1997

1997

# Chapter ten:

# The Roles of *Sphagnum* in Peatlands

Professor Richard S. Clymo
*Queen Mary and Westfield College, UK.*

## Introduction

The genus *Sphagnum* is morphologically isolated as the only one in its family, order and class of bryophytes. It contains perhaps 150 to 200 species, of which about a score are common. The best known of its special features is the two types of leaf cell (hyaline and chlorophyllose) arranged in a regular elongate diamond pattern. A similar but less differentiated pattern is seen in the fossil *Protosphagnum* from the Russian Permian about 200 million years old (Neuberg, 1960), and remains of plants indistinguishable from present day species are seen in some brown coals from Yunnan Province, south-west China, about one million years old (Lu and Zhang, 1986).

Most, but not all, species of *Sphagnum* grow in (and are restricted to) habitats that have acid, solute-poor, water. Most such systems accumulate peat - the dead, and partly decayed, remains of the plants that once grew at their surface. Northern hemisphere peatlands of this kind cover about 350 Mha (a square of side about 1900 km if all were to be herded together), have an average depth of about 2.3 m, have an average dry bulk density of about 0.11 g cm$^{-3}$, and an average carbon percentage of about 52% in their dry mass (Gorham, 1991). The total carbon in such systems is about 250 Pg (250 Gt) - about the same as the total mass of carbon in atmospheric carbon dioxide. We may guess that about half the peatland carbon is in *Sphagnum*, alive and (mostly) dead: *Sphagnum* is far and away the most successful bryophyte and, by the criterion of the amount of carbon incorporated, is possibly the most successful plant genus of any kind.

What makes *Sphagnum* so successful? There seem to be three main reasons:

1. it thrives in (most species can only tolerate) water with an unusually low concentration of dissolved solutes;
2. it makes the water around itself unusually acid;
3. it decays unusually slowly.

The first two of these factors result in *Sphagnum* being most abundant in situations where the live plants depend entirely on precipitation for their water. In these acid, solute-poor, conditions few vascular plant species can survive, and most of those that can are specialised. Slow decay leads to the accumulation of peat and to the most conspicuous example of natural ecological engineering - the huge peatlands of Minnesota, James Bay and the west Siberian plain.

It is well known that *Sphagnum* holds water like a sponge. Most of this water is held in capillary films between imbricate (overlapping) leaves, not (as is commonly supposed) in the hyaline cells (though these cells do contribute). Differences in water relations among species are the main cause of the restriction of particular species to particular microhabitats (e.g. pool, hollow, lawn or hummock) - but these differences do not account for the general success of *Sphagnum*.

Finally, *Sphagnum* has formidable powers of regeneration given suitable conditions and time.

In this chapter, I consider first the general economy of a growing peatland surface, then the three main causes of *Sphagnum's* success, then the water relations of *Sphagnum* and finally the regenerative powers of *Sphagnum*. Further detail on most of these may be found in Clymo and Hayward (1982), though there has been a lot of work on *Sphagnum* since that review was made.

## The general economy of a *Sphagnum*-dominated peatland surface

Imagine a rainwater-dependent peatland approached on foot on a fine day. From a distance it may seem to be mainly covered by dwarf shrubs (mostly members of the *Ericaceae*) and linear-leaved sedges (such as those in the genera *Eriophorum*, *Trichophorum* and *Rhynchospora*). Closer inspection reveals *Menyanthes* in pools, *Rubus chamaemorus* on hummocks, and insectivorous plants of genera such as *Drosera*, *Utricularia* and *Sarracenia*. Closer still one can see that all these rooted vascular plants are set in a nearly continuous carpet of *Sphagnum*. These moss plants grow at the apex producing a continuous series of new branch primordia. The internodes and branches extend as the branches produce the characteristic leaves with green chlorophyllose and hyaline cells. The branches are of two types: spreading, and pendent around the stem. The pendent branches act as a wick allowing water to reach the apex externally (Hayward and Clymo, 1982). The branches and leaves form a porous but optically dense canopy which absorbs all but 1% of the incident light in its top 2-3 cm (Clymo and Hayward, 1982). Below this euphotic zone, light is so limited that respiration exceeds photosynthesis, the leaves (and most of the branch and stem cells) die, the green colour disappears, and the plants become light brown or straw-coloured. Nevertheless all the leaf and branch structures remain and the whole canopy, in which dry matter occupies barely 1-2% of the volume, is very porous. Water and gases can permeate freely, molecular oxygen in the air is abundant, and aerobic decay by fungi and bacteria is the dominant process in this moss litter layer. Some plants, such as *Rubus chamaemorus* and *Menyanthes*, decay rapidly and disappear almost completely leaving those that decay slowly, such as *Sphagnum* to dominate the moss litter (even if they did not do so to begin with) (Clymo, 1984a).

