success of this and similar initiatives will be vital to the conservation of the very biological resources that initiated and sustain human civilization.

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How *Sphagnum* bogs down other plants

Nico van Breemen

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.

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There may be more carbon (C) incorporated in *Sphagnum*, dead and alive, than in any other genus of plant[1]. 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[2] 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[3] (see Box 1) needs to be adjusted by recognizing its active role in creating those very conditions in order to gain competitive advantage[4]. Yet this aspect receives little attention in literature on *Sphagnum*. In the light of recent interest in organisms as ecosystem engineers[5], and in feedbacks between plants and soil[6–8], *Sphagnum*'s ability to outcompete other plants for light by creating acidic, nutrient-poor, cold and anoxic peat bogs deserves every attention.

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 → *Scheuchzeria*/*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[2].

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, water-saturated catotelm[9]. Bogs are recharged mainly by meteoric water. *Sphagnum* lacks rhizoids and internal water-conducting tissue, and some species are very susceptible to desiccation. It therefore depends on water from rain, or from the water table in the acrotelm, drawn up through the capillary spaces formed by overlapping pendent branches that hang down against the stem[1] (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[1]. 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 98% 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 $10^{-7}\,cm\,s^{-1}$, 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 formation[11]. But *Sphagnum* peat itself also stimulates water stagnation in initially well-drained mineral topsoils, as was observed under *Sphagnum* peat debris piled on mineral soil[12]: 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 substances[11].

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 plants[13]. 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 bogs[14,15]. Loss of N and P from *Sphagnum* litterbags in bogs far exceeded that of organic matter itself[16], 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 fens[15]. 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,

Box 1. Bog formation and terminology

Wetlands include non-peat-forming, intermittently flooded marshes, and peat-forming, permanently wet mires[9]. Mires are usually classified as: (1) bogs, which are fed by rainwater (ombrotrophic) and therefore poor in solutes; or (2) fens, which are fed by ground water (minerotrophic) and therefore usually richer in solutes from terrestial sources, notably Ca^{2+}.

Raised bogs form when shallow open waters are filled up by organic matter to semi-terrestrial fens, followed by accumulation of water-saturated peat above the original water surface ('terrestrialization'; see Fig. 1). This requires that annual precipitation exceeds evapotranspiration. In temperate climates, raised bogs are rarely higher than 6 m and more than a few kilometres across. More extensive, but shallower, blanket bogs form in wet climates (annual rainfall >1600 mm, with a low summer precipitation deficit) by increasing stagnation of water in relatively flat or gently sloping terrestrial soils (paludification). Bogs usually have a complex microrelief, including an alternation of hollows and hummocks with elevation differences of several decimetres and horizontal dimensions of metres.

Hollows and hummocks may be alternated by flat areas, so-called lawns. Peatmoss, *Sphagnum*, often dominates the vegetation of bogs in temperate and cold climates. It requires low pH and low Ca^{2+} concentration[1], conditions that are achieved by a predominant downward flow of meteoric water, so that the plant is isolated from minerotrophic ground water.

