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REGENERATION OF *SPHAGNUM*

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SUMMARY

When disc-shaped horizontal slices of peat cores, three from a bog in mid-Wales and three from a bog in Hampshire, were kept for several months in a saturated atmosphere in a cool greenhouse numerous new shoots of *Sphagnum papillosum* (Lindb. *S. magellanicum* Brid. and *S. recurvum* P. Beauv. were produced.

The new shoots arose on peat discs from at least 30 cm below the surface and water table and from regions in which the *Sphagnum* appeared to be brown and dead. A timescale, inferred from the cumulative dry mass and the peak in ^{137}Cs concentration (which was assumed, conservatively, to reflect the 1963 peak influx), indicates that the matrix of the deepest discs from which new shoots arose was from 25 to perhaps 60 years old.

Many of the new shoots of *Sphagnum* arose as innovations from the outer cortex of buried stems. In most cases the first leaves on these had the usual dimorphic leaf cell pattern. Other shoots, which initially produced leaves with monomorphic cells, arose from protonemata, comprising irregularly lobed plates of tissue and sparsely branched filaments with oblique cross-walls. A few of the protonemata arose from old stems, a feature not reported before, but the vast majority had no attachment to old plants and are thought to have grown from spores.

Light and air were necessary if new shoots were to appear. But very few innovations or protonemata were found in the green discs from near the surface of the core. This suggests some kind of hormonal control of innovations akin to apical dominance in vascular plants and a more general allelopathic inhibition of spore germination and protonemal growth by green *Sphagnum*.

Fern gametophytes of at least two taxa (*Dryopteris*-like and *Pteridium*-like) grew on the peat discs with distribution patterns similar to those of new *Sphagnum* shoots. Seedlings of five taxa of vascular plants – all species growing close to the core-sites – appeared on the peat discs but much more erratically than *Sphagnum* and the ferns. Stems of five species of leafy liverwort, presumed to have been derived from subterranean axes rather than from gemmae or spores, were also recorded, but no other bryophytes were seen.

The discovery that morphogenesis in *Sphagnum* is far more fluid than hitherto assumed has far-reaching physiological, ecological and possibly genetical implications. The development of protonemata under semi-natural conditions, recorded here for the first time, confounds the results of culture experiments which had indicated that *Sphagnum* protonemata were unlikely to grow on peat.

Key words: *Sphagnum*, peatland ecology, morphogenesis, protonemata, ^{137}Cs.

INTRODUCTION

The bog moss *Sphagnum* is widespread and there is more of it than of any other bryophyte. Indeed, considered in terms of its total mass, live and dead, it must be regarded as one of the most important of all plants (Clymo & Hayward, 1982). Despite its considerable ecological and economic importance we are not aware of any experimental study which attempts to explore the regenerative behaviour of *Sphagnum* in or on peat.

On agar the spores of *Sphagnum* germinate to produce a chlorophyllose filament (Nehira, 1984). This in turn produces a highly chlorophyllose plate one cell thick resembling the gametophyte of a fern. Around the margins and basal region further

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mulitcellular filaments develop. These are usually referred to as rhizoids (Hill, 1978). Eventually one or more vertical leafy shoots arise from the central region of the oldest part of the plate. In a typical case, the first few leaves are monomorphic (i.e. with only one cell type), the cells being chlorophyllose [Fig. 8(e)]. In the succeeding leaves some areas become dimorphic in that up to one third of the cells die and lose their contents, but they do not develop conspicuous hoops of thickening before doing so [Fig. 8(g)]. Finally leaves are produced which show the full dimorphic cellular pattern characteristic of the genus, with about one third of the cells becoming hyaline with hoops of thickening and pores. (Why do one third of the leaf cells become hyaline? In the early stages of leaf development about ten divisions produce a plate of close-packed diamond-shaped cells. Each cell then divides once. One daughter cell then divides again. Only one of the granddaughters eventually becomes a hyaline cell and therefore about one third of the cells are hyaline.) This morphogenetic sequence, from filament to plate to leafy shoot, may conveniently be called one-dimensional to two-dimensional to three-dimensional growth (abbreviated 1D→2D→3D hereafter). The sequence is readily observed in laboratory cultures, but seems never to have been recorded in the field. Consequently, it is usually tacitly assumed that *Sphagnum* spreads solely by vegetative means, although many species regularly produce capsules in the summer months.

Individual 'adult' haploid plants of *Sphagnum* are usually considered to have a strictly determined organography. A large apex of unlimited growth produces stem leaf primordia and branch primordia. In most species the branches occur in groups (fascicles). These are normally of determinate growth and themselves produce branch leaves. In undamaged stands of *Sphagnum* new shoots of unlimited growth are produced in two ways. In the first, the stem apex appears to divide into two new apices of approximately equal size. Whether this involves an equal division of the apical cell itself or involves a change in the pattern of development of a branch primordium is unclear. In the second way, a lateral shoot may be produced from the main stem a centimetre or more below the apex. Such laterals, generally referred to as innovations, may eventually become stems in their own right.

In 1963 one of us (R.S.C.) noticed that brown, apparently dead, *Sphagnum magellanicum* left unintentionally for two months in a sealed polythene bag on a north-facing window sill produced new shoots. Such new shoot regeneration has been observed several times, and with various *Sphagnum* species but particularly with *S. recurvum*. The observation is of morphological and physiological interest in itself, and may also have ecological and genetic implications. It could, for instance, explain the ability of a *Sphagnum* carpet to recover from random or systematic damage. It could also provide a basis for interpreting the genetic composition of such a carpet. If the newly regenerated shoots are from vegetative shoot production, the carpet would be expected to remain genetically uniform but if new shoots arise from spores then genetic variation would be expected.

We record here the results of some experiments on peat cores taken from two widely separate sites, one in mid-Wales and the other in southern England. They show that *Sphagnum* regeneration can occur not only vegetatively (or asexually) from apparently dead mature gametophyte tissues, but also from spores. Moreover, it can occur from as much as 30 cm below both the green parts of the plants and the water table. Our observations also reveal that the development of *Sphagnum* is far more plastic than is usually supposed.

Materials and Methods

Sites and cores

Six 20-cm diameter × 50 to 60-cm deep cores of *Sphagnum* and underlying peat were collected in PVC tubes. The first three (GL1–GL3) were collected on 13 September 1984 from sites about 20 m apart on Gors Lwyd, a basin mire at about 386 m altitude, on the border between Dyfed and Powys in mid-Wales (National Grid reference SN 857756). This site was chosen solely for convenience. A description of the vegetation, stratigraphy and water chemistry of the mire is given by Slater (1976). Mean precipitation rate for 1916 to 1950, 9 km south at Esgair Gader (503 m), was 1821 mm a^{-1}; 11 km away at Lyn Gynon (457 m) it was 1824 mm a^{-1} (Anonymous, 1958). Precipitation at the latter site was evenly distributed throughout the year – coefficient of variation 0·23 – with the driest month (May)/mean month = 0·68. Similar values were recorded for five stations within 15 km of the sample area and between 457 and 503 m altitude. Gors Lwyd itself is about 70 m lower, but the bog is in a valley and is probably very wet at most times. The cores came from vegetation similar to Slater's 'Association A', except that, by chance, they lacked *Molinia caerulea*. All three cores contained three species only: *S. papillosum*, *S. recurvum* and a few (< 5) small plants of *Eriophorum angustifolium*. (Nomenclature follows that of Clapham, Tutin & Warburg (1981) for vascular plants, Smith (1978) for mosses and Corley and Hill (1981) for liverworts). Core GL1 had about equal cover of the two species of *Sphagnum*; GL2 and GL3 had about 90 % cover of *S. papillosum* with about 10 % of *S. recurvum*. The water table at the time when core samples were taken was only 3 to 4 cm below the surface of the *Sphagnum* carpet. On three visits – July, August and September each in different years – the area sampled could be crossed only with difficulty.

The results from these cores were so surprising that it was decided to collect further cores from another totally different bog site. On 2 February 1985 seven cores were taken from Cranesmoor, a valley bog in the New Forest (National Grid reference SU 185029). This site is about 160 km from Gors Lwyd, and has a very different climate. The vegetation and water chemistry are described by Newbould (1960). The bog is at about 40 m altitude. Mean precipitation rate 1916 to 1950 8 km north at Fordingbridge at the same altitude was 830 mm a^{-1} (Anonymous, 1958), evenly distributed throughout the year – coefficient of variation 0·26 – but with the driest month (June)/mean month = 0·36. Evaporation probably exceeds precipitation from April to September (Newbould, 1960), and the bog remains wet and survives only because water is channelled into a valley over or through solute-poor rocks.

Results from three of the seven cores (CM1, CM4 and CM6) taken are shown here. The remaining four cores were used to study the regenerative capabilities of subterranean axes of bog hepatics (Pocock & Duckett, 1985). The findings from these are to be reported separately (Duckett & Clymo, unpublished data). The first core, CM1 came from the extensive *Sphagnum* carpet itself, in an area shielded from flowing water (Newbould, 1960). The core had a complete cover of *S. papillosum*, with a few small plants of *Eriophorum angustifolium* and *Erica tetralix*. In the immediate neighbourhood *Calluna vulgaris*, *Molinia caerulea* and *Rhynchospora alba* were common. The water table was at 3 cm below the surface of the *Sphagnum* carpet when sampled, but qualitative observation of the site on numerous visits at all seasons of many years indicates that the water table sinks lower here in most summers than it appears to do at Gors Lwyd. The second core, CM4, came from

an enclosed area upstream from a sandy causeway built across a valley. This area also had a complete cover of *S. papillosum* but the core also included one small plant of *Erica tetralix*. Species common in the neighbourhood were *Eriophorum angustifolium*, *Molinia caerulea*, *Rhynchospora alba*, *Narthecium ossifragum*, *Schoenus nigricans*, *Drosera rotundifolia* and *Sphagnum magellanicum*. The water table was 3 cm below the carpet surface. The area is constantly wet throughout the year – it is in effect a shallow pond in one of the two main stream lines – and the peat is unhumified and of very low density, so the plants can rise and fall with the water table, just as on a Schwingmoor. The third core, CM6, was taken just to one side of the same stream line about 250 m downstream from the causeway, and about 20 m from a pine-covered island. It had a complete cover of *S. magellanicum* with a few small plants of *Erica tetralix*. Species common in the neighbourhood were *Eriophorum angustifolium*, *Molinia caerulea*, *Rhynchospora alba*, *Calluna vulgaris*, *Narthecium ossifragum* and *Juncus acutiflorus*. The core was taken in a low hummock, with the water table 6 cm below the surface. Because the hummock is immediately next to the stream it is likely that the water table does not fluctuate much.

