions however (Table 2); individual species behaved differently in response to shade and, to a lesser extent, in response to water-table depth (Fig. 2). For all three species there was an 'optimum' shade and for *S.*

TABLE 2. Mean values of growth of three species of *Sphagnum* in the pot experiment carried out in a garden in London, on the effects of shade and water-table depth on growth. Values have been back transformed from logarithms. For details of treatments, see text. Values in parentheses indicate length (cm) to which plants were cut at the start of the experiment. Italic values in brackets are *F* values from an analysis of variance. Mean values for the main effects on growth in length are not given because the interactions are significant. The interaction mean values are shown in Fig. 2.

		Degrees of freedom	Mass (mg plant ⁻¹)	Growth in Mass (mg(mg cm ⁻¹ stem ⁻¹) ⁻¹)	Length (cm plant ⁻¹)
Species		2	[85.2***]	[40.1***]	[52.7***]
<i>S. capillifolium</i>			3.0	6.2	
<i>S. papillosum</i>			8.5	7.3	
<i>S. recurvum</i>			6.2	13.1	
Shade Layers	Absorbance	4	[39.2***]	[32.7***]	[26.2***]
0	0.00		9.2	14.4	
1	0.54		7.4	12.0	
2	0.80		5.8	8.1	
3	0.91		4.0	6.5	
4	0.96		2.9	4.7	
Water-table depth (cm)	Plant length (cm)	4	[1.1]	[0.7]	[18.8***]
0	(5)		4.8	7.6	
3	(5)		5.4	8.7	
6	(11)		5.4	8.4	
10	(11)		5.9	9.1	
14	(15)		5.6	8.4	
Interactions:					
Species × shade		8	[1.6]	[1.9]	[13.2***]
Species × water-table		8	[1.1]	[2.9*]	[7.2***]
Shade × water-table		16	[1.5]	[1.9]	[2.3*]
Residual mean square		30	0.016	0.018	0.011

* $0.01 < P \leq 0.05$.

** $0.001 < P \leq 0.01$.

*** $P \leq 0.001$.

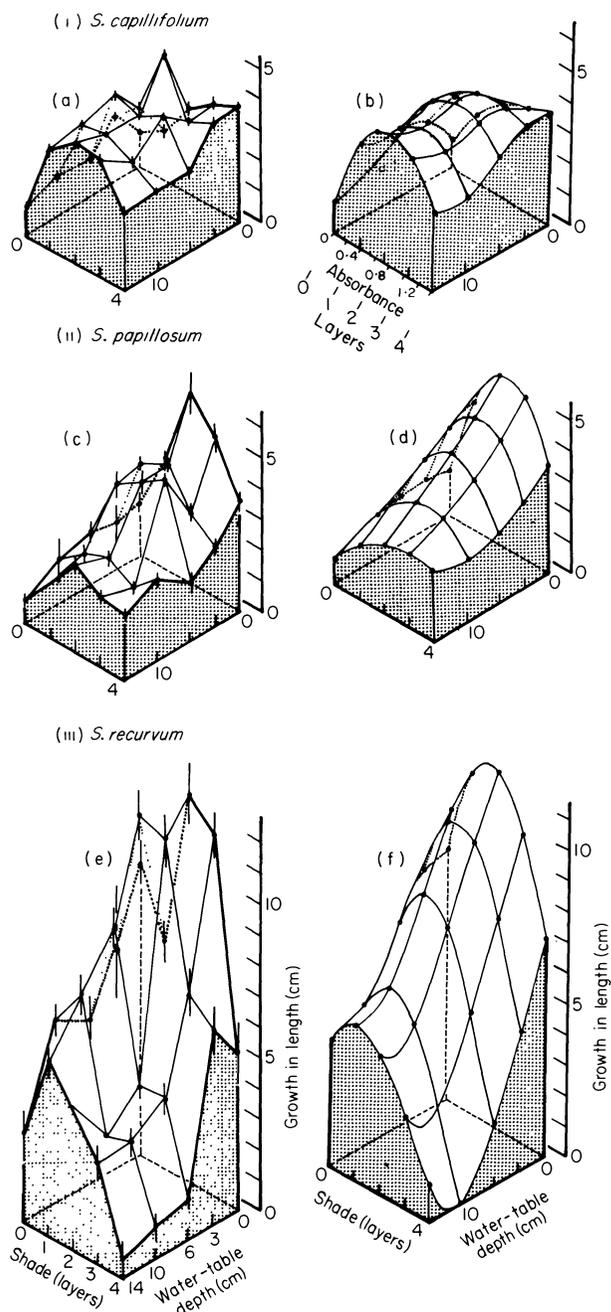


FIG. 2. Growth in length of *Sphagnum* in relation to shade and water-table: (a), (c), (e) growth (bars represent 95% C.L.); (b), (d), (f) surfaces fitted to the results in (a), (c) and (e), respectively, by a least squares fit to the cubic equation

