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# Transport of carbon and phosphorus compounds about *Sphagnum*

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[Plates 1 and 2]

The bog mosses, *Sphagnum*, lack any obvious anatomical specialization inside the stem but have a well-developed system of water conduction in capillary spaces among pendent branches around the stem. It has hitherto been assumed that this was the main route for solute transfer too. We describe experiments showing that there is rapid and quantitatively important transport within the stems.

The tracers $^{32}P$ and $^{14}C$ were supplied to *S. recurvum*. When applied below the top of the plant they moved to the apex whether external mass flow was upward or downward. Autoradiographs showed high concentration of tracers in the stem. Steaming the stem above and below the site of application prevented tracer movement.

An experiment lasting four weeks on *S. papillosum* showed that after $^{14}C$ labelling almost all that part of the alcohol-soluble fraction that moved did so from older parts to the apex, with very little transfer to the insoluble fraction, to neighbours, or into the gas phase. For the soluble fraction in the capitulum, the conductance for $^{14}C$ from below was about the same as that of its loss in respiration. The conductance to the insoluble fraction was about twice as great, and to neighbours about half as much.

A longer experiment showed that predominately acropetal transport continued for at least 22 weeks in five species. By that time about 25% of the remaining $^{14}C$ label was incorporated in the new tissues.

The stem of *S. recurvum* contains a central mass of parenchyma 20–50 cells across. The end walls of the parenchyma cells have perforations approximately 100 nm across at a density of 7–13 $\mu m^{-2}$. A single cell wall has about 1500 perforations. They probably house plasmodesmata.

These results indicate that *Sphagnum* has an effective mechanism for retaining and relocating solutes within it. This property, coupled with the ability to grow in a very low supply of solutes, and to make the environment acid by cation exchange, may be seen as causes of the widespread success of *Sphagnum*.

## INTRODUCTION

Peatlands cover about 3% of the Earth's land surface (Matthews & Fung 1987). The bog moss, *Sphagnum*, is an important component of a large part of this peat-

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forming vegetation: it is not only the most important bryophyte (in terms of mass) but in the same category as the most abundant vascular plants. Unlike them it has no anatomically specialized internal conducting system (Hébant 1977) though it does have an effective external water-conducting system.

An individual *Sphagnum* plant has a single apical cell in the centre of a domed apex about 0.5–2 mm across. The apex develops primordia destined to become stem leaves or branches. The branches in turn produce leaves. The crowd of developing branches and leaves forms a dense mass – the capitulum – around the apex. Internodes on the main stem then elongate thus separating the branches. The branches are in fascicles and, in most species, are of two sorts: spreading and pendent. In a carpet of *Sphagnum* the spreading branches of neighbouring plants allow lateral transport of water (Clymo & Hayward 1982). The pendent branches form a capillary wick around the stem and provide an effective vertical transport path to the capitulum, the movement of water being driven by evaporation (Hayward & Clymo 1982). The much-vaunted hyaline cells in the leaves are not directly concerned with transport as they are, in effect, caverns that lead nowhere. Differences among species in the abundance and size of pendent branches are related to, and probably are the cause of, their ecological distribution (Hayward & Clymo 1982; Rydin 1985).

External transport of water about *Sphagnum* is thus known to be effective, and internal transport of water is comparatively poor (Cavers 1911; Clymo & Hayward 1982). Some mosses – *Polytrichum* for example – do have specialized cells in the stem, and these have a function in transporting solutes, but *Sphagnum* lacks such differentiation. It has therefore been generally assumed that solutes are transported about *Sphagnum* in the external stream of water. Yet there are observations that suggest that this may not be entirely true.

1. The concentration on a dry mass basis of elements such as N, P, K, Mg and S in the capitulum is greater than it is lower down the plants (Malmer 1962; Clymo 1978; Damman 1978; Pakarinen 1978; Malmer & Nihlgård 1980; Malmer & Wallén 1986) and the upper parts of the plant retain almost all of the N, P and K that fall on them in precipitation (Malmer 1988). Most species of *Sphagnum* are adapted to oligotrophic conditions – even quite low concentrations of nitrate or phosphate in water will kill them (Clymo 1987) – so scavenging from rain or dust by the actively growing tissue might account for these high concentrations.

2. In 1963 there was a peak in the influx of $^{137}Cs$ produced during testing of nuclear weapons immediately before the U.S.A.–U.S.S.R. moratorium on such tests. Much of this $^{137}Cs$ was mobile (a result confirmed by measurements after the accident at Chernobyl in 1987) yet in 1973, ten years later, it was possible to find a small peak in activity about 10 cm below the top of *Sphagnum* plants and a much larger one in the capitula. About half the $^{137}Cs$ that fell in 1963 was still present in capitula in 1973 (Clymo 1978). Again, scavenging may be invoked, but in this case would have to be from upward transport. This seems implausible because in the climate in which these plants grew precipitation much exceeded evaporation for most of the year.

3. When brown and apparently dead *Sphagnum* from 30–40 cm below the surface is exposed to air and light then innovations grow from patches of cells on

the stem (Clymo & Duckett 1986). Close to the surface, where the stem is still in contact with the capitulum, innovations are rare except when the capitulum is damaged. These observations suggest apical dominance controlled by hormones. It is scarcely believable that the concentration of hormone in an external stream of water could be controlled, and therefore some form of internal transport must be invoked.

4. One interpretation of field experiments in which the top parts of *Sphagnum subsecundum*† were labelled with $^{14}C$ (Skre *et al.* 1983) is that there was downward transport from the green, apical part of the plant to the brown part below.

In this article we describe experiments to seek direct evidence of the path of transport of solutes about *Sphagnum*. We imagine three possible routes: internal, external in solution, and external in the gas phase. (This last route might be significant for carbon dioxide coming from respiration or from decay of dead plants below the surface.) We chose two tracers: $^{14}C$ and $^{32}P$. The half-life of $^{32}P$ (14 days) is sufficiently short that the isotopes can be separated by making records immediately ($^{14}C$ and $^{32}P$) and again after several months ($^{14}C$ alone); and $^{14}C$ may reveal gaseous transport.

We made three experiments. The first was to follow the physical and chemical redistribution of $^{14}C$. It lasted four weeks and is referred to here as the C4 experiment. The second experiment was to follow the redistribution of $^{14}C$ over a longer time (22 weeks). We call it the C22 experiment. The third experiment was to compare the movement of $^{14}C$ and $^{32}P$ in different flow régimes and to discover the effects of killing the stem. It lasted four weeks. We refer to it as the CP4 experiment.

The order of the experiments was determined by practical considerations. We present them in the order CP4, C4, C22.

## Methods

In all three experiments *Sphagnum* plants were labelled with $^{14}C$ or $^{32}P$ then put into a carpet ('matrix') of unlabelled plants in place of a plant removed from the matrix. These carpets were in cylindrical pots or beakers of 10 cm diameter. The cylindrical mass of plants had been collected in the field with a minimum of disturbance using a corer with a diameter of 10 cm. The experiments were made in a cool north-facing glasshouse on the roof of a building in London at times between August 1987 and March 1988. Heating kept the temperature above 5 °C and during the winter natural daylight was supplemented by mercury vapour lamps giving a flux at the plant surface of about 250 μE‡ $m^{-2}$ $s^{-1}$. The lights were on between 04h00 and 11h00, and again between 13h00 and 20h00, thus leaving a 'dark' period of 8 h.

Five species were used. *Sphagnum fuscum*, *S. tenellum* and *S. balticum* were collected in July 1987 from the ombrotrophic mire Ryggmossen, Uppland, eastern Sweden, at which place they are the commonest species. *Sphagnum papillosum*

† Nomenclature follows Hill in Smith (1978).

‡ 1 einstein (E) = 1 mol photons; 1 μE = $6 \times 10^{17}$ photons.

and *S. recurvum* were collected in England from Cranesmoor (National Grid reference SU 185029), Moor House (NY 760325) and Dersingham Mire (TF 676288) at various times between September 1987 and February 1988.

*The* $^{14}C$ *and* $^{32}P$ *four week experiment* (*CP*4)

This experiment was designed to show the movement of the tracers in *Sphagnum* plants around which the water flow was upward, downward or still, and to show the effects of killing a small part of the stem on tracer movement.

