EXPERIMENTS ON BREAKDOWN OF *SPHAGNUM* IN TWO BOGS

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INTRODUCTION

Accumulations of organic matter have for long excited interest. Depths of peat greater than 30 cm are usually formed in waterlogged conditions and it is usually supposed that the peat accumulates owing to a slow rate of breakdown. This appears to be true of at least two *Sphagnum* dominated bogs where it has been found that the rates of production are in the range 2–12 metric tonnes/ha/year (unpublished data). These amounts are not unusually large for the region and climate in which they occur.

Whether or not different species of *Sphagnum* break down at the same rate is not known, nor has there been much investigation of the factors affecting the rate of breakdown. There is a good deal of evidence (for example, Waksman & Stevens 1928a, b; Theander 1954; Kox 1954) to show that various chemical constituents of *Sphagnum* are lost at different rates, but it is not known to what extent the slow loss from old peat in natural conditions can be explained by its large proportion of residual constituents resistant to decay in these conditions.

The experiments reported here have been made to investigate these questions.

METHODS

In most of the experiments *Sphagnum* plants were brought into the laboratory, separated into capitula and mature sections (approximately 0–2 cm and 2–6 cm respectively), spread out, and allowed to dry for 7 days. The plants were turned every day. In one part of Experiment 3 material of *S. papillosum* was collected from a depth of 60 cm ('peat'). Its structure was well preserved, most of the leaves being still attached to the branches. Samples of air-dry material were then dried at 105° C for 24 h and the oven-dry weight determined. Other samples of about 100–400 mg of the air-dry material were weighed and put into bags of nylon net about 12 cm × 6 cm, which had been numbered with spirit based ink. They were also colour coded with 3 mm lengths of coloured PVC tube. The plants were then wetted with distilled water and the open side of the bags was sewn up. Nylon or terylene thread was used for all sewing. The mesh of the net was hexagonal and its largest diameter was about 1·0 mm. In one experiment about 15 mg of various solids was added to each bag. The bags were tied to nylon cords and replaced in the bog in places dominated by a carpet of actively growing *Sphagnum* spp. (mostly *S. recurvum*, *S. papillosum* and *S. magellanicum*).

In most experiments three ranges of level were used. In that described as 'surface' the bags were placed on edge between the live *Sphagnum* plants at the surface just sufficiently far down to be not easily visible to the casual passer-by. In practice this level covered the range 0–10 cm below the surface.

In the next level, described as 'water-table' the bags were placed with long axis vertical

across the position of the water table at the time. This covered the range 6–18 cm below the surface.

In the '75 cm' level, bags were placed at 75 cm below the surface. This was done with as little disturbance as possible by holding the bag between the rough surfaces of two strips of hardboard 80 cm × 5 cm. The bag could then be thrust down to 75 cm and the hardboard strips withdrawn one at a time, leaving the bag in position.

In Experiment 4 a series of continuous belts of bags reaching down to 60 cm was used.

The bags were subsequently recovered, cut open, and the contents dried at 105° C and weighed. Percentage recovery was calculated from the weight after correcting for water in the original air dry sample (about 9%).

Up to 12 months after the bags were put out there was no difficulty in deciding how much of the material was that originally introduced and how much had got into the bags subsequently, because the plants remained as a coherent mass. With surface samples, however, after 18 months it became difficult to make this distinction and results became erratic. They have therefore been rejected.

In addition, in Experiment 1 a series of Whatman No. 1 filter papers was sewn into bags.

In part of Experiment 2 the weighed, air-dried, *Sphagnum* spp. were put into the centre of a 10 cm length of 3·5 cm diameter polythene tube, and sandwiched between plugs of *Sphagnum* of another species. These open tubes were soaked in bog water and then put horizontally into the bog surface centred at about 3 cm below the surface.

Two bog sites were used for the experiments. The first was in the Moor House National Nature Reserve, Westmorland, northern England, on the area known as Burnt Hill, at a height of 575 m above sea level. The site is part of an extensive blanket bog, the edges of which are eroding, but the centre, where the experiments took place, still has a nearly complete cover of *Sphagnum* spp. broken by a reticulate pattern of pools which may eventually become erosion foci (Bower 1959).

The other bog was near Godalming, Surrey, southern England, at Thursley Common, at a height of 30 m above sea level. The bog could be classed as a valley bog and the experimental site is in a part shielded from obvious water flow.

