How Sphagnum bogs down other plants

Nico van Bremen

There may be more carbon (C) incorporated in Sphagnum, dead and alive, than in any other genus of plant. The success of Sphagnum is due to its ability to create a habitat in which few other plants can flourish. The literature abounds in remarks about Sphagnum smothering other plants. Klinger even considers the widespread ‘forest decline’ as part of a general autogenic succession towards climax Sphagnum bogs. Clearly, the traditional view that Sphagnum is simply well-adapted to wet, nutrient-poor mires (see Box 1) needs to be adjusted by recognizing its active role in creating those very conditions in order to gain competitive advantage. Yet this aspect receives little attention in literature on Sphagnum. In the light of recent interest in organisms as ecosystem engineers, and in feedbacks between plants and soil, Sphagnum’s ability to outcompete other plants for light by creating acidic, nutrient-poor, cool and anoxic peat bogs deserves every attention.

Recent research on the organo-chemical composition of Sphagnum and on the fate of its litter has further clarified how this plant builds acidic, nutrient-poor, cold and anoxic peat bogs. The bog environment helps Sphagnum to outcompete other plants for light. Its morphology, anatomy, physiology and composition make it an effective ecosystem engineer and at the same time benefit the plant in the short term. This may have facilitated the evolution of the genus.

Vegetation succession during bog formation

The classical autogenic succession during the formation of a raised bog from a lake is lake mud → Phragmites fen mud → Alnus fen → Pinus/Betula bog → Schoenoxiphium/Carex/Sphagnum bog = Sphagnum bog (Fig. 1). Many more pathways are possible, but most studied sequences end with Sphagnum bogs, and successful invasion of established Sphagnum bogs by trees is rare (Fig. 2). The frequent claim that forest is the climax vegetation on bogs seems to be poorly substantiated.

Hydrology of Sphagnum bogs

Sphagnum bogs have a highly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called acrotelm. The acrotelm is underlain by the slowly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called geotelm. The geotelm is underlain by the slowly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called hydromor. The hydromor is underlain by the slowly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called acrotelm. The acrotelm is underlain by the slowly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called geotelm. The geotelm is underlain by the slowly permeable, 10–40 cm thick surface layer where ground water fluctuates—the so-called hydromor.
the water table in the acrotelm, drawn up through the capillary spaces formed by overlapping pendent branches that hang down against the stem (Fig. 3). When the water table drops, the capillarity increases as pores between the leaves, pendent branches and stems narrow when plant parts are sucked together. Sphagnum species observed at increasing height above the water table (that is, when moving from pools to hummocks) have an increasing capacity to conduct water by such capillary action. Much water can be held in the porous, hyaline cells, which make up about 80% of the plant’s volume (Fig. 3). Through their pores (diameter 5–20 μm), hyaline cells can rapidly absorb water, which can be held against suctions of 10–100 kPa. When emptied during drought they impart a whitish appearance to Sphagnum carpets, causing high albedo and reflection of incident radiation.

About 96% of a living Sphagnum carpet is pore space; 10–20% is in hyaline cells, and the rest is on the outside of the plant. Towards the base of the acrotelm, dead or senescent stems bend down, and total pore space decreases by collapse and compression. This increases the bulk density, from 0.02 g cm⁻³ in the acrotelm to 0.1 to 0.2 g cm⁻³ in the catotelm, while the contribution of hyaline cells to the total pore space increases to 70% (Ref. 10).

Water movement in a raised bog is almost wholly lateral, through the highly permeable acrotelm (saturated hydraulic conductivity, K, in the order of 1 cm s⁻¹). Given its high porosity, surprisingly little water is transmitted through the 0.5–6 m thick catotelm (K = 10⁻³ to 10⁻¹ cm s⁻¹, decreasing with increasing contribution of Sphagnum)¹⁰. The thin water-impervious iron pan, often formed in podzolic soils in wet climates, may help blanket bog formation¹¹. But Sphagnum peat itself also stimulates water stagnation in initially well-drained mineral topsoils, as was observed under Sphagnum peat debris piled on mineral soil¹²: within decades, an impervious iron pan had developed under 5–8 cm of peat. Thicker peat created thicker layers of anoxic mineral soil (without iron pan) because of decreased soil porosity resulting from the eradication of burrowing soil fauna and clogging of pores by humic substances¹¹.