Green shoots (7 cm long) of *S. recurvum* were labelled with either $^{14}C$ or $^{32}P$ in the top 0–1 cm (capitulum), the middle 3–4 cm or the basal 6–7 cm section. The shoots labelled in the middle were of two types: intact, and previously steamed. The steaming treatment consisted of playing a jet of steam from a Pasteur pipette for 30–40 s on sections of 1 cm immediately above and below the as yet unlabelled 3–4 cm section. The section to be steamed was gripped lightly between two rubber bungs having central holes. The steam was passed into one hole over the plant, and out of the other hole. The rubber served to protect the plant on either side of the steamed section. After 1–2 days the steamed zones turned white and did not recover during the experiment. The unsteamed parts of the plants both above and below remained green. Steamed plants grew as much as intact ones did during the experiment; the zone of active growth was well above the steamed zone.

Tracers were applied to the appropriate section: $^{32}P$ in $NaH_2PO_4$ at a rate of 4 μCi† in 10 μl; $^{14}C$ in $NaHCO_3$ at a rate of 1 μCi in 25 μl (capitulum) or 0.4 μCi in 10 μl (other two sections). The untreated parts were covered with aluminium foil and the rest illuminated for 6 h. The treated plants were then washed twice in distilled water and put into place in a carpet of unlabelled plants of depth 9 cm in a beaker. Each beaker contained three $^{14}C$-treated plants and three $^{32}P$-treated plants, arranged alternately in a regular grid. A gas-tight transparent lid covered the beaker.

The beakers were given one of three flow régimes (Clymo & Mackay 1987).

1. Upward flow. Air, dried over $CaCl_2$, was pumped in through a hole in the lid and escaped through another hole, causing evaporation averaging 1.1 mm per day. The beaker, which had a hole in its base, stood in a box within which water was kept at 1 cm depth. Water lost by evaporation was thus replaced from the box. The path of water movement probably occupies less than 0.5 % of the carpet cross section, so the velocity was probably 10–20 mm $h^{-1}$.

2. Downward flow. Distilled water was sprayed on the plants every other day at a rate of 1.8 mm per day, the surplus escaping through a hole in the base of the beaker.

3. No flow. No water added or removed.

In (2) and (3) the lids were removed for a few minutes every day to allow some gas exchange. The water level in all beakers was kept at 8 cm below the initial level of the capitula.

This factorial experiment thus contained two tracers (in the same beaker); four modes of application (capitulum, middle intact, middle steamed, basal); three flow

† 1 curie (Ci) = $3.7 \times 10^{10}$ Bq.

régimes; and two replicate beakers. The beakers were in two randomized blocks in the glasshouse, and received supplementary light. The beakers were re-randomized half-way through the experiment, which lasted for 30 days from 9 December 1987 to 8 January 1988.

Two treated plants from the start of the experiment and one or two from each beaker at the end of the experiment were blotted dry then pressed flat between absorbent paper and allowed to dry in air. They were transferred to X-ray film for autoradiography. After this they and two dried matrix plants from three beakers were cut into 1 cm sections, weighed, then ground in a mortar with 6.5 ml of water. A subsample of 1.5 ml of this macerate was transferred to tubes containing 3.5 ml of Instagel. Light flashes were counted with a Packard 360 liquid scintillation counter. In $^{32}P$ counting, interference by $^{14}C$ was avoided by counting in an energy-window centred on $^{32}P$ and well above that of $^{14}C$. Quenching was negligible, and was almost the same for all samples. Results were corrected for background activity. In $^{14}C$ counting, interference by $^{32}P$ was avoided by making $^{14}C$ counts after two months, when $^{32}P$ activity had reduced to about 5% of that when the plants were killed. Corrections were made for quenching and background.

### *The $^{14}C$ four week experiment (C4)*

This experiment was designed to follow the movement of $^{14}C$ (which may travel by the internal, external and gaseous paths) in more detail, and to follow the chemical transformations during an ecologically moderate length of time. Shoots (4 cm long) of *S. papillosum* were labelled by submerging them in an upright position in 330 ml of simulated rainwater to which 1 mCi of $^{14}C$ as $NaHCO_3$ had been added. The plants were left in the sealed container in daylight for 8 h. The shoots were washed three times in distilled water then transferred into a matrix of unlabelled *S. papillosum* at natural density in beakers. Four labelled shoots were put, spaced out, in each of 24 beakers. Of these, 12 were shaded with black nylon gauze (about 35% transmission). The beakers were put into tunnels of transparent nylon film, relatively impermeable to gases, in the glasshouse. Moistened air was passed through the tunnels and $CO_2$ trapped in NaOH solution at the outlet. The trap was changed at each plant-sampling. The water level in the beakers of plants was kept at 2.5 cm below the top of the capitula.

Two shaded and two unshaded beakers were sampled immediately (0), and after 0.5, 1, 3, 9 and 27 days (between 22 September and 19 October 1987).

One labelled shoot and adjoining matrix plants from each beaker were blotted, flattened, dried, and put onto X-ray film. The other three labelled shoots were divided into capitulum (0–1.5 cm), and the lower 1.5–4 cm stem and branches. Some branches were brownish in colour. The plants were put into 10 ml of 70% ethanol at 4 °C for 3 days. After extraction the shoots were washed twice in ethanol, dried and weighed. Two 5–10 mg subsamples were dried, ground in a mortar, and a subsample added to Instagel before counting, as in the CP4 experiment. Subsamples of the NaOH trap were diluted and their radioactivity counted. The results were corrected for quenching and background.

The alcohol extracts were separated into cationic, anionic and neutral fractions (corresponding, in the main, to amino acids, organic acids and sugars) by passing

them successively through Dowex 50 and Dowex 1 ion-exchange resins. The radioactivity in each extract was estimated on a 25 µl subsample. Cold standards were added to each fraction, then the constituents were separated by two-way paper chromatography on 25 cm × 20 cm Whatman 3 MM paper. The cation fraction was separated by using phenol:water (100 g:33 ml) and butanol:acetic acid:water (90:10:29 by volume). Amino acids were located with ninhydrin. The anion fraction was separated using phenol:formic acid:water (100 g:10 ml:29 ml) and the organic phase of *tert*-amyl alcohol:formic acid:water (80:10:40 by volume). Organic acids were located with a combination of $NH_4SCN$ and $FeCl_3$ solutions in acetone (Firmin & Gray 1974). The neutral fraction was separated (Calvin & Bassham 1957) by using phenol:water (100 g:39 ml) and *n*-butanol:propionic acid:water (92:47:61 by volume). Sugars were detected with saturated $AgNO_3$ in acetone followed by 0.5 M NaOH in acetone (Firmin 1973). Autographs of chromatograms were made on X-ray film. Radioactive spots were eluted and their activity counted.

### *The* $^{14}C$ 22 *week experiment* (*C*22)

The C4 experiment showed that a lot of $^{14}C$ remained in the soluble phase for a surprisingly long time. We therefore tried in the C22 experiment to follow the incorporation of $^{14}C$ into the insoluble phase for a much longer time and in a variety of species.

Shoots of *S. fuscum*, *S. tenellum*, *S. balticum*, *S. recurvum* and *S. papillosum* were used. At the start of the experiment the shoots were 4 cm long, except for *S. tenellum* for which the green part of the plant was less than 4 cm long. For this species we used 3 cm plants. The central, shortest, branch in the capitulum was marked by a dot of red spirit ink, and the first fully expanded branch by a dot of black ink, to allow us to distinguish newly formed branches from those that already existed at the start of the experiment but which were carried up passively by the elongation of stem internodes. Material above the red mark was wholly new; that between red and black was partly new and partly old; that below the black mark was almost all old.

The marked shoots were labelled with $^{14}C$ in the same way that those of *S. papillosum* had been in the C4 experiment. The labelled shoots were transferred to a matrix of plants of the same species. The number of labelled shoots in each beaker was determined by their size and the field density. It was: *S. fuscum* 8; *S. tenellum* 8; *S. balticum* 6; *S. recurvum* 4; *S. papillosum* 4. For each species there were two unshaded beakers and two shaded ones (as in experiment C4). The beakers were put inside nylon film tubes and air was passed slowly through the tubes. Carbon dioxide was trapped in NaOH solution. For part of the experiment separate collections were made during the day and during the night to seek diurnal patterns. The experiment was made from 22 October 1987 to 22 March 1988.

At harvest one labelled plant from each beaker was dissected into the below-black, black–red and above-red (old, mixed and new) sections. These were dried, weighed, and their $^{14}C$ activity measured as in the C4 experiment. The same measurements were made on two shoots of each species from the start of the experiment (with no above-red section of course) and on two matrix plants from one beaker for each species.

*Scanning electron microscopy*

Pieces of stem of *S. recurvum* were soaked for 30 min successively in 70% ethanol, chloroform, methanol, and acetone to remove the contents of the cells. The stems were then put into absolute ethanol before critical-point drying. The dried stem was sectioned (or split) with a razor blade. The sections were then sputter coated with Au and Pd and examined in a JSM 35 scanning electron microscope operated at 20 kV.