In addition to losses of weight from bagged material some other features of the bog profile were examined.

Temperature was measured at 0·5, 10 and 30 cm below the surface.

The uppermost level of detectable blackening on a freshly cleaned silver or copper wire was recorded. This deposit was indistinguishable from that produced by putting the wire into a solution of hydrogen sulphide. The deposit was usually blotchy near its upper limit, particularly in the winter months, which may indicate local differences of concentration on the scale of 1–2 mm.

Estimates of sulphur metabolizing bacterial activity were made on material collected in sterile bottles with a sterile syringe with a long glass tube attached to it. Samples were taken from various depths at Thursley bog on 31 August 1964. The bottles were filled to the top and air excluded. These estimates were made by Dr D. Kelly to whom I am most grateful. Production of H_2S was estimated in enrichment cultures on a medium containing Na^+, K^+, Ca^{++}, Mg^{++}, Fe^{++}, Cl', SO_4'', H_2PO_4', thioglycollate and an energy source (lactate). Air was excluded from the cultures which were incubated at 25° C. These conditions were used by Postgate (1963) for the enrichment of *Desulfovibrio*. Considerable activity was stimulated by this treatment (Fig. 3). It is noteworthy that Benda (1957) isolated from peat an organism, which she considered to be *D. desulfuricans*, which could reduce sulphate and sulphite to H_2S, but could not reduce thiosulphate.

Samples were also tested for acid production in the *Thiobacillus* medium of Vishniac & Santer (1957) which contains $Na_2S_2O_3$; and in 0·4% $Na_2S_2O_3$ solution, both at 25° C. No clear evidence of acid production in these conditions was found, even in surface (aerobic) samples.

EXPERIMENTS AND RESULTS

First experiment

Five variables were factorially combined. There were two sites (Moor House and Thursley), three levels in the bog, three species of *Sphagnum*, two parts of the plants, four sampling times and five replications. The main results are shown in Tables 1 and 2

Table 1. *Analysis of variance of percentage loss in weight of* Sphagnum *in Experiment* 1

Treatment	Degrees of freedom	Mean square	F test of significance
Level (A)	2	7537	
Parts (B)	1	4949	
Species (C)	2	2315	$P \ll 0{\cdot}005$
Site (D)	1	2178	
Time (E)	3	2054	
Interactions			
AD	2	607	$P < 0{\cdot}005$
BCD	2	326	$P < 0{\cdot}01$
AC	4	150	
DE	3	142	
BC	2	139	$P < 0{\cdot}05$
ACE	12	87	
Error	567	43·4	
Total	719		

Arcsin transformation of percentage losses in weight (Snedecor 1956). There were factorial combinations of three levels in the bog (surface, water-table and 75 cm below surface), two parts of *Sphagnum* plants (capitulum or 2–6 cm), three spp. (*S. acutifolium*, *S. papillosum*, *S. cuspidatum*), two sites (Moor House and Thursley), four sampling times (June/July, August/September, January/February, and April), and five replications. There are altogether thirty-one main effects and interactions. Only those with $P < 0{\cdot}05$ are shown.

Table 2. *Mean values of percentage losses in weight of* Sphagnum *in response to treatments in Experiment* 1

Retransformed data. Interactions of significance < 0·005 have been ignored.

AD	LEVEL	Surface		Water-table		75 cm	
	SITE	Moor House	Thursley	Moor House	Thursley	Moor House	Thursley
		12·2 (17·7)*	13·6	8·4 (7·0)*	10·5	1·3 (3·0)*	2·3
B	PART	Capitulum	Mature (2–6 cm)				
		10·6	5·6				
C	SPECIES	*S. acutifolium*	*S. papillosum*	*S. cuspidatum*			
		10·1	4·9	9·2			
E	TIME	10 weeks	20 weeks	41 weeks	51 weeks		
		4·6	7·0	8·7	12·3		

* Values in parentheses are means for twenty Whatman No. 1 filter papers at Moor House.

and in Figs. 1 and 2. Logarithmic transformation of the data was not as effective as the arcsin transformation in removing the dependence of variance on mean value (Snedecor 1956). The interpretation of interactions in these terms is difficult. All the main effects