In none of the cores from both Gors Lwyd and Cranesmoor was there any sign that the *Sphagnum* plants had produced sporophytes recently, though the remains of dehisced capsules were not uncommon at both sites.

Treatment of cores

The coring equipment (Clymo, unpublished data) caused negligible (< 1 cm) compression of the core and retained all the water *in situ*. The core tubes were sealed, and transported in the vertical position to London. Within two weeks the core tube was lowered around the still vertical core, 3 cm at a time, and the core was cut transversely into 3 cm thick $\times$ 20 cm diameter discs. On one core, pH and 'redox potential' (potential of a Pt electrode) were measured. The peat discs were placed separately, each in a 40×50 cm polythene bag, with the open end of the bag folded under to prevent evaporation except through the polythene. Air was included in the bag, and the polythene was held off the upper surface of the disc to allow gas circulation. Water which drained from the wetter discs was removed.

In the first three (GL) cores one semicircular half of the peat disc was covered with aluminium foil to keep it nearly dark. All the samples, still in their original vertical orientation, were placed in a 'summer cloud'-painted glasshouse with one continuously lit 'Daylight' fluorescent light. The discs received about 0·13 to 0·25 % of incident (autumn and winter) daylight. Heaters ensured that the temperature did not fall below 10 °C. At intervals the discs were removed from their polythene bags and the number of green shoots of *Sphagnum* was recorded. Shoots growing out from the edge of the disc or within 1 cm of the edge were recorded separately, but are not shown in the Figures. After 13 weeks (18 December), the aluminium foil was removed and subsequent counts made of green shoots which appeared in the previously darkened part. After 17 weeks (16 January), the discs were removed from the bags for detailed examination. New shoots were counted (and in many cases carefully dissected out and photographed) with either a Leitz Dialux microscope using bright-field optics, or a Wild dissecting microscope using transmitted light. Finally, after 19 weeks, (31 January 1985) the remaining material in the bags was turned upside down, thus exposing a new surface to the light. Further counts were made on 5 March of any new green shoots.

The CM cores were collected, sliced, and put in bags in the glasshouse in a similar fashion except that there was no foil treatment. The discs were put in the glasshouse on 5 February 1985 and counts of shoots made at intervals until 5 June, i.e. over 17 weeks. The final counts of new shoots were made using a dissecting microscope.

Sample age

It is highly desirable to know the age of any peat from which regeneration occurs. A technique was required which would give an approximate estimate of the age of the samples, but which would be inexpensive. The age range expected was 0 to 100 years. Unfortunately, there is at present no such reliable technique – even an expensive one. Identifiable and datable local pollen events may be useful (Livett, Lee & Tallis, 1979; Tallis, 1985) but the method is time-consuming and works only for peat from areas where there are such suitable events. The ^{210}Pb method is expensive. It may be useful for some peats, but for others, where independent dating tests are also available, it has proved to be unreliable (Oldfield *et al.*, 1979). The Pb may be more mobile than is often assumed, particularly in the open unhumified material of the cores obtained in this work. The 'moss-increment' method has been used several times (e.g. El-Daoushy, Tolonen & Rosenberg, 1982; Olson 1983; Tolonen, Davis & Widoff, 1986) but has not yet been sufficiently checked and appears to be useful only in cases where there is a clearly discernible seasonal change in moss morphology. For the period 0 to 100 years, standard ^{14}C dating is of no use. High-accuracy ^{14}C 'wiggle matching' (Pearson, 1983) is still only at the development stage and is also very expensive. In principle, however, a proportional time scale can be obtained by measuring any substance which is known to be added at constant rate and which is immobile once it has arrived. The elements Mg, Ti and Al were studied and measured as possible time markers by Clymo (1978), but later work (Damman, 1978; Clymo, unpublished) makes it clear that these are of only restricted use for dating. Total inorganic matter – 'ash' – is easy to measure. Even easier is total organic matter, with allowance made for loss by decay. Proportional time scales are tethered only at zero. The 'free end' must be tied down either by knowledge of the absolute rate of addition of the substance or of the age of one particular horizon (or by both). The best chance of dating one specific horizon seems to lie in using the 1963 peak in nuclear-bomb test nuclides, for example ^{137}Cs. The element Cs is chemically similar to K, and probably moves by diffusion and mass flow in peat, and also by transport within living material. These possibilities and analyses of four profiles have caused some authors (e.g. Pakarinen & Tolonen, 1977; Oldfield *et al.*, 1979) to conclude that, on the evidence then available, ^{137}Cs 'does not provide a valid method of dating in ombrotrophic peat'. But Olson (1983) made a more extensive study of ^{137}Cs in North American peats and concluded that, used with caution, it could often be useful for dating. This conclusion has also been reached by Clymo (1978 and unpublished). An ordinary low-background gamma counter is all that is needed. As such a machine was available we used the ^{137}Cs method to date the peat cores used in this study.

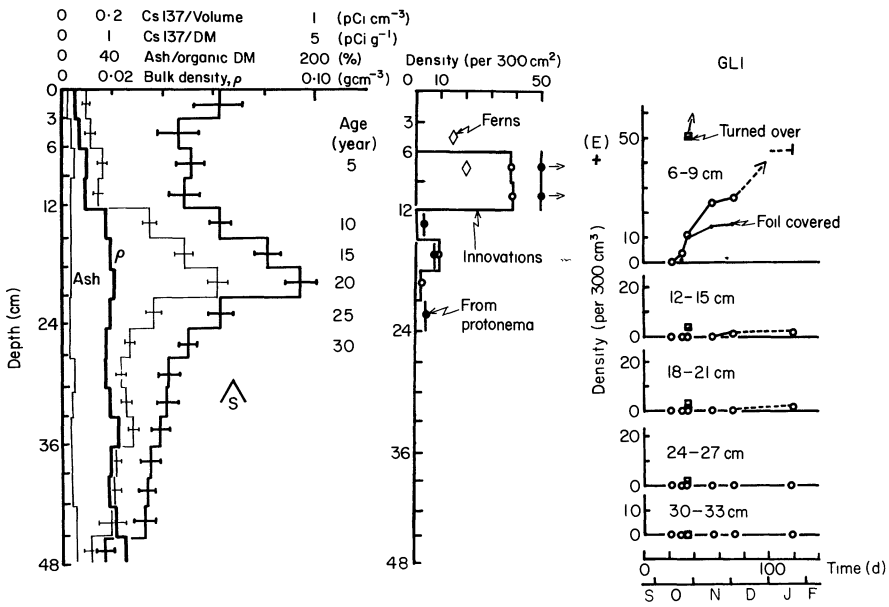
We measured bulk density, ash concentration and ^{137}Cs activity after all the dissections and regeneration observations had been completed. One half of a 3 cm thick disc (volume 450 cm^3) was oven-dried at 105 °C, cooled and weighed. The dry material was then ashed in a muffle furnace at 550 °C for 8 h, and the ash weighed. The ash was packed into a 4·6 cm^3 polypropylene tube. In samples where

there was more than 4·6 cm^3 of ash a weighed subsample was used. The ^{137}Cs activity was assayed using a standard Beckman BioGamma automatic counter. The detector was a doped NaI crystal. Three channels were used with widths 5, 10 and 15 % of the peak energy for ^{137}Cs (662 keV). There is unlikely to be any interference from other isotopes even in the widest of these windows (Olson, 1983), and there was no evidence of any systematic difference between results from different channels. Every fifth count was of an empty tube ('background count'), and each count lasted 100 min. A standard was counted every day. Sample count rates averaged 1·5 times the background count rate. Counting errors were assembled for the sample, for the bracketing background counts, and for the bracketing standards (including an assessed 5 % error in the standard value itself). The error in each count was weighted in proportion to its partial differential. The times were assumed to be error free. In a typical case the sample contributed 60 %, the background 30 %, and the standard 10 % to the overall counting error. The data were searched for evidence of drift or erratic shifts in machine sensitivity or background count-rate, but none was found. Measurements from two peat profiles were duplicated. The standard error of duplicates was 5 % of their mean value. The counting errors were generally smallest for the widest window, and it is therefore these values that are reported here.

RESULTS

All the cores were similar in showing (Figs 1 to 6) an increase of bulk density with depth, a peak in ^{137}Cs activity below the surface, growth of abundant innovations and sporelings of *Sphagnum* to 20 to 30 cm depth, and the appearance of fern gametophytes to the same depths. Nevertheless, even the cores which had seemed to be most similar when collected (GL1 to GL3) showed marked differences in other features. The cores must therefore be considered individually and statistical treatments cannot be applied. The ash, bulk density and ^{137}Cs profiles are considered first because they are the basis for ages used in the rest of the results. The rate of appearance of shoots and the results of the shading experiments are given next. Finally, the extraordinary variety or morphogenetic observations is reported.