$$L = a + bW + cS + dWS + eW^2 + fS^2 + gW^3 + hS^3 + iW^2S + jWS^2$$

where L = growth in length (cm), W = depth of water-table (cm), S = absorbance of gauze shade, a to j are parameters whose value defines the shape of the surface. The values are estimated by the minimization procedure.

(i) *S. capillifolium*; (ii) *S. papillosum*; (iii) *S. recurvum*.

papillosum and *S. recurvum* a fall in the water-table reduced the rate of growth in length at the shade optimum. In unshaded conditions, water-table depth had a large effect on rate of growth in length of *S. recurvum* and to a lesser extent of *S. capillifolium* but had relatively little effect on *S. papillosum*. These results are again consistent with those of Clymo (1973) and also those of Sonesson *et al.* (1980) who measured the elongation of *S. riparium* (which is in section *Cuspidata* and related to *S. recurvum*) in different degrees of shade.

It is clear that growth in mass and length vary in different ways in response to the treatments. Stem length between branch fascicles increases and branch length decreases (i.e. the plants became more straggling, or etiolated) with either or both greater shade and higher water level. The effects of shade and water depth on etiolation are shown in Table 3.

TABLE 3. Mean values of etiolation (growth in length/growth in mass) for the three species of *Sphagnum* used in a pot experiment, carried out in a garden in London, on the effects of shade and water-table depth on growth. Units of measurement are $\text{cm plant}^{-1} (\text{mg} (\text{mg cm}^{-1}\text{stem}^{-1})^{-1})^{-1}$. Values have been back transformed from logarithms. The main effects of species, shade and water-table are all highly significant ($P < 0.001$).

Layers	Shade		<i>S. capillifolium</i>	<i>S. papillosum</i>	<i>S. recurvum</i>
	Absorbance				
0	(0.00)		0.16	0.11	0.20
1	(0.54)		0.31	0.31	0.41
2	(0.80)		0.53	0.48	0.51
3	(0.91)		0.66	0.63	0.54
4	(0.96)		0.91	0.57	0.29
Water-table depth					
	(cm)				
	0		0.55	0.49	0.65
	3		0.56	0.45	0.51
	6		0.43	0.41	0.37
	10		0.37	0.27	0.28
	14		0.32	0.24	0.20

Surface roughness measurements

Natural conditions

Measurements of surface roughness were made on lawns of *S. papillosum* in field conditions on Brishie Bog on the Silver Flowe N.N.R. and at a site in a pool-and-hummock complex between Bog Hill and Spur Hill at Moor House N.N.R. (National Grid reference NY 771328). The results from both sites (there was no significant difference between the sites) are shown in Fig. 3. A negative correlation between variance and depth of water-table was found but the relationship was not linear. A plot of log variance against water-table depth was near a straight line but no functional relationship is implied.

Experiments

By the middle of the growing season following that in which the cores were collected (44 weeks from the introduction of the water level and shade treatments) values of surface roughness were as shown in Table 4. There were significant effects attributable to species, shade and water-table depth and there was also a significant interaction between species and shade. These trends continued throughout the growing season; both shading and

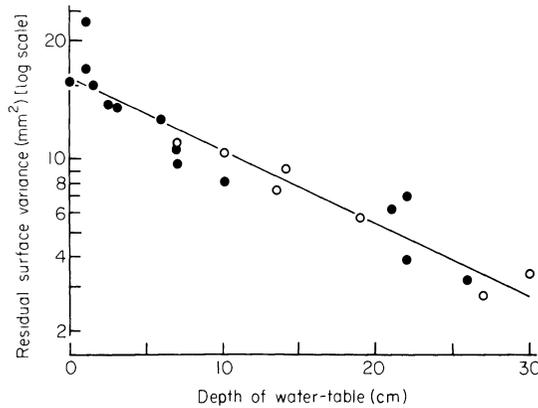


FIG. 3. Surface roughness of natural lawns of *Sphagnum papillosum* in relation to depth of water-table. The line shows the regression:

$$\log_{10}(y) = 1.33 - 0.0297x; r^2 = 0.90,$$

where y is the residual surface variance (mm^2) and x the water-table depth (cm). (●), Moor House; (○), Silver Flowe.

