

Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems

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Peatland restoration measures usually require the rewetting of the disturbed ecosystem. In northern latitudes, the increase in wetness of the bare peat substrate causes frost heaving. In this paper, we described the problem of frost heaving in cutover peatlands and an array of means whereby it can be diminished. Several avenues of research should be pursued with the use of nursing plants to reduce frost heaving and promote *Sphagnum* establishment and growth. For large scale restoration of peatland ecosystems, *Polytrichum strictum* appears to be a good potential nursing plant to *Sphagnum*. However the importance of competition between polytric and *Sphagnum* is unknown and we do not know under which conditions the association is beneficial or not.

Key words: colonisation, degraded mire, peat erosion, regeneration, rehabilitation, revegetation, *Sphagnum*.

Introduction

In their natural state, peat bogs are a unique ecosystem in which atmospheric carbon is sequestered as peat for long-term periods. Composed primarily of *Sphagnum* and sedges in the boreal regions, peat is extracted for horticultural or fuel purposes on large expanses by modern milling technology (Frilander et al. 1996). Prior to harvesting, the site is prepared by scraping off the existing vegetation and digging drainage ditches to dry the site.

When the peat deposit has been exhausted, the site is either abandoned or taken into after-use like agriculture, berry farming, forestry, creation of bird lakes or restored to functional peatlands (Selin 1996). Even twenty years after abandonment, there is often little natural regeneration of peat mosses on many sites (Salonen

1992, Pfadenhauer & Klötzli 1996, Fig. 2 in Desrochers *et al.* 1998 for post-vacuum sites, Tuittila et al. 2000b). But for sites with less than 30 cm of peat left, a good diversity of vascular plant communities can be found on cutaway peatlands (Salonen 1992, Rowlands 2000). Reasons for poor peat moss regeneration include: lack of a viable seedbank, inappropriate hydrological regime, harsh microclimate and peat instability (Salonen 1987, Joosten 1992, Schouwenaars 1993, Poschlod 1995, Anderson 1997, LaRose 1997, Huopainen et al. 1998, Price et al. 1998). In light of these difficult conditions, human intervention is necessary to hasten the regeneration process and return these sites to carbon accumulating ecosystems (Joosten 1995, Pfadenhauer & Klötzli 1996, Rochefort 2000).

In the peatland restoration method now practiced on a large scale in North America

(Rochefort et al. in press) the first step is to scrape off the surface of the abandoned site in order to facilitate contact between diaspores and the substrate. Next, the top 10 cm of vegetation from a donor peatland site is harvested and spread over the bare surface in a 1 to 10 ratio; that is, the material from one square meter of donor site is spread over 10 square meters of bare peat (Campeau & Rochefort 1996). The newly spread diaspores are covered with a protective straw mulch at a rate of 3000 kg ha⁻¹. This mulch reduces solar radiation and temperature fluctuations while increasing moisture, and as a result, the survival and growth rate of *Sphagnum* and other re-introduced plants is increased (Quinty & Rochefort 1997, Rochefort et al. 1997, Price et al. 1998). A light phosphorus fertilizer is applied to stimulate the growth of the plant fragments and the germination of bryophyte spores (Boatman & Lark 1971, Rochefort et al. 1995). As the regeneration potential of *Sphagnum* is severely impaired by desiccation (Sagot & Rochefort 1996), it is essential to increase the humidity on post-harvested bogs. This is accomplished by blocking the drainage ditches, which raises the water table (Price 1996).

In addition to the basic method, water reservoirs may be created to increase water storage and soil moisture (Beets 1992, LaRose et al. 1997). Reprofilng and microtopography have been considered to enhance humidity and create sheltered microsites. However, although *Sphagnum* establishes better in depressions, when the positive relief is taken into account the overall effect of microtopography is a drier site with equal or less *Sphagnum* establishment than flat areas (Bugnon & Rochefort 1997, Ferland & Rochefort 1997, Price et al. 1998).