## Results

### *The* $^{14}C$ *and* $^{32}P$ *four week experiment* (*CP*4)

An analysis of variance showed no significant difference among the flow régimes, indicating that mass transport in the external solution was unimportant in this experiment.

The effects of putting the label in different positions and of steaming sections of stem are shown as autoradiographs (figure 1). Quantitative results, combining flow régimes, are shown in figure 2. There was negligible activity in the water surrounding the plants. Where tracer had been applied to the capitulum (0–1 cm) there was no indication of downward (basipetal) movement during the experiment, though 5–10% had spread down during the initial labelling, perhaps by capillary movement among the pendent branches. Where tracer was applied in the middle section (3–4 cm) about 45% of $^{14}C$ and 30% of $^{32}P$ had moved to the capitulum by the end of the experiment. There was no evidence of downward movement. Where tracer was applied to the basal section (6–7 cm) there was upward redistribution too: about 25% of $^{14}C$ had moved to the capitulum, whereas about 30% of $^{32}P$ was fairly uniformly spread up the whole length of the plant.

The most important result may be seen with the plants that were labelled in the middle after the sections above and below (2–3, 4–5 cm) had been steamed. In these cases there was no evidence of movement of either $^{14}C$ or $^{32}P$ during the experiment, though some tracer had moved (during the initial labelling) outside the segment to which it had been applied.

The radioautographs show the distribution in some detail. Where $^{14}C$ or $^{32}P$ has moved acropetally it seems to be in high concentration in the stem and in the tips of capitulum branches.

High concentration does not necessarily indicate the path of movement of course: just as plausibly it indicates a sink of accumulation. But the absence of any effect of flow régime coupled with the results of steaming sections of stem do indicate that most of the transport in this experiment was inside the living stem.

### *The* $^{14}C$ *four week experiment* (*C*4)

Analyses of variance of the activity in soluble and insoluble fractions showed no significant effect of shading so the results for shaded beakers were combined with those for unshaded ones in further analyses. The pattern of changes when the results were expressed on a dry mass basis was very similar to those on a plant basis, so only the latter are shown.

The general pattern of change is shown in figure 3. About 30% of the $^{14}C$ in the

plants at the start of the four week experiment was released during it: about 8% (of the original) was found in neighbouring plants (almost all in their capitula), and about 18% in the NaOH trap. About 4% was unaccounted for.

The net loss from labelled capitula (21%) was less than that from stem and branches below (48%). In the capitula there was a threefold increase in activity in the alcohol-insoluble fraction, at the expense of the soluble fractions, particularly the neutral one. In stem and branches, however, there was little change in the insoluble fraction. Activity in the soluble fractions decreased, but by less than it did in the capitula. We suppose this decrease resulted from respiratory losses and from internal transport towards the apex, as we found in the CP4 experiment. Changes in the capitula represent the net effects of import through the stem and export to neighbours or out of the carpet of plants altogether.

The most heavily labelled amino acids (table 1) were asparagine (which increased in relative importance over the 27 days of the experiment), and glutamic acid which decreased. Together they constituted 65–80% of the labelling. Other labelled amino acids were aspartic acid, glutamine, arginine, valine and leucine. About 20% of the activity was in pyrrolidone-5-carboxylic acid (PCA), a breakdown product of glutamic acid or glutamine.

Only some of the labelled compounds in the anionic and neutral fractions were satisfactorily identified. Malic acid increased from 15 to 70% of the anionic fraction during the experiment. More than 50% of the neutral fraction was in glucose and fructose.

All these changes must be seen against a background of general decline in the soluble fractions: the proportion of individual compounds may have increased but their absolute activity decreased.

### *The* $^{14}$C 22 *week experiment* (*C*22)

During the five months from mid-October to mid-March *S. papillosum* extended least (6 mm unshaded, 17 mm shaded) and *S. recurvum* most (55 and 83 mm). Details may be seen in figure 4. *Sphagnum recurvum* was noteable for showing not only a large increase in length in the 'mixed' section (between red and black dots) but also in the 'old' section (below the black dot). For this species internode elongation continues more than 1 cm below the top of the capitulum.

The dry mass of the new section is a conservative measure of dry mass growth: it makes no allowance for increase in the mixed section. Dry mass growth was poorly correlated with growth in length, ranging from 1.9 mg (*S. fuscum*) to 7.8 mg (*S. papillosum*). These differences occur because the plants differ in diameter.

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### Description of plate 1

Figure 1. The CP4 experiment. Plants labelled with $^{14}$C in capitulum ('top'), basal 1 cm, middle 1 cm, and middle 1 cm after steaming the sections immediately above and below, together with autoradiographs. The leftmost of each pair is immediately after labelling; the rightmost is after four weeks growth in beakers with downward water flow. The arrows show where the radioactive solution was applied. Vertical bars indicate steamed sections. The activity in each 1 cm section is expressed as the percentage of total activity in the shoot.

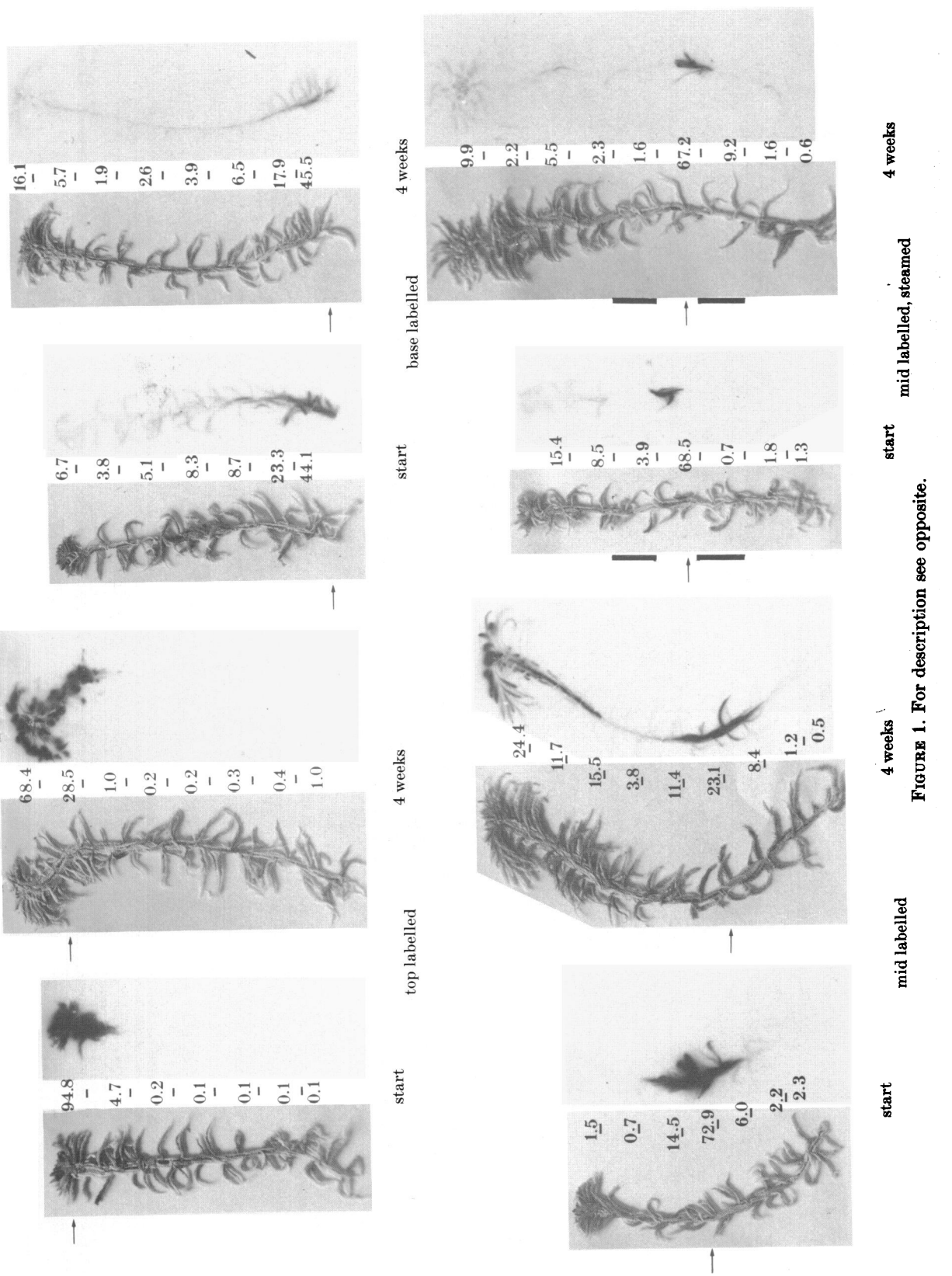


FIGURE 1. For description see opposite.