TABLE 4. Surface roughness, assessed by residual variance (mm^2) of lawns of three species of *Sphagnum* grown in controlled conditions for 44 weeks. Values are the mean of duplicates, but for single measurements for *S. recurvum*. Values in parentheses are light absorbance by shading material. Italic values in brackets are F values from an analysis of variance. The F -value of the interaction species \times shade was [12.3*].

Shade [172***]	Water-table depth (cm) [35**]	<i>S. capillifolium</i>	Species [39**] <i>S. papillosum</i>	<i>S. recurvum</i>
Shaded (0.80)	3	17	33	26
	15	13	27	23
Unshaded (0.0)	3	9	12	19
	15	2	7	10

* $0.01 < P \leq 0.05$.

** $0.001 < P \leq 0.01$.

*** $P \leq 0.001$.

raising the water-table increased the surface roughness of all species although water-table in the range of conditions investigated here had the smaller effect.

A MODEL OF THE GROWTH OF A SPHAGNUM CARPET

The various influences on *Sphagnum* growth are generally considered in isolation. If their overall effect is to be studied they must be applied to the system together and allowed to act together. Two sorts of effect may be imagined:

(i) where the overall effect is that of the application of more than one factor in a simple additive way; or

(ii) where the factors may interact in such a way as to produce a result which is not predictable from the main effects alone.

In the model of a *Sphagnum* carpet, which is now described, measured interactions were included, but all other effects were simple additive ones. The model allows an examination of the consequences of putting the pieces together in a situation where a sufficiently detailed factorial experiment would be too large to be practicable. It also provides some calculated effects which can be checked independently—values for surface roughness are the most obvious.

The model is shown pictorially to the left of Fig. 4 where *Sphagnum* plants are shown growing vertically in a pure lawn which is flat and horizontal with a well defined water-table below it. The capitula are not always all at the same level, however, and so the question must be considered: What happens to an individual if its capitulum is not at the general surface but is either above or below it? To the right of Fig. 4 are shown the radiant flux and the water supply to which the capitulum of such an individual might be subject. Both of the profiles have two distinct parts: one above, the other below the mean surface.

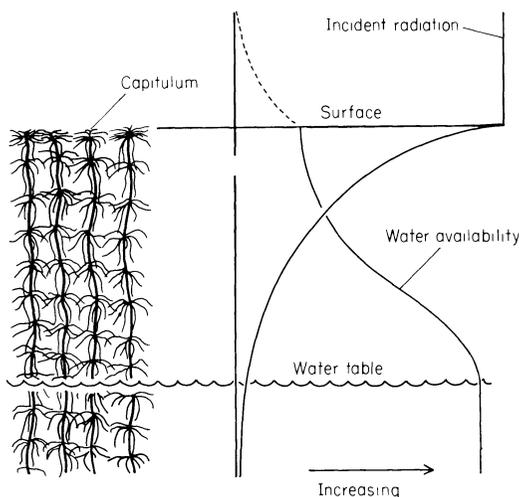


FIG. 4. A conceptual model of a *Sphagnum* lawn with, to the right, profiles of light flux and water availability to the capitulum of an individual which is not growing level with the rest of the lawn and whose capitulum is either above or below the mean surface. The part of the moisture profile shown by the broken line is speculative and has not been demonstrated by experiment.

For short distances above the surface, incident radiant flux is constant at a value determined by the general climate and 'external' shading from vascular plants (*Calluna vulgaris*, etc.). Below the surface, flux falls exponentially with depth or, more precisely, with cumulative dry matter, i.e. Beer's Law can be applied. The slope of the attenuation line depends on the species involved and on the previous history of shading and water-table (Clymo & Hayward 1982); shaded conditions and a high water-table both reduce absorbance, i.e. absorbance is inversely related to 'etiolation' (see above).

The moisture profile between the surface and the water-table depends on several factors including species and the previous position of the water-table. Both hydraulic conductivity and density of the peat also affect supply. There is consequently no simple mathematical description of water supply analogous to Beer's Law for light, although in specific conditions the moisture profile can be described (Hayward & Clymo 1982). Fortunately,

this problem can be avoided by using the results from the growth experiment described above as growth was related to depth of the water-table, not to water supply. Polynomial equations fitted to those results have thus been used in the model to describe growth in terms of both length and dry matter by substituting values for shade (calculated from Beer's Law) and the depth of the water-table below a particular capitulum.