Figures 1 to 6. Results for peat cores from Gors Lwyd (GL1, GL2, GL3) and from Cranesmoor (CM1, CM4, CM6). (a) Profile of ash mass/organic dry mass (%); dry bulk density (g cm^{-3}); ^{137}Cs activity/organic dry mass (pCi g^{-1}); and, in core GL1 only, ^{137}Cs activity/volume (pCi cm^{-3}). The depth at which the peat became strongly sulphidic is shown by a tented 'S'. At the right are tentative – probably minimum – ages, inferred from the ^{137}Cs and bulk density measurement (see text for details). (b) Profile of density of new shoots or seedlings, all /300 cm^2 basis. A value of 50 is equivalent to individuals about 2 cm apart. Continuous histogram, *Sphagnum* innovations; vertical bar, *Sphagnum* developed from protonema; ◇, fern gametophytes of at least two taxa. Where the density was high an exact count was not made: an arrow indicates 'more than'. Other taxa are shown by +(0 to 9 plants) or ▲ (10 or more). Those found were: L, liverworts (at least 5 species – see text for names); Et, *Erica tetralix*; D, *Drosera rotundifolia*; E, *Eriophorum*; M, *Molinia caerulea*; N, *Narthecium ossifragum*. (c) Time course of appearance of *Sphagnum* (innovations and plants newly developed from protonema). Most counts were made by simple visual inspection, but for the last a microscope was used. A dashed line indicates that this value is not directly comparable with earlier ones. Where the density was high an exact count was not made. (----) Indicates 'more than' at the time shown by the right hand terminal bar. For the GL cores results for foil-covered (●) and uncovered (○) halves – both scaled /300 cm^2 – are shown separately. ⬓, After the discs were turned over. For them the time scale is correct but the calendar month is invalid.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0 40 Ash/organic DM 200 (%)
0 0·02 Bulk density, ρ 0·10 (gcm⁻³)
Density (per 300 cm²)
0 10 50
Depth (cm)
Age (year)
Ash
ρ
S
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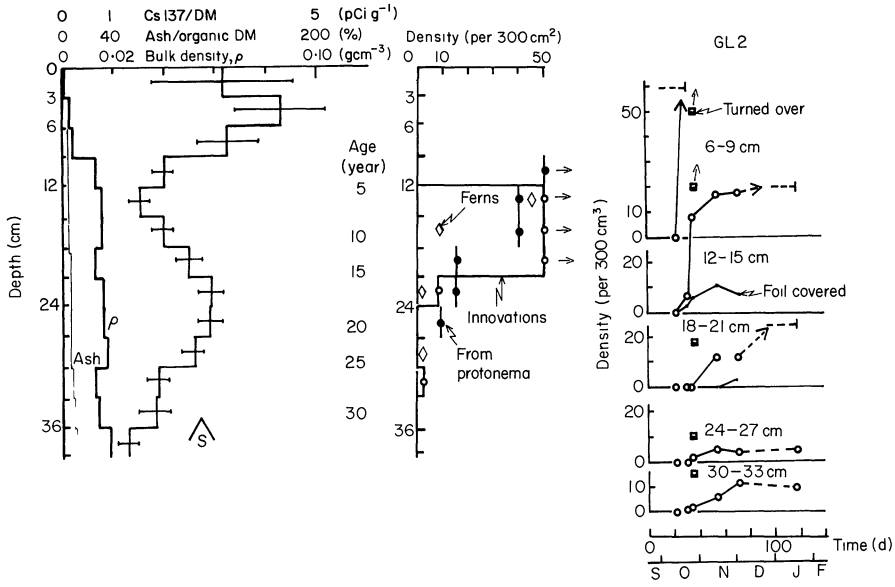
Innovations
From protonema
GL1
(E)
Turned over
6-9 cm
Foil covered
12-15 cm
18-21 cm
24-27 cm
30-33 cm
Density (per 300 cm³)
Time (d)
S O N D J F

Fig. 1.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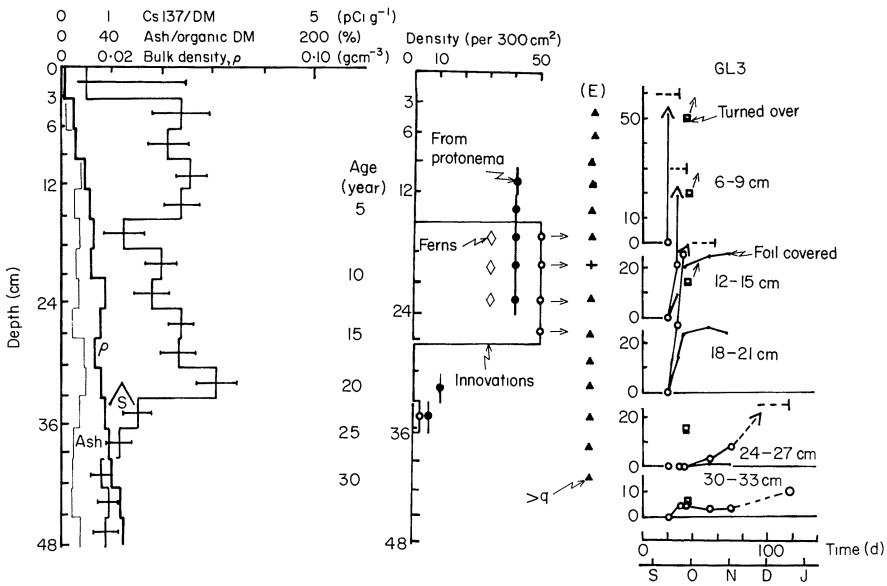
0 40 Ash/organic DM 200 (%)
0 0·02 Bulk density, ρ 0·10 (gcm⁻³)
Density (per 300 cm²)
0 10 50
Depth (cm)
Age (year)
Ash
ρ
S
Ferns
Innovations
From protonema
GL2
Turned over
6-9 cm
12-15 cm
Foil covered
18-21 cm
24-27 cm
30-33 cm
Density (per 300 cm³)
Time (d)
S O N D J F

Fig. 2.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0 0·02 Bulk density, ρ 0·10 (gcm⁻³)
Depth (cm)
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Ash
Density (per 300 cm²)
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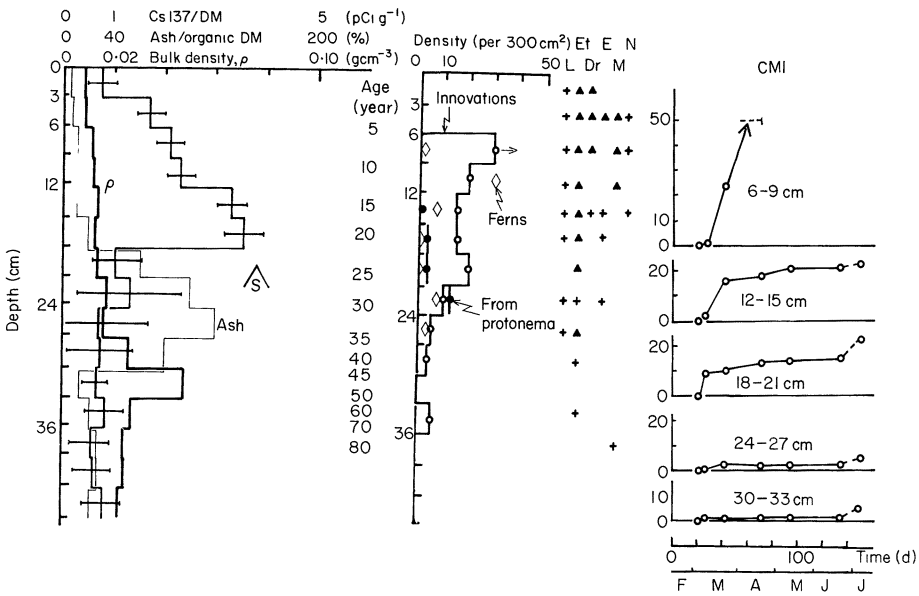
>q
(E)
GL3
Turned over
6-9 cm
Foil covered
12-15 cm
18-21 cm
24-27 cm
30-33 cm
Time (d)
S O N D J

Fig. 3.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0 40 Ash/organic DM 200 (%)
0 0·02 Bulk density, ρ 0·10 (gcm⁻³)
Depth (cm)
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Density (per 300 cm²) Et E N
0 10 50 L Dr M
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CMI
6-9 cm
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Time (d)
F M A M J J

Fig. 4.

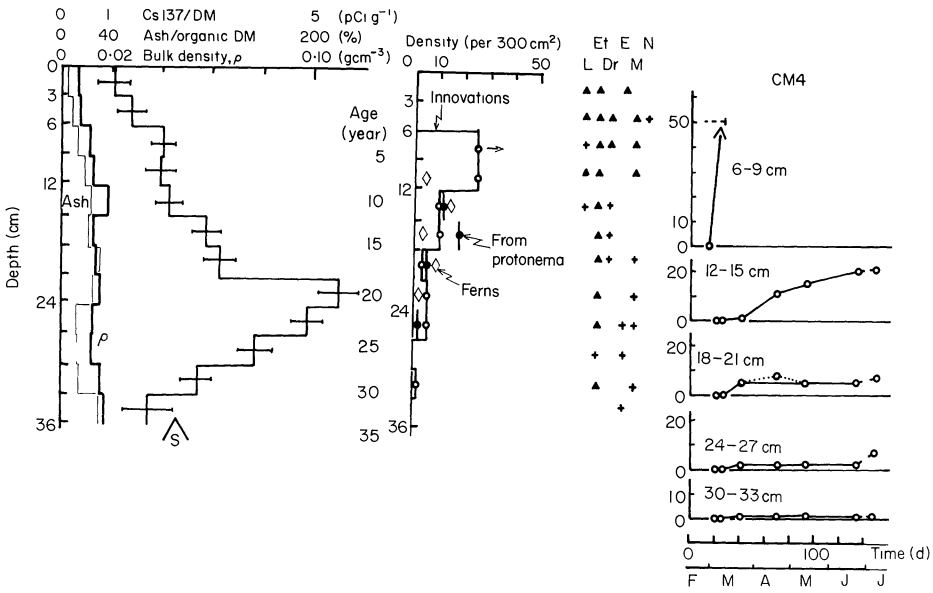
Cs137/DM
Ash/organic DM
Bulk density, ρ
Density (per 300 cm²)
Et E N
L Dr M
Age (year)
Innovations
From protonema
Ferns
Ash
Depth (cm)
CM4
6-9 cm
12-15 cm
18-21 cm
24-27 cm
30-33 cm
Time (d)
F M A M J J

Fig. 5.

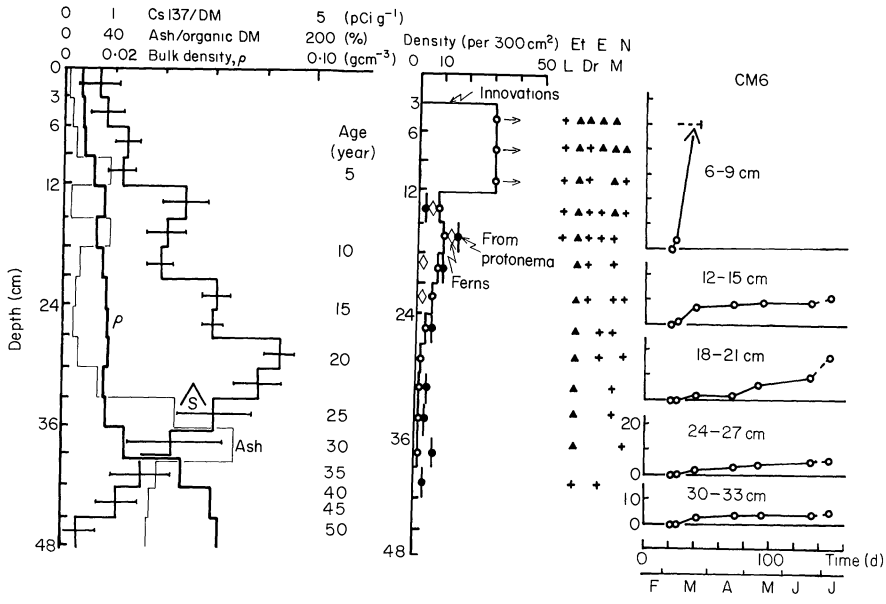
Cs137/DM
Ash/organic DM
Bulk density, ρ
Density (per 300 cm²)
Et E N
L Dr M
Age (year)
Innovations
From protonema
Ferns
Ash
Depth (cm)
CM6
6-9 cm
12-15 cm
18-21 cm
24-27 cm
30-33 cm
Time (d)
F M A M J J

Fig. 6.