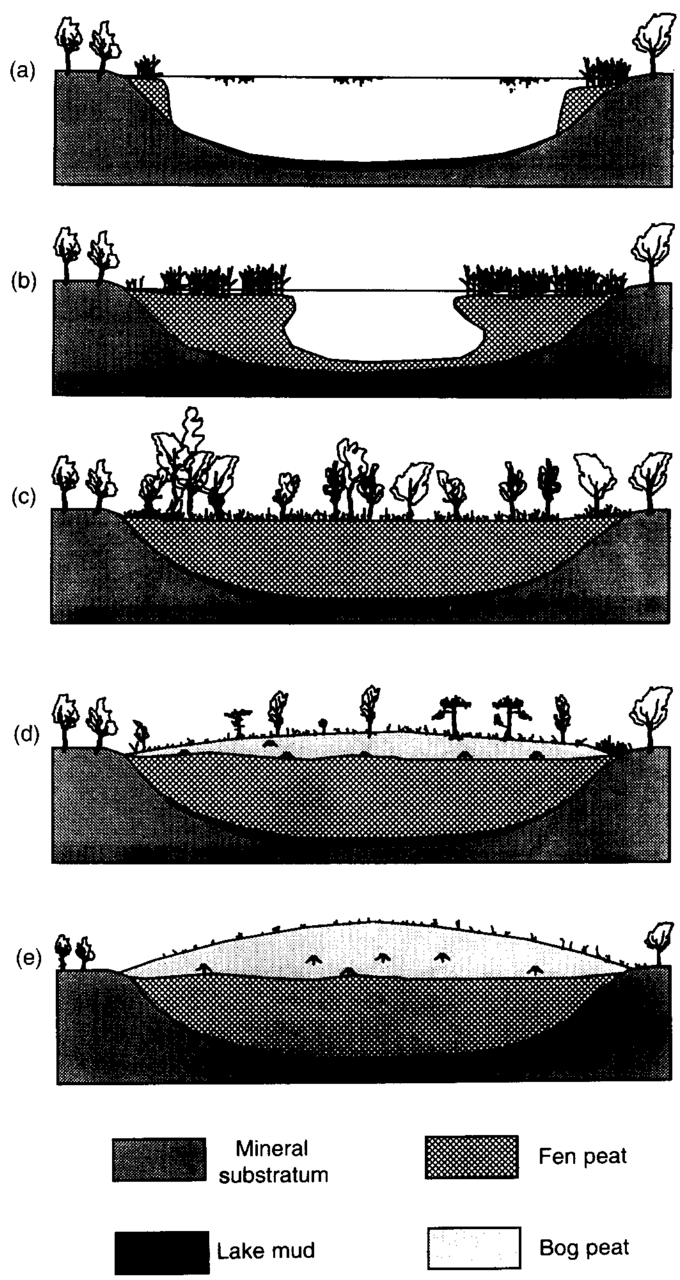

Fig. 1. Development of a raised bog: (a) lake mud; (b)–(c) fen; (d)–(e) bog.