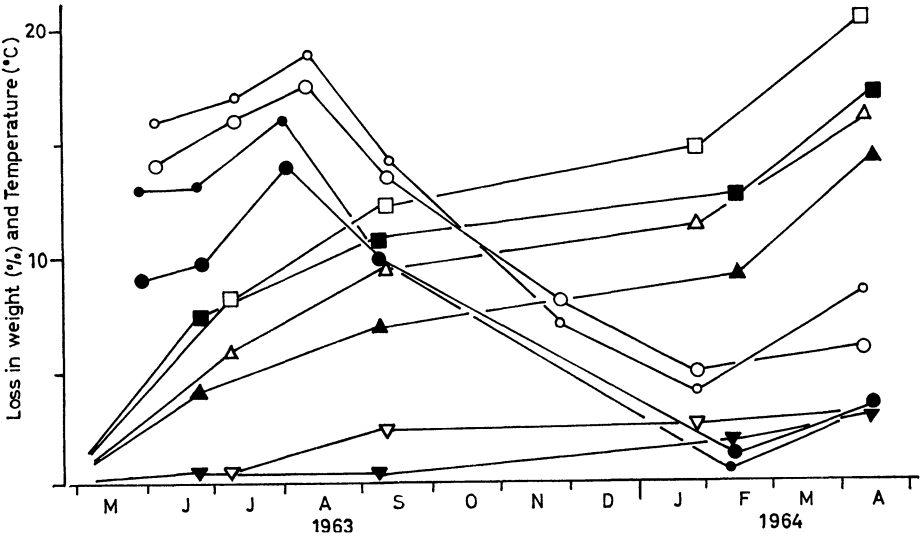

FIG. 1. Percentage loss in dry weight (retransformed means of three species and two parts of plants) in relation to time for both sites and three levels in the bog, and of temperature at two depths in relation to time. Open symbols, Thursley; solid symbols, Moor House; □, ■, bags at surface; △, ▲, bags at water-table; ▽, ▼, bags at 75 cm below the surface; ○, ●, temperature at 10 cm; ○, ●, temperature at 30 cm.

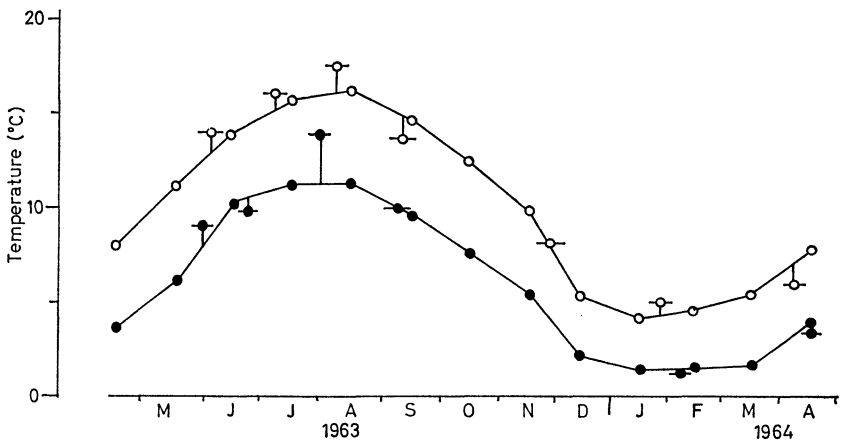

FIG. 2. Temperature in relation to time. Point measurements at 30 cm below the surface in Thursley bog (-○-) and Moor House (-●-). These may be compared with the nearest places with daily records, for which the monthly averages are shown connected by a continuous line. ○, 2 ft (about 60 cm) below the soil surface at Alice Holt, 13 km from Thursley bog; ●, 1 ft (about 30 cm) below the soil surface at Moor House about 1 km from the experimental site.

are however considerably larger than all but one of the interactions and significance is, of course, a function of the size of the experiment. The interactions will not, therefore, be considered further.