Age profiles

If the rate of addition of organic and of inorganic matter were constant one would expect the proportion of 'ash' (i.e. inorganic matter) to increase down the profile as decay removed the organic matter. In GL1, GL2 and GL3 (Figs 1 to 3) to 33 cm depth this is approximately true, though the absolute values in GL3 are about twice those of the others. The ash proportion is lower again in the bottom third of GL3, and erratic in all the CM cores. In CM1 (Fig. 4) and CM6 (Fig. 6) there are places where there is a greater mass of ash than of organic matter. Most of this ash was diatom frustules dominated by *Frustulia rhomboides* (Ehr.) de Toni, *Anomoeoneis serians* (Bréb.) Cleve, and *A. brachysira* (Bréb.) Cleve. These layers probably represent a time when there was a pool on the surface. There are many pools on Cranesmoor today. It is obvious that 'cumulative ash' cannot be used uncritically as a dating method. But the approximate constancy of the proportion of ash in GL1, GL2 and the top two-thirds of GL3 all indicate that the loss of organic matter by decay in these cores does not exceed 10 to 20%. Decay during the experiment was either uniform in all slices or at worst, caused the 10% difference between top and bottom.

With the exception of CM1 (Fig. 1), the cores became strongly sulphidic at 30 to 36 cm below the surface, i.e. at 27 to 30 cm below the water table. In the one core in which measurements were made this level coincided with a marked fall in redox potential. It seems likely therefore that the top 30 cm or so, though waterlogged, is still mainly aerobic and hence best considered as part of the acrotelm. In all sites except CM1 water was flowing slowly, so O_2 was not, we assume, in short supply. But it is surprising to find such an apparently low rate of decay in such circumstances.

For the present purposes, therefore, the cumulative mass of dry matter below the surface is regarded as being proportional to age. The ^{137}Cs profiles show great variety – as previously found by Olson (1983). When expressed on a volume basis (Fig. 1), the activity near the surface appears to be low, but that is because the bulk density there is low. Therefore it seems better to make comparisons on an organic dry-mass basis, and this is what is shown for all cores. The error bars shown are $\pm$ standard error in the counting (only). In some cases they are large because there was little organic matter, and correspondingly little ash, in a sample. In others the errors are large because there was a very high proportion of ash and only a small part of it would fit in the counter. The cumulative influx of ^{137}Cs in precipitation is about 7 fCi cm^{-2} (mm $a^{-1})^{-1}$ (Cawse, 1983). This would give about 12 pCi cm^{-2} at Gors Lwyd and about 6 pCi cm^{-2} at Cranesmoor. The totals recorded in the three cores were 4·2, 2·6 and 3·6 pCi cm^{-2} at Gors Lwyd and 2·5, 3·6 and 6·2 at Cranesmoor. All cores except CM6 had ^{137}Cs activity significantly above zero even in the lowest slice at 36 to 48 cm depth. The apparent retention in CM6 (Fig. 3) was thus 102%, and in the other cores from more than 22% to more than 60%. All but CM4 (Fig. 5), for which the apparent retention was at least 40%, were in flushed areas, and the real influx can only be guessed. Cawse (1983) found that long-term ^{137}Cs retention in ombrotrophic peat was only half that in a grassland soil.

The same variability as in total activity is also found in the profile of activity. Core GL3 (Fig. 3) shows moderate activity to 33 cm depth, then a sharp fall; GL2 (Fig. 2) shows a peak at the surface, and a second peak at 18 to 30 cm; GL1 (Fig. 1) is similar, but the lower peak is from 15 to 21 cm and is more pronounced. The Cranesmoor cores all show no surface peak but a steady rise to a peak in the range

15 to 33 cm below the surface. In some cases the subsurface peak is approximately symmetrical. In others it is skewed upwards and in others skewed downward. This variability in size of the surface peak and in skewness of the lower peak is remarkably similar to that found by Olson (1983) in twelve peat cores in north America.

It seems clear that there are differences in the extent of biological transport, of diffusion, and of mass flow for ^{137}Cs. The differences are as large within the GL cores, which seem on other criteria to be very similar, as they are in the more diverse CM cores.

For dating purposes, the lower peak has been taken as 1963 – the year before the moratorium on aerial tests of nuclear bombs, when deposition reached a high maximum. This is likely to underestimate the age because subsequent downward movement is likely to be greater than that upward.

Rate of shoot appearance and effects of shading

Two sorts of new *Sphagnum* shoot were observed: (1) shoots arising from pre-existing gametophyte tissues. These are of several types described in the next section, but for convenience are referred to as innovations; (2) shoots developed on protonemata. Because these two shoot types can be distinguished only after careful dissection, using a microscope, they had to be grouped together in earlier counts to avoid disrupting the peat disc. Because the shoots on protonemata take longer to reach a size at which they are clearly visible to the unaided eye, it is likely that the early counts are of innovations alone, and that in later counts protonemal shoots form an increasing proportion of the total.

Perhaps the most important observation is of the simple abundance of new *Sphagnum* shoots. Fifty in a 300 cm^2 slice may be visualized as shoots about 2 cm apart on average; ten corresponds to an inter-shoot distance of about 4 cm. This abundance varied with depth and age (which are confounded). The following observations were generally true for all cores studied.

(1) There were apparently very few new shoots of either type in the surface 6 cm or so. It is easy to overlook a small green innovation amongst a forest of older green plants, but it was very clear that the abundance of new shoots in the lower brown discs was much greater than in any 'green' disc. In CM6 (Fig. 6) shoots first became abundant in the second (3 to 6 cm) disc. In GL3 (Fig. 3) innovations became abundant only at 15 to 18 cm depth. In general innovations became abundant nearer the surface in the CM cores than they did in the GL cores. In the GL cores both *S. papillosum* and *S. recurvum* innovations were found and in the CM cores most were of *S. papillosum*, with some *S. magellanicum*. (Innovations have been seen from other cores of *S. capillifolium* (Duckett & Clymo, unpublished) and *S. fuscum* innovations were recorded by Karunen & Kälviänen (1985) from stems as deep as 40 cm in a hummock when the stems were exposed to light, air and water.)

(2) The shoots appeared in greatest abundance at 6 to 30 cm depth, associated with *Sphagnum* which was by that depth about 5 to 15 years old.

(3) The abundance of shoots generally decreased with depth and age, but some still appeared even at 33 to 36 cm deep in GL3 (Fig. 3) and CM1 (Fig. 4), and at 39 to 42 cm deep in CM6 (Fig. 6). The age of the parent material at these depths was estimated conservatively, at about 25, 60 and 35 years respectively.

(4) The decline in new shoot abundance with depth was fairly abrupt in the GL

cores. It was less so in the CM cores and could be regarded as approximating a negative exponential with a half life of about 5 to 15 years.

(5) Most of the shoots appeared in discs which had been water saturated but were above the sulphidic zone. But a few appeared in discs of GL3 (Fig. 3), CM1 (Fig. 4) and CM6 (Fig. 6) which were in the sulphidic zone when collected, though they became aerobic soon after slicing.

An important feature of the results is that the behaviour of *Sphagnum* in GL cores was very similar to that in the CM cores, although the cores came from different sorts of mire in different climates and were experimented on at different times of the year. This strengthens the case for believing that the behaviour observed may be widespread, or even general and that it is not an idiosyncrasy of plants from just one particular site.

This similarity extended also to the appearance of fern gametophytes in both sets of cores (Fig. 11). There were at least two taxa: one was *Pteridium*-like, with a plain margin [Fig. 11(a), (c)], the other was *Dryopteris*-like [Fig. 11(d), (f)] with a papillate margin and surface (Atkinson, 1973). The gametophytes ranged from 1 mm to 2 cm across after 17 weeks. The smallest lacked sex organs. Larger individuals (> 2 mm) bore either antheridia, amidst the rhizoids on the older parts [Fig. 11(g)] and the wings [Fig. 11(b)] or archegonia with recurved necks [Fig. 11(e), (f)]. Individuals over 8 mm across were either female or protandrously hermaphrodite. The ferns appeared over a more restricted range of depths than did the *Sphagnum* shoots, and they were also less abundant. The similarity of the profile of appearances of gametophytes in all the cores, even those from different sites, suggests that their appearance is not simply a consequence of local climatic effects or contamination. Even so, the two sets of cores differed markedly in the abundance in which other plants appeared. GL1 produced nothing, GL2 a solitary *Eriophorum* seedling, while GL3 produced 20 to 30 *Eriophorum* seedlings in almost every disc. The CM series produced a much greater variety and abundance of other species. Five species of liverwort (*Cladopodiella fluitans*, *Cephalozia bicuspidata*, *Kurzia pauciflora*, *Odontoschisma sphagni* and *Cephalozia connivens* were common in the top 15 cm. Among the vascular plants, seedlings of *Erica tetralix*, *Drosera rotundifolia*, *Eriophorum*, *Molinia caerulea* and *Narthecium ossifragum* were abundant to varied extents and depths. Most of these taxa are bog-plants and grew locally at both sites. Even though they did not grow from the core samples, they were as common at Gors Lwyd as at Cranesmoor (though not in the immediate vicinity, i.e. within 1 to 2 m, of the core sites). The ferns do not grow on either bog. *Pteridium aquilinum* is common around both bogs, but other ferns are uncommon. Just as curious as the appearance of fern gametophytes was the absence of protonemata of mosses other than *Sphagnum*. A green film appearing on the surface of many discs, particularly those from between 15 and 25 cm was due to the presence of abundant euglenoids rather than of filamentous algae or protonemata.

The *Sphagnum* shoots appeared soon after growing conditions were made suitable [Figs 1(c) to 6(c)]. The first were seen about 20 d after the experiment began. The number of shoots appearing tended toward a plateau with the time for half-maximum values of about 40 to 60 d. The concept of a half-time is, however, no more exact than was that of exponential decline. These ideas are still useful, perhaps, as convenient quasi-quantitative models.

