The Bryologist 103(3), pp. 503–508

INVITED ESSAY

New Frontiers in Bryology and Lichenology

Sphagnum—A Keystone Genus in Habitat Restoration

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Given the massive aerial extent of peatlands in Canada, how can we justify expenditure to conserve or restore this habitat? Although the vast majority of Canadian peatlands occur in the northern boreal region (170 million ha; Gorham 1990), the degradation and commercial exploitation of peatlands is concentrated in the south. Thus, spatially restricted peatland habitats in southern Canada are disproportionately affected by intensive human landuse where they may be flooded during reservoir construction, drained for agriculture and sylviculture, mined for peat extraction, or simply disappear under industrial and urban development. The peatlands of southern Canada are home to a rich flora, including many rare plant species (*Arhetusa bulbosa*, *Listera australis*, *Utricularia geminiscapa*), as well as unusual assemblages of insects (Odonata: *Somatochlora brevicincta* and Coleoptera and birds (Palm warbler, Lincoln sparrow), and accordingly, the fragmentation and loss of peatland habitats can have a significant long term impact on regional biodiversity (Calmé & Desrochers 1999; Findlay & Houlahan 1997; Pellerin & Lavoie 2000; Poulin et al. 1999). In the last 50 years there has been an increasing recognition of the ecological services and goods that peatlands provide for the human population (Parkyn et al. 1997–Conserving Peatlands); e.g., i) peatlands are used by humans for hunting, gathering medicinal and food plants, and for recreational activities such as birdwatching and botany, ii) they act as a partial hydrological buffer against flooding and they filter and ameliorate the quality of groundwater, iii) within the forested landscape, peatlands act as seed source after forest fire or clear-cutting, iv) they are a source of archeological information preserving human artefacts for millennia, and v) peatlands provide archives from which it is possible to reconstruct long term changes in plant and animal communities, past climates, and pollution regimes. Perhaps most importantly, Canada's peatlands perform a significant global function in regulating the Earth's atmospheric chemistry, acting as a source and sink for atmospheric gases (Clymo 1998; Moore et al. 1998).

Peatlands also provide valuable economic commodities: live *Sphagnum* plants are collected from peatlands and sold as ''floral moss'' to use as germination beds and growth medium for orchids. Northern hemisphere peatlands have been historically known to provide good quality horticultural peat and fuel peat. More recently, fibric peat has been commercially used to produce a multi-purpose absorbant board, which is turned into disposable nappies, sanitory towels, germination beds and absorbants for oil spills and moderately decomposed peat is used as biofilters, while more decomposed 'humic peat products' are being developed for therapeutic use. Wild berries collected from peatlands (cloudberries, cranberries) are collected for local consumption and the former are commercially exploited is certain areas for the production of cloudberry liquor.

As we begin to appreciate more the ways in which peatlands contribute essential ecological services to the human population, provincial governments, environmental agencies (e.g., Wetland International, International Mire Conservation Group, North American Wetlands Conservation Council, Ducks Unlimited), research groups and commercial users of peatlands have begun to seek ways to sustainably manage the human exploitation of peatland ecosystems. For recent examples of these advances in Canada see Poulin & Pellerin (2000) for Québec, Bush (2000) for Saskatchewan, and Thibeault (1997) for New Brunswick.

In this review I will consider the *restoration* of degraded peatlands. Modern restoration work in Canada has focussed on post-mined peatlands, where peat extraction has taken place either by i) the hand block-cut method, which was used up until the late 1960's or ii) the vacuum harvesting method, which superseded block-cutting and is intensively used today. For details on each of these methods and how they affect the topography of peatlands see Crum (1988; pp. 182–188).

0007-2745/00/503–508$0.85/0

Defining the goals of restoration. It is impossible to evaluate the success of a restoration project without first defining a series of well-stated goals. For example, if peatland restoration is the return of a vegetation cover that includes only peatland species, resists invasive plants, and has a characteristic plant structure when viewed obliquely, then one could say that 90% of all abandoned areas of peatland in eastern Canada have successfully regenerated naturally, this statistic reflecting the general situation for both hand block-cut and vacuum mined sites. This is excellent if we compare the record of natural regeneration in Canada to European peatlands, where abandoned sites are being invaded by bracken, rhododendron, *Molinia,* and sometimes a dense cover of birch.

