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GROWTH RATE OF *SPHAGNUM RUBELLUM* WILS. ON PENNINE BLANKET BOG

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INTRODUCTION

Sphagnum rubellum Wils. is quantitatively a fairly important component of the present surface of uneroded blanket bog (on which *Calluna vulgaris* (L.) Hull and *Eriophorum vaginatum* L. are dominant) in the Pennine Hills of England. Its importance may be greater than its bulk suggests for three reasons.

(1) It (and other species of *Sphagnum*) may be largely responsible for producing the acidic environment (Clymo 1967).

(2) It decays more slowly than other bog species (O. W. Heal *in litt.*; Clymo 1965) and comes to be over-represented in peat.

(3) By growing upwards around *Calluna* stems it creates an environment in which the stems produce adventitious roots, thus rejuvenating the *Calluna* and making it potentially immortal. This phenomenon, remarked on by Rawes & Welsh (1969) and by G. I. Forrest and R. A. H. Smith (*in litt.*), contrasts with the finite lifespan of *Calluna* plants growing in the East Anglian Breckland (Watt 1955) and in other dry situations.

Previous reports of the growth of *Sphagnum* in blanket bog have been restricted to measurements for 1 or 2 years at most. This paper reports the growth of *S. rubellum* during five years at three sites on the Moor House National Nature Reserve in the northern Pennines.

METHODS AND SITES

Growth was measured against the emergent 10-cm arm of cranked wires (shaped like a car starting-handle) pushed into the *Sphagnum rubellum* carpet parallel to the plant stems and clear of *Calluna* shoots. The cross-bar of the crank was level with the capitula in April 1968. In April 1969, 1970 and 1973 the length of emergent wire was measured. In 1973 9% of the wires located were found to be buried, and it was necessary to add the growth above the wire tip. The maximum addition was 40 mm. A narrow-bore glass tube with a scale on one side and a 2-cm polythene disc on the end served to define the position of capitula and simplify measurements. Evaluation of this method of measuring growth in length was given by Clymo (1970).

Conversion to net dry matter growth rate was made using measurements of the dry weight of the section of plants from 1 cm to 4 cm below the apex in 7·5 cm diameter circular samples. The dry matter below the capitulum may be considered as the 'product' of the machinery represented by the capitulum, and the 'product' within the defined cylindrical volume gives the 'product density'. The plastic response of the plants is such that the mass in the top 1 cm (including the capitulum) over a given area is nearly constant, but the 'product density' is more variable (Clymo 1970).

Groups of about four sample wires were marked by bamboo canes about 50 cm away. The bamboos were put initially in a regular pattern, about 3 m apart. They were then moved to the nearest patch (minimum area 10 cm × 10 cm) of live *Sphagnum rubellum*. Three subjective categories of *Sphagnum* health were recognized, based on plant colour and carpet integrity. It was hoped that this would improve precision if the results were applied to other nearby sites. Most wires were in the 'healthy' category.

Three sites were used, all at altitude about 550 m; details of the environment are given by Smith (1973).

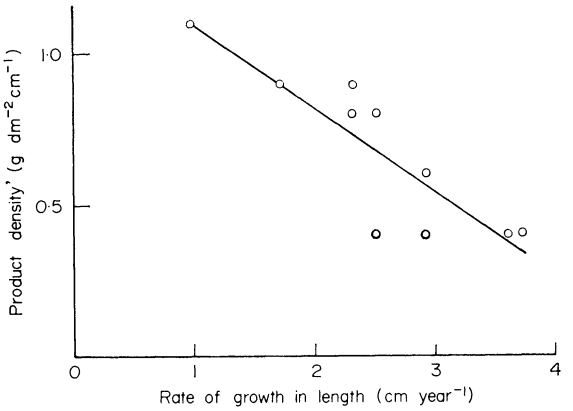

FIG. 1. *Sphagnum rubellum* 'product density' relationship with rate of growth in length. 'Product density' = bulk density of stem + branches in 1–4 cm section. The rate of growth in length is the mean annual rate for the five years 1968–73.