Let us follow what becomes of this newly dead moss litter. The green surface grows onward and upward gradually burying our layer. The load of new matter above our layer increases and the 10-20 fold greater load of associated capillary water increases too. At the same time the loss of matter by decay weakens the *Sphagnum* plant structures. Eventually the larger structures collapse, the dry bulk density increases 3-5 fold, and the space between remaining structures decreases by the same factor. The resistance to flow of water in channels is inversely proportional to a power, approximately four, of the width of the channel. As a result of the structural collapse, the resistance to the flow within the dead moss increases approximately $3^4$-$5^4$ (i.e. 81-625 fold). Water, from above can no longer move easily downwards but is diverted sideways. As long as precipitation exceeds evaporation the peat, as it now is, below the collapse remains saturated. In periods of excessive precipitation the water table rises into the porous layer but, the higher it rises, the easier it is for water to flow away sideways, so the whole system is beautifully self-limiting. During a dry period the water table drops into the collapsed layer, but the first rains rapidly refill the pores and the water rises again to near the point of collapse. These mechanisms keep the water table within 3-5 cm of its mean position for 60-80% of the time (Clymo, 1992).

Just below the water table, aerobic decay continues but the rate of diffusion of oxygen in water is only 1/10,000 of that in air, so oxygen is used up faster than it can be replaced: the peat becomes anoxic. Bacteria able to exist anaerobically replace the aerobic fungi and bacteria. There is no obvious intrinsic reason why anaerobic metabolism should be slower than aerobic metabolism - anoxic sludge digesters in sewage works operate at a high rate - but in practice the decay rate of anoxic *Sphagnum* peat is about 100-1000 fold slower than that of oxic *Sphagnum* peat. Thus we get the spectacular accumulations of organic matter in peat bogs.

The whole process is dynamic: it depends on continued plant growth, continued precipitation, and continued fungal and microbial activity. It is, to a great extent, caused by *Sphagnum*, but it also creates the conditions in which most *Sphagnum* grows.

## Relationship with solutes

The leaves of *Sphagnum* have only one layer of cells and no fatty cuticle (rooted vascular plants have much thicker, multi-layered, leaves and cuticles). There is no obstruction to direct absorption of solutes and, contrary to long-held beliefs, *Sphagnum* has an effective internal transport system for carbon- and phosphorus- containing compounds at least (Rydin and Clymo, 1989). In experiments *Sphagnum* is able to incorporate nitrate and phosphate rapidly from solutions of unusually low concentration (Clymo and Hayward, 1982), and has an inducible nitrate reductase (Woodin and Lee, 1987). Adding ammonium nitrate at 2 or 4 g $m^{-2}$ $year^{-1}$ (= 0.7 or 1.4 mol $m^{-2}$ $year^{-1}$ = 20 or 40 kg $m^{-2}$ $year^{-1}$) stimulated the productivity of *S. balticum* but had no effect on the productivity of *S. magellanicum* growing in similarly wet lawns (Aerts *et al.*, 1992). But sodium di-hydrogen phosphate added at 0.2 or 0.4 g $m^{-2}$ $year^{-1}$ (= 0.052 or 0.10 mol $m^{-2}$ $year^{-1}$ = 2 or 4 kg $m^{-2}$ $year^{-1}$) had no effect on the productivity of *S. balticum* but increased the productivity of *S. magellanicum*. These rates of addition are barely ten times those that fall in precipitation nowadays and are tiny compared with agricultural rates. Supplying nitrogen and phosphorus, at annual rates that were no more than one to five times the amount already in *Sphagnum* plants, reduced growth and proved lethal to some species (Clymo, 1987). This egregious behaviour has advantages and disadvantages: on the one hand, *Sphagnum* is able to flourish in situations where most plant species cannot; on the other hand, most *Sphagnum* species cannot spread into solute-rich situations.