**Nutrient supply and content**

Nutrients enter bogs mainly by wet and dry atmospheric deposition. Sphagnum and other mosses efficiently intercept nutrients from the atmosphere, from leachates and from litter of overstorey plants¹³. Minerotrophic fens and ombrotrophic bogs are central concepts in mire ecology (see Box 1), but their differences in nutrient content and supply are not always straightforward. While pH and the contents of soluble calcium (Ca) and magnesium (Mg) and total phosphorus (P) are almost invariably higher in fens than in bogs, readily available P and nitrogen (N) increased when going from fens to bogs¹⁴,¹⁵. Loss of N and P from Sphagnum litterbags in bogs far exceeded that of organic matter itself¹⁶, while the reverse is true for decomposition of (vascular) plant material in mineral soils. Also, net mineralization of N and P was significantly higher in Sphagnum-dominated bogs than in phanerogam-dominated fens¹⁵. This suggests a dearth of C for microbes, caused by the refractory nature of C in Sphagnum. During initial decomposition of Sphagnum, apparently small quantities N-rich (e.g. protoplasmic) compounds are used by a sparse microbial community. So, while the C:N ratio of total Sphagnum litter is quite high (e.g. C:N ≈ 50), the C:N of the small amount of biodegradable material is low relative to that of the (mainly fungal) decomposers, leading to the release of an appreciable fraction of the (little) N that is decomposed. Although raised bogs ultimately depend on atmospheric supply of nutrients, the water table in the acrotelm, drawn up through the capillary spaces formed by overlapping pendent branches that hang down against the stem (Fig. 3). When the water table drops, the capillarity increases as pores between the leaves, pendent branches and stems narrow when plant parts are sucked together. Sphagnum species observed at increasing height above the water table (that is, when moving from pools to hummocks) have an increasing capacity to conduct water by such capillary action. Much water can be held in the porous, hyaline cells, which make up about 80% of the plant’s volume (Fig. 3). Through their pores (diameter 5–20 μm), hyaline cells can rapidly absorb water, which can be held against suctions of 10–100 kPa. When emptied during drought they impart a whitish appearance to Sphagnum carpets, causing high albedo and reflection of incident radiation.

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Sphagnum peat

Fig. 2. Stratigraphic sequences in (a) British and (b) North American peat profiles. Arrows connect pairs of superposed strata; numbers refer to recorded instances of the particular transition; dashed arrows indicate reversals of the normal sequence. Of the 36 North American peat profiles, 11 cases are forest, and 25 cases are Sphagnum bog. Redrawn, with permission, from Ref. 49.

Fig. 3. Morphology and anatomy of Sphagnum. (a)–(e) S. papillosum: (a) sporophyte-bearing shoot (with pendent branches, see arrow); (b) branch leaf; (c) stem leaf; (d) network of chlorophylllose (stippled) leaf cells, surrounded by porous hyaline cells; (e) cross-section of leaf; (f) same for S. magellanicum; (g) and (h): cross-section and external view of stem of S. papillosum, showing the large, porous hyaline cells, with fibril thickenings of cell walls, at the outside. Reproduced, with permission, from Ref. 50.

retranslocation of nutrients from senescent Sphagnum is no doubt important. Sphagnum lacks a microscopic structure for internal transport, but vertical internal transport of solutes does take place, probably through submicroscopic perforations in the wall ends of stem parenchyma cells11.

Productivity

Net productivity in pure Sphagnum stands may increase from 150 g m$^{-2}$ yr$^{-1}$ on hummocks, via 500 g m$^{-2}$ yr$^{-1}$ in lawns, to 800 g m$^{-2}$ yr$^{-1}$ in pools1. In actual bogs, vascular plants may dominate net ecosystem productivity18. Different Sphagnum species inhabit the different bog habitats. This distribution is clearly caused by competition because species dominate the habitat where they produce better than others, not necessarily where their potential growth is highest1. Sphagnum has a low energetic efficiency (0.2% of the annual incoming solar radiation in the UK), but uses nutrients quite efficiently: Sphagnum production was 2 t kg$^{-1}$ P, and 0.1 t kg$^{-1}$ N at an annual net production of 4 t ha$^{-1}$ yr$^{-1}$. By comparison, production of Scots pine (Pinus sylvestris) was 0.7 t kg$^{-1}$ P, and 0.07 t kg$^{-1}$ N at an annual net production of 13 t ha$^{-1}$ (Ref. 19).