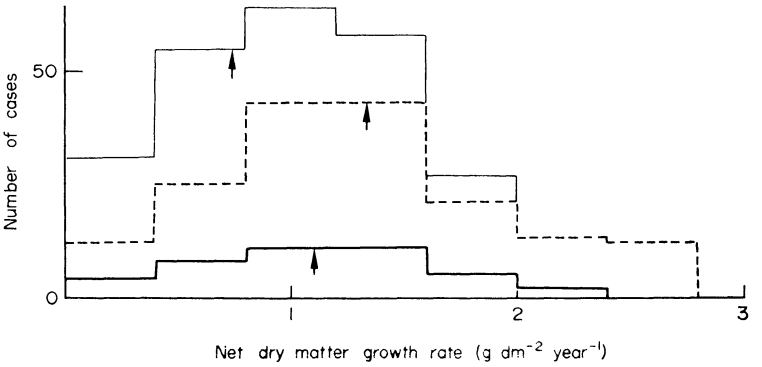

FIG. 2. Distribution of net dry matter growth rate of *Sphagnum rubellum* (averaged over the five years 1968–73) in relation to subjective assessment of plant health. Within each range the number of cases is cumulative: 'healthy' (heavy line) at the bottom; 'indifferent' (pecked line) above; 'poor' (thin line) at the top. The arrows mark the medians.

(i) Sike Hill (NY 769331), the main I.B.P. site at Moor House, contiguous with the area in which Forrest (1971) measured productivity of the whole system. The vegetation was dominated by *Calluna vulgaris* and *Eriophorum vaginatum*. *Sphagnum* (about 80% *S. rubellum*) covered about 15% of the area. The site had a slope of about 2° towards south. It was unfenced and may have been grazed by sheep at some times of the year,

and by grouse at any time. The above-ground biomass of *Calluna* averaged 870 g m^{-2} in 1968 (Forrest 1971).

(ii) Bog Hill (NY 767326), about 0·5 km distant from Sike Hill, differs in being fenced and in having a larger above-ground biomass of *Calluna* (960 g m^{-2} in July 1971) on the experimental area. *Sphagnum rubellum* covers about 20% of the area.

(iii) Burnt Hill (NY 754328), about 2 km distant, has a summit (where the experiments were made) whose vegetation shows a 'pool and hummock' complex. *Scirpus cespitosus* L. is common (besides *Calluna* and *Eriophorum vaginatum*). The *Calluna* bushes are smaller and more sparse than those on the other sites with above-ground biomass of 320 g m^{-2} in July 1971. The hummocks in the wetter area where the measurements were made have a fairly continuous cover of *Sphagnum rubellum*.

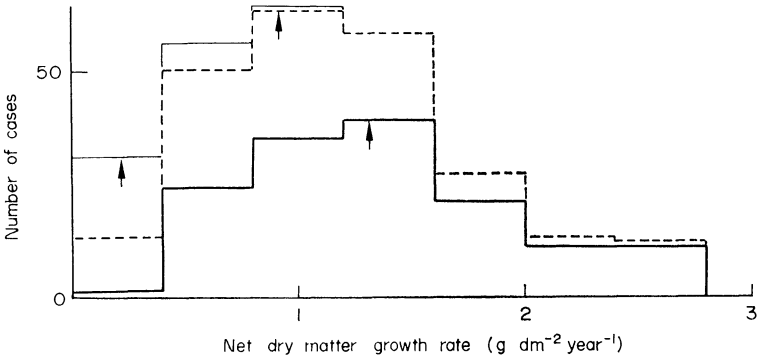

FIG. 3. Distribution of net dry matter growth rates of *Sphagnum rubellum* (averaged over the five years 1968–73) on three sites. Within each range the number of cases is cumulative: Sike Hill (heavy line) at the bottom; Bog Hill (pecked line) above; Burnt Hill (thin line) at the top. The arrows mark the medians.