The last result requiring comment is that from the shading experiment. Only the GL cores were shaded. In all three cores and at every depth where shoots

appeared there were many fewer in the shaded half than in the unshaded one. There were *some* shoots in the shaded halves, but this may have been because the foil covering did not totally prevent light penetrating laterally. All the shoots were green. After the foil was removed many more shoots then appeared on the now uncovered half. The lower surface of the discs was completely free of any new shoots – but new shoots are either positively phototropic or negatively geotropic or both. When the discs were eventually turned over, the previously lower surface produced abundant shoots, as the results in Figures 1(c) to 6(c) show. It is relevant to record that in many discs shoots appeared at greatest density around the edges of the disc. Contamination by material carried down during coring was feared, and the edges were excluded from all the counts. But later dissection showed that the plants at the edge were innovations from stems that were clearly part of the proper disc. A more likely explanation is that light could penetrate through the 3 cm deep edge of the disc as well as through the upper surface, and that a larger proportion of potential innovations thus received sufficient light to stimulate them to grow.

Morphogenesis of Sphagnum *regenerants*

Developments from pre-existing adult gametophyte tissues. Careful dissection of the basal regions of innovations revealed that they may arise in several different ways in all three species of *Sphagnum* which grew in the discs (*S. magellanicum*, *S. papillosum* and *S. recurvum*).

Over 90 % of new shoots from both GL and CM cores emerged from the immediate vicinity of fascicles of branches [7(a), (d)]. The innovation bases were inserted in the elongated thick-walled cells of the outer cortex which contain abundant chloroplasts (Hébant, 1977). Such new shoots were most frequently produced from stem fragments which were particularly 'woody'. Here the cortical cells were bright green for several millimetres in the vicinity of the new growths. In most instances only one new shoot arose from a single stem, but up to three were seen on some [Fig. 7(d)].

Approximately 5 % of the new shoots could be traced back to the tips or sides of branches [Fig. 7(c)] and a further 5 % to the cortex of stems in regions several millimetres removed from the remains of fascicles [Fig. 7(b)].

Whatever their origin, ultimately all the new shoots began to function as normal leafy stems with an apex of unlimited growth producing stem leaves and fascicles of branches in the normal manner. However, in the early stages of their ontogeny other features were observed. The first leaves produced by the majority of the shoots emerging from the vicinity of old fascicles of branches had the dimorphic cell structure typical of adult plants [Fig. 7(a))]. Other shoots produced monomorphic leaves at first and only gradually produced dimorphic ones through a succession of intermediate stages [Fig. 8(c) to (g)]. These juvenile leaves were most often encountered on shoots which had arisen either away from old fascicles of branches [Fig. 8(d)] or from stems several millimetres below the surface of a disc [Fig. 8(c)]. The basal regions of new shoots with the latter origin bore widely spaced leaves and irregularly branched multicellular filaments with oblique cross walls and few chloroplasts [Fig. 8(a), (b)]. The filaments arose either in clusters just below the insertion of a leaf [Fig. 7(e)] or from the point of emergence of the new shoot [Fig. 8(b)]. In some instances the filaments produced plates of tissue upon which leafy gametophytes subsequently developed [Fig. 8(b)].

Development, probably from spores. Physical contact between filamentous protonemata and ruptured spore coats was not observed, although it was sought for many hours in dissections. Several filament systems were separated in their entirety from the subjacent organic matter, however, and these were found to be entirely separate from living tissues in old *Sphagnum* stems or the outgrowths described above [Figs. 9 and 10]. These filaments were most readily observed growing over the dead leaves of *Sphagnum* [Fig. 9(a)] or on the remains of stems and leaves of *Eriophorum* [Fig. 9(b)].

The filamentous protonemata were sparsely and irregularly branched. Virtually all the cells contained numerous chloroplasts and were usually separated by oblique cross-walls. When two-dimensional plates grew, they always arose from

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EXPLANATION OF FIGURES 7 TO 11

All the specimens came from Gors Lwyd.

Abbreviations: AM, archegonia; A, apical notch; I, innovation; BP, pre-existing branch; LP, pre-existing leaf; SP, pre-existing stem; NS, new shoot; PF, protonemal filament; PP, protonemal plate.

Fig. 7. New shoots of *Sphagnum* arising from pre-existing gametophyte tissues. In all such situations new shoots were immediately distinguishable from pre-existing tissues on the basis of their colour. The striking contrast between bright green outgrowths and brown pre-existing tissues is obviously lost in monochrome. (a) Innovations of *S. papillosum* arising from the vicinity of a pre-existing fascicle of branches. The first leaves on the new stem have dimorphic leaf cells indentical to those on adult stems. (b) Innovation of *S. papillosum* arising from the cortex of a stem some distance from a pre-existing fascicle of branches. (c) Three new shoots arising from a pre-existing branch of *S. recurvum*. (d) Three new shoots of *S. papillosum* growing out from the stem cortex adjacent to a pre-existing fascicle of branches. (e) Portion of a new shoot of *S. papillosum*, dissected from approximately 5 mm below the surface of a peat disc, showing clusters of filaments growing out from just below the points of leaf insertion.

Fig. 8. Regeneration from pre-existing shoots of *Sphagnum*. (a) New stem of *S. papillosum* from approximately 1 cm below the surface of a peat disc. Note the widely spaced leaves and multicellular filaments with oblique cross walls (arrowed). (b) Base of a new shoot of *S. papillosum* dissected from a pre-existing stem, showing numerous sparsely branched filaments one of which has produced two-dimensional plates of tissue. (c), (d) Young shoots of *S. recurvum* (c) and *S. papillosum* (d) with largely monomorphic leaf cells. (e) to (g) Different leaves from a regenerating stem of *S. recurvum* showing the gradual development of the dimorphic cell structure. (e) Leaf with very few hyaline cells. (f) The same ratio between hyaline and chlorophyllose cells as seen in adult leaves, but wall thickenings are largely absent in the former and the latter are much wider than in adult leaves. (g) Dimorphic cell structure characteristic of mature adult leaves.

Fig. 9. Development of *Sphagnum* protonemata, probably from spores. (a) Numerous protonemal plates arising from the tips of filaments growing over the surface of dead *Sphagnum* leaves. (b) Protonemal plates and filaments partially dissected from the remains of an *Eriophorum* stem. (c) Tip of a new shoot, with entirely monomorphic leaf cells, arising from a protonemal plate. (d) Base of a new shoot developing from the basal region of a protonemal plate. Note the secondary plate (arrowed) and the numerous filaments arising from the vicinity of the new shoot. (e), (f) Young protonemal plates.

Fig. 10. Development of *Sphagnum* protonemata, probably from spores. (a) Irregularly lobed protonemal plate with several filaments growing out from the older regions of the margin. Note the initiation of secondary plates and the tips of the filaments (arrowed). (b) Montage in two focal planes of two highly lobed protonemal plates each of which has produced a single shoot with monomorphic leaf cells. A secondary plate (arrowed) is beginning to develop at the tip of one of the filaments extending from the basal region of the original plates.

Fig. 11. Fern gametophytes originating on peat discs. (a) Ventral aspects of a cordate gametophyte of the *Pteridium* type showing numerous archegonia along the central cushion. Note the plain margin. (b) Ventral aspect of a *Pteridium*-like gametophyte bearing numerous antheridia on the wings and a few necrotic archegonia with darkly stained venters behind the apical notch. (c) The plain margin of a *Pteridium*-like gametophyte. (d) Marginal papillae on a *Dryopteris*-like gametophyte. (e) Archegonia with recurved necks from a *Pteridium*-like gametophyte. Post-mature archegonia with darkly stained venters exhibit separation of the upper tiers of neck cells (arrowed). (f) Ventral surface of the central cushion of a *Dryopteris*-like gametophyte showing scattered papillae and archegonia with recurved necks. (g) Numerous antheridia amidst the rhizoids on the basal region of a *Dryopteris*-like gametophyte.