There are similar relations with the concentration of calcium and hydrogen ions. In nature, most species of *Sphagnum* are restricted to waters that are acidic and have only low concentrations of calcium. In experiments (Clymo, 1973), however, the same species seem able to grow well in either high calcium concentrations or high pH (low hydrogen ion concentration); it is the combination of high calcium concentration and high pH that is lethal, and this is the combination almost always found in nature. A few species (examples are *S. squarrosum* and *S. fimbriatum*) are able to grow in waters that have moderately high calcium concentrations with, at least initially, high pH. These are the species that are able to establish in fens and thus act as John the Baptist to the main bog species of *Sphagnum*.

## How does *Sphagnum* make the water around it acid?

Up to 30% of the dry mass of the cell walls of hummock species of *Sphagnum* is composed of uronic acid residues linked in long chain polymers (Clymo, 1963). A uronic acid is similar to a sugar but the terminal carbon has a charged acid $COO^-H^+$ attached instead of the neutral $-CH_2OH$ found in sugars. Such large polymeric molecules are not soluble in water: if they were, the plants would rapidly disintegrate. The uronic acids are made by the plant in the $H^+$ form but the bond between $COO^-$ and $H^+$ is relatively weak so the $H^+$ may be competitively replaced by any other (positively charged) cation. The process is very rapid - it is essentially complete within 5-20 minutes. Rainwater, away from sea coasts, contains about 1 mmol $l^{-1}$ of cations, mostly sodium, potassium, ammonium, calcium and magnesium. These compete with the $H^+$ on the uronic acid polymers and displace it into the water around the plants. This is the process of cation exchange, well-known in water softening, which in the case of *Sphagnum* makes the water acid. If the plants were not growing then, as with a water softener, there would come a time when all the exchangeable $H^+$ had been exchanged and the plants would no longer acidify the rain (and they would have been becoming steadily less effective from the start). But *Sphagnum* does grow and continuously produces new exchange sites loaded with $H^+$, so it continues to acidify rain that flows over it. In average conditions of precipitation and cation concentration and for *Sphagnum* growing in carpets, the plants can maintain a pH of about 4.0-4.2 around them (Clymo, 1967). On a hummock during periods with little precipitation and fast *Sphagnum* growth, a pH of 3.0 is possible both in theory and in practice (Clymo, 1984b).

There has been some argument (e.g. Shotyk, 1988) about the role of cation exchange in producing acidity in peat bogs because one can show that in many cases organic acid anions contribute a significant part of the total concentration of soluble anions in peat bog waters. But cation exchange with *Sphagnum* undoubtedly occurs, and on a scale sufficient to be able to account for the observed pH. The real problem is to explain where the soluble organic acid anions have come from. There is, in the cell walls of *Sphagnum*, a fraction of the polymers which is slowly soluble. This fraction contains many residues of a very unusual uronic acid: D-lyxo 5 hexo-sulopyranuronic acid also known as 5-keto-D-mannuronic acid or 5-KMA (Painter, 1991a; b; 1995). This is able to form cross-links between chains and to result in large soluble negatively charged (anionic) polymers, named sphagnans by Painter, that give the water a yellow or brown colour. Indeed it seems plausible that the colour of peat bog water is due to these molecules and not, as is often supposed without any evidence, to phenolic substances. It may therefore be that the rapid primary process, complete within half an hour, producing acidity around *Sphagnum* is cation exchange but that there is a secondary process involving the much slower leaching of residues of 5-KMA that were originally in the H form but which have become associated with other cations before both rejoin the $H^+$ in the water around the plants.