However, on closer inspection one finds that the *Sphagnum* and herb layers of revegetated Canadian peatlands are severely depleted, accounting for only 10% of the abandoned surface. Furthermore, data from field surveys show that the recolonization of abandoned vacuum mined peat fields is especially problematic—fewer than 1% of the vacuum mined surfaces are colonized by *Sphagnum* and these sites show a tendency towards birch invasion (Lavoie & Rochefort 1996). It therefore does not appear that the flat, extensive, vacuum mined peat fields naturally regenerate into a functioning peatland, at least not in the short term (<25 years). Intuitively its seems that the predicted establishment of a birch or poplar woodland, and the lack of a well developed *Sphagnum* carpet, would not be conducive to the rapid recovery of a functioning peat-accumulating system.

We define the goals of peatland restoration as reestablishing 1) a plant cover dominated by Sphagna or brown mosses, depending on the status of the residual peat and 2) the diplotelmic hydrological layers that characterize intact 'active' peatlands. Peatland restoration also implies the return of a functionality that ensures ecosystem maintenance in the long term e.g., achieving an adequate level of productivity, returning the mined site to a peat accumulating system, re-establishing the cycling of nutrients, returning a vegetation structure and microhabitats from which emerge faunal and floral diversity, and making sure that the ecosystem is resistant to biological invasion.

How the interest in peatland restoration and Sphagnum reintroduction started? Up until 1990, there was no discussion about nor research into peatland restoration in North America. The Canadian peat industry and a Canadian pharmaceutical company have been two of the major players in helping to develop a Canadian expertise in peatland restoration, and particularly on the biology of *Sphagnum* during its ''regeneration phase''. It was after watching the outcries of British environmentalists who denounced the bad management of the last natural mires in England that the Canadian peat industry became proactive in their resource management. The first significant step was a peatland reclamation workshop in Fredericton, NB, at the beginning of 1992 organized by the horticultural peat industry. All Canadian industries with an interest in peat were invited to the workshop, along with peatland scientists and representatives from provincial governments regulating the use of peat. Peatland researchers from Europe, who had already begun to work on such topics, were invited to give seminars. By the end of this two-day workshop, the guidelines of an after-use policy for peatlands had been delimited and links between university researchers, interested government bodies, and the industry were later to develop into collaborative research. The basis of this first policy has remained relatively unchanged (http://peatmoss.com/) and states a primary after-use objective: the return of bog to natural wetlands habitat through natural succession.

From that moment, restoration research was on its way. The industrial use of peat by the pharmaceutical industry began in 1989, when the absorbant properties of *Sphagnum*—which had been used for centuries by native peoples, who used it as diaper—was marketed on an industrial scale. An absorbent *Sphagnum* board was produced and used in the fabrication of sanitary napkins. To ensure a sustainable supply of its primary resource, the pharmaceutical industry has for the past 10 years invested in research to develop a farming system for *Sphagnum* fibers. The idea was to reuse post-mined peat fields to install a *Sphagnum* producing system that could yield good *Sphagnum* fibers on a cycle of 10 to 15 years. For separate economic reasons, the industrial production of the absorbent board will terminate this year.

Sphagnum moss is a key plant in the ecology and development of most Canadian peatlands (van Breemen 1995). *Sphagnum* mosses possess several morphological, anatomical, physiological, and organo-chemical properties that help them in nurturing their environment by forming acidic, nutrient-poor, heat-insulating, and slowly permeable peat. In the past fifteen years, the ecology of *Sphagnum* (habitat niche) has been widely studied in natural mires. The literature on growth, production, and the most important niche dimensions of many species is quite extensive (e.g., Gignac et al. 1991; Rochefort et al. 1990). There is, however, a remarkable gap in our knowledge of life history strategies of *Sphagnum,* especially regarding the dispersal and establishment potential of these species. The latest