Organochemical properties and decomposition of Sphagnum and Sphagnum peat

Fresh Sphagnum mainly consists of polysaccharides5, made up of glucose and galacturonic acid units. The latter are sugars in which the CH$_2$OH side-chain at C6 has been replaced by a carboxylic acid group, which give Sphagnum its high cation exchange capacity and are largely responsible for its acidic character1. Sphagnum lacks lignin (early reports about lignin in Sphagnum are now attributed to contamination with vascular plants20). Sphagnum is rich in phenols, including the genus-specific, very stable Sphagnum acid [p-hydroxy-beta-(carboxymethyl)-cinnamic acid]21. Sphagnum acid is present in a polyphenolic network polymer that is probably linked covalently to cell wall biopolymers22. Sphagnum acid is present in a polyphenolic network polymer that is probably linked covalently to cell wall biopolymers22. This combination confers one lignin-like property (poor substrate quality) to Sphagnum tissue, without providing the structural strength typical of woody tissue. Indeed, in spite of its lack of lignin and its high polysaccharide content 'almost nothing eats Sphagnum'1. Anatomical and biochemical
details of Sphagnum may be preserved in peat for millennia, with the bulk of the polysaccharide still present after 70,000 years. In the acrotelm, Sphagnum litter decomposes more slowly (mass loss 10–20% yr⁻¹) than leaves of most other plants in their natural habitat (40–80% yr⁻¹). Most of the decay takes place in the first 4–6 months, with much slower mass loss afterwards. The bog environment slows down decomposition of cellulose. However, the refractory nature of Sphagnum litter is mainly responsible for its slow decomposition: (1) Sphagnum litter decomposed equally slowly in its natural environment and in near-neutral, more-fertile mineral soil; (2) other plants, including typical bog species, decomposed much faster in the bog than Sphagnum; and (3) the rates of decomposition of Sphagnum observed in hollows were higher than in hummocks, because of species' differences, not environmental differences. The main reason for the recalcitrance of Sphagnum litter is chemical protection of cell wall polysaccharide, mainly by the polyphenolic network polymers, but also by lipid surface coating (containing C₆₀-C₁₂₆ hydroxy acids, C₁₇-C₄₆ dicarboxylic acids, fatty alcohols and fatty acids).

Some 20–30% of the Sphagnum litter is decomposed in the acrotelm. Because most other bog plants decompose faster, the fraction of Sphagnum material tends to increase with depth. When reaching the upper catotelm, most Sphagnum leaves have been detached from the stems, and decayed cell walls are visible by SEM, albeit only locally. Further decomposition in the anoxic catotelm is very slow, with rates of 0.1 to 0.001% per year. Sphagnum peat is famous for its excellent preservation, not only of Sphagnum, but also of remains of human and animal bodies, and of organic artifacts. This was attributed to a tanning-like process involving 5-keto-α-mannuronic acid, associated with sphenan (a complex pectin-like material that is coaxially linked to cellulose and amylloid-like chains in Sphagnum). Sphenan would suppress microbial activity by strongly binding N, by inactivating exo-enzymes and by sequestering essential multivalent metal cation by chelation. While Painter found no polyphenols responsible for tanning in Sphagnum peat, tannin-like compounds have been observed in Sphagnum more recently. Continuous waterlogging is essential for preserving peat. Aeration and decomposition following drainage irreversibly increases the permeability of the peat, which then becomes unsuitable as a substrate for Sphagnum.

Growth of vascular plants in Sphagnum bogs

Sphagnum bogs form an adverse environment for many plants. Stunted, xeromorphic trees and shrubs usually grow on the better-drained parts (e.g., hummocks) of deep bogs, but hollows and lawns are often treeless. Ratios of tree species on raised bogs. They are (1) low nutrient availability (2) anoxia, (3) low temperatures and (4) high acidity.

Synthesis: how Sphagnum engineers adverse conditions for other plants

Under favourable external conditions, Sphagnum growth, once initiated, stimulates peat growth and forms raised bogs. The morphological, anatomical, physiological and organo-chemical properties of Sphagnum give it attributes (see Fig. 4) that help form acidic, nutrient-poor, heat-insulating and slowly permeable peat. Depressed growth of vascular plants increases (1) light availability and (2) wetness, via decreased evapotranspiration, both of which positively feed back to the growth of Sphagnum, and thus to peat growth. Accumulation of peat is further promoted by feedbacks involving physico-chemical processes and depression of decomposers (Fig. 4).

Sphagnum combines properties of autogenic and alloecosystem engineers (Fig. 5). It autogenically changes the supply of resource to others by building bogs out of its own dead tissue. Decreasing the permeability of the mineral substrate through iron-pan formation and clogging pores with organic material is allogetic engineering. Clearly, growth of Sphagnum positively feeds back to itself, and is affected little by the adverse conditions it creates for other plants. Just like trees, Sphagnum uses dead tissue (peat, rather than wood) to outcompete others for light. However, it does so not by using the dead tissue to prop up its photosynthetic apparatus above that of others, but by attacking its competitors, literally, at the root.