The most important results may be summarized. First, the rate of loss of *S. papillosum* is only half that of *S. acutifolium* and *S. cuspidatum*. Secondly, even though fresh *Sphagnum* was used, the losses at 75 cm in the bog were only a small fraction of losses at the surface. Thirdly, the losses at Moor House were less than those at Thursley. This may be partly related to temperature differences. The infrequent measurements made at 30 cm depth on the experimental sites correlate reasonably with mean monthly measurements (based on daily readings) from the nearest meteorological stations (Fig. 2), and these confirm that the Thursley environment is 4–5° C warmer than that at Moor House throughout the year. Surface temperatures fluctuate much more widely and rapidly than those at 30 cm, but if the heat conductivities of the two bogs are not very different, then average temperatures at the surface will also be higher at Thursley. Any connection there may be between temperature and rate of loss is clearly not simple; it would not for instance explain the relatively larger losses between January and April than between August and January.

Second experiment

In this experiment the losses from three species in bags were compared with those in polythene tubes. The results are detailed in Tables 3 and 4.

Differences between species were found as in the first experiment. The differences in losses of plants in tubes and losses of those in bags may have occurred because the tubes (at 3 cm) were nearer the bog surface than the bags (spanning 0–10 cm).

Table 3. *Analysis of variance of percentage loss in weight of* Sphagnum *in Experiment* 2 *comparing bags with polythene tubes*

Treatment	Degrees of freedom	Mean square	F test of significance
Container (A)	1	1009	$P \ll 0{\cdot}005$
Species (B)	2	744	$P \ll 0{\cdot}005$
Interaction AB	2	19	N.S.
Error	54	48·8	
Total	59		

Arcsin transformation of losses after 103 days (starting 20 May) at surface of Thursley bog. Factorial arrangement of containers (two) and species (three); ten replicates.

Table 4. *Mean values of percentage losses in weight of* Sphagnum *in response to treatments in Experiment* 2 *(retransformed data)*

A	CONTAINERS	Bags	Tubes	
		11·8	22·5	
B	SPECIES	*S. acutifolium*	*S. papillosum*	*S. cuspidatum*
		17·0	9·2	24·4

Third experiment

S. papillosum in a series of bags was put at the surface of Thursley bog. One set of five bags contained capitula, one set contained *S. papillosum* 'peat' collected from a depth of 60 cm, the rest all contained mature parts of *S. papillosum*. One of these sets was dried at 105° C before being put out. The last six sets had about 15 mg per bag of chemicals added. These were sodium, potassium or calcium nitrate, sulphate or phosphate or peptone. The experiment originally contained ten replicates of each treatment. Five of these were put in a part of the bog subject to some flushing. When these bags were recovered the

mass of material was found to be permeated by a tawny, gelatinous material containing a large proportion of broken down *Sphagnum* and diatoms. Most bags had gained 10–50% in weight, irrespective of treatment. The gains were very irregular. It seems that the process of breakdown in these places is different from that in the unflushed areas and the results from these places have accordingly been left out. Though all the chemical treatments resulted in rather greater rates of loss than in the control, none of these effects was important compared with the larger losses by capitula, and the smaller losses of oven-dried material and 'peat' (Tables 5 and 6).

Table 5. *Analysis of variance of percentage loss in weight in Experiment* 3 *(arcsin transformation of percentage losses)*

	Degrees of freedom	Mean square	F test of significance
Treatments	10	138·7	$P \ll 0{\cdot}005$
Error	44	8·84	
Total	54		

Sphagnum papillosum in bags at the surface of Thursley bog for 103 days. There were eleven treatments (details are shown in Table 6) and five replications.

Table 6. *Mean values of percentage loss in weight of* Sphagnum papillosum *in Experiment* 3

	Mean loss in weight	*P* (F test)
Control (mature air dry)	8·7	—
Capitula	25·8	$<0{\cdot}005$
Mature dried in oven at 105° C	4·4	$<0{\cdot}01$
'Peat'	3·0	$<0{\cdot}01$
Mature + 15 mg Na_2SO_4	13·2	N.S.
$NaNO_3$	8·9	N.S.
$CaNO_3$	11·4	N.S.
$CaSO_4$	9·6	N.S.
$CaHPO_4$	9·1	N.S.
KH_2PO_4	13·1	N.S.
Peptone	11·6	N.S.

Retransformed data. Significance of individual comparisons with the control (1 degree of freedom) is shown if $P < 0{\cdot}05$

Fourth experiment

Columns of ten contiguous bags containing mature *S. papillosum* were placed in Thursley bog. Losses were estimated after 103 days. There were originally five columns, but two of these were in the flushed region referred to in the third experiment and have consequently been left out. Percentage losses (mean values of three replicates) are shown in Fig. 3. Also shown in Fig. 3 are results of measurements made on four replicate samples collected with sterile technique on 31 August, 3 m from one of the experimental sites. The activity of sulphate reducing organisms (from five depths) in enrichment culture is shown, together with the pH of the original samples. Fig. 3 also shows the fluctuation of the top of the sulphide zone (shown by blackening of a silver wire) throughout a year at this same place.