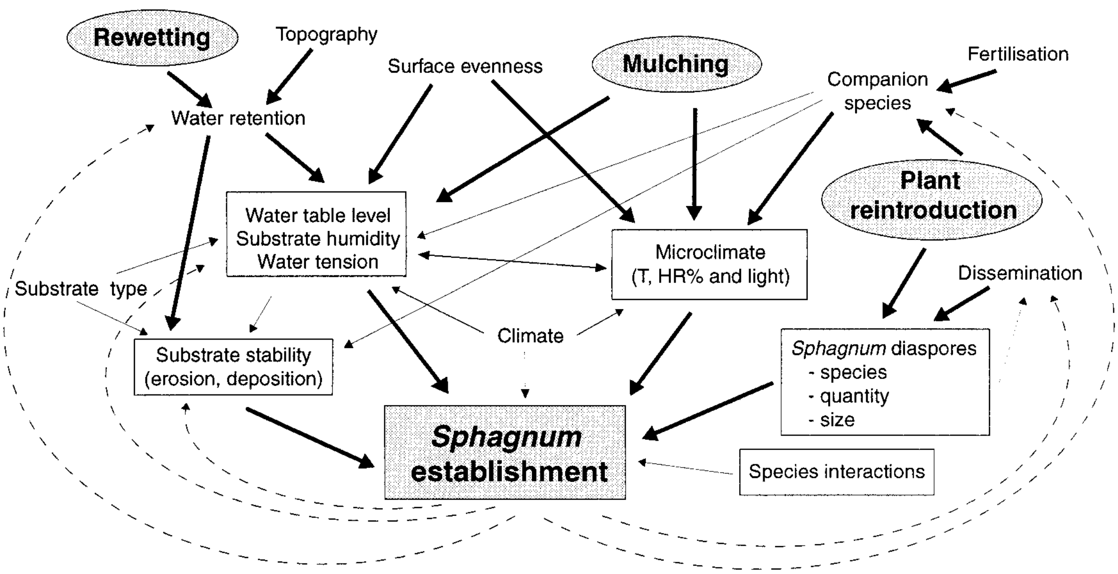

FIGURE 1. Diagram to summarize the factors affecting the success of *Sphagnum* establishment on bare peat substrates. Thick arrows indicate relationships that are substantiated by data from the PERG (Peatland Ecology Research Group). Thin arrows show relationships not yet proven. Dashed arrows indicate feedbacks.

economic use of peat and the better management of this resource have both provided an impetus towards a fuller understanding of *Sphagnum* biology during its early stages of establishment, including colonization of bare peat substrates (regeneration niche). The next section will summarize the advances made in the last 10 years and discuss future research needs.

Factors influencing Sphagnum establishment on bare peat substrates. We already know from the few post-vacuum mined peatlands that have been abandoned for at least 15 to 20 years, that *Sphagnum* plants do not readily colonize extensive bare peat surfaces (<1% cover for all the mined peatlands surveyed in eastern Canada). Recent advances in research restoration conducted in eastern Canada have shown that there are three interventions that are paramount to the success of *Sphagnum* establishment on bare peat surfaces: (I) the active reintroduction of moss diaspores, (II) the presence of a protective mulch cover, and (III) rewetting of the site (ellipses in Fig. 1). Other factors or interventions listed in Fig. 1 will act to improve *Sphagnum* establishment to various degrees by acting on similar (e.g., microclimate, water retention) or different mechanisms (e.g., surface stability) than the main interventions. The process of restoration summarized in Fig. 1 are discussed below.

(I) Natural dissemination or active reintroduction of *Sphagnum* diaspores to the restoration site is essential for the return of *Sphagnum* moss (Rochefort & Bastien 1998; Rochefort et al. 1995; Fig. 1–plant reintroduction). Post-vacuum mined sites are clearly not recolonized by *Sphagnum* mosses (Lavoie & Rochefort 1996) and this even if some sites have been abandoned for 15 to 20 years (Desrochers et al. 1998). It appears that diaspores naturally dispersed to post-vacuum mined peatlands are either too small and to few to enable regeneration. Because of their size, *Sphagnum* spores would have a better chance to disseminate to bare peat substrate. Their capacity to establish in these conditions, is however poorly documented. Therefore, active reintroduction of plants is suggested as a first, essential action for restoration. Several experiments done by PERG (Peatland Ecology Research Group—http://alpha.eru.ulaval.ca/gret-perg) has shown repeatedly that reintroducing shredded bog vegetation is a needed step in the establishment of a moss carpet.