(*Facing p.* 70)

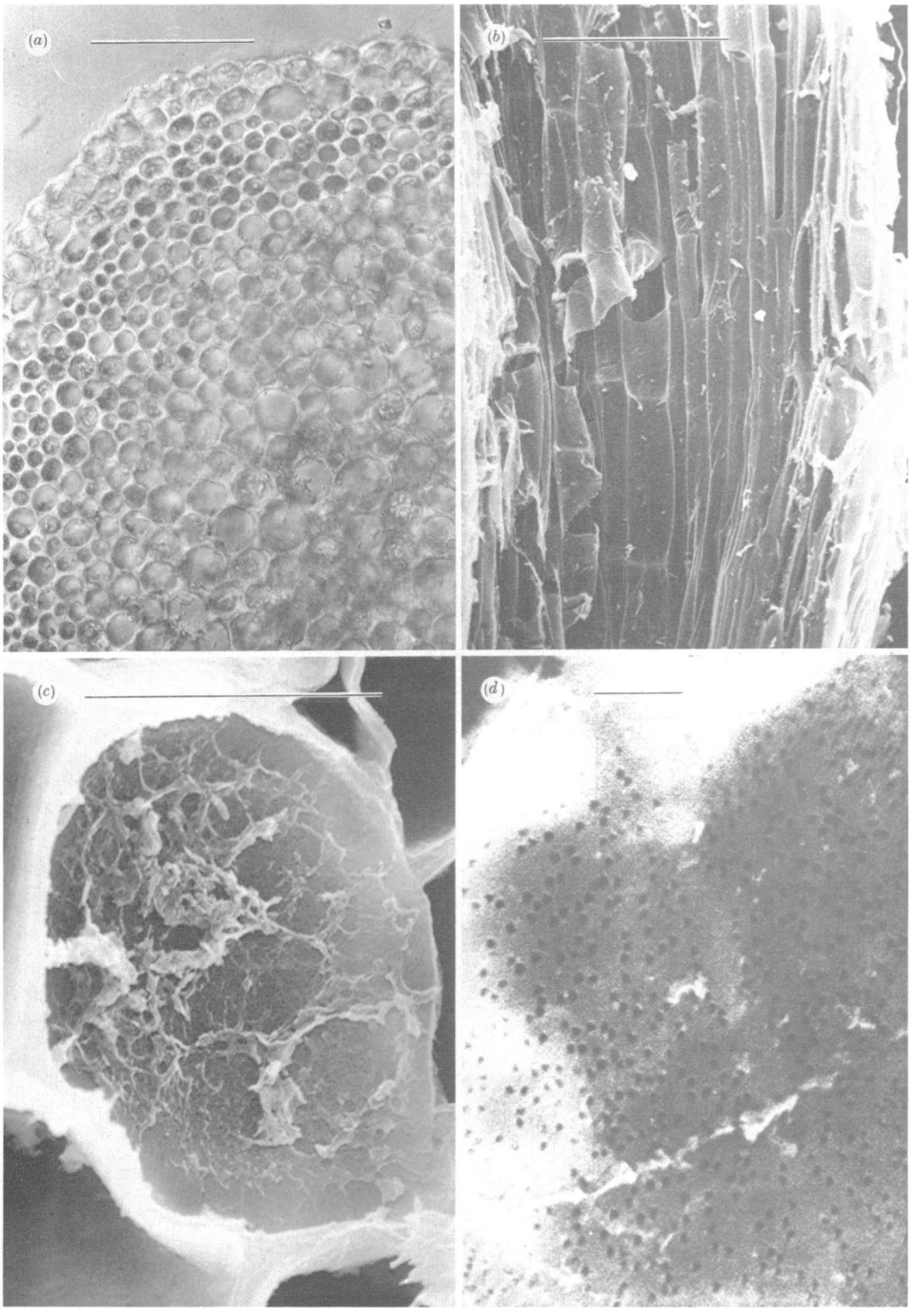


FIGURE 6. For description see opposite.

Analyses of variance showed that shading had no significant effect on the concentration or proportion of radioactivity, either as a main effect or in interactions, so the results for unshaded and shaded plants were combined.

The proportion of radioactivity still present at the end of the experiment ranged from 28 to 44% for four species (figure 4). This suggests a half-life in the plants of 12–19 weeks. The fifth species, *Sphagnum recurvum*, appears to have retained almost all its label, a result we cannot explain. In all species the concentration of $^{14}C$ in the wholly new section at the end of the experiment is similar to that remaining by then in the mixed and old sections (figure 5). In many cases it was greater. Only in *S. recurvum* was it rather less. There had been compensating decreases in concentration in the old and mixed sections during the experiment, except in *S. recurvum*.

The proportion of activity in the different sections showed a similar pattern in all species, with old, mixed and new sections having about 40, 35 and 25% at the end of the experiment (figure 5) compared with about 65 and 35% in the old and mixed sections at the start. Again *S. recurvum* is rather different.

These differences are reflected in the analysis of variance at the end of the experiment (table 2). 'Species' has a big effect on concentration, and 'section' on proportion. In both the different behaviour of *S. recurvum* causes a significant interaction.

Some activity was found in neighbouring matrix plants: about 1–2% in this experiment. The ratio of rates of $CO_2$ trapping in NaOH during the day to that during the night was 1.0:2.8, indicating that the rate of $CO_2$ efflux during the day is only 36% of that at night.

### *Structure of stems of Sphagnum*

The structure of *Sphagnum* stems differs among species (Nyholm 1969). In *S. recurvum*, as figure 6 shows, the whole stem is parenchymatous. It snaps suddenly if bent. The parenchyma is 20–50 cells across, each cell being of diameter about 10 and 20 μm in the outer and inner parts of the stem, respectively. The cells are about 100–200 μm long.

The longitudinal walls of these parenchyma cells are almost imperforate, but the end walls are densely perforate. The holes are about 75–100 nm across (figure 6) and at a density of 7–13 $\mu m^{-2}$. A single end wall has about 1500 perforations. We assume that in life the perforations were filled by plasmodesmata. Similar perforations occur in primary pit fields on the walls of parenchyma in the stem apex of *S. recurvum* (Baker 1988). This density of perforations is similar to that in the

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DESCRIPTION OF PLATE 2

FIGURE 6. Structure of the stem of *Sphagnum recurvum* at 3–5 cm below the apex. (*a*) Transverse (hand) section of live stem, mounted in water, light microscope, 100 μm (0.1 mm) scale bar. Note the absence of a conducting strand. (*b*) Longitudinally fractured stem prepared as described in the text, s.e.m., 100 μm scale bar. Elongate cells with horizontal end walls. (*c*) Transverse end wall prepared as described in the text, s.e.m., 10 μm scale bar. Most of the cytoplasm has been removed. Numerous perforations are just visible. (*d*) Part of a transverse end wall showing perforations, s.e.m. 1 μm scale bar.