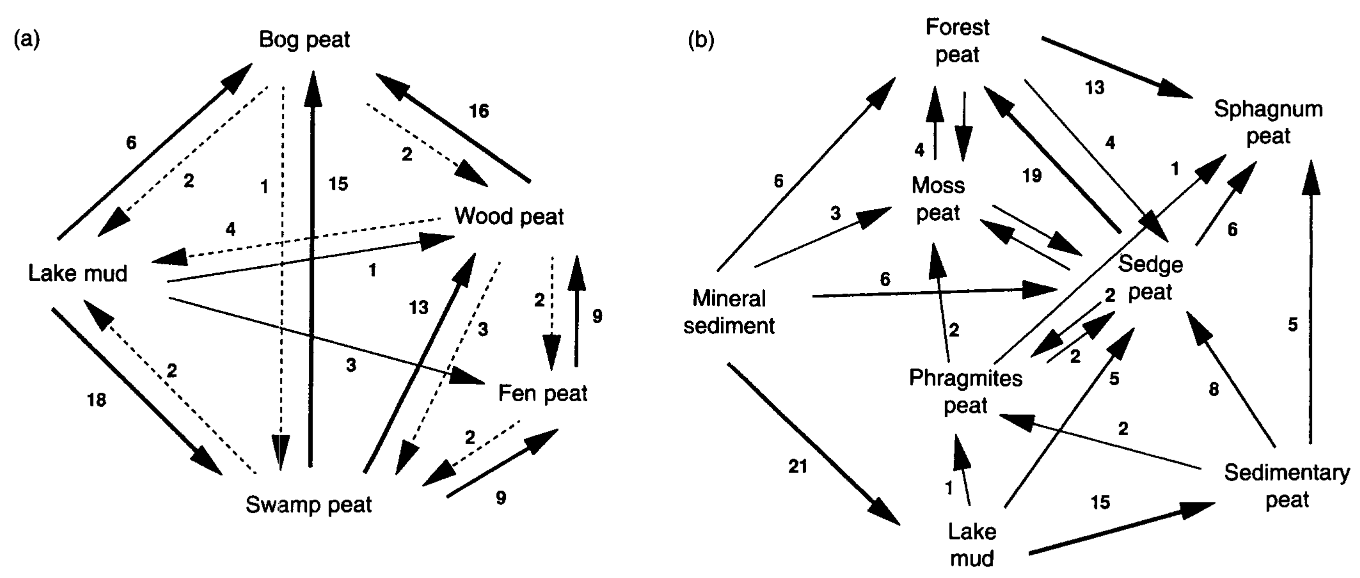

Fig. 2. Stratigraphic sequences in (a) British and (b) North American peat profiles. Arrows connect pairs of superposed strata; numbers refer to recorded instances of the particular transition; dashed arrows indicate reversals of the normal sequence. Of the 36 North American peat profiles, 11 cases are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

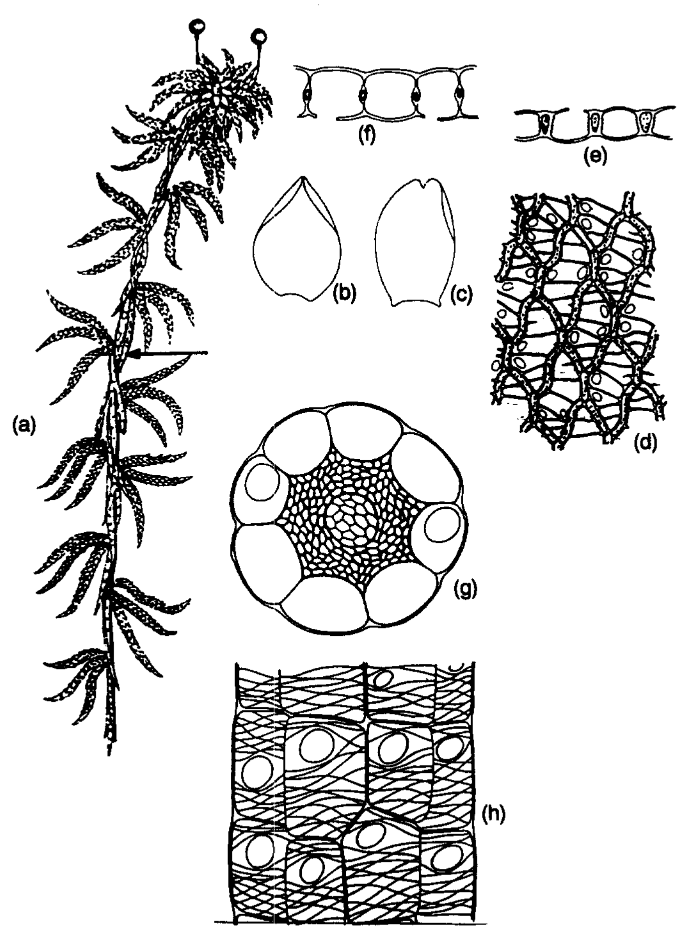

Fig. 3. Morphology and anatomy of *Sphagnum*. (a)–(e) *S. papillosum*: (a) sporophyte-bearing shoot (with pendent branches; see arrow); (b) branch leaf; (c) stem leaf; (d) network of chlorophyllose (stippled) leaf cells, surrounded by porose hyaline cells; (e) cross-section of leaf; (f) same for *S. magellanicum*; (g) and (h): cross-section and external view of stem of *S. papillosum*, showing the large, porose 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 end walls of stem parenchyma cells[17].