(II) The presence of mulch is the second essential intervention. The straw mulch density that is recommended in peatland restoration (1,500 kg/ha) has been shown to improve the substrate conditions and the microclimate surrounding reintroduced diaspores (Fig. 1–Mulching). A straw mulch cover increases surface soil moisture by 15% (Price 1997), decreases the amplitude of temperature changes between days and nights, decreases evaporation from the underlying soil and soil water tension, sustains a water table closer to the peat surface, and increases relative humidity at the peat interface, thus enhancing the regeneration of a *Sphagnum* moss carpet (Price et al. 1998). The potential fertilizing effect provided by leaching of nutrients from the straw mulch is, however, negligible. Although mulch applied in the recommended density intercepts 50 to 60% of incoming light, it was found that such a decrease in light intensity do not adversely affect *Sphagnum* regeneration. Parallel to mulching experiments, different ground covers, windbreaks, and irrigation techniques were tested to protect reintroduced *Sphagnum* diaspores against dessication, but none of these manipulations yield any significant result toward better *Sphagnum* establishment (Quinty & Rochefort 1997; Rochefort & Bastien 1998; Rochefort et al. 1997).

(III) Rewetting of the site by blocking the former drainage system is the third essential action, which enables the success of *Sphagnum* establishment (Fig. 1–Rewetting). Wheeler and Shaw (1995) discussed at length the importance of rewetting for peatland restoration and the fundamentals of how *Sphagnum* moss responds positively to increased substrate humidity and water level.

Other peripheral factors or actions that, in combination to the three primary actions, will improve moss establishment, are discussed below. The choice of *Sphagnum* species is an important determinant for the success of moss establishment (Fig. 1–Species; Campeau & Rochefort 1996; Rochefort & Bastien 1998 and unpublished data). Species of the *Acutifolia* group (e.g., *S. capillifolium, S. fuscum, S. russowii*) have a greater ability to colonize bare surfaces than other species, especially the *Sphagnum* group (*S. magellanicum, S. papillosum*). Facilitation or competition processes that could occur by reintroducing different *Sphagnum* species together is currently under study. In fact, there is a dearth of information regarding the question of competition among *Sphagnum* species (Rydin 1993) and much could be gained by studying *Sphagnum* interactions during their regeneration phase. The quantity of diaspores reintroduced during restoration will also directly affect the success of *Sphagnum* establishment (Fig. 1–quantity; Campeau & Rochefort 1996; Quinty & Rochefort 1997). The more diaspores reintroduced, the better the establishment success of *Sphagnum.* This positive linear relationship holds until diaspores more or less completely cover the ground without any overlap. When working mechanically on a large scale, we can translate the sowing of diaspores into a ratio of 1:10 i.e., one square meter of collected material from a donor site should be spread on 10 square meters of bare peat. Diaspores size also plays a role in promoting establishment, and it is generally believed that larger diaspores have a better chance at survival and establishment (Fig. 1–size; Rochefort et al. 1995 and unpublished data).

Like mulching, vascular plants or other mosses (particularly species of *Eriophorum* and *Polytrichum strictum*) may be used as nursing plants to improve *Sphagnum* establishment (Fig. 1–companion species; Boudreau & Rochefort 1999; Ferland & Rochefort 1997; Grosvernier et al. 1995). The exact process by which nurse plants ameliorate substrate and microclimatic conditions remains properly quantified. On the other hand, we do know that if a light fertilization of phosphorus is applied, *Polytrichum* and vascular plant growth is stimulated, augmenting those hydro-climatic conditions favorable to *Sphagnum* establishment (Fig. 1–fertilization; unpublished data). We also suspect that nurse plant species have a greater ability to stabilize the peat substrate than *Sphagnum* species, having a greater resistance to frost heaving. Nurse plants probably also have an effect on substrate humidity (either positive the same way a mulch would act, or negative through evapotranspiration), but this remains to be confirmed.