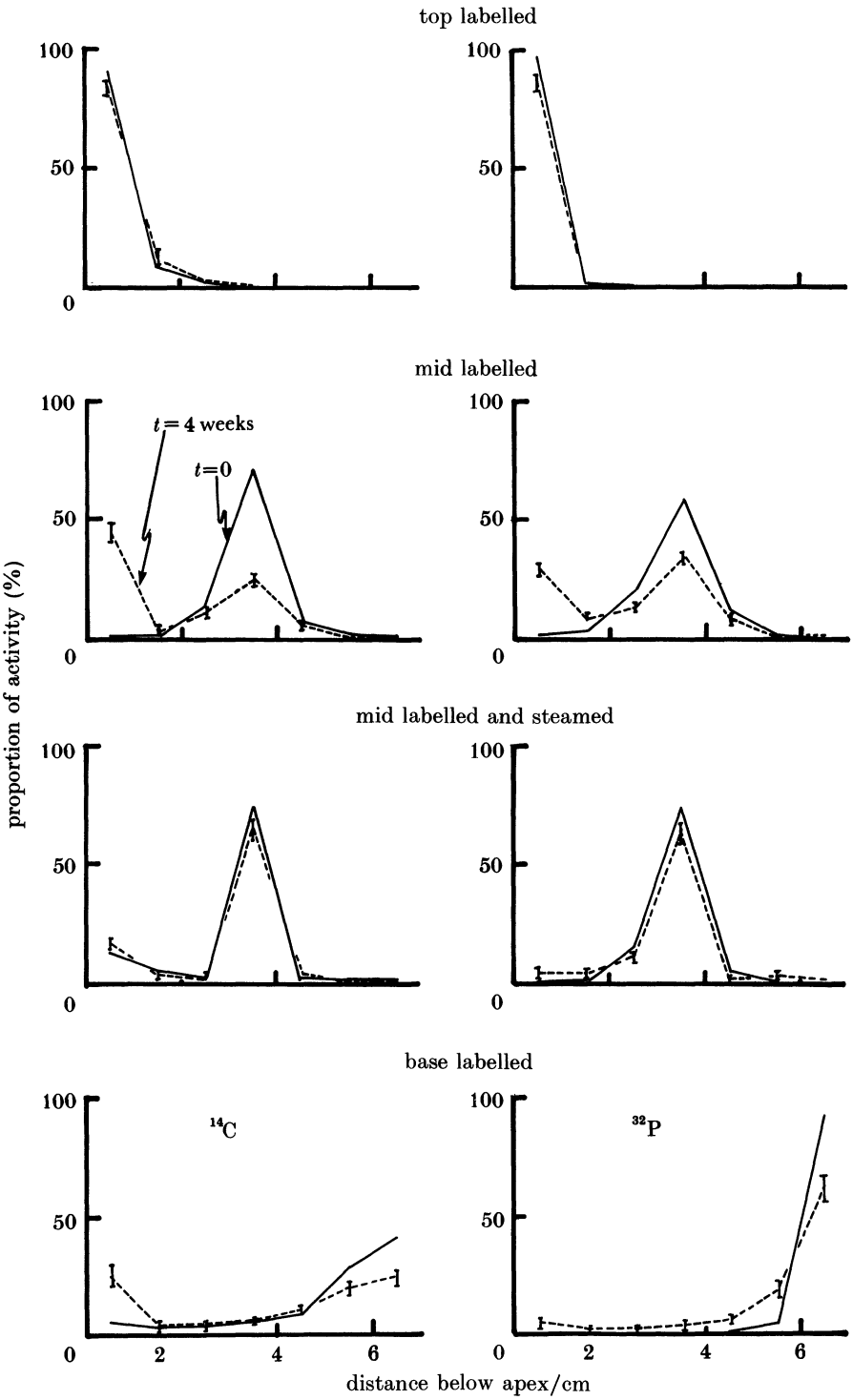


FIGURE 2. The CP4 experiment. Activity of $^{14}C$ (top) and $^{32}P$ (bottom) in 1 cm sections of shoots as the percentage of total activity in the shoot. Solid lines show results immediately after labelling ($\bar{x}$, $n = 2$); broken lines are results after four weeks ($\bar{x}$, s.e.m., $n = 6$ for top and base labelled, $n = 5$ for middle labelled). Results for the three water flow régimes (see text) are lumped. During the four weeks of the experiment the apical internodes had elongated. Distances were measured from the shoot bases, and the nominal 0–1 cm section includes that material now above the original zero datum.

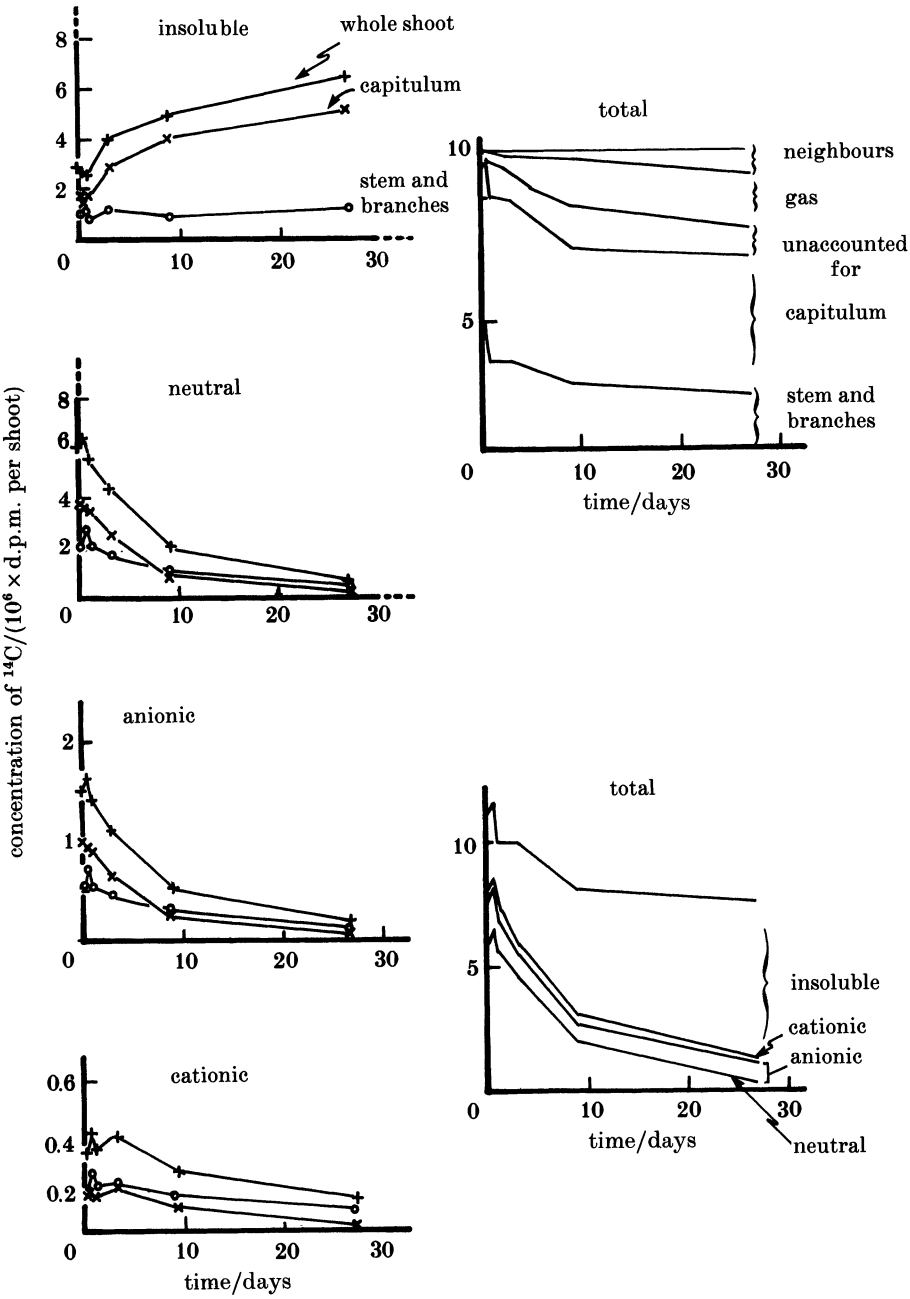


FIGURE 3. The C4 experiment. Time-course of concentration of $^{14}C$ in various chemical fractions (insoluble in 70% ethanol, neutral, anionic and cationic) and physical positions (stem + branches, capitulum, neighbours, gas, and unaccounted for). The graphs on the left show individual traces; those on the right are cumulative.