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 pools[1]. In actual bogs, vascular plants may dominate net ecosystem productivity[18]. 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 highest[1]. *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 polysaccharides[5], made up of glucose and galacturonic acid units. The latter are sugars in which the CH_2OH 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 character[1]. *Sphagnum* lacks lignin (early reports about lignin in *Sphagnum* are now attributed to contamination with vascular plants[20]). *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 biopolymers[20]. 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[20]. 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[22,23]. The bog environment slows down decomposition of cellulose[15]. 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[24]; (2) other plants, including typical bog species, decomposed much faster in the bog than *Sphagnum*[24]; and (3) the rates of decomposition of *Sphagnum* observed in hollows were higher than in hummocks[23,25] because of species' differences, not environmental differences[23]. The main reason for the recalcitrance of *Sphagnum* litter is chemical protection of cell wall polysaccharide, mainly by the polyphenolic network polymers[20], but also by lipid surface coating (containing C_{14}–C_{26} hydroxy acids, C_{20}–C_{24} dicarboxylic acids, fatty alcohols and fatty acids)[26].

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[27]. Further decomposition in the anoxic catotelm is very slow, with rates of 0.1 to 0.001% per year[28]. *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-D-mannuronic acid, associated with sphagnan (a complex pectin-like material that is covalently linked to cellulosic and amyloid-like chains in *Sphagnum*[29]). Sphagnan would suppress microbial activity by strongly binding N, by inactivating exo-enzymes and by sequestering essential multivalent metal cation by chelation. While Painter[29] found no polyphenols responsible for tanning in *Sphagnum* peat, tannin-like compounds have been observed in *Sphagnum* more recently[20]. 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*[30].

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 diameter growth in Alaskan *Sphagnum* bogs to those under the best conditions on mineral soil nearby ranged from 0.27 (*Tsuga heterophylla*) and 0.16 (*Pinus* spp.) to 0.09 (*Pseudotsuga menziesii*)[31]. The poor growth is clearly due to adverse conditions below ground. Fewer living, and more dead, fine roots of *Tsuga heterophylla*, and *Chamaecyparis nootksatensis* were observed under *Sphagnum* than in its absence[2]. The adverse belowground factors could include low soil temperatures, drought stress, excess water, high acidity and low nutrient supply. Few studies were directed to test any of these hypotheses.

Sphagnum peat conducts heat poorly, causing a relatively short growing season for vascular plants on boreal peats[32]. By contrast, the shallow euphotic zone (<5 cm) of the *Sphagnum* carpet tends to be relatively warm, lengthening the growing season of *Sphagnum* itself[1]. Xeromorphism in bog plants was not associated with higher water potentials and stomatal resistance than recorded in normal individuals outside the bog, and is more likely caused by lack of nutrients than by drought[33]. Lack of oxygen and/or toxicity of reduced substances (e.g. Fe^{2+}, H_2S) obviously impede plants not adapted to anoxic conditions. Bog trees avoid the anoxic catotelm by having a shallow root system. *Empetrum nigrum* was affected by prolonged waterlogging on bogs[34]; *Molinia caerulea* grew well in flushes, but became stunted in stagnant water high in H_2S (Ref. 35).

The low pH and Ca concentrations in bogs effectively exclude calcicole plants. But *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} (Ref. 36). In solution cultures, such concentrations seriously affected *Schoenus nigricans*[36] and *E. nigrum*[34]. However, the experiments involved inorganic ionic Al, while in bogs most dissolved Al is organically complexed[37], 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[38]. 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[39,40]. This contrasts with the higher availability of N and P in bogs than in fens observed in Germany and The Netherlands[14,15].

In conclusion, the available literature gives some direct and much circumstantial evidence that four factors are mainly responsible for adverse conditions for vascular plants 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 organochemical 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[10], 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 allogenic ecosystem engineers[5] (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 allogenic 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