Topographical modifications refer to structures created at a macro-scale (affecting several hundreds of meter squares of surface) i.e., the creation of shallow basins, bunding across the slope of peat fields or reprofiling the surface to reverse the camber which originally enhanced lateral drainage. Topographical modifications of peat fields have been shown to increase water retention, ameliorating those hydrological conditions that improve *Sphagnum* recovery (Fig. 1–topography; Bugnon et al. 1997; Price et al. 2000). However, when too much water is retained, inducing long periods of flooding on large areas, the formation of waves and wavelets can cause erosion of the peat surface, displacing the freshly reintroduced plant material and mulch or depositing peat particles over the mosses. Substrate instability induced by these water movements has a negative effect on *Sphagnum* establishment. At a smaller microtopographical scale, increases in surface roughness have been shown to deteriorate hydro-microclimatic conditions conducive to *Sphagnum* growth and survival. (Fig. 1–surface evenness; Rochefort & Bastien 1998). Surface preparation tests (ploughing, harrowing, and track-and-ridge topography) all aimed at creating wetter and more sheltered microsites in order to improve establishment of *Sphagnum* mosses were shown to provide no net overall benefit to *Sphagnum* because of desication in areas of positive relief (Price et al. 1998; Quinty & Rochefort 1997). In conclusion, the more even the peat surface where plants are reintroduced, the greater the success of establishment. This remains true for the surface of a macro-scale structure i.e., within a macrotopographical structure (e.g., a shallow basin) the bottom surface should be flat. The quality of the peat substrate is also suspected to influence *Sphagnum* establishment (Fig. 1–substrate type; Buttler et al. 1998 and PERG unpublished observations). Less decomposed peats (von Post H1 to H2) are more favorable for *Sphagnum* regeneration, having greater stability and better hydrological conditions. The effects of drainage on peat properties are relatively well known (Price 1996), but the effect of different peat types on *Sphagnum* establishment needs further research.

Clearly, when a threshold level of re-establishment is reached, *Sphagnum* establishment will act as a positive feedback (dashed arrows, Fig. 1). Once a partial moss carpet is established, there are fewer problems of substrate instability, water retention is increased through interception, and substrate humidity conditions are believed to be ameliorated. Also, with a partial moss carpet, natural short distance dispersal can occur and the moss carpet can act as a seedbed for vascular plants that have been observed to increase in abundance three to four years after moss carpet establishment. One important factor that has not yet been studied in detail is the significance of yearly climatic variation (length of growing season, rainfall, temperature) on *Sphagnum* establishment and colony stability (Fig. 1–climate; Rochefort et al. 1997).

Why this topic will yield significant advances in the next millennium. For the past 100 years, peatland scientists have been studying natural peatlands to understand how these ecosystems function and develop. The attempt to recreate peatland ecosystems is the acid test of our ecological knowledge (Jordan et al. 1987). For example, can we infer regeneration patterns from the known niche breath of the main *Sphagnum* species?

The dynamics of *Sphagnum* during the regeneration phase of peatlands have been little studied because empty habitat space is not as often observed in natural mires as in other ecosystems. The increase in the number of anthropogenic disturbances of *Sphagnum*-dominated peatlands, through activities such as peat cutting, building of pipelines, cranberry culture, and use of All Terrain Vehicles provide us with exciting experimental opportunities to study dispersal, establishment, colonization, and competition in Sphagna. The knowledge gained by studying the regeneration of a *Sphagnum* carpet on bare peat surfaces could give precious insights into factors explaining the distribution and abundance patterns of species in natural habitats, as well as the conditions needed for primary peat formation following major disturbances e.g., after glacial or marine regression.

In his presidential address at the 75th anniversary of the British Ecological Society, Peter Grubb (1990) suggested that a measure of the maturity of ecology is the ''*ability to predict the result of new kinds of manipulation or changing conditions that have not been experienced before*''. Thus, it is in this sense that peatland restoration ecology can contribute to the wider scientific community—providing the opportunity to study plant interactions over an important temporal gradient (regeneration) on bare peat substrate.

Acknowledgments

I am very grateful for the work of many former graduate students and research associates who have contributed so much to understanding of *Sphagnum* biology during its regeneration phase in restoration ecology. I thank Christopher Ellis who helped to improve the manuscript and Suzanne Campeau for drawing Figure 1.

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