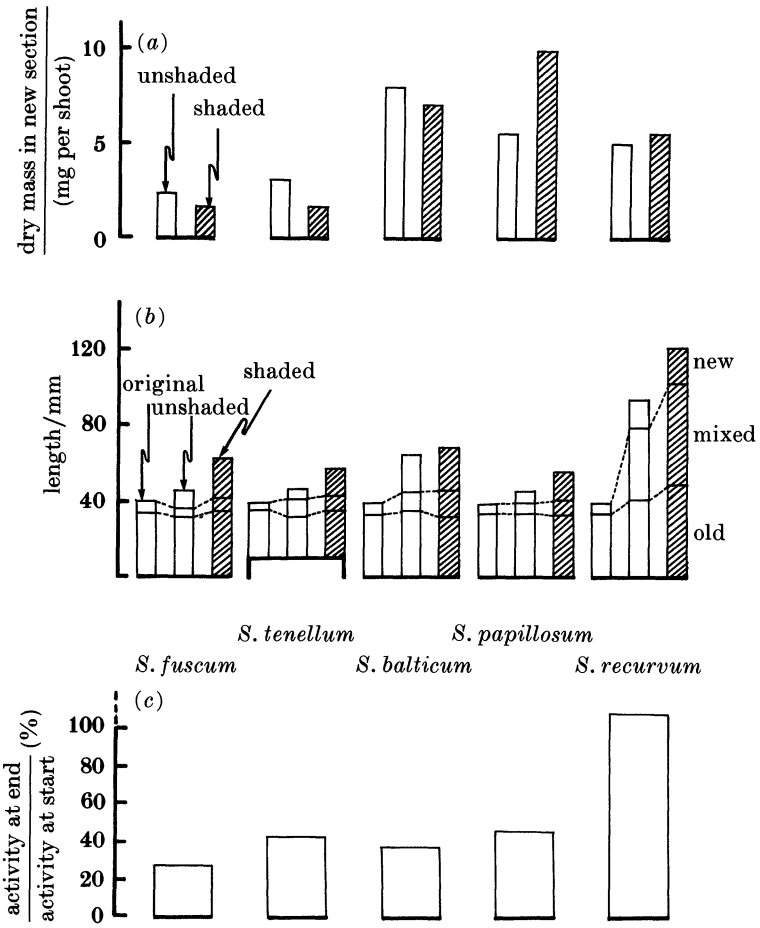


FIGURE 4. The C22 experiment with five species. At the start the youngest branch and the youngest fully expanded branch were marked. At the end of the experiment after 22 weeks everything below the lower mark is 'old' mass; between the marks is 'mixed' old and new; above the top mark is 'new'. (*a*) Mean dry mass ($n = 2$) in the new section in unshaded and shaded conditions. (*b*) Mean original length, and length after 22 weeks in unshaded and shaded conditions ($n = 2$); *S. tenellum* plants were 1 cm shorter than those of other species at the start and appear in the diagram on a pedestal. The two broken lines linking sets of columns draw attention to the position of the marks separating original, mixed, and new sections. (*c*) Mean proportion of $^{14}C$ activity present in the plants at the start of the experiment and still present in the plants after 22 weeks ($n = 4$).

TABLE 1. $^{14}C$ ACTIVITY IN AMINO ACIDS AFTER 0.5, 9 AND 27 DAYS AS A PERCENTAGE OF TOTAL ACTIVITY IN THE SPOTS DETECTED ON THE AUTORADIOGRAM

| | activity (%) | | |
|---|---|---|---|
| | 0.5 days | 9 days | 27 days |
| glutamic acid | 37 | 35 | 17 |
| asparagine | 28 | 48 | 66 |
| PCA | 23 | 17 | 17 |
| aspartic acid | 8 | n.d. | n.d. |
| glutamine + arginine | 4 | n.d. | n.d. |

PCA, pyrrolidone-5-carboxylic acid.
n.d., not detected on the autoradiogram.

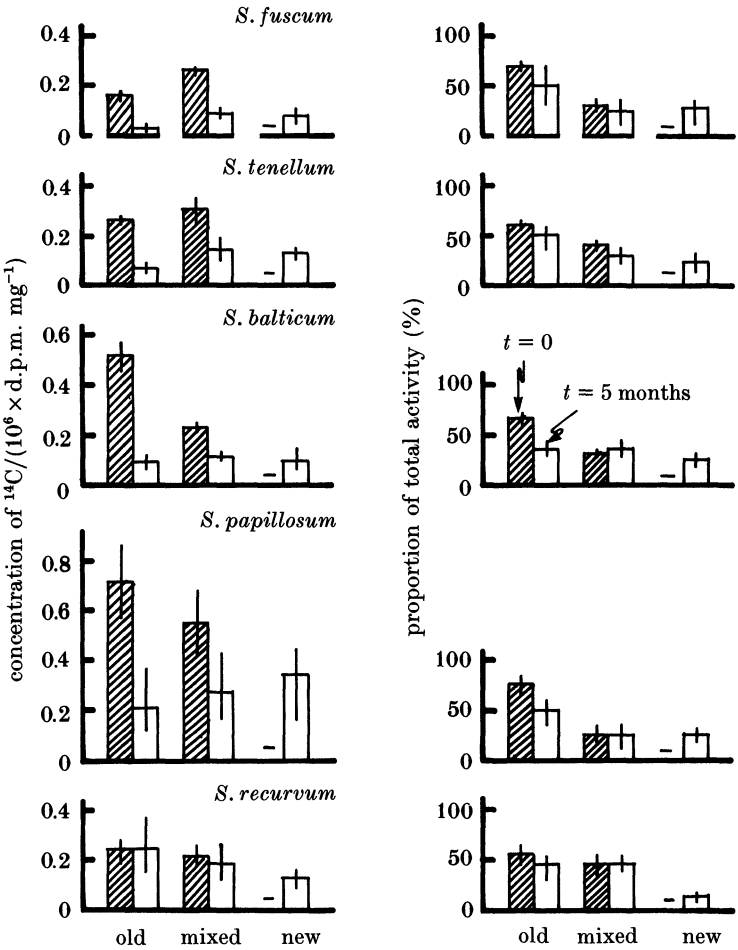


FIGURE 5. The C22 experiment. Distribution of $^{14}C$ in old, mixed and new sections of five *Sphagnum* species immediately after labelling and after 22 weeks (mean and range). Hatched bars: at start ($n = 2$); open bars: after 22 weeks ($n = 4$). The new section was formed during the experiment. The left diagrams show concentration of $^{14}C$ in the plant parts and the right diagrams show proportional distribution of $^{14}C$ as the percentage of the total activity in the shoot.

TABLE 2. SUMMARY OF THE ANALYSES OF VARIANCE OF RADIOACTIVE CONCENTRATION AND PROPORTIONAL DISTRIBUTION OF $^{14}C$ IN THE SHOOT IN NEW, MIXED AND OLD SECTIONS OF THE FIVE SPECIES OF *SPHAGNUM* AFTER FIVE MONTHS

| | | concentration of radioactivity | activity in section / total activity |
|---|---|---|---|
| source | d.f. | *F* | *F* |
| section | 2 | 1.26 n.s. | 28.0*** |
| species | 4 | 19.7*** | + |
| section × species | 8 | 2.17* | 2.72* |
| error | 45 | | |

d.f., degrees of freedom; n.s., not significant.
* $p < 0.05$; *** $p < 0.001$.
+, each species totals 100%.

deuter cells of *Dawsonia polytrichoides* (Hébant 1977) and in end walls of parenchyma cells of *Polytrichum commune* (Eschrich & Steiner 1968) whereas the density in the oblique end walls of leptoid cells in *P. commune* is about twice as great. The individual holes in *S. recurvum* are of similar dimensions to those in *P. commune* leptoids and *Dawsonia polytrichoides* deuters.

## Discussion

### *Are metabolites transported in Sphagnum stems?*

The usual view of transport in bryophytes is that where there is a differentiated tissue in the stem, with specialized elongated cells resembling those in vascular plant xylem or phloem, then one may expect to find evidence of internal transport. *Polytrichum* is a clear case. It has specialized cells – leptoids and hydroids – and there is experimental evidence of transport of $^{14}C$ in the stems both above and below ground (Eschrich & Steiner 1967; Collins & Oechel 1974). Trachtenberg & Zamski (1978) suggested that transport may occur in the symplast.

There has been a general presumption, however, that those mosses that lack obvious specialization of the internal tissue of the stem, such as *Sphagnum*, probably do not have a specialized system of transport inside the stem though Hébant (1977) pointed to indirect evidence of transport in *Mnium* and *Dicranum*, both of which lack leptoid-like cells. Our observation of about 1500 perforations in the end wall of otherwise unremarkable parenchyma cells in the stem (figure 6) now provides a mechanical structure that may plausibly be considered the seat of transport processes.

Our CP4 experiment with $^{14}C$ and $^{32}P$ tracers in *S. recurvum* shows clear evidence that there is transport in the stem. The direction of mass flow in the capillary system outside the stem had no detectable effect on the transport of either $^{14}C$ or $^{32}P$, and this argues against passive transport in something analogous to a transpiration stream. This conclusion is supported by the discovery that transport was prevented when the stem was killed by steaming. We conclude that in this experiment, at least, much the most important mechanism of transport operated inside the stem.

The transport seems to be entirely acropetal in this CP4 experiment with plants of *S. recurvum* that were green through their whole length. There is evidence of acropetal transport in *Marchantia polymorpha* (Rota & Maravolo 1975; Gaal *et al.* 1982). In *Polytrichum*, transport occurs to underground axes as well as to apices (Collins & Oechel 1974), and there is evidence of transport from gametophyte to sporophyte in several cases (Proctor 1977, 1982; Thomas *et al.* 1979). There is one report (Skre *et al.* 1983) of basipetal transport in *S. subsecundum* labelled in the field with $^{14}C$ in $CO_2$. After 2 h about half the activity was in the green section of the plants and the rest in the underlying brown section. Results for the next 35 days were rather erratic but in general showed that 60–90% of the label in the green shoots disappeared whereas the amounts in the brown section decreased by less or, in one case in autumn, increased. The authors concluded that there had been basipetal transport before the onset of winter. But it seems equally plausible that there was a slower rate of loss from the brown section, consistent with the

results of our C4 and C22 experiments. The extent of initial labelling in the brown section remains puzzling.