The effect of the height that an individual plant is exposed above the general surface on water supply to, or on growth rate of, the plant, has not been investigated experimentally and is indicated by a broken line in Fig. 4. In the computer model therefore, the amount of growth calculated from the height of the capitulum above the water-table has been modified by multiplying it by a value which was varied to simulate different exposure effects. The exposure effect, E , was determined from a simple exponential function:

$$E = \exp(k \cdot DL)$$

where k is a constant and DL is the height of an individual above the average level of the six surrounding plants (Table 5). (Capitals denote names of variables used in the computer program.) With $k = 0$, the rate of growth was unaffected. By making k positive or negative, the rate of growth could be increased with exposure or decreased.

The components of the model and their inter-relationships are shown in Fig. 5. Most of the model, that part within the box, concerns individual *Sphagnum* plants in the lawn separately. Five parameter values are required besides those describing growth rate and the attenuation of light. These five parameters are listed in Table 5 together with typical values. In the following results the number of plants, n , was set at 25 throughout. These plants were arranged in a 5×5 grid with alternate rows offset by half a column so that each plant was surrounded by six equidistant others. The whole array was wrapped around toroidally to minimize edge effects; i.e. the plants at the left edge are considered as adjacent to those at the right edge, and those at the top as adjacent to those at the bottom.

TABLE 5. Parameters required in the model of *Sphagnum* growth shown in Fig. 5.

Symbol	Description	Typical value(s)	Units
Chosen before each run			
C(1)	Number of plants, n , in the lawn	25	—
C(2), C(3)	k in the equation: $E = \exp(k \cdot DL)$ for effect of exposure on elongation and productivity respectively*	-1.39 (growth halved when $DL = 0.5$ cm)	cm^{-1}
C(4)	External absorption of light by <i>Calluna vulgaris</i> etc.	0 and 0.3 (tested up to 1.0, i.e. 10% transmission)	—
C(5)	Depth of water-table below mean surface level	0-14	cm
Built into the model			
GL(1..10)	Parameters for growth function determining elongation (found from growth experiment)	See Table 6	cm plant^{-1}
GM(1..10)	Parameters for growth function determining productivity (found from growth experiment)	See Table 6	mg plant^{-1}
AC(1..4)	Parameters for function determining extinction coefficient (from Hayward 1980)	See Table 6	—

* DL is the distance of an individual above the mean height of the six surrounding plants (SRND). In Fig. 5, $DL = X(j) - \text{SRND}$. The effect operates only when DL is positive, i.e. the individual is emergent.

TABLE 6. Values for parameters (estimated from measurements, see text) of equations used in the model of *Sphagnum* growth. The two species in the model were: (i) *S. capillifolium* and (ii) *S. papillosum*

Parameter	Length, Z^* (cm plant ⁻¹)		Mass, Z^* (mg plant ⁻¹)		EXT†	
	(i)	(ii)	(i)	(ii)	(i)	(ii)
a	0.79	1.5	1.7	10.9	0.89	0.71
b(W)	0.57	0.097	0.72	1.3	0.085	0.022
c(S)	5.1	10.6	5.5	3.5	-0.73	-0.58
d(WS)	0.057	-0.77	-0.60	-3.6	-0.093	-0.027
e(W^2)	-0.082	-0.014	-0.028	0.027		
f(S^2)	-3.8	-7.2	-9.0	5.2		
g(W^3)	0.0030	0.00026	-0.00030	-0.0069		
h(S^3)	1.2	0.30	3.9	-4.4		
i(W^2S)	0.018	0.018	0.031	0.13		
j(WS^2)	-0.28	0.36	-0.046	1.22		

* 'Growth functions' were polynomial equations, fitted to the results of the growth experiment. They were of the form: $Z = a + bW + cS + dWS + eW^2 + fS^2 + gW^3 + hS^3 + iW^2S + jWS^2$ where W = depth of water-table (cm), S = absorbance of shading plant material, and a to j are parameters whose value defines the shape of the surface. The values are estimated by the minimization procedure. The equations were valid over the ranges 0-14 for W and 0-1.3 for S .

† 'Extinction coefficient' equations (from Hayward 1980) were of the form: $EXT = a + bW + cS + dWS$. The equation is valid only within the range 3-15 for W and 0-0.8 for S . Outside these limits EXT was assumed to remain constant.

rather than cumulative dry matter (Hayward 1980) in order to avoid complicating the model. The extinction coefficient (EXT) was calculated from the mean water-table depth, $C(5)$, and the external shade, $C(4)$ (Hayward 1980). The parameters of these equations are given in Table 6.