Although this North American restoration approach has been successful in many cases (Rochefort et al. in press) there are some patches and sectors of restored sites where mire vegetation did not establish and it appears to be largely caused by substrate instability connected to frost heaving (Quinty & Rochefort 2000, Campbell et al. 2002). Unforeseen in earlier work on peatland restoration, frost heaving problems may be exacerbated by the rewetting of former drained peatlands. As most peatlands are located in the

boreal and temperate zone (Lappalainen 1996) experiencing freezing weather, peat substrate instability caused by frost heaving might be among the main factors impeding total success of restoration projects. As vegetation is known to reduce the incidence and severity of frost heaving, the use of nurse plants in restoration may be part of the solution to the problem. The purpose of this review is to describe the problem of frost heaving on bare peat surfaces and to promote research on the use of nursing plants to alleviate its detrimental effect on plant establishment.

Frost heaving

The problem with frost heaving

As early as 1907, Hesselman observed that drained areas of peat bogs remained virtually devoid of vegetation because of the destructive action of needle ice on tree seedlings (Fig. 1a). Studies by Tallis (1997) and Anderson (1997) on damaged mire surfaces led them to recognize frost heaving as a factor limiting plant recolonization. In addition to damaging plants, recent work in summit peats on the fells in Finnish Lapland revealed that frost action, especially needle ice formation, destroys the structure of the surface peat and activates the process of deflation (Luoto & Seppälä 2000).

In addition to peatlands, frost heaving has been recognized as a factor limiting recolonization of plants on bare soil in: recently burned forests, abandoned agricultural fields, the alplands of British Columbia, tussock tundra of the arctic, steep mountain lands in New Zealand and the grassland steppe of the Pacific northwest (Brink et al. 1967, Dunbar 1974, Rietveld & Heidmann 1976, Regehr & Bazzaz 1979, Gartner et al. 1986, Sheley & Larson 1994).

The effects of frost heaving are twofold. First, a soil that has been affected by frost heaving is more susceptible to erosion (Brink et al. 1967, Luoto & Seppälä 2000). Second, young plants may be killed or damaged. The four types of frost heaving damage inflicted on seedlings are (Graber 1971):

1. Heaving out: The root system is exposed to the air after successive frost heave cycles.

2. Partial heaving: The plant is only partially lifted out of the soil. Severe damage to the root system and subsequent mortality is common.

3. Stem girdles: Mechanical abrasion of the stem and damage to the epidermis and cambium.

4. Seedling decapitation: Severing at the cotyledons or primary root.

Once a seedling has survived a frost heaving period, it stands a much greater chance of surviving to reproductive age. For example, although the cheatgrass (*Bromus tectorum*, a winter annual weed) seedling population was reduced by 40% during a two week frost heaving period, all the seedlings which survived became adults (Sheley & Larson 1994).

The mechanism of frost heaving

The heaving of soils is not due to the expansions of water upon freezing, as was commonly thought until Bouyoucos & McCool (1928) and Taber (1929, 1930) correctly described the phenomenon. Needle ice is formed by the segregation of soil water that freezes into ice lenses or needles near the ground surface during calm and clear evenings where the temperature approaches zero (Outcalt 1971). The water at the surface of the soil begins to freeze. As freezing occurs, the liquid water content of the soil is reduced, lowering the freezing point of the soil solution and causing a negative pressure at the freezing front. Water flows from the surrounding soil down the pressure gradient to the freezing front, forming needle ice.

As morning approaches, the temperature rises and the needle ice melts. During the next night with suitable conditions, the cycle of freezing and thawing is repeated. Eventually, the temperature drops enough that the soil does not thaw during the day. The freezing front descends into the soil, forming "concrete frost" which does not melt until the spring (Graber 1971).

Factors influencing the growth of needle ice

The basic atmospheric condition for needle ice formation is a clear night sky favouring maxi-

mum heat loss from the surface. When air temperature falls below the freezing point of water, crystal growth begins. If the heat flux toward the surface is too great (*e.g.* the temperature drops) or the soil water flux decreases (*e.g.* the soil becomes too dry), the soil water tension at the freezing plane will increase and the freezing plane will descend in the soil (Soon & Greenland 1970, Outcalt 1971). In Eastern Canada, conditions conducive to frost heaving occur in the fall from about October to November, and in the spring from about April to May.