Although the number of replicates is small, two points seem to be fairly clear. First, the sulphide level is related, as might be expected, to the sulphur reducing potential of the

microorganisms. Secondly, breakdown rates are greatest at the surface, lower in the region over which the sulphide level oscillates, and lowest below the permanently sulphidic level. This conclusion is supported by the (undesigned) observation of the PVC markers used in colour coding the bags. Those from bags at the surface were not visibly altered on recovery; those from 75 cm depth were uniformly light grey outside, though the colour could be seen unchanged on cutting. Experimentally pieces of coloured PVC could be bleached to a light grey in a solution of H_2S in water. The PVC recovered from the water table series showed a complete range from unchanged to bleached. This was presumably connected with differences in the range and time of oscillation of the upper edge of the sulphide layer. In almost all cases the bags with bleached PVC had lost less weight than those where the PVC was still coloured. This effect, examined for the third harvest

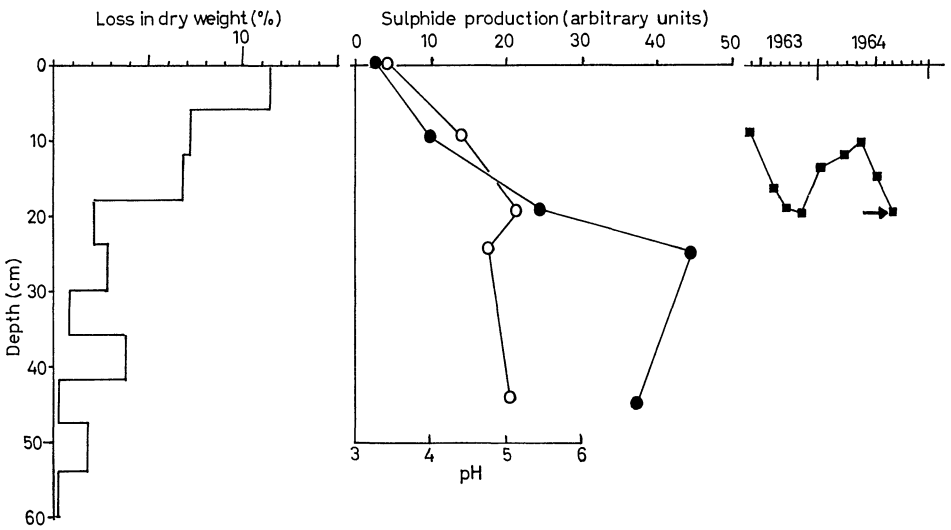

FIG. 3. Depth at Thursley bog related to percentage loss in dry weight of *Sphagnum papsillosum* (left). Upper limit of sulphide at various times of year (■), pH at 31 August (○) and H_2S production in arbitrary units after 13 days in enrichment culture (●). The arrow shows the upper level of sulphide at the time when the samples for pH and microbiological activity were taken.

time, was very highly significant ($P<0{\cdot}005$). Many other features of the environment (pH for example, Fig. 3) are correlated with water table and sulphide level; the position of the upper sulphide level has been used as an indicator because at Thursley bog at least, the water table fluctuates much more rapidly and by larger amounts than does the top of the sulphide zone.

DISCUSSION

Two main questions are raised by these results.

What are the causes of the losses observed and to what extent does the chemical state of the plants and environment affect the rate of breakdown? The results are also relevant in the interpretation of recurrence and retardation surfaces in peat profiles and in the reconstruction of past bog surfaces from peat remains.

First, what are the causes of the losses observed? There are at least three main possibilities; loss of whole leaves in handling, loss of whole leaves by natural water

movements, and loss by predation (animal, fungal or bacterial) or by chemical breakdown.