When the length of an individual was greater than that of its neighbours (DL positive) the rate of growth was modified to take account of increased exposure as previously explained.

The measurements of surface roughness described above are particularly important in the context of the model because the value of surface roughness is independent of the assumptions made in the model and can be calculated from it. The model calculates surface roughness as the variance of the lengths of all the plants in the model carpet. This measure is similar to that used in the field but not identical; the lengths measured in real lawns were not necessarily those to the apices of discrete individual plants.

The complete model was written in FORTRAN and run as a subroutine of a general program SYSFLO written by one of us (R.S.C.). It controls input, manages iterations for a series of time steps and produces printed and graphical output. Forrester's (1961) conventions were followed. At each iteration, all new values of variables (lengths and weights) were calculated before any rates. The order of individual plants and the order in which the new value of variables was calculated were thus of no importance.

Results from the computer model

The model described in the previous section does not allow for individual variation between plants; all behave in the same way in a particular set of conditions. It could easily be made stochastic, but there is too little known at present to make this worthwhile. The model was therefore 'forced' at the start to simulate individual differences by choosing the initial values so that the lengths (distributed at random) followed a normal distribution with a mean of 0 cm (datum level) and a standard deviation of 0.5 cm. The only exception

was that two plants were set at -1 cm and $+1$ cm respectively (2 S.D.) and the effect of shading and exposure was subsequently recorded in detail for these two plants.

The model was first run with pure lawns of each of *S. capillifolium* and *S. papillosum* and various combinations of the constants $C(2)$ to $C(5)$. The model was tested with depths to the water-table of between 0 cm and 14 cm with absorbance ('external' shade) up to 1.0 (10% transmission; equivalent to a path length through *Calluna vulgaris* of 6–9 cm (Grace & Woolhouse 1972)).

The most noticeable feature of these runs was that the model *Sphagnum* population tended towards one of two states depending on the particular combination of parameters used. The population either went into a steady state with the average rates of growth constant and surface roughness stabilized, or it became unstable with some plants falling irrevocably behind and others growing at an increasing rate away from the mean surface.

Two typical results, showing stable and unstable behaviour, are shown in Fig. 6. There were two sets of conditions under which the model became unstable. The first of these occurred in cases with no external shade, $C(4) = 0$, and with combinations of high water-table and only a small negative exposure effect. The instability was increased when the exposure effect was made zero or positive (i.e. with increased growth above the surface). These unstable conditions were mainly caused by long plants growing away from the surface. This consequence is expected, but such plants are never observed in nature, so it is probable that k is in reality negative.

The model also became unstable when there was some external shade and the depth to the water-table was great. Changing the value of k (positive or negative) in the equation for exposure effect made little difference. In this case the instability was largely due to short plants being 'left behind'. The model was not designed to respond to such events and plants which behaved in this way (and which would have died in reality) simply left a 'hole' in the model lawn. In nature this hole would be filled by sideways movement or growth of neighbours, or by the splitting of apices to produce two plants where before there was one (Clymo & Hayward 1982).

Some of the model results of surface roughness are shown in Fig. 7. The result of changing the exposure effect with no external shade is shown in Fig. 7 (a) for *S. capillifolium*. As expected, the results show a decrease in surface roughness with more negative values of k and also with lower water-tables, with exception of a small (the graph is plotted on a log scale) increase with the lowest water-tables in combination with the most negative values of k . It is improbable that an effect of this size could be detected in the field or in experiments.

The effect on surface roughness of depth of the water-table down to 6 cm and of shading with absorbance of from 0 to 1.0 for both *S. capillifolium* and *S. papillosum* is shown in Fig. 7(b) and (c). *Sphagnum capillifolium* behaved much as it did in reality in the experimental lawns described above (see Table 4). Water-table depth had a similar effect on the surface roughness of *S. papillosum* although it was in general smaller with lower water-tables. Shade had a larger effect, generally increasing roughness, except where the absorbance of light was 0.3 when it was apparently at a minimum. These results do not conflict with those of Table 4 where the effect of shade on *S. papillosum* was much greater than was that of water level.