Moisture conditions most likely to produce heaving occur when the soil pores are filled with water (Fahey 1979). As the soil surface begins to freeze, the heat released flows up the temperature gradient, towards the soil surface. As long as the water supply to the freezing zone is adequate, the amount of heat created by freezing equals the amount of heat radiated from the soil surface, and the freezing front remains stationary in the soil. In this case, ice lenses develop in the soil and heaving occurs. If water becomes limiting, the amount of heat radiated from the soil surface is greater than that released by freezing, and the freezing front moves downward into the soil. In this case, water freezes in place and heaving does not occur (Taber 1930, Heidmann 1976).

The moisture content of soil is positively related to frost heaving; wet soils are susceptible, dry soils are not (Haasis 1923, Grant & Saini 1973, Russell et al. 1978). Large differences in heaving have been observed for adjacent conifer seedlings, these differences being entirely attributed to differences in soil moisture (Heidmann & Thorud 1976).

Soil particle size is an important factor to consider when determining if a soil is susceptible to frost heaving. Ice segregation can be expected in non-uniform soils containing $\geq 3\%$ of grains smaller than 0.02mm, and in uniform soils containing $\geq 10\%$ smaller than 0.02mm (Casagrande 1931 in Heidmann 1976). According to Beskow (1947), the maximum particle size that will produce measurable heaving in 24 hours is 0.1mm. According to Taber (1929), segregation will occur readily if the soil particle diameter is less than a micron, and under favourable conditions where particles are 2 to 3 microns. In muck soils, such

as those characteristics of peat bogs, the needle ice development has been described as “striking”, with needles reaching “considerable heights” of over 12 cm (Bouyoucos & McCool 1928, Brink et al. 1967).

Soil permeability is a determining factor in frost heaving susceptibility. Permeability is a function of many factors, including soil texture. Soils with a large pore size, such as sandy soils, are highly permeable. However, the moisture suction will be low; water cannot easily flow to the freezing front, and such soils will have little heaving. In contrast, fine-grained soils such as clays, have small pores and are able to develop a large suction. However, they are not very permeable; water cannot easily flow through the small pores to the freezing front, and heaving is limited. Silty soils, with their intermediate permeability and moisture suction are extremely susceptible to frost heaving (Penner 1959).

The control of frost heaving

The most effective way to control frost heaving is to reduce the water content of the soil. However, this management option is incompatible with the water requirements of *Sphagnum* and other peatland plants (Price et al. 1998).

Chemical additives

Various chemicals, which change the properties of the soil and the soil water, have been added to the soil. For example, the addition of gypsum will lower the freezing point of water. Dispersing agents, waterproofing agents, cementing agents, nucleating agents and salts have all been tested as means to reduce frost heaving. In general, they have been developed for road construction, and in one case tree planting. The use of chemical additives in peatland restoration would add to the cost and efficiency would need to be tested on peat substrates. Chemical additions, against frost heaving, are reviewed by Heidmann (1976), and Heidmann & Thorud (1976).

Surcharge

In the context of frost heaving, overburden stress (or surcharge) is defined as the load that must be lifted by the segregating ice. An increase in the surcharge reduces frost heaving by decreasing the ability of water molecules to replace those, which have been frozen (Taber 1930, Goulet 1995). Therefore, means to increase the overburden pressure, such as placing heavy weights on the soil, may decrease the heaving. Once again, this solution is more likely to be useful to engineers constructing roads than to biologists restoring bogs.

Radiation balance

By reducing the amount of soil heat lost to the atmosphere, the soil water may be prevented from freezing, thus reducing frost heaving. This may be accomplished using mulches, snow pack, shade or plant cover.

Mulches such as straw, forest litter or even wooden laths have been found effective against frost heaving (Bouyoucos & McCool 1928, MacKinney 1929, MacGillivray & Hartley 1973). Mulches reduce the number of freeze thaw cycles at the surface of the soil or avoid heaving altogether by delaying the soil freezing until continuous low temperatures set in (Belotelkin 1941, Kohnke & Werkhoven 1963).