If the losses were in handling the observed results would be valueless. It is suspicious that the greatest losses were from the two species with leaves small enough to pass easily between the mesh of the bags (*Sphagnum acutifolium* and *S. cuspidatum*). The losses of weight of filter papers in Experiment 1 however (Table 2) were similar to those of the plants. Furthermore, in Experiment 2 comparing losses from bags with those from tubes, the same differences between species appeared and losses were greater from tubes than bags (Table 4). The plugs of *Sphagnum* (of alien species) in the ends of the tubes were examined carefully for detached leaves of the experimental material. Very few were found. Both these results indicate that handling losses were small. One might also have expected the losses to be greatest from those bags placed at greatest depth but this is the reverse of the observed results. It seems then that handling cannot account for more than a small proportion of the observed losses.

These arguments apply in part to the possibility of loss of whole leaves by bulk water movement and make this, too, an unlikely explanation of the main part of the losses. In addition, if losses were mainly by bulk water movement it might be expected that losses from bags at the water table level would be much larger than those at either surface or 75 cm bags. This is not the case.

It appears therefore that the main losses are caused by the same agents of breakdown as operate in natural conditions, probably animals, fungi and bacteria. Losses by chemical reactions (not mediated by living organisms) do not appear to be important in aerobic conditions over periods of a few months since no losses could be detected from sterilized *Sphagnum* kept in flasks in the laboratory.

No attempt was made in this work to determine the relative importance of the different organisms in breakdown. During the experiments some herbivorous or detritus feeding animals visible to the unaided eye were found in the bags. These included *Lumbriculus variegatus*, herbivorous mites, and Chironomid larvae, though none of these was found more than three times. In addition *Tetracanthella* sp. and Tipulid larvae have been found in *Sphagnum* collections. Other reports are of a characteristic fauna including herbivorous beetle larvae (Anon. 1954), Rhizopods (Paulson 1952; Heal 1962), mites (Tarras-Wahlberg 1952), and a variety of other animals (Smirnov 1961). It has not however been established how far these animals actually eat the *Sphagnum* except in one case (Smirnov 1961) where of a number of animals examined only one species of Chironomid larva was found of whose diet *Sphagnum* formed an appreciable part. It seems that direct attack by animals on fresh *Sphagnum* may be rather unimportant as an explanation of losses in weight.

Fungi and bacteria are abundant in the surface (aerobic) layers of many bogs (Waksman & Stevens 1929; Waksman & Purvis 1932; Burgeff 1961). At Thursley bog wefts of ascomycete hyphae are abundant in some places at least, and are associated with disintegration of *Sphagnum*. Sulphur metabolizing bacteria, too, are present and can be easily activated (Fig. 3).

The importance, or even presence, of viable microorganisms at depths greater than 1 m in raised bogs is in dispute. Waksman & Stevens (1929) and Waksman & Purvis (1932) report large numbers of bacteria living anaerobically below 90 cm depth, though their sampling methods are not given in detail. Burgeff (1961) reports his inability to show microbiological activity in peat from depths of more than 70 cm and, indeed, considered peat from these depths to be sterile and used it in aseptic culture experiments without

further sterilization. Burgeff (1961) also reports, however, that *Desulfovibrio desulfuricans* occurs to a depth of 1 m and the production of gas at depths of at least 3·5 m (Waksman & Purvis 1932) suggests that some microbiological activity may still have been occurring at depths greater than a metre in the raised bog which they studied. Gas production is also commonly observed in anaerobic conditions nearer the surface.

It may be concluded that breakdown by microorganisms is probably the main cause of the loss of matter from *Sphagnum* when dead. Eventually the broken down material must leave the bog ecosystem as gas, or in solution in run-off.