The model was next run with mixed stands of different species. For these tests the model was arranged with one of the species forming a flat carpet in which were placed two plants of the other species. In various tests these plants were arranged to be either level with the general surface or 1 cm above or below the surface as in previous runs. Figure 8 shows

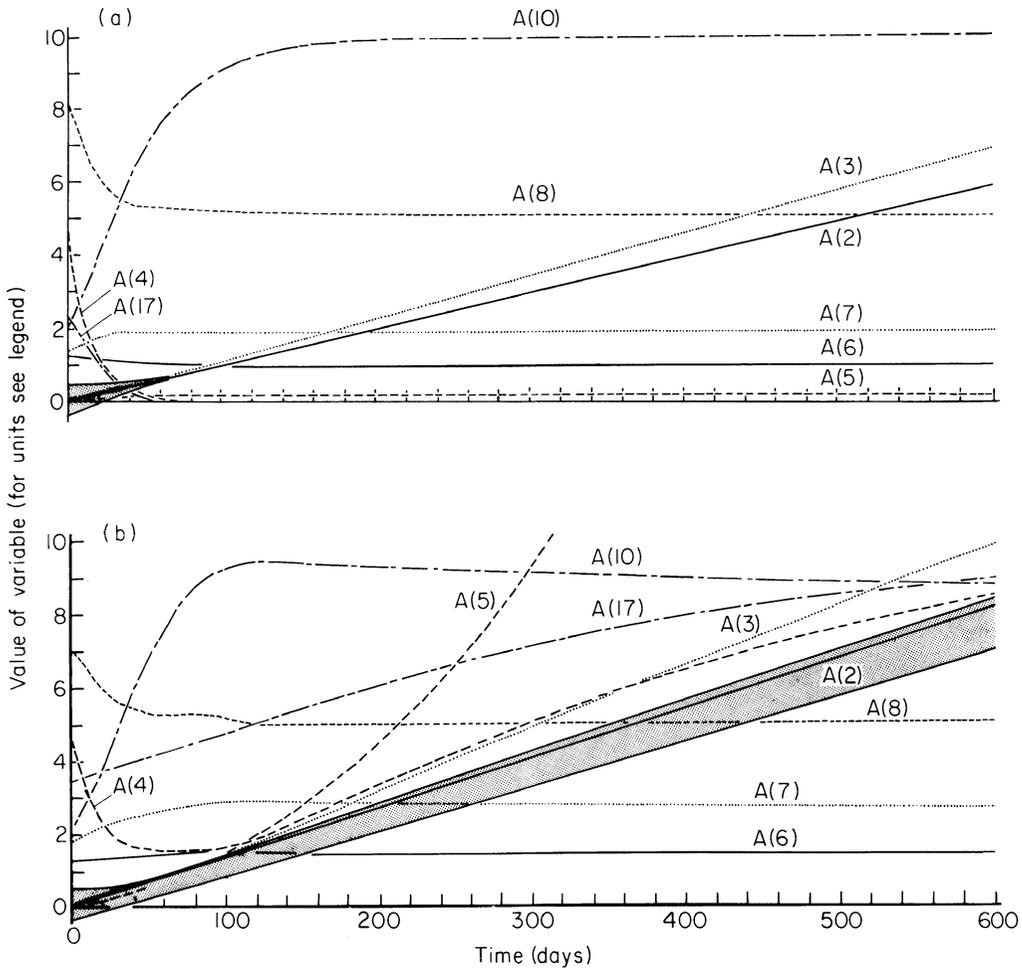


FIG. 6. Results of computer simulation for the growth of *Sphagnum capillifolium* run for 600 time steps of one day: (a) with no external shade and the water-table 3 cm below the surface; (b) with absorption by external shade of 0.3 and water-table at 12 cm. Variable names are those used in Fig. 5 and their values have been scaled on a common axis by multiplying by the italic values shown below in brackets: A(2), average length (cm) [0.40]; A(3), average mass (mg) [0.25]; A(4), variance in length (surface roughness) (cm²) [20]; A(5), variance in mass (mg²) [1.0]; A(6), average rate of elongation (cm day⁻¹) [40]; A(7), average rate of production (mg day⁻¹) [40]; A(8), average etiolation (cm mg⁻¹) [10]. Growth in length of plants initially 1 cm above and below the mean surface is shown by shading around A(2). Exposure effect with $k = -1.39$, A(10) [10], and shade, A(17) [2.5], are shown for these two plants respectively. After 600 days, the value of A(5) in (b) was 35 mg².

some of the results obtained as the mean growth in length of the second species in relation to that of the main species. Both of these graphs show similar effects. In both cases, when there was no external shade, *S. papillosum* grew faster than *S. capillifolium* did when the water-table was near the surface. With the water-table below 2 cm, the rate of growth in length of the two species was about the same, although *S. capillifolium* growing in a lawn of *S. papillosum* grew slightly faster when the water-table was between about 2 cm and 8 cm depth. In all these cases the model reached a steady state. Plants initially above or