A snow cover of sufficient depth acts like a mulch. Its effect against frost heaving has been recorded in both agricultural areas and regenerating forests (Haasis 1923, Holmes & Robertson 1960).

Shading the ground acts against frost heaving by conserving soil heat at night and by reducing radiation intensity and consequent soil thawing during the day. Soil, which does not thaw during the day, will not heave at night (Graber 1971). Shading also delays the melting of protective snow packs in the spring (Rietveld & Heidmann 1976).

Vegetation modifies the temperature and moisture content of the soil and heat transfer between the soil and the air (Belotelkin 1941, Anderson 1947). The most effective plant cover is dense and uniform (Decker & Ronningen 1957). Plants such as alfalfa, mosses, trees and

grasses have been found to reduce frost heaving in a variety of environments (Jones & Peace 1939, Larson 1960, Krumbach & White 1964).

As vegetation is known to reduce the incidence and severity of frost heaving, the use of nurse plants in restoration may be part of the solution to this problem.

Nurse plants

A nurse plant is a plant facilitating the growth of a plant of another species during at least some of its life cycle. The plant, which is nursed, is called the beneficiary. The nurse plants themselves do not require a nurse plant to establish: they are pioneers (Nuñez et al. 1999). Nurse plant interactions are common in conditions of high physical disturbance, stress or predation whereas under more favorable conditions, competitive interactions dominate (Bertness & Shumway 1993, Hacker & Gaines 1997).

The functions of a nurse plant

Nurse plants help other plants in many ways. Nurse plant effects are mostly abiotic and structural. For example, the shade cast by nurse plants may lower the evaporative demands of the beneficiary, decrease soil surface temperatures and stem temperatures, increase soil moisture, reduce pest damage, promote seed dispersal in safe sites, stabilize soil and reduce frost heaving (Lathief & Ortiz 1984, Gill & Marks 1990, Valiente-Banuet & Ezcurra 1991, Callaway 1992, Fulbright et al. 1995, Susán et al. 1996, Martinez & Moreno-Casasola 1998, Raffaele & Veblen 1998). Other facilitative effects are a direct result of the nurse plant. For example, increasing nutrients via leaf litter or nitrogen fixation (Walker & Chapin 1987, Belsky 1994).

In alpine and arctic environments, where the soil is thin, coarse and unstable with low plant cover, nurse-plant establishment is common. Typically, these nurse plants have a flat cushion growth form which is hypothesized to reduce wind velocity and thus transpiration stress. Lower wind velocities also allow the deposition and accumulation of fine wind-born soil materials (in-

cluding seeds) promoting accelerated soil development, increased moisture storage, and greater nutrient availability (Welden 1985). Deposited seeds are provided with a sheltered environment in which they can germinate and the seedlings are protected against the desiccating effects of wind exposure, large temperature fluctuations and may gain protection from foraging animals (Griggs 1956, Kikvidze 1993, Nuñez et al. 1999).

The effects of a nurse plant may be both positive and negative. For example, in the Sonoran Desert, nurse plants facilitate cactus seedlings establishment by reducing high temperatures near the soil surface and provide a microhabitat with a higher soil nitrogen level. However, shading and competition for water with the nurse plants markedly reduce seedling growth (Franco & Nobel 1989, 1998). A second example may be found in the steppe of western Nevada, where the shrub *Artemisia* nurses the seedlings of *Pinus monophylla* enhancing its survival by favorably altering the microclimate. However, the conifer seedlings under the nurse shrubs were found to be smaller than in the open or where shrubs had been cut, indicating that while the overall effect of *Artemisia* on survival is positive, negative interactions also exist (Callaway et al. 1996). Overall, however, the positive interactions outweigh the negative interactions, and the beneficiary benefits.

The use of nurse plant as a complement to peatland restoration is increasingly receiving attention. Experiments by Boudreau & Rochefort (1998) in Canada, demonstrated that more *Sphagnum* mosses established beneath the cover of two nurse plants, *Eriophorum vaginatum* var *spissum* and *Eriophorum angustifolium*, than on bare peat. In Finland, Tuittila et al. (2000a) showed that many peatland species benefited from the sheltering effect of *Eriophorum vaginatum* tussocks in cutaway peat fields. In Ireland, tussocks of *Juncus effusus* appear to play a similar role as the tussocks of *Eriophorum vaginatum* (Robert Rowlands, pers. comm.). Anderson (1997) reported on the use of grasses as a nurse plant in the damaged moorlands of the Pennine Way, England. A study by Ferland & Rochefort (1997) determined that *Sphagnum* growth on post-harvested peatlands was enhanced by the presence of nurse plants in eastern Canada. Various stud-

ies such as Grosvernier et al. (1995), Buttler et al. (1996) and Robert et al. (1999) have suggested that the wetland moss polytric (*Polytrichum strictum*) may be a useful nurse plant in wetland restoration.

***Polytrichum*: Pioneer moss and nurse plant on bogs**

Pioneer moss

Polytric is a pioneer moss locally abundant on abandoned peatlands. Unlike other mosses, members of the family Polytrichaceae have an internal water conducting system, which allows them to conduct water under conditions of moisture stress (Bayfield 1973). Their leaves are sun leaves, adapted for photosynthesis under higher light intensities and drier conditions than other mosses (Callaghan et al. 1978, Skre et al. 1983, Clayton-Greene et al. 1985, Silvola 1991). In times of water stress, the leaves fold up against the stem, reducing water loss (Mögenson 1985).

One of the most interesting features of polytric, from the viewpoint of peatland restoration, is its tolerance to burial (Faubert & Rochefort 2002) and its binding effect on loose soil. Tolerance is due in part to a high degree of clonal integration. In *P. commune*, nitrogen absorbed by one plant part is evenly shared with the others (Eckstein & Karlsson 1999). Carbon is translocated to underground parts and apical buds via interconnecting rhizomes (Skre et al. 1983, Thomas et al. 1990, 1998). Emerging shoots depend on nutrients translocated from above ground parts to grow and reach the surface (Collins 1976, Callaghan et al. 1978). Even when entire clones are catastrophically buried, such as by sand or volcanic ash, food reserves in the rhizomes provide enough energy for emergence from depths up to 6 cm or more (Birse et al. 1957, Collins 1969). The lower stem of some members of the genus *Polytrichum*, including *P. strictum*, is covered with a dense layer of rhizoids. These rhizoids capture small particles such as ash and sand stabilizing the soil (Leach 1931, Collins 1969). In very windy areas such as the Antarctic, banks of *P. alpinum* resist wind erosion due to cohesion of

shoots bound together by the dense tomentum of rhizoids (Fenton & Lewis Smith 1982).

Polytrichum has a high potential for regeneration both from vegetative fragments and from spores. New plants can form from isolated protoplasts, leaves and fragments (Gay 1976, Wilmot-Dear 1980, Li & Vitt 1994). Each sporophyte capsule contains millions of spores (Campbell, 2002). These spores are ubiquitous in seed banks, remaining viable even when buried (Jonsson 1993, Rydgren & Hestmark 1997). Some authors consider that establishment via spores is impossible or extremely unlikely (Hobbs & Pritchard 1987, Miles & Longton 1990), whereas others consider it to be regularly successful, or at least possible (Callaghan et al. 1978, Johnson 1981, Clement 1985, Derda & Wyatt 1990, Innes 1990, Maltby et al. 1990). Restoration trials in Canada, in which large carpets of polytric form in less than a year strongly suggest successful establishment via spores (personal observation).

Polytrichum as a nurse plant

Due to its high regeneration potential, and tolerance to desiccation and substrate instability, polytric can successfully colonize cutover peatlands. Once it has established, it behaves as a center of establishment and a nucleus for the subsequent growth of patches of persistent species, as described by the succession theory of Yarranton & Morrison (1974). But this facilitation effect may be species dependent for the polytric species and the beneficiaries (Rozé et al. 1991, Corradini & Clément 1999) and the specific relations for peatland species have to be researched.

Species which benefit from the protection of various members of the polytric family include black spruce seedlings, white spruce seedlings, various woody plants and *Sphagnum* (Marsh & Koerner 1972, Buttler et al. 1996, Filion & Morin 1996, Parker et al. 1997). Polytric has been shown to increase drought survival of conifer seedlings by stimulating root growth. It appears to fulfil the same function at our study sites in Canada for fir seedlings (Fig. 1b). Studies of *P. pilferum* demonstrated its ability to stabilize sandy slopes

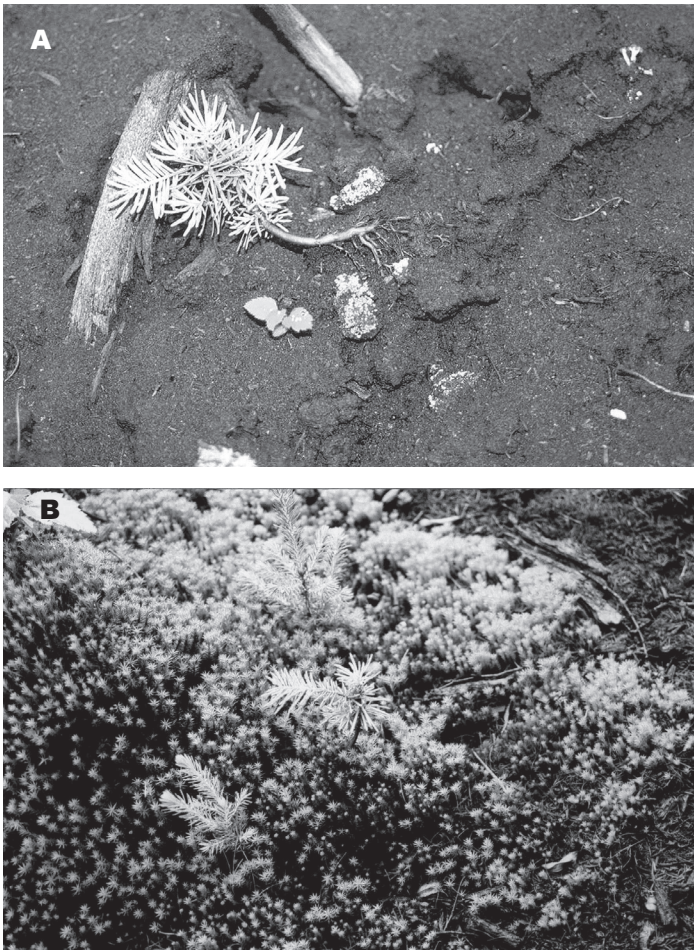


Fig. 1: Conifer seedlings. A) Fir seedlings (*Abies balsamea*) frost heaved on a cutover peatland. The bare peat substrate has been mostly devoid of vegetation for 15 years. B) Thriving conifer seedlings within a mat of polytrich mosses.

and provide a suitable microhabitat for woody plant invasion (Marsh & Koerner 1972). Other hypothesized benefits include facilitating seedling penetration, reducing mortality from frost heaving, preventing the formation of a crust, which could isolate diaspores from soil water and creating a favorable microclimate (Grosvernier et al. 1995, Parker et al. 1997). Its closely packed stems provide shelter and a relatively moist atmosphere (Bayfield 1973).

Studies with other moss species have shown that bryophyte carpets may act as seed traps and reduce the predation of large seeds (Tooren 1988). During hot and dry periods following heavy rains, seed germination is higher in bryophyte carpets perhaps because they act as moisture reservoirs (Johnson & Thomas 1978). Improved moisture

content, reduced temperature fluctuations and soil stabilization in bryophyte carpets permit the colonization of vascular plants in bare pit heaps (Richardson 1958).

In using polytrich as a companion plant, we encourage its spread across the cutaway peatland. However, the goal of restoration is to return the post-harvested site to a functional peatland ecosystem, and by extension, to establish a layer of *Sphagnum*, not polytrich. Therefore, it is important to know that *Sphagnum* will displace polytrich when it no longer requires nursing (Fig. 2).

Reviewing the nurse plant literature we can see that in many cases as the beneficiary plant grows, the interaction may shift from facilitation to competition (Callaway & Walker 1997). In many instances the beneficiary plant eventually