The sphagnans are important in other ways too. They may be responsible for the tanning of peat-bog bodies (such as Tollund Man and Lindow Man) and they seem to have bacteriostatic properties: brown bog water was taken on voyages by the Vikings because it remained fresh for longer than colourless water did. Painter (1991a; b;1995) suggests that the bacteriostatic property is a result of the ability of sphagnans to sequester metal cations thus depriving bacteria of essential metals. He also suggests that the same mechanism may, at least in part, account for the slow decay of *Sphagnum* peat.

## Why does *Sphagnum* decay so slowly?

One must consider decay in oxic and anoxic conditions separately. In the surface oxic layers the rate of decay is related to temperature and water content but in a similar way for most species of peatland plant (Bliss *et al.*, 1981). There are, however, large and approximately linearly correlated differences in decay rate and concentration of nitrogen (Clymo and Hayward, 1982). Material, such as the leaves of *Calluna vulgaris*, with a nitrogen concentration of 1.5% on a dry mass basis, loses 50% of its dry mass in a year. But *Sphagnum*, with 0.5% nitrogen, loses only 15% in a year, and some species of *Sphagnum* lose even less. Such low rates of loss cause *Sphagnum* to become proportionately over represented in the material which is submerged by the rising water table and which becomes anoxic. This resistance to decay is supplemented by unpalatability to animals - vertebrate and invertebrate. There are few, if any, authenticated examples of an animal ingesting *Sphagnum* except inadvertently.

Slow decay of *Sphagnum* in anoxic conditions is perhaps the main reason why deep deposits of peat accumulate. But the reason(s) for slow decay are still obscure. The temperature is not particularly low: a metre or two down, the temperature is nearly constant at the annual mean which is 8-10°C in some 10 m deep peat deposits. Nor is the concentration of nitrogen particularly low: it seems that much of the nitrogen is sequestered so that as carbon is lost so the C/N quotient increases (Malmer and Wallén, 1993). Painter's suggestion that sphagnans sequester metals and so inhibit bacterial growth is a plausible hypothesis and should be tested.

## The water relations of *Sphagnum*

Suppose that rain fell on a carpet of *Sphagnum* on a low hummock until an hour ago, since when water has drained away. In this state, the mass of water in the top few centimetres is about 30-40 times the oven-dry mass of the plants (Clymo and Hayward, 1982). Of this total, the water associated with the hyaline cells of the leaves and the porous cells of stem and branches is about six times the dry mass, and water in fine capillaries in the cell walls is about two times the dry mass. This means that water held in capillary spaces between leaves is about (22)-27-(32) times the dry mass. The percentages of water in fine capillaries: porous cells: between leaves is thus approximately 6: 17: 77. In wet conditions therefore most of the water is in relatively large spaces between leaves where it moves easily up and down outside the *Sphagnum* plants. During longer dry periods the water in these spaces is the first to be lost and the water in the porous cells moves less easily. In prolonged dry periods even water in the porous cells disappears and the plants become papery in appearance. But *Sphagnum* plants are more resistant to desiccation than is usually supposed and most that have become papery for several weeks will recover when rain comes. The ability to withstand desiccation is uncorrelated with the normal habitat: *S. auriculatum* which usually grows in hollows or pools is among the most resistant species; *S. cuspidatum* of hollows and pools is of intermediate resistance; *S. papillosum* of lawns is among the least resistant; while *S. capillifolium* of hummocks is of intermediate resistance (Clymo, 1973).