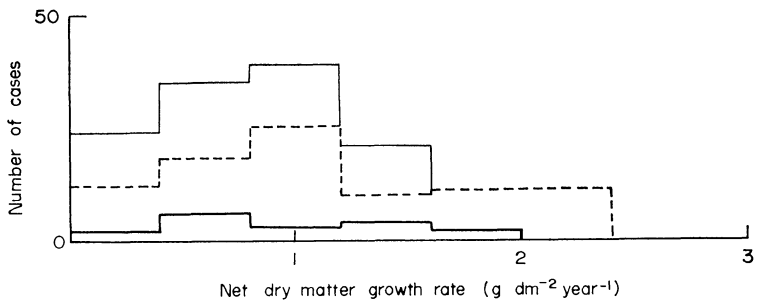

FIG. 4. Distribution of net dry matter growth rates of *Sphagnum rubellum* (averaged over the five years 1968–73) on three sites for 'healthy' plants. Within each range the number of cases is cumulative: Sike Hill (heavy line) at the bottom; Bog Hill (pecked line) above; Burnt Hill (thin line) at the top.

RESULTS

Some of the spots originally marked by wires were subsequently not found again. There were two reasons for non-recovery.

(1) The wire was found, but it had been pulled up. Often these wires were crumpled and in five cases wrapped round the nearby marker bamboo—even in one case knotted.

This happened at all three sites, including the fenced Bog Hill site. The area is remote and visited rarely other than by scientists. If it is assumed that humans were not responsible, the most likely agents seem to be grouse; on one occasion a grouse was indeed seen to peck at a wire. Some wires may have been knocked out or whipped out by wind-waved *Calluna* branches.

(2) The general location of wires could not be found because the marker bamboo had disappeared—causes unknown, but in at least one case the experimental area had been partly overlaid (in error) by experiments of other workers.

These non-recoveries would be important only if they were selective—with losses, for example, of completely buried wires or of the least buried ones. In general, however, the majority of non-recoveries were due to loss of the bamboo markers. On Bog Hill, for example, of 49 bamboos (marking 204 wires) 37 were found (76%). Potentially these 37 bamboos located 151 wires, of which 132 were found (88%). Of the missing 19 only 2 were from groups where at least one of those recovered was buried. The overall recovery at this site was 66%. At Sike Hill it was 21% (though recoveries from those bamboos which were found were 87%) and at Burnt Hill it was 92%.

Table 1. *Net annual dry matter growth rate of* Sphagnum rubellum *at three sites measured over different times (units are g* dm^{-2} $year^{-1}$*;* $\bar{x}$, *mean;* $S_{\bar{x}}$, *standard error of mean;* n, *cases*)

Length of time (years)		Site: Sike Gill	Bog Hill	Burnt Hill
1 (1968–69)	$\bar{x}$	0·86	No data	0·75
	($S_{\bar{x}}$)	(0·10)		(0·15)
	n	276		71
2 (1968–70)	$\bar{x}$	1·11	1·24	0·96
	($S_{\bar{x}}$)	(0·13)	(0·14)	(0·13)
	n	118	153	57
5 (1968–73)	$\bar{x}$	1·09	1·35	0·80
	($S_{\bar{x}}$)	(0·08)	(0·06)	(0·04)
	n	41	127	94*

* Some wires must have been missed at the earlier times.

The results, though fragmentary, are therefore not likely to be seriously biased by selective losses.

Measurements of dry matter per unit area and depth (Fig. 1) show that the plants growing faster in length have a lower 'product density'. The linear regression through the points in Fig. 1 was used in making the net dry matter growth rate estimates over 5 years, shown in Figs. 2–4. Obviously this regression cannot be extrapolated far.