### *Relative rate of transfer of $^{14}C$ about Sphagnum*

To try to disentangle the dynamics of the transport and chemical transformation processes we now consider a simple model of the processes (figure 7). It follows conventions suggested by Forrester (1961): full lines represent flows of substance ($^{14}C$ in this case) and broken lines are flows of information. We assume that all the flows of $^{14}C$ are directly proportional to the size of the source, and are unaffected by the size of the sink. Implicit is the assumption that if the driving force is related to concentration differences then there are negligible changes in the volume of the compartments and that the concentration in the net receiving compartment has a negligible effect. For the four weeks of this experiment the first assumption is probably true to within 10% or so. The justification for the second assumption differs for different compartments. In the case of gas the concentration in the gas phase remains very low as gas is removed; in the case of neighbours the concentration of $^{14}C$ is much less than it is in the treated plants; in the case of transfer from the soluble to the insoluble fraction in the capitulum the evidence shows that the net movement is strongly to the insoluble fraction; and the same argument applies to the transfer from older parts to the capitulum. None of this demonstrates that the sinks have no effect, but for a first trial the assumptions seemed to us to

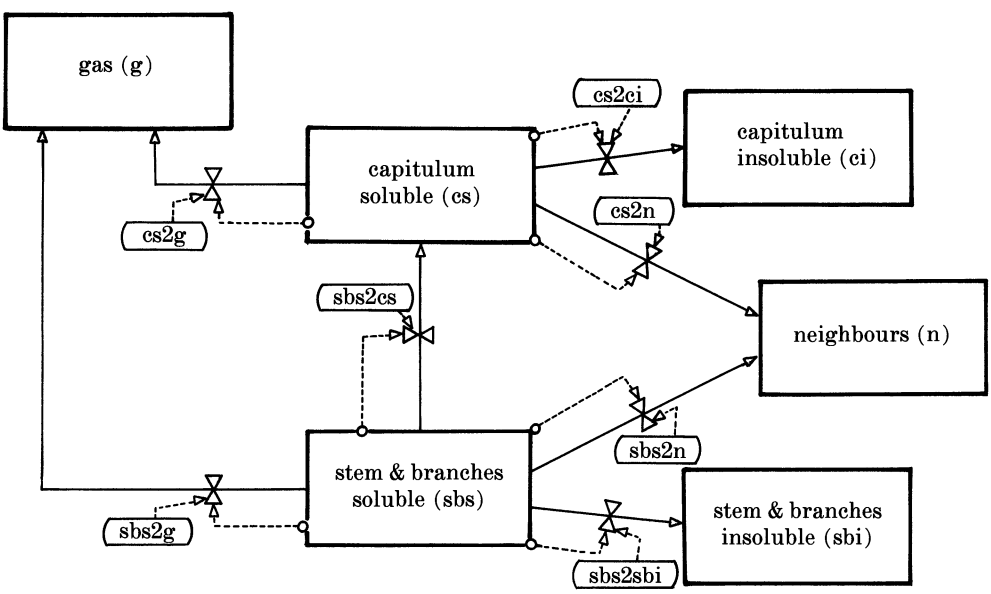


FIGURE 7. Model of $^{14}C$ flow in *Sphagnum*. Conventions are those of Forrester (1961). The boxes represent amounts in different fractions. These same fractions were measured at intervals in experiment C4. Solid lines show flow of $^{14}C$; broken lines are flow of information and indicate control of the valves. In all cases we assumed a simple proportional control: the rates of flow were directly proportional to the amount in each box (see text for explanation). Each valve also has a rate-control coefficient, shown encircled.

be acceptable. It is important to realize that what we are following is the transfer of $^{14}C$, not total change in the molecular species in which it is incorporated.

We use the median values of the C4 experiment (figure 3), thus avoiding problems created by the occasional extreme value.

The total $^{14}C$ on a shoot basis, relative to the largest value (at 0.5 days) is shown at the right of figure 8. Relative totals for 0.5, 1, 3, 9 and 27 day samples ranged between 91 and 100% with no obvious pattern. The '0' day sample had only 80%. The proportions of the different components in this sample were very similar to those in the 0.5 day sample, however. As we are concerned with changes in proportions we decided (*a*) to omit the '0' day sample and (*b*) to scale samples on different days to the same total (100).

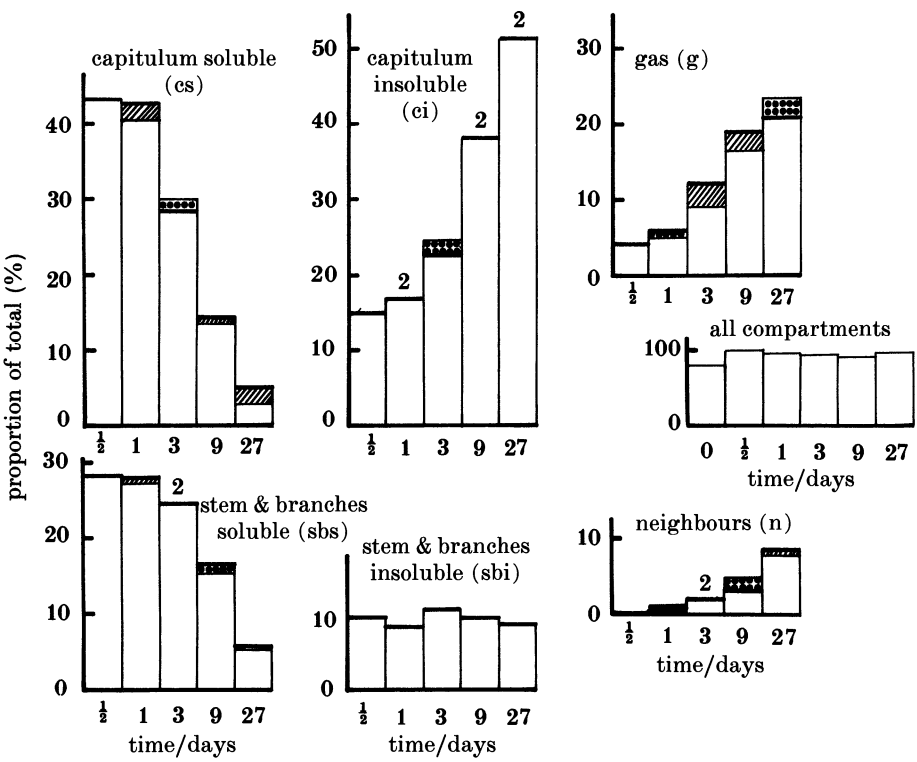


FIGURE 8. Results of the CP4 experiment and of fitting the model shown in figure 7. The first column (0.5 days) is used as the starting point for the model, so there is no fitted value there. Hatched: fitted is less than observed. Dots: fitted exceeds observed. A '2' above a column shows that observed and fitted are indistinguishable at this scale. The 'stem + branches insoluble' fraction scarcely changes and was omitted from the minimization procedure. At the middle right is the measured total $^{14}C$ on a shoot basis at different times, relative to 100 for the sample at 0.5 days.

Figure 8 shows that the changes in the 'stem and branches, insoluble' fraction were erratic and small. We therefore omitted the part of the model (figure 7, lower right) that concerns this fraction.

This leaves six parameters – the rate coefficients in figure 6 – to be estimated.

The initial values in the boxes are the 0.5 day results, thus leaving 20 independent observations to fit six parameters, i.e. 14 independent values. It is obvious that we should not expect to get highly precise estimates.

In operation we chose parameter values arbitrarily then ran the model of figure 7 with 0.1 day increments to produce model values for each of the fractions for which there were measurements. The fit between measured and modelled was poor, of course. We then used a simplex technique (Nelder & Mead 1965) to adjust the six parameter values in such a way as to minimize the sum of squares of deviations between the measured and modelled values of the five fractions. Other criteria gave similar results.