There are differences among species, however, that are closely related to the microhabitat in which each species usually grows. When the water table is only one centimetre below the surface the rate of evaporation of water from the surface is similar in all species, but when the water table is 10 cm below the surface then the evaporation from *S. capillifolium* of hummocks is greater than from *S. papillosum* of lawns, and this in turn is greater than from *S. cuspidatum* of hollows (Clymo, 1973). The cause of these differences is the numerous small spaces between leaves of *S. capillifolium* compared with the fewer, larger spaces in *S. papillosum* and the very few spaces in *S. cuspidatum*, which has few pendent branches and those it has do not form a continuous capillary path to the apex of the plant (Hayward and Clymo, 1982). As the water table drops so the water tensions increase and the larger capillary spaces empty. *S. capillifolium*, with its abundant small spaces, maintains a continuous external capillary path while most of the paths in the larger *S. papillosum* are broken. It is interesting to note that, in experiments, both *S. cuspidatum* and *S. capillifolium* grew best in hollows, although *S. capillifolium* was the least successful of the two. On hummocks, however, even though it was not at its best, *S. capillifolium* grew better than other species, because of its superior water-conducting ability (Clymo and Reddaway, 1972).

## Regeneration

*Sphagnum* establishment in a new site is most likely to be from spores, which germinate to form a filament, then a plate, and from that develop the conspicuous three-dimensional growths with stem, branches and leaves. The apex may become so large that it 'divides' (there is discussion about the details of this process). The apex exerts dominance over the stem and branches below it, but if the apex weakens or dies then one or more new stems may grow from patches of cells in the axils of branches below, and these new apices and stems may take over from the original one (Clymo and Duckett, 1986). We do not know if any, or the majority, of the apices we see on the surface of a 6000 year old peatland are the same genet as the plants that originally established the peatland. The molecular techniques exist to decide this question, and the *Sphagnum* plants we see are haploid, but the necessary work would be tedious and expensive.

If one takes one centimetre thick slices of peat from a 30 cm diameter core of *Sphagnum* and the peat it has formed and keep them in sealed transparent bags in the light then there is abundant regeneration of *Sphagnum* down to 30 cm depth. This is from a depth where the peat may be 50 years old or more. The *Sphagnum* regenerates from spores (which may have washed down) and from leaves and, especially, from the patches of cells in the axils of branches (Clymo and Duckett, 1986). Whether or not this ability to regenerate is ever exercised in nature we do not know.

## Conclusion

*Sphagnum* is not only the most successful of the bryophytes; it is a notably successful plant by any standards.

# Conserving Peatlands

*Edited by*

**L. Parkyn**
**R.E. Stoneman**
*Scottish Wildlife Trust*
*Edinburgh*
*UK*

**and**

**H.A.P. Ingram**
*University of Dundee*
*Dundee*
*UK*

CAB INTERNATIONAL
Wallingford
Oxon OX10 8DE
UK

Tel: +44 (0)1491 832111
Fax: +44 (0)1491 833508
E-mail: cabi@cabi.org

CAB INTERNATIONAL
198 Madison Avenue
New York, NY 10016-4341
USA

Tel: +1 212 726 6490
Fax: +1 212 686 7993
E-mail: cabi-nao@cabi.org

A catalogue record for this book is available from the British Library, London, UK.
A catalogue record for this book is available from the Library of Congress, New York, USA.

ISBN 0 85198 998 5

Printed and bound in Great Britain by
Biddles Ltd, Guildford and King's Lynn

# Contents

**Part One: PEATLANDS OF THE WORLD**

**Part Two: THE PEAT ARCHIVE**

**Part Three: PEATLAND BIODIVERSITY**

**Part Four: FUNCTIONING PEATLANDS**

**Part Five: MIRES AS CULTURAL LANDSCAPES**

**Part Six: THE NEED AND MEANS FOR SURVEY AND INVENTORY**

**Part Seven: COMMERCIAL USES OF BOGS**

**Part Eight: PEAT FREE HORTICULTURE**

**Part Nine: CONSERVATION MANAGEMENT, REHABILITATION AND MONITORING**

**Part Ten: LEGISLATIVE PROTECTION**

**Part Eleven: RAISING AWARENESS**

**Part Twelve: THE WAY AHEAD**