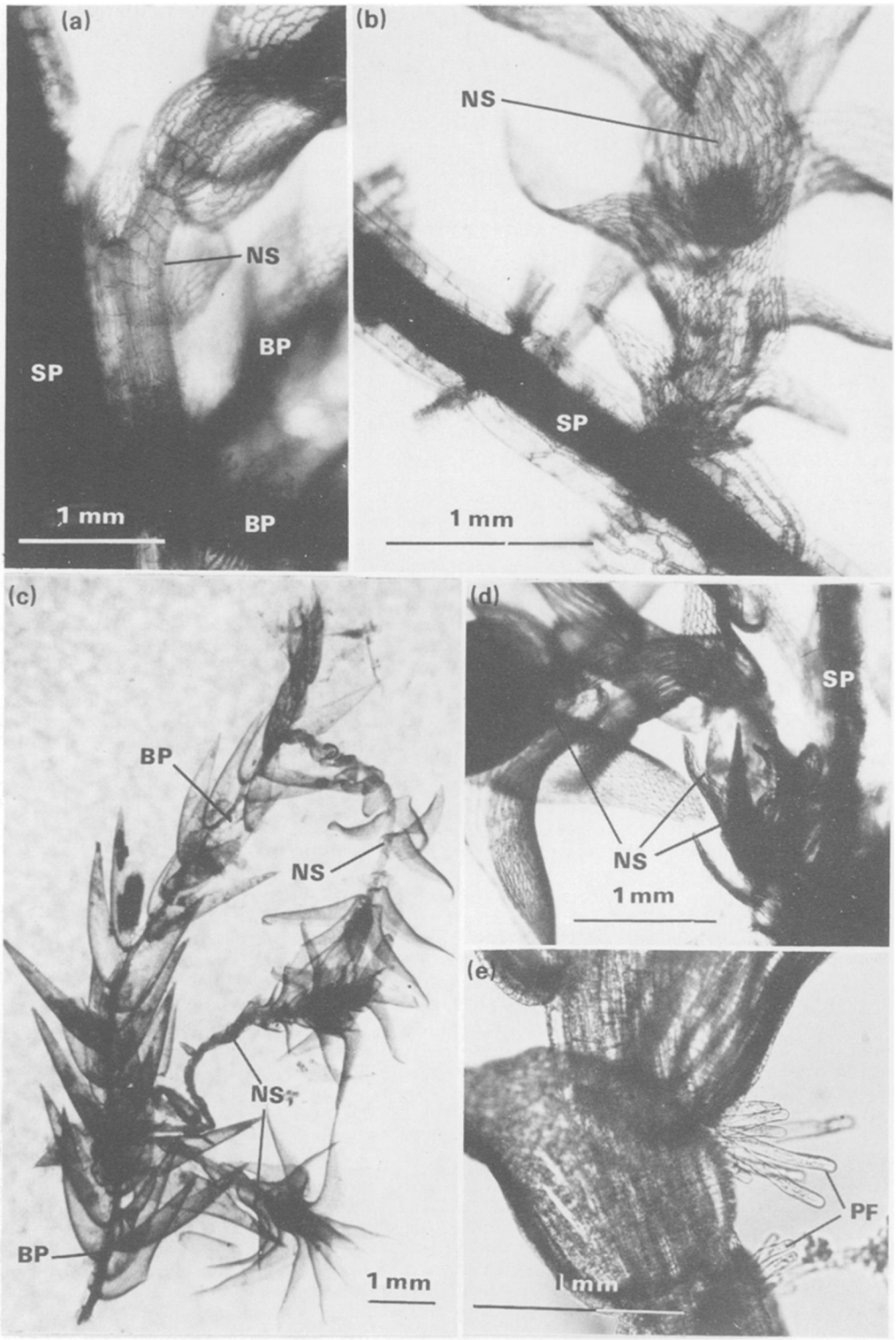
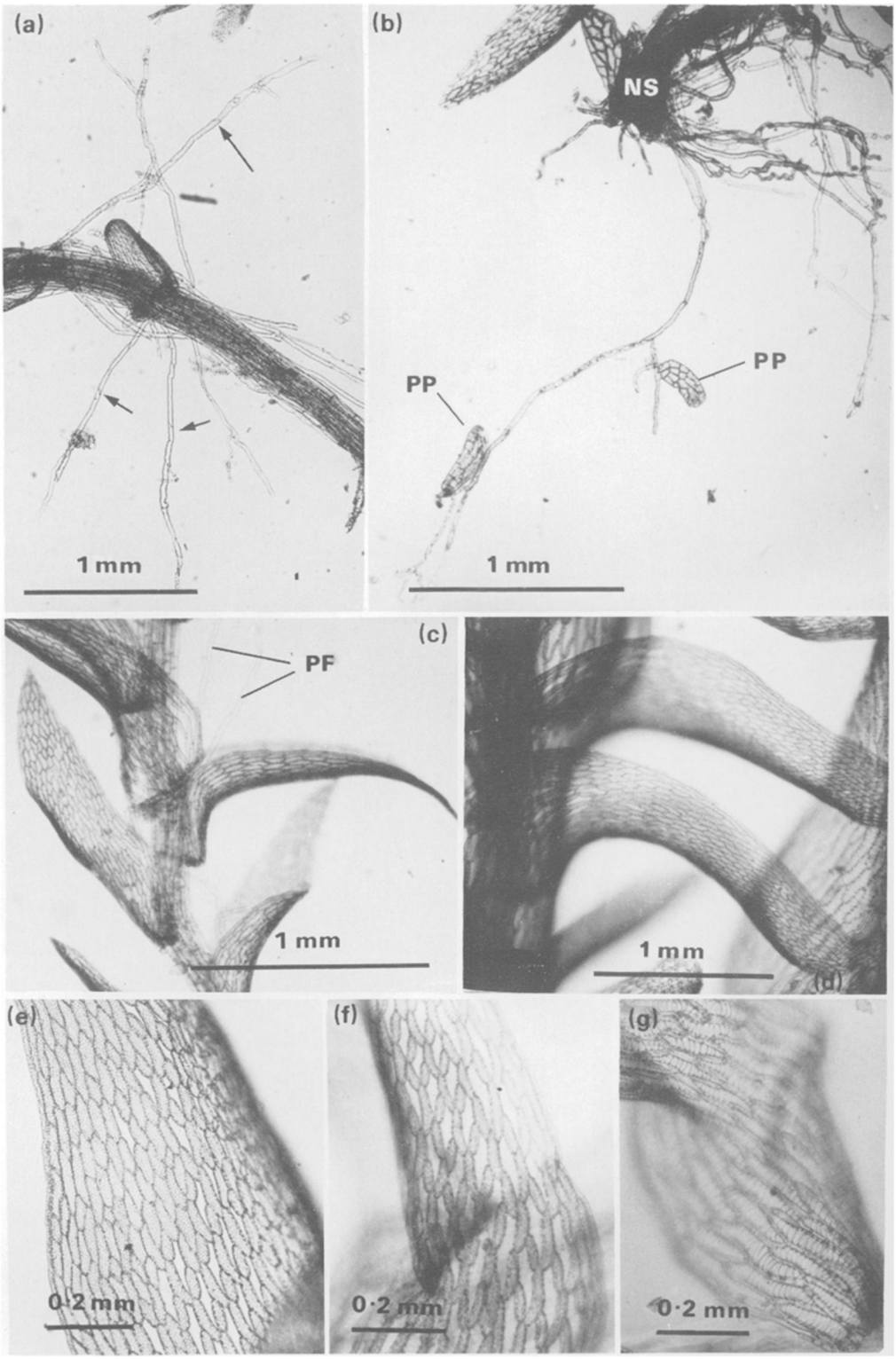


Fig. 7



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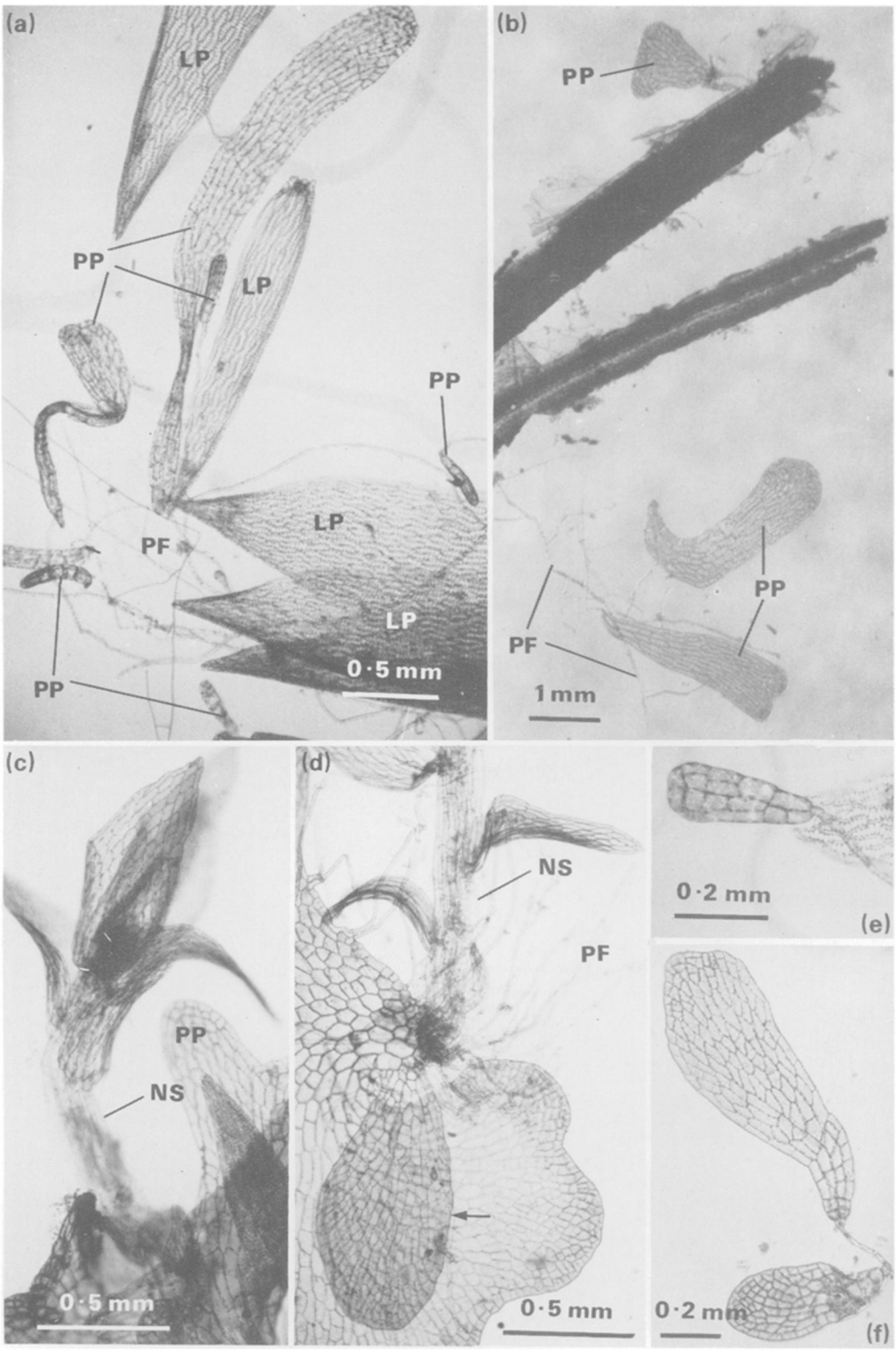
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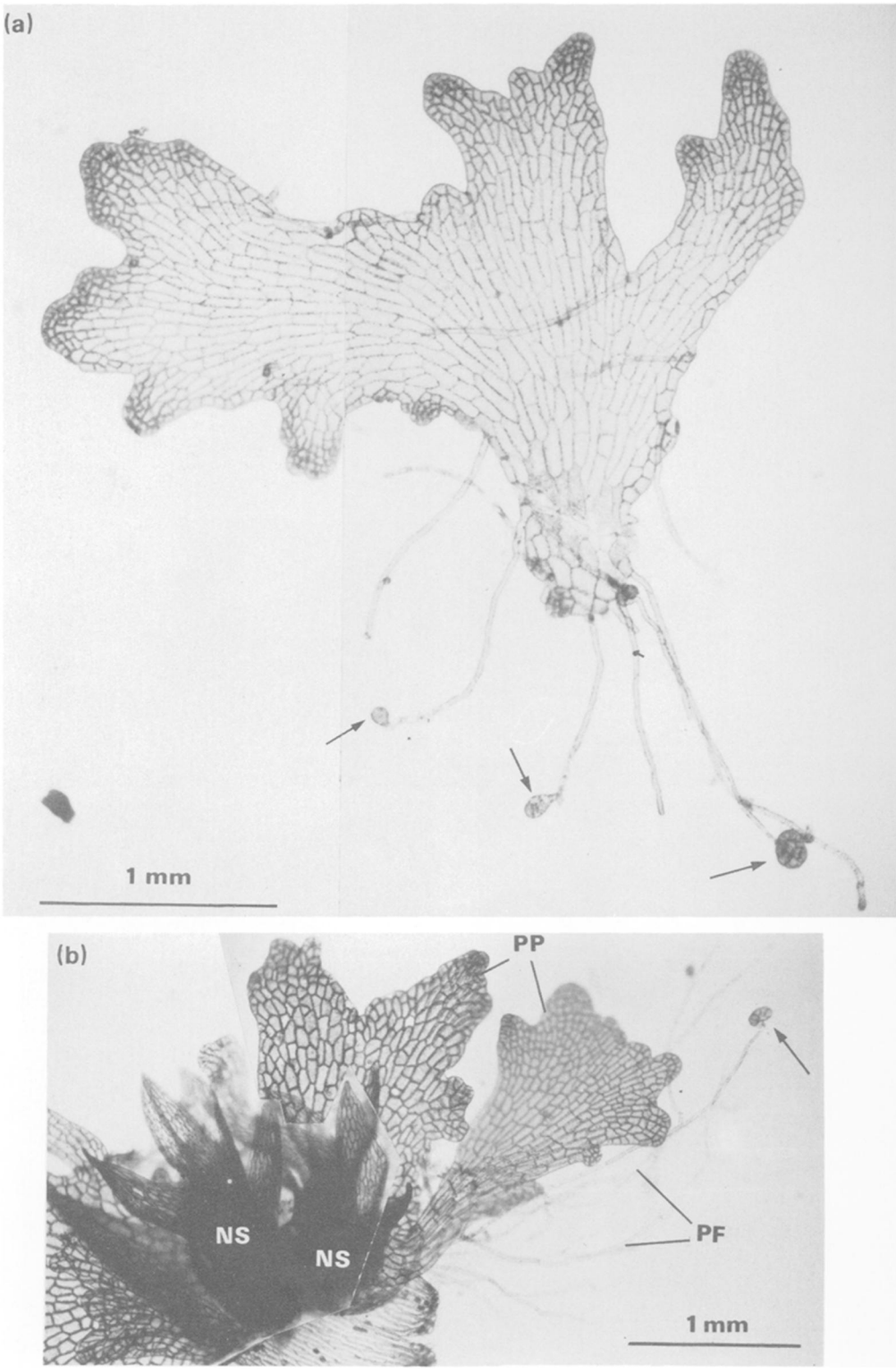