Effects of light and water on *Sphagnum* growth

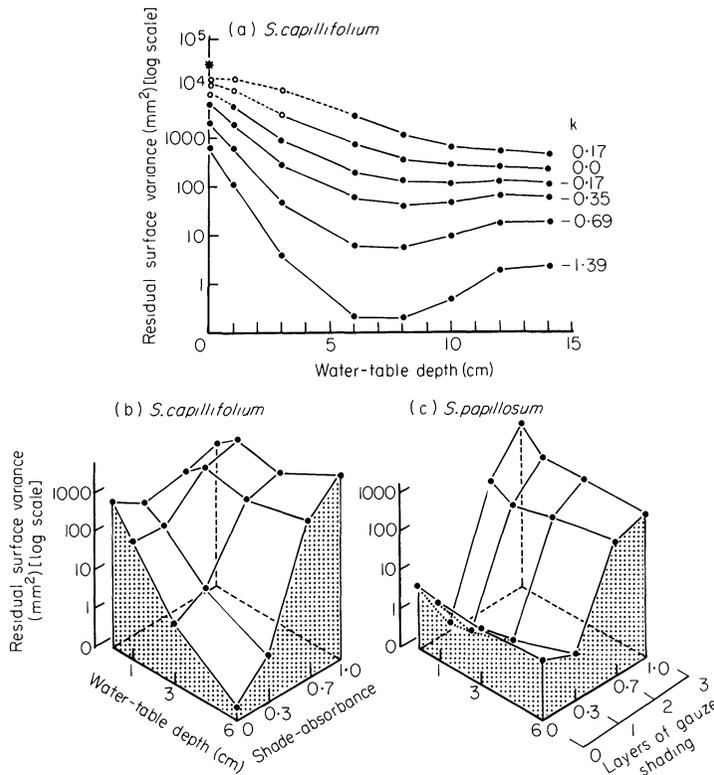


FIG. 7. (a) Surface roughness (log scale) of model lawns of *Sphagnum capillifolium* with a variety of water-table depths and no external shade. Each set of points was recorded with a variety of exposure effect. Values at the right are *k* in the equation of exposure effect (see Table 4). (---○---), indicates conditions where the model was unstable (plotted points are then the minimum values attained); * shows the surface roughness of the lawn at the start of a run when lengths were normally distributed random numbers with S.D. = 0.5. (b) Surface roughness of model lawn of *Sphagnum capillifolium* (with same units as (a)) with different combinations of water-table depth and external shade. The exposure effect was set to -1.39. (c) As (b), but *Sphagnum papillosum*.

below the surface tended to stabilize at the same level as those starting at the general surface level.

Sphagnum papillosum consistently produced greater growth in mass except at the lowest water-table depths examined, where growth was similar to that of *S. capillifolium*. This may simply be a consequence of the values of mean stem weight used to convert the units of growth in mass to mg (mg cm stem⁻¹)⁻¹. The important point is probably that the difference is greater the nearer the surface the water-table is.

With the external absorbance of light set at 0.3, the differences in growth in length were greater; *S. papillosum* now grew faster than *S. capillifolium* with the water-table down to 5 cm. A large exposure effect prevented *S. papillosum* plants from stabilizing very far above the surface of a *S. capillifolium* lawn with a high water-table but in the reverse situation, *S. capillifolium* plants were some distance below the surface at the end of the run. With the water-table at 0 cm, these plants were still slowly falling further behind at 200 days, so the model community was probably unstable in these conditions. It was certainly unstable when *S. papillosum* was grown with a low water-table in a *S. capillifolium* lawn,