Sphagnum also competes intragenerically. Their higher capillarity, higher productivity under nutrient-poor conditions, and lower nutrient requirements give it attributes (see Fig. 4) to enhance light and water availability. As a consequence, Sphagnum competitively excludes calcicole plants. However, Sphagnum bogs are not more acidic than surface horizons of many mineral soils that carry healthy acid-tolerant plants, including trees and shrubs that grow poorly on bogs. Dissolved aluminium (Al) in bogs may reach concentrations of up to 3 mg l⁻¹, with a mean of 1 mg l⁻¹. In solution cultures, such concentrations seriously affected Schoenus nigricans and E. nigritum. However, the experiments involved inorganic ionic Al, while in bogs most dissolved Al is organically complexed, and therefore less toxic.

The presence of Sphagnum reduces supply of nutrients to vascular plants by a combination of effective interception of nutrients form the atmosphere and slow mineralization. Fertilization experiments in the UK, Ireland, and Scandinavia often, but not always, pointed to low nutrient supply, particularly of N and P, and sometimes of potassium (K), as a major reason for lower aboveground productivity of vascular plants in bogs than in fens and marshes. This contrasts with the higher availability of N and P in bogs than in fens observed in Germany and The Netherlands.
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**Figure 4. Pathways of peat formation (solid arrows) and feedbacks increasing the growth of Sphagnum (dashed arrows).** Dotted arrows show feedbacks involving physico-chemical processes and depression of decomposers. The ovals show the morphological, anatomical, physiological and organochemical properties of Sphagnum.

**Figure 5. Autogenic and allogenic engineering by Sphagnum (see Ref. 5).** The hourglass symbol indicates the points where drainage of the mineral substratum and resource flows are altered.

**Table 1. Specific properties of Sphagnum that increase its fitness in the short term, and in the long term (through promoting peat formation)**

<table>
<thead>
<tr>
<th>Property</th>
<th>Short-term benefit</th>
<th>Long-term benefit</th>
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<tbody>
<tr>
<td>Organomineral composition</td>
<td>Anti-herbivory action</td>
<td>Peat formation</td>
</tr>
<tr>
<td>Microstructural (hyaline cells)</td>
<td>Water conservation</td>
<td>Finely porous, impermeable peat</td>
</tr>
<tr>
<td>Macrostructural (pendent branches)</td>
<td>Capillary water supply</td>
<td>Collapses easily to dense peat</td>
</tr>
<tr>
<td>High nutrient retention</td>
<td>Efficient nutrient use</td>
<td>Low nutrient supply to environment</td>
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</table>

conditions, higher uronic acid content and more recalcitrant dead tissue allow hummock species to outcompete hollow species (by forming hummocks). So hummock species are superior in most properties causing positive feedback in Fig. 4. Paradoxically, these outspoken ‘Sphagnum properties’ help their potential vascular competitors: hummocks are sufficiently oxygenated for the growth of many bog shrubs and trees. Moreover, woody plants even help Sphagnum build hummocks by providing structural support.

**Evolutionary aspects**

Geologically speaking, Sphagnum is relatively young, with species diversity increasing during the Tertiary and Pleistocene. This suggests that Sphagnum evolved along with vascular plants with which it competes on peat bogs. A clonal patch of Sphagnum and its underlying bog can be regarded as an extended phenotype, which, as such, is subjected to natural selection. The very properties of Sphagnum responsible for bog formation, which thereby increase its fitness over long timescales, are also beneficial to the individual plant in the short term (Table 1). This may have contributed to the evolution of successful bog-building individuals. Individual Sphagnum plants are potentially very long-lived. If a single clone would form the bulk of individual raised bogs, long-lived successful Sphagnum could proliferate easily by successive sporophyte generations.

Sphagnum is quantitatively unimportant on tropical raised bogs, which are forested. So, raised bogs can form without Sphagnum, which raises the question if, in the tropics, other plants use Sphagnum’s evolutionarily stable strategy. Up to six forest vegetation types can be found in transects from shallow to deep peat, without trees unique to peat bogs, so the answer is probably no. However, in New Zealand, Empodisma minus produces a sponge-like rootmass, which appears to help form raised bogs in New Zealand; thus, it might use the same strategy.
**Future research**

Important aspects of the typical properties of Sphagnum and its peat that are still poorly understood include: (1) the exact role of phenolics in the recalcitrant nature of its tissue; (2) the processes determining the availability of N and P in fens and bogs; and (3) the cause of the low permeability of the highly porous Sphagnum peat. Much future research on Sphagnum bogs will no doubt be triggered by their importance for the global change issue. Northern peatlands contain 20–30% of all organic C and N in the world’s soils. Effects of future climate change, and of increased atmospheric CO₂ and atmospheric deposition of N, partly through shifts in the competitive balance between Sphagnum and vascular plants, could significantly influence the global atmospheric budget of the greenhouse gases CO₂, CH₄ and N₂O.

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