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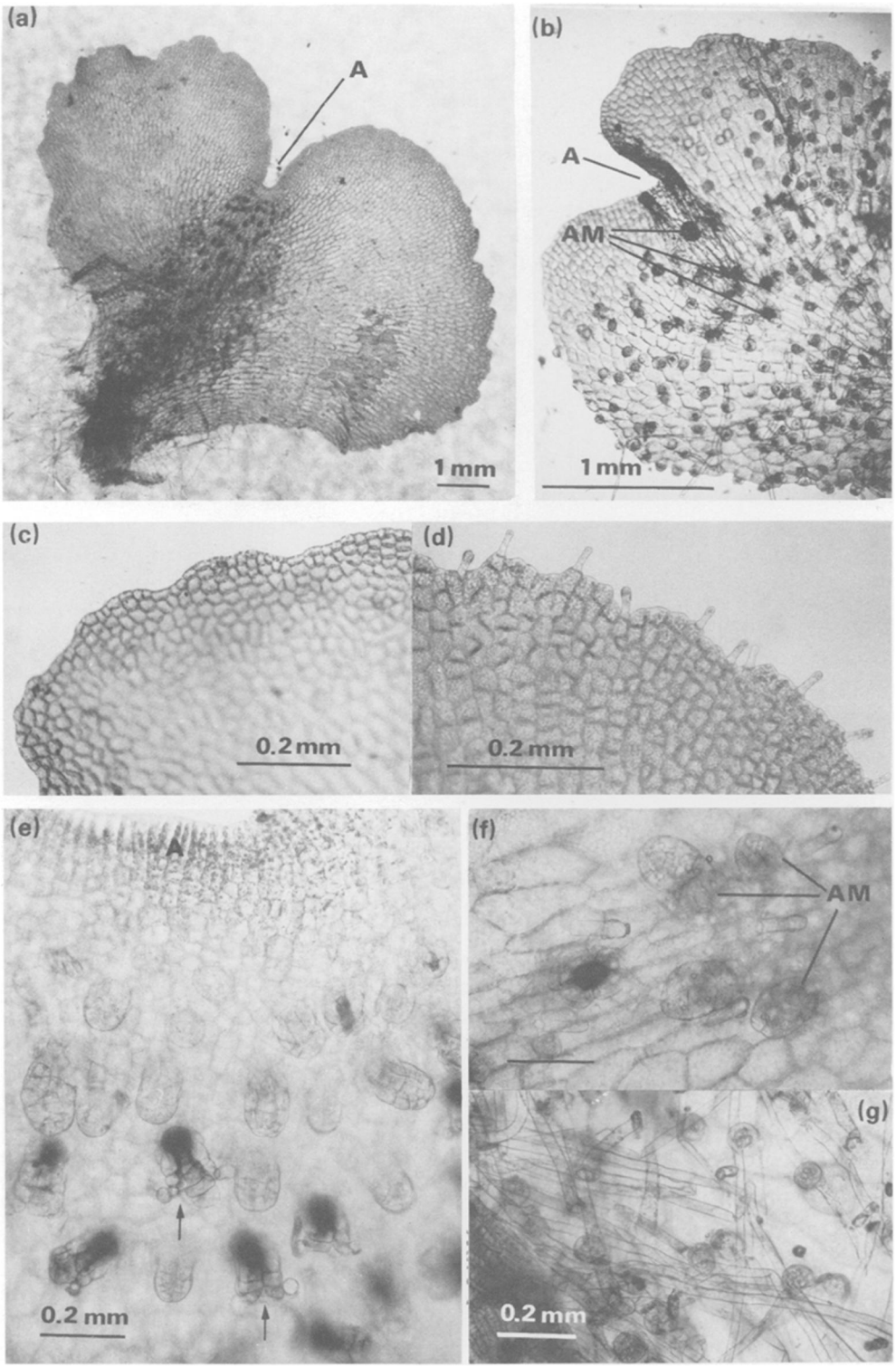

Fig. 11.

the tips of such filaments [Fig. 10(a)] not from interstitial cells. With successive cell divisions, the outline of the plates changed from circular to ovoid to spathulate [Fig. 9(e), (f)]. Older plates became irregularly lobed as a result of localized activity of the marginal meristem [Fig. 10(a)]. Additional filaments, developing from the margins (and more occasionally the central region) of the older parts of the lobed plates subsequently produced secondary plates at their apices [Fig. 10(a)]. Other two-dimensional plates sometimes developed directly from single cells near the base of the original plates [Fig. 9(d)].

The two-dimensional protonemata of *S. papillosum*, *S. magellanicum* and *S. recurvum* (identified from the leafy shoots they produced) were morphologically indistinguishable. In all three species they reached a size of up to 1 cm across.

Most of those plates which were more than 3 mm across bore leafy shoots [Figs. 9(c), (d) and 10(b)]. Only one shoot arose from each plate in over 90% of the individuals examined in detail. Dissection of clusters of shoots of the same size almost invariably revealed a corresponding group of plates in close proximity, each bearing but a single shoot. The first few leaves were monomorphic [Figs. 9(c) and 10(b)], as they are in cultures too.

DISCUSSION

The work reported here has shown that regeneration of *Sphagnum* from innovations and protonemata is abundant from depths of more than 30 cm below the surface. The plants from which innovations develop may be 25 to 30 years old, or more, and some at least are in sulphidic anaerobic conditions. The appearance of new shoots is light-dependent and their morphogenetic patterns are fluid.

These results raise a number of questions. How plastic *is* the morphogenesis of *Sphagnum*? Where does the protonema come from? What controls regeneration? What are the ecological implications of this work? Why do the spores of other bryophytes not germinate in these experiments? We consider these questions in turn.

The morphogenesis of Sphagnum

The morphogenesis of the sporelings of *Sphagnum* on peat discs mirrors that in axenic cultures (Nehira, 1984): in both cases an initally filamentous phase gives rise to a lobed plate, which in turn produces a leafy gametophyte. On peat the filamentous phase is more extensive than it usually is on agar containing a full range of inorganic salts. This accords with the findings of Boatman and Lark (1971) that one-dimensional growth is dominant at very low phosphate concentrations. Under such conditions, as on peat, more than one plate may be produced from each filament system.

Although the production of secondary protonemata from adult gametophyte tissues is well known in other mosses (Bopp, 1984; Knoop, 1984), as far as we are aware it has not hitherto been recorded in *Sphagnum*. This discovery of filaments on regenerating shoots contradicts general statements that 'rhizoids' are absent in *Sphagnum* except on protonemata. It would seem more than likely that they are normally overlooked: small and etiolated shoots are scrupulously avoided by taxonomists for good reasons.

The results of this study raise the question: what is the true nature of the filamentous phase in *Sphagnum*? Whether derived from shoots or spores it has the following attributes: colourless walls, numerous chloroplasts, oblique cross-walls and sparse irregular branching. The first two are normally associated with

caulonema (Bopp, 1984), the last with rhizoids (Crundwell, 1979) and oblique cross-walls are common to both. Nevertheless, even in bryopsid mosses, in spite of an increasing accumulation of morphological and physiological data, the distinction between caulonema and rhizoids is far from clear (Knoop, 1984). In the absence of information on the precise manner of growth of the 1D phase in *Sphagnum* and its responses to light, gravity and hormones, the general term filament is preferable to caulonema or rhizoid. The strictly terminal origin of the 2D plates in *Sphagnum* (as opposed to the lateral development of gametophores in Bryopsida) suggests that the filamentous phase may not be strictly homologous with morphological counterparts in other mosses.

The present observations suggest that the term innovation encompasses branches of unlimited growth which may have originated in different ways.

Perhaps the simplest explanation for the origin of those in the vicinity of existing fascicles of branches is that they develop from branch primordia derived from the stem apex, but which failed to develop on the surface of the capitulum. Released from the morphogenetic control of the stem apex such dormant buds would become stems rather than branches. We are examining this possibility by serial sectioning to see whether or not capitula contain a few primordia which fail to develop into leaf or branch at the usual time.

The retention of a capacity for indeterminate growth by the apices of buried *branches* again points to the controlling influence of the stem apex. In culture (Duckett & Clymo, unpublished data) detached branches show apical regeneration into new stem systems. These findings indicate that the fate of a particular primordium in *Sphagnum* is not fixed at the time of its initiation. Under the control of the apical meristem it will usually become a stem leaf or a side branch of determinate growth, but removed from this influence it can develop into a major axis. It is noteworthy that Baker & Boatman (1985), from experiments on the effects of carbon dioxide on *Sphagnum cuspidatum* similarly conclude that innovations and fascicular branches are homologous (Schimper, 1858). The lack of any absolute distinction between side branches and stems is seen clearly in species such as *S. molle* which often has branches of indeterminate growth.