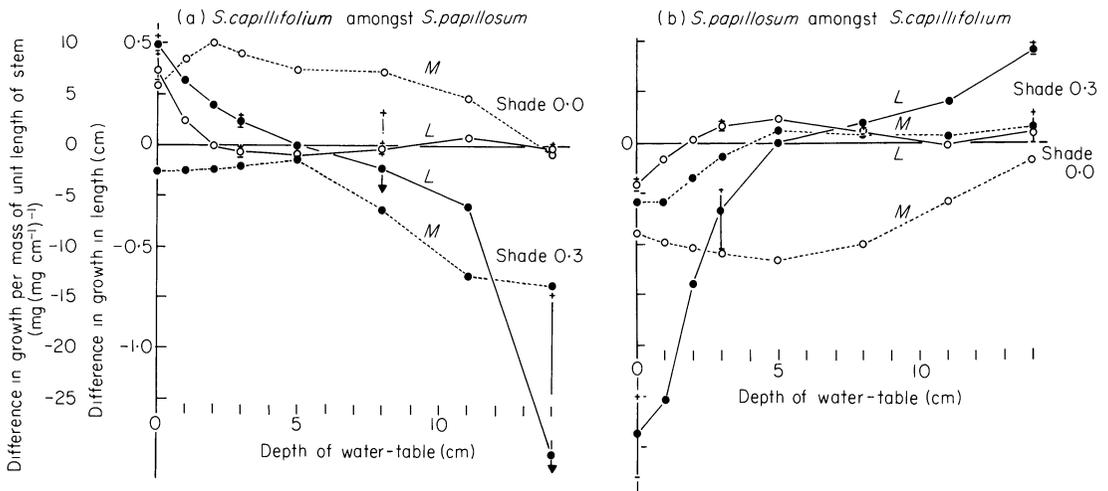


FIG. 8. Results of a model of *Sphagnum* growth: the effect of introducing a second species into a *Sphagnum* lawn. Graphs show difference in growth between the second species and the rest of the lawn when all the plants started at the same level. The symbols + and - show the difference in growth of plants initially at 1 cm above or below the surface, at water-table depths of 0, 3, 8 and 14 cm. In each graph, difference in growth in length (*L*, —) and in mass (*M*, ----) is shown for a period of 200 days with absorbance by external shade of 0.0 (○) and of 0.3 (●). The value of *k* in the equation for exposure effect (see Table 4) was -1.39 throughout. (a) *S. capillifolium* growing in a lawn of *S. papillosum*; (b) *S. papillosum* growing in a lawn of *S. capillifolium*. In (b), the *S. papillosum* plants initially at -1 cm, at water-table depths of 8 and 14 cm, both finished at -2.6 cm (shown by arrows).

particularly when the plants were initially below the surface. Instability caused by dense shade in association with a low water-table has been seen before, when lawns of single species were considered.

DISCUSSION

The existence of a relationship between water-table depth and surface roughness is confirmed, and it can be simulated too. There are at least two mechanisms which could account for this observation. The first concerns the effect of water supply on emergent plants. If the water-table is near the surface, the rate of growth in length of a plant just above the surface will be high, despite the exposure effect. But as it grows away from the surface, the exposure effect will cause the rate to fall so that in a steady state the plant is growing at the same rate as the rest of the lawn but just above it (Fig. 2). If the water-table is lowered, the rate of growth in length of an emergent plant is immediately reduced and the rest of the lawn catches up. Thus surface roughness is inversely related to depth of water-table.

The second mechanism concerns the effect of shading on a plant which falls behind, and may reinforce the reduction of surface roughness where there is no external shade. The rate of growth in length is greatest when the radiant flux incident on a lawn is high but a plant is shaded by its neighbours a few millimetres above. Such a plant would then tend to return to the surface, though with a reduced apex size, because growth in mass is reduced by shading. Another effect is also apparent from the results in Fig. 2. When there is external shading, any increase in shade from neighbouring *Sphagnum* plants will tend to reduce the

rate of growth in length of a shorter individual and it will fall behind irrevocably. This effect was observed in the model.

Several interesting points arise from the model runs with mixed lawns. First, the two species each appear to outperform the other in their own 'natural' habitat. Even if individuals of one species are in a minority, they will grow better than those of the other species if the water-table is either low, for *S. capillifolium*, or near the surface, for *S. papillosum*. Whether such individuals could compete to the extent of eliminating the predominant species cannot be determined without studying their branching and reproductive abilities.

Secondly, the depth of the water-table at which the growth of the two species is equal seems to be about 2 cm below the surface, with no external shade, falling to 5 cm deep with an absorbance of light by external shade of 0.3. Although *S. capillifolium* is usually considered to be a hummock species, it *can* grow successfully in places where the water-table is nearly at the surface (Ratcliffe & Walker 1958; Clymo & Hayward 1982). Nevertheless, this result does imply that *S. papillosum* growing on a hummock, where the water-table may be 20–30 cm below the surface, is at a disadvantage. This may, of course, be compensated by other factors such as its ability, compared with *S. capillifolium*, to multiply.

Thirdly, the differences between the two species are greater when they are shaded externally. Again, hummocks, which are often shaded more than open lawns, would seem to put *S. papillosum* at a disadvantage.

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