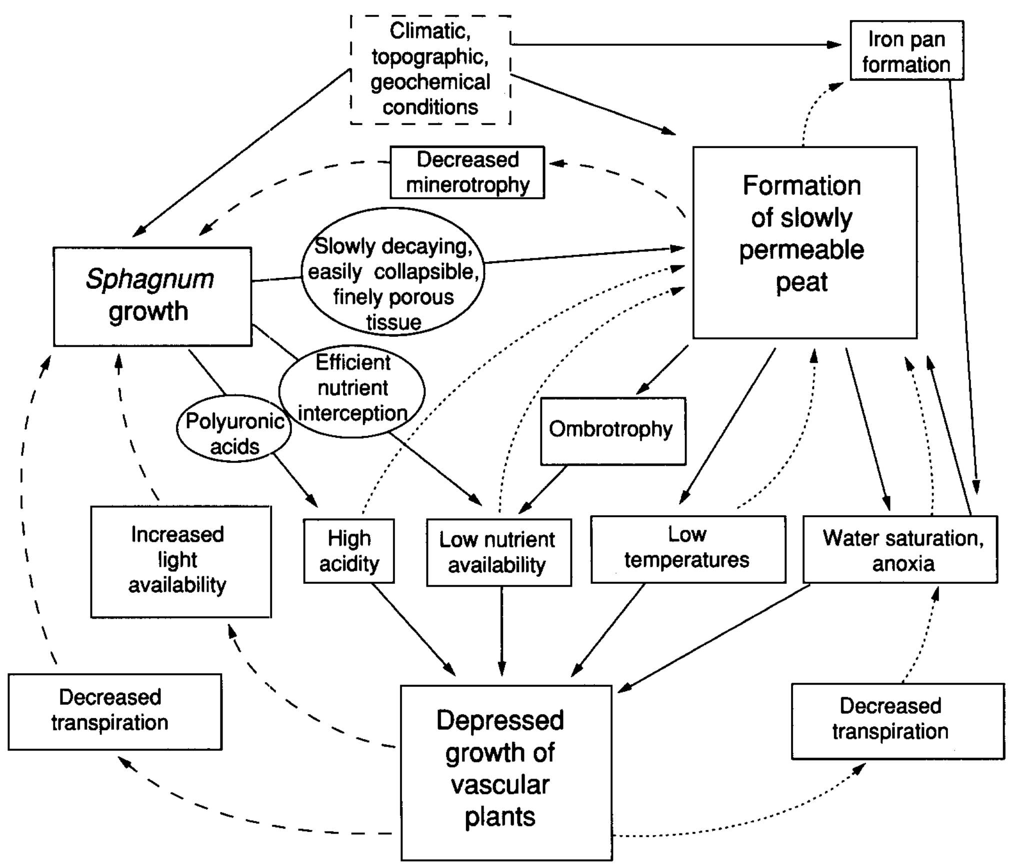

Fig. 4. Pathways of peat formation (solid arrows) and feedbacks increasing the growth of *Sphagnum* (dashed arrows). Dotted arrows show feedbacks involving physico-chemical processes and depression of decomposers. The ovals show the morphological, anatomical, physiological and organochemical properties of *Sphagnum*.

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[38].

Evolutionary aspects

Geologically speaking, *Sphagnum* is relatively young, with species diversity increasing during the Tertiary and Pleistocene[41]. 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[5,42], 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[43]. 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[43], 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[44]; thus, it might use the same strategy.

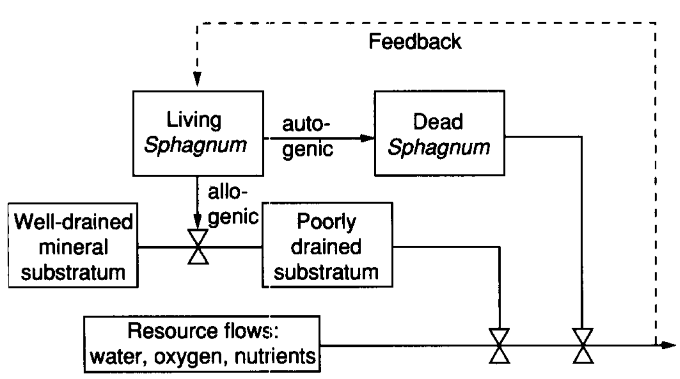

Fig. 5. Autogenic and allogenic engineering by *Sphagnum* (see Ref. 5). The hourglass symbol indicates the points where drainage of the mineral substratum and resource flows are altered.

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

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

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[45]. Effects of future climate change, and of increased atmospheric CO_2 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 CO_2, CH_4 and N_2O (Refs 38,46–48).

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