There is no way that one can be sure with this technique that the global optimum has been found but if one finds the same point from numerous different starting points and with differing rates of contraction, and the fit to the data is good, then it is reasonable to accept the best solution. We made 23 optimizations: each took about 30–40 min on a microcomputer. Of these, 15 gave very similar values for the optimization criterion. The other eight were noticeably poorer. The 15 were not identical: the greatest was 0.3% larger than the smallest. To three significant digits they all gave the same value for four of the six parameters (table 3). The other two parameter values were four or five orders of magnitude smaller. The values are shown in table 3, and the fitted values in figure 8. Repeated location of a similar set of values is satisfactory, though the precision with which the parameters are estimated is not great, and in the two cases of small values is very poor.

TABLE 3. ESTIMATES OF VALUES OF THE RATE COEFFICIENTS OF THE MODEL IN FIGURE 7

| parameter | symbol | value (% $d^{-1}$) | PE[a] |
|---|---|---|---|
| capitulum soluble to gas | cs2g | 0.060 | 0.11 |
| stem + branch soluble to gas | sbs2g | 2e-7 to 8e-8 | + |
| stem + branch soluble to capitulum soluble | sbs2cs | 0.063 | 0.14 |
| capitulum soluble to insoluble | cs2ci | 0.111 | 0.08 |
| capitulum soluble to neighbours | cs2n | 0.024 | 0.22 |
| stem + branch soluble to neighbours | sbs2n | 6e-6 to 2e-8 | + |

[a] PE, standard error/mean.
+, low precision.

This model and optimization lead to several tentative conclusions, perhaps best treated as hypotheses worth further testing. They concern the rate coefficients, which may be imagined as being the inherent conductances of the pathways. The actual rates will depend on the driving forces too.

(*a*) The rate coefficient for, and the actual rate of transfer of, $^{14}C$ from the soluble fraction in stem and branches to either the gas phase above the *Sphagnum* or to neighbours is very small, and negligible compared with transport to the capitulum.

The rate coefficient for transport to the capitulum, 0.063 per day, is equivalent to a half-time of about 11 days.

(*b*) From the point of view of the capitulum, the rate coefficient for efflux of $^{14}C$ from the soluble fraction to the gas phase – respiration – is nearly the same as that of influx from the stem and branches below. The coefficient for transfer to the insoluble phase is about twice as great, and of transfer to neighbours is about half as great, as that of respiration. In a complete carpet one might expect that transfer of carbon-containing compounds from neighbours would, on average, balance losses to them.

Transport to the capitulum from below may be through the stem, around the stem, or in the gas phase. It is possible to make a crude estimate of the proportion of $^{14}C$ transferred in the gas phase during the C22 experiment. The relative rate at which $^{14}CO_2$ collected in the NaOH trap during the day and night was 1:2.8. If we ignore diurnal changes in respiration rate then this implies that during the 16 h day an amount of $^{14}CO_2$ equal to 75% of the amount actually trapped in NaOH failed to reach the trap because it was reabsorbed by the plants: a total of $1.67 \times 10^6$ disintegrations per minute (d.p.m.) per shoot.

The parameter values in the model indicate that transfer from the stem plus branch fraction was almost entirely to the capitulum, and this was about 26% of the total $^{14}C$ (figure 8). This gives $2.44 \times 10^6$ d.p.m. per shoot. An extreme view is, then, that 1.67/2.44 (68%) of the transfer is in the gas phase, and 32% in the stem.

A more plausible assumption is that $^{14}CO_2$ was evolved by the capitulum and that some of this could be reabsorbed too. The capitulum contained about as much $^{14}C$ in the soluble phase, on average, as was in the stem plus branch fraction (figure 8). This suggests $1.67/(2 \times 2.44)$, or 34%, of transfer is in the gas phase and 66% in the stem.

In the CP4 experiment about 45% of the $^{14}C$ moved to the capitulum, but only 30% of the $^{32}P$. This result is consistent with the existence of an extra path for $^{14}C$, carrying about one third of the total $^{14}C$ that moved.

The very small amounts of $^{14}C$ transferred to the capitula of steamed plants in the CP4 experiment and to neighbouring matrix plants in all three experiments suggest, however, that these may be over-estimates of the importance of the gas-phase route.

In summary, *Sphagnum papillosum* has a mechanism that transfers soluble carbon compounds from the older parts to the capitulum at a much greater rate than they are lost by respiration or transfer to neighbours. The inherent conductance of this pathway – mostly inside the stem – is about the same as that of respiration by the capitulum, and about half that at which soluble compounds are transferred to an insoluble form.

These processes of predominately acropetal transport continue over long times and in other species of *Sphagnum*, as the results of the C22 experiment (figure 5) show. After five months about 25% of the initial $^{14}C$ had appeared in totally new growth largely, we suggest, as a result of transport in the stem.

*The composition of the soluble fraction*

Among the soluble fractions, *Sphagnum* incorporates more carbon into organic acids than into amino acids, in contrast with *Plagiochila asplenioides* (Suleiman 1981). However, this need not indicate a difference between *Sphagnum* and other bryophytes: according to Maass & Craigie (1964) *S. papillosum* contains a lower concentration of amino acids than other species of *Sphagnum* do (0.08% in *S. papillosum* compared with an average of 0.4% in the eleven other species they investigated). In our experiment, 60–70% of the soluble activity was found in the neutral fraction. This is similar to that in *Plagiochila* (Suleiman 1981). In an earlier experiment (Clymo 1967) 41% of $^{14}C$ was in the insoluble fraction in *S. papillosum* one day after labelling, a value that was reached after three days in our experiment with the same species. With these comparisons in mind, it seems likely that differences in distribution among fractions observed in different studies may depend more on experimental conditions than on the bryophyte genus or species studied. The neutral fraction seems always to dominate among the soluble fractions in bryophytes (Maass & Craigie 1964; Clymo 1967; Suleiman 1981).

Glucose and fructose are known to be the most important sugars in *Sphagnum* (Theander 1954; Maass & Craigie 1964), and malic acid is a major component in the anionic fraction (50–70% of the organic acids for different species of *Sphagnum* (Maass & Craigie 1964)). Our results show that $^{14}C$ enters these same compounds in large amounts. A similar pattern appears in the liverwort *Plagiochila asplenioides* (Suleiman 1981). All the amino acids that we identified are already known in *Sphagnum*. In addition to asparagine and glutamic acid (which we found in greatest quantities), aspartic acid, glutamine, serine, arginine and threonine have been reported as quantitatively important in *Sphagnum* (Maass & Craigie 1964; Thönes & Rudolph 1983). The quotient between the amounts of $^{14}C$ in asparagine and glutamic acid was 3.9 after 27 days in our experiment, quite close to a quotient of 3.4 for concentrations in *S. magellanicum* grown in culture (Thönes & Rudolph 1983).

The proportional distribution of $^{14}C$ among fractions appeared to be stabilizing at the end of the C4 experiment, indicating that further chemical changes after 27 days may be small. The upward transport of $^{14}C$ continues into newly formed biomass, however, as our C22 experiment showed. Differences in growth morphology may account for the smaller fraction of the radioactivity in new biomass in *S. recurvum* than in the other species. *Sphagnum recurvum* forms less dense carpets than the other species and this enables light to penetrate further down, so that a greater proportion of the basal parts may be photosynthetically active. Because of the remarkable growth in length of this species it was difficult to keep the shoots together and the light penetration was even greater than usual. As in the C4 experiment, $^{14}C$ accumulated in the top section.

*Ecological implications*

In its abundance, as well as in anatomy and morphology, *Sphagnum* is distinct from all other bryophytes. It can make the water around it unusually acid (Clymo 1963; Brehm 1971; Clymo 1984) by cation exchange of ions such as $Na^+$, $K^+$, $Ca^{2+}$,

$Mg^{2+}$ in rain for $H^+$ on the plants; it can tolerate (or even requires) unusually low supplies of inorganic nitrogen and phosphorus compounds (Press *et al.* 1986; Rudolph & Voigt 1986; Clymo 1987); and it has a remarkable capacity for external transport of water (Hayward & Clymo 1982).

The conditions required by, or consequent upon, these three features result in the accumulation of peat that is waterlogged, acid and poor in solutes. This, in turn, restricts the species of vascular plants to those that can tolerate these conditions.

Many of these shrubs conserve nitrogen, phosphorus and potassium (as well as organic solutes) within them, shuttling solutes from the aerial parts to subterranean roots, rhizomes or shoot bases as winter approaches and back to aerial parts in spring (see, for example, Sæbø 1968, 1970, 1973, 1977; Chapin *et al.* 1975; Chapin & Bloom 1976; Malmer & Nihlgård 1980).

It seems clear that in these ombrotrophic conditions nutrient limitation and conservation are an important feature of plant life. The work reported in this article allows us to add the capacity to relocate solutes internally as one of the features of *Sphagnum* that contribute to its success. The detailed mechanism deserves further investigation.

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