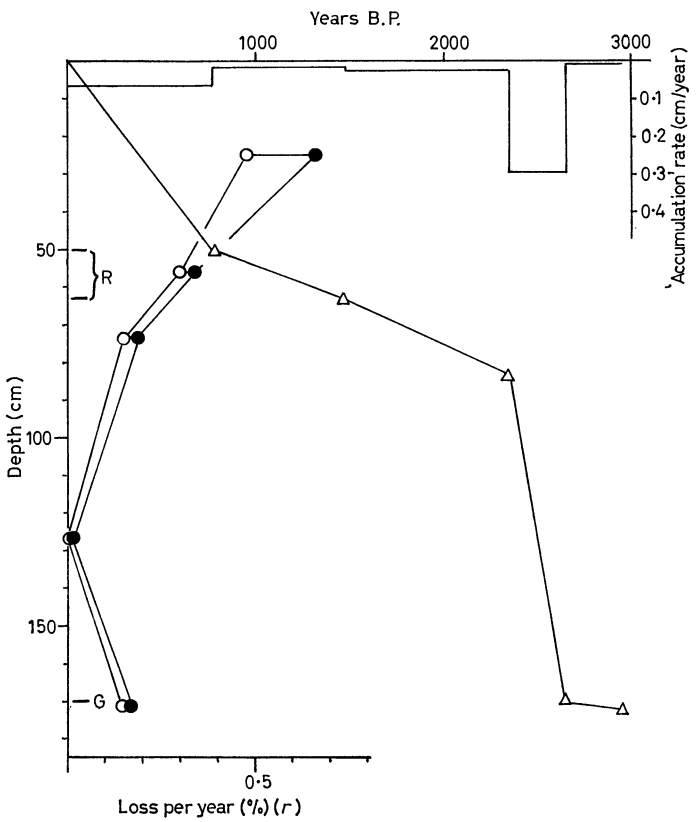

FIG. 4. Data for Tregaron bog drawn or calculated from Turner (1964). △, Depth in relation to age (by radiocarbon dating of peat samples); histograms, rate of growth in cm/year (with no allowance for compression); Calculated mean annual percentage loss (*r*) assuming original production of 5 tonnes/ha/year (○) or 10 tonnes/ha/year (●); R indicates a recurrence surface, G shows Grenzhorizont. Further details in the text.

The second main question set by these results is to what extent the rate of breakdown is affected by the chemical state of the plants and environment?

The low rates of loss observed in Experiments 1 and 4 at 75 cm depth (Table 2, Fig. 3), even though the material used was fresh *Sphagnum*, demonstrate that it is primarily the environment which is responsible for the low rate of loss. There are, however, some effects on the rate of loss connected with the plants. Differences between species have been mentioned already (Tables 2 and 4). The rather rapid loss from capitula might occur because they contain a larger proportion of inorganic materials (Malmer 1962) which

could stimulate growth of microorganisms (though this effect would not normally occur in natural conditions). Experimental addition of chemicals, however, had no marked effect on rate of breakdown (Table 6). It seems more likely that capitula contain relatively large amounts of easily metabolized organic materials. There is good evidence that different chemical constituents of the plants disappear at different rates (Waksman & Stevens 1928a, b; Theander 1954; Kox 1954). It might also be expected in consequence that the rate of breakdown would gradually become slower, even if the remaining material were in the same environment. This may explain the slow rate of loss from 'peat' in Experiment 3 (Table 6). This conclusion is reinforced by a consideration of the dating of peat left at the present day. For example the data of Turner (1964) from Tregaron Bog may be examined. Ages established by ^{14}C proportions are shown in Fig. 4 related to depth of peat. Rates of growth of the peat calculated from these data are also shown. No allowance has been made for compression. Density measurements on twenty-nine samples of peat of widely varying humification from Moor House gave a mean value of 12·2 g/100 ml (standard deviation 2·7) and using these figures an estimate can be made of the mass of peat of various ages left at present. Assuming further that the rate of loss per year has been constant, this rate can be calculated for any original rate of production, since

$$m_t/m_0 = (1-r)^t \qquad (1)$$

where r = proportional loss per year, t = time in years, m_0 = initial production per unit area, m_t = mass left after t years. Calculated values of r are shown in Fig. 4 for production values of 5 and 10 metric tonnes/ha/year. For older peats the rate of the original production becomes relatively unimportant. The values of r calculated in this way are almost certainly overestimates, as will be shown below. It is therefore noteable that the values for the period 2400–2600 years ago (for which period the assumption of uniform rates of loss is least objectionable) are less than 0·1% per year. This is an order of magnitude smaller than the losses of fresh *Sphagnum* placed at 75 cm in these experiments and may serve to support the conclusion that the rate of loss of material does decrease as the more easily attacked constituents are removed. The second feature of note in the calculated values of r (Fig. 4) is their wide variation in size. It seems unlikely that rates of loss can really differ so widely in similar environments, especially since the material laid down 2800 years ago has a value of r roughly ten times that of more recent material (2400–2600 years old). It would be more in accord with the experimental observations and with the observed variation in the degree to which macro structure is preserved to suppose that breakdown rates once into the sulphide zone are low and fairly uniform for all materials. Observed differences in rate of peat accumulation would then result mainly from differences in the rate at which plant materials passed into the sulphide zone (or at which the zone rose and covered them). In neither case can the results be adequately described by equation (1) alone, as Olson (1963) has also concluded.