On the other hand, innovations which develop some distance from old side branches may well be strictly adventitious, i.e. their primorida arise *de novo* from the chlorophyllose cells in the inner cortex of the stem. The notion of adventitious origin is strengthened by the observation that whilst shoots developing away from old branches almost invariably produce monomorphic leaves initially, the first leaves on those adjacent to fascicles of branches usually possess from their beginning the dimorphic cell structure found on mature shoots. Monomorphic leaves lacking hyaline cells have also been induced in cultures under particular unusually high concentrations of inorganic nitrogen and carbon dioxide (Baker & Boatman, 1985).

In this investigation the only organs which showed no sign of regenerative ability were leaves. Karunen & Kälviäinen (1985) likewise state in a study of subsurface samples of *Sphagnum fuscum*, that leaf cells never produce new plants, all regeneration being from groups of cells on branches near the junction with the main stem.

The source of protonema

Although protonema attached to a spore coat was never observed, the fact that the vast majority were not attached to living tissues of old *Sphagnum* indicates that it is probable that most of these juvenile stages did in fact arise from spores.

Protonemal shoots appeared from depths where the 'peat' was 20 to 30 years old. Has the protonema arisen from spores which have washed down only recently, or is there a long-lived spore bank? At first sight a spore bank seems implausible for two reasons. First, the spores are barely 30 to 40 μm in diameter (Tallis, 1962). Secondly, spores in *Sphagnum tenellum* capsules remain viable for only a few weeks when stored in air at about 4 °C. If the capsules of *S. cuspidatum* are stored in distilled water at 2 °C, however, the spores remain viable 'for several months' (Baker & Boatman, 1985) – at least six months for *S. palustre* and *S. capillifolium* in our experience. But the spores of *Sphagnum* are packed with lipids, contain little starch, and have plastids with very small grana (Brown, Lemmon & Carothers, 1982; Mogensen, 1981). These are all characteristics of long-lived spores in contrast with those of taxa such as *Equisetum* and *Osmunda* which contain a lot of starch, have large grana, and remain viable for less than a week if allowed to dry out at room temperature. Even these spores remain viable for up to a year, however, if stored in water at 4 °C. A *Sphagnum* spore bank with a half-life of 5 to 10 years is not improbable therefore, but we cannot at present eliminate the possibility that the spores have been washed down and are much younger than the matrix in which they germinated. Much the same possibility applies to the fern spores.

Perhaps the nearest analogue of *Sphagnum* spore survival in bogs is that of bryophyte spores in pond and reservoir muds. Rare species such as *Physcomitrium sphaericum* and *Micromitrium tenerum* appear sporadically when the water recedes (Duckett & Duckett, 1980). Such growth may occur twenty years of more since the mud last dried out. There is no other source of spores, so the plants which appear must have grown from spores which have survived for twenty years or more. These spores also contain a lot of lipid and little chlorophyll. Some annual bryophytes which appear erratically at long intervals in arable fields may also derive from long-delayed spore germination. Longton & Schuster (1984) give other examples.

Control of regeneration

This work has shown that in the top few centimetres of a green *Sphagnum* carpet protonemata and innovations, in the sense which we have defined, are absent or at least are much less abundant than they are in older material when exposed to light and air. In natural carpets of *Sphagnum* the light absorption coefficient is at least 0·7 cm^{-1} (Clymo & Hayward, 1982). The light flux is thus attenuated to 0·01 of that incident on the surface by the time that a depth of no more than 4 cm is reached. In most carpets this 'euphotic zone' is less than 4 cm deep. It is quite difficult to imagine how dense is the shade cast by the *Sphagnum* canopy. Light dependence is thus an effective mechanism for keeping spores and potential innovations dormant. How light dependence is determined is not yet known, but it is known that *S. subnitens* produces archegonia and antheridia only in short (6 to 8 h) days (Benson-Evans, 1964) though this is not *a priori* a reason for assuming that spore germination is likely to follow the same pattern.

Why, then, are protonemata and innovations not abundant in the surface layer of the *Sphagnum* carpet? We suggest that innovations may be kept dormant – that *Sphagnum* may have apical dominance even though it has no obvious internal transport system (Jones, 1978; Schofield & Hébant, 1984). The maintenance of a particular range of concentrations of a growth hormone distributed to a distance of several centimetres by diffusion alone poses obvious problems. It may be that

the central stele of the *Sphagnum* stem is more physiologically specialized than its structure indicates (Schimper, 1858; Hébant, 1977). Transport of a growth hormone (or hormones) around the outside of the plant in water films seems likely to be an unreliable control mechanism, because these films of water are flushed out whenever rain falls on the plants.

The patterns of branching of many mosses is so regular as to suggest that apical dominance may be the rule both in endohydric and ectohydric species: one has only to look at the regularly pinnate shoots of *Hylocomium splendens*, and to see the way in which a lateral growth becomes the new main stem if the old one is damaged. Precisely the same release occurs in *Sphagnum* when the capitulum is damaged, though a bifurcation in the main stem can also happen without apparent damage.

But what then prevents spores germinating? Live *Sphagnum* shoots are known to inhibit germination of spores of *Sphagnum* (and of ferns) on agar (Duckett & Clymo, unpublished data). This points to a more general allelopathic chemical control operating on these spores. It is of interest that the spores of *Sphagnum* and of the two taxa of ferns (*Pteridium*-like and *Dryopteris*-like; Atkinson, 1973) behave so similarly: a common control mechanism seems possible. It is worth recalling that gemmae of *Marchantia* and *Tetraphis* remain dormant as long as they are attached to the parent plants. A general inhibition of germination could also account for the observation that *Sphagnum* protonema has never been recorded around live 'adult' *Sphagnum* even in those places where the plants are bound together by a web of fine liverworts and where physical conditions for *Sphagnum* protonema growth would seem to be suitable.

Ecological implications

Current knowledge of colonization by, and regeneration of, *Sphagnum* is inconsistent. On the one hand are field observations that these processes occur easily and frequently. On the other hand are laboratory experiments which seem to show that they do so only in conditions which are very unlikely to occur at all in the field (Baker & Boatman, 1985).

For example, drains ploughed in preparation for afforestation in upland Britain are rapidly invaded by *Sphagnum* – particularly *S. recurvum*. A small acid soak on the lawn in front of Kenwood House in London was ploughed during the 1939/45 war (J. Hillaby, pers. comm.). By 1961, within a few years of natural recolonization, it contained six species of *Sphagum*. The appearance of five species of *Sphagnum* at Wicken Fen, Cambridgeshire, where the genus was unknown, except subfossil, prior to 1962 (Perring, Sell & Walters, 1964) is a further example of colonization from a distance (Crompton & Whitehouse, 1983). Yet Boatman & Lark (1971), for example, showed that to get the full development of protonema from 1D→3D growth in liquid culture needed orthophosphate concentrations between 130 and 1300 $\mu g\ l^{-1}$. The lower the concentration the more 1D growth dominated the 2D growth. The concentration of orthophosphate in bog water is much lower than this range: for example, Gorham (1956) found $< 0{\cdot}1\ \mu mol\ l^{-1}$ in bog pools at Moor House in the English Pennines where *Sphagnum* is abundant. One of us (RSC) observed that *Sphagnum* protonema grew faster on full strength Moore's Medium agar, which contained orthophosphate at $1500\ \mu mol\ l^{-1}$, than it did on dilutions by 10, 100 and 1000, but in those experiments the full development from 1D→3D did actually occur at all concentrations. Recently Baker & Boatman (1985) have reported experiments in which development of the normal morphology of adult

S. cuspidatum in liquid culture, starting from shoots newly arisen on protonema, seemed to be carbon-limited. Normal morphology was not obtained in still cultures or even in those through which air was bubbled; it occurred only when air enriched to 0·5 % CO_2 was bubbled through the cultures. Jones (1978) also concluded that in liquid cultures the addition of simple sugars in addition to inorganic salts allowed full development. He suggested that aerial cultures were able to complete their development because the sugars produced by the plants were not dispersed throughout a large volume of solution.

Not only are these laboratory results difficult to explain *per se*, but they are also difficult to reconcile with our ecologial observations. We have now shown that *Sphagnum* protonema can develop completely from 1D→3D without any difficulty given no more than light, air, water and whatever inorganic or organic solutes are available in newly formed peat. We conclude that in axenic cultures one or more factors essential to the early development of *Sphagnum* appear to be lacking.

It is curious that protonemata of *Sphagnum* have not been seen in the field. Admittedly, they are inconspicuous and transient, but one of us (J.G.D.) has twenty years experience of hunting for equally inconspicuous liverworts and, in spite of specific searches, has never found *Sphagnum* protonemata.

The nature of regeneration after random or extensive damage is likely to have implications for the genetic constitution of a *Sphagnum* carpet. Innovations arise by mitosis only and therefore have the same genetic identity as the plants which produce them and which they replace. Spores however, arise after meiosis and plants growing from them may be genetically different from the parent plants. This will probably make the carpet genetically heterogeneous. As the 'adult' plants are haploid gametophytes, homozygosity and heterozygosity are irrelevant. If easily recognized genetically determined characters could be found, the genetic constitution of a carpet could be investigated. A start might be made by mapping the distribution of male and female plants, which can often be distinguished in late summer.

Other bryophytes

The five species of liverwort recorded in the CM cores all grew from subterranean axes, not spores (Duckett & Clymo, unpublished observations). No bryophyte, other than *Sphagnum*, produced protonema. Taxa such as *Polytrichum* spp., *Dicranum* spp., *Dicranella* spp., *Hypnum jutlandicum* and *Pohlia nutans* are all common in the region of the bogs sampled, and produce abundant spores – probably more abundant than those of *Dryopteris*. It seems that something in the *Sphagnum* peat is inhibitory to spore germination. It might be as simple as the relatively high concentration of H^+, or it could be the presence of some complex organic compound. Low pH seems the more likely because other bryophytes do appear when the pH is raised artificially (Clymo, unpublished).

The simple experiments reported here have shown that the morphogenesis of *Sphagnum* is far more plastic than has commonly been assumed, and point to physiological and ecological (and possibly genetic) problems of considerable interest.

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Note added in proof

Since completing this article, subsurface slices of peat containing the parasitic liverwort, *Cryptothallus mirabilis*, have been collected from beneath a lawn of *Sphagnum recurvum* and *S. palustre* growing in *Alnus/Betula* carr (Hothfield Common, near Ashford, Kent, National Grid Reference TQ 967463) and maintained for over three months under artificial light in the laboratory. As in the two previous experiments, numerous new shoots of *Sphagnum* have arisen as innovations from pre-existing stems and from protonemata. Fern gametophytes have also appeared but no bryophytes other than *Sphagnum*.