The subjective assessments of plant health correlate (both on median and mean) with the net dry matter growth rates, but the spread of results is large, and the mean for the 'healthy' category on Burnt Hill is well below that for Bog Hill.

The mean net dry matter growth rate of *Sphagnum rubellum* on Bog Hill is nearly twice that on Burnt Hill.

Table 1 shows a comparison of net dry matter growth rates based on measurements made in 1969, 1970 and 1973. An analysis of variance gives $P \simeq 0{\cdot}01$ for site differences, and $P \simeq 0{\cdot}03$ for time of measurement.

DISCUSSION

At least two factors might cause estimates of net annual growth averaged over a long time to be smaller than those from a shorter time. These are compression of the *Sphagnum* carpet, and decay.

The major stress on these surface layers is probably that of the weight of snow; 30 cm of snow might produce a stress of about 3 grams force cm^{-2}. Such stress will have a marked effect only if the surface layer of peat is not frozen. On Burnt Hill (where temperatures at the surface and 5 cm below were recorded on a hummock and lawn for 1969–72) the temperature was at or below 0° C for most of the time during which snow was accumulating. One might expect that if compression did occur the plant stems would buckle or become bent at an angle. Such buckling was not observed, and if whole plants did bend then the wires must have done the same since most of the wires recovered were still parallel to the plant stems.

Decay rates in these conditions are probably about 5% per year (Clymo 1965; O. W. Heal *in litt.*). The decay rate probably declines with time because the more easily attacked plant constituents are removed first, leaving more refractory materials. Over five years it is unlikely that more than 25% of the original material will have gone. Losses due to decay probably do not result in a directly proportionate collapse in length—equivalent to removing a whole row of bricks from a wall—but resemble the removal of random bricks. This removal does not at first affect the height, though eventually when sufficient have been removed collapse must occur.

For these reasons it is thought that the 5-year averages are not likely to contain a large systematic error. The similarity of the 2-year and 5-year averages may be used either to support this supposition or to indicate that the years 1968–70 were typical of the longer term 1968–73. It seems that either the net dry matter growth rate in 1968–69 was compensated by a higher than average rate in 1969–70 or the low values in 1968–69 result from bias. The mean growth in length recorded for 1968–69 was only 8 mm, and in a situation as ill-defined as a *Sphagnum* carpet a bias of 3 mm could easily have occurred. Such a bias would become relatively less important as time passed.

The growth rate of *S. rubellum* is greatest on Bog Hill and least on Burnt Hill. These differences are not easy to interpret because of variations in *Sphagnum* and *Calluna* cover and distribution which are coupled with differences in grazing, and probably in water supply too. *Sphagnum* growth rate is positively correlated with the above-ground standing crop of *Calluna*. It may be that only relatively fast-growing *Sphagnum* survives where the *Calluna* is dense, so that the Bog Hill measurements were made on a naturally selected upper part of the range of growth rates.

If the argument that there has been no great degree of compression is accepted, then these estimates of net dry matter growth rate are probably close to those of the net productivity. The 'product density' factor by which the length increment is multiplied represents material between 1 and 4 cm below the surface spanning the age of about 1–3 years, and from which perhaps 10–20% of the original net production has been removed in decay.

The average net productivity of *Sphagnum rubellum* in its natural situation on these three sites was therefore about 1·3 g dm^{-2} $year^{-1}$ (130 g m^{-2} $year^{-1}$) with a range between sites of a factor of about 1·7. This productivity is about 7% of the total on Sike Hill (Forrest 1971) and 43% of that on hummock habitats on Burnt Hill (Clymo & Reddaway 1971).

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SUMMARY

Growth in length of *Sphagnum rubellum* Wils. was measured over a 5-year period at three sites at 550 m altitude on blanket bog in which this species was a component of the vegetation. Net productivity estimated with these and other measurements averaged about 130 g m^{-2} $year^{-1}$. This is about 10–40% of the total net productivity.

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