These results have relevance also to some other features of bog ecology.

First they are connected with the interpretation of recurrence and retardation surfaces. These are recognized primarily by changes in the degree of preservation of the plant macro structure, particularly of *Sphagnum* remains. It is usually considered that climate is the master factor which controls their development (e.g. Conway 1948, 1954). Those features of the climate leading to more rapid peat accumulation would be usually those connected with water supply to the bog surface. If the conclusions reached about the importance of the time before submersion below the sulphide layer are correct, recurrence

surfaces might be quantified in terms of the ratio of number of years for freshly produced material to pass below the sulphide layer before and after the recurrence horizon formed. (The data for such an estimate do not at present exist.) A relatively short distance between the mean water table (and sulphide level) and *Sphagnum* capitula would also be favourable to *Sphagnum* growth, as experiments in the laboratory have shown. Consequently more rapid peat accumulation is probably also generally associated with increased *Sphagnum* production. These two features need not *necessarily* occur together however, as is sometimes supposed. A case in point might be that of the C_3 horizon in Conway's (1954) profile, Kinder VI. This horizon is marked by a large decrease from previous values in tree pollen frequency (with no considerable change in the proportion of tree pollen) and indicates an increase in rate of peat accumulation. There is however no associated recurrence surface; the degree of breakdown of structure does not change. These observations might be explained if there was an increase in production at the bog surface, but little change in the time before which plants passed below the sulphide level.

Another factor which may affect the development of recurrence or retardation horizons is a change of species of *Sphagnum*, since different species lose weight at different rates. *S. acutifolium* and *S. cuspidatum*, losing about 5% per year, would have lost 32% of the original matter if 5 years passed before they were covered by the sulphide layer, or 53% if 10 years elapsed. *S. papillosum* in the same circumstances losing 2·5% per year would have lost only 12% and 22% of its original mass. These differences between species might of themselves produce recurrence or retardation surfaces, particularly when the individually larger parts of *S. papillosum* are also considered. It is conceivable (though unlikely) that a recurrence surface would result from a change to slightly drier conditions, if this resulted in the extensive replacement of *S. cuspidatum* by *S. papillosum*.

The second aspect of bog ecology to which these results relate is the reconstruction of past surface vegetation from the remains found in peat. If the results of experiments on *Sphagnum* and filter paper are of general application to plant materials, then some bog plants are growing in positions which will lead to their preferential preservation. For example, *Eriophorum angustifolium* at Thursley bog usually has its shoot base 5–25 cm below the surface and in a few cases roots of *E. angustifolium* had grown through bags at 75 cm depth at Thursley. These tissues may be already at or below the sulphide level when they die. The mass of shoot bases and roots of *Eriophorum* will then be over-represented in the peat compared with *Sphagnum* spp. Where a relatively long time elapsed before *Sphagnum* passed below the sulphide level the identifiable remains in peat would be mainly of *Eriophorum*, though the surface which gave rise to the peat contained a large proportion of *Sphagnum*.

Finally, these results have a bearing on the postulated 'succession' of hummocks and hollows. There are however so many other variables involved that discussion at this stage would be unprofitable.

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SUMMARY

Experiments are described in which weighed amounts of *Sphagnum* were sewn into nylon mesh bags and replaced in two bogs. The bags were recovered at intervals and loss of weight measured. The main results were:

1. Losses at the surface, water-table and 75 cm down were roughly in the ratio 13:9:2.
2. Losses were more rapid in a lowland bog (with higher temperatures) than in an upland bog.
3. Losses of *S. papillosum* were only half those of *S. cuspidatum* and *S. acutifolium*.
4. The addition of inorganic salts or peptone had little effect on rates of loss.

Reasons are given for supposing that the main loss is due to microbiological activity. It is suggested that the most important variable in determining the proportion of original material which survives as peat is the time which elapses before the plants pass below a level close to the uppermost position at which sulphide can be detected.

The implications of these results in the interpretation of recurrence and retardation surfaces, and in reconstruction of past bog surfaces from peat remains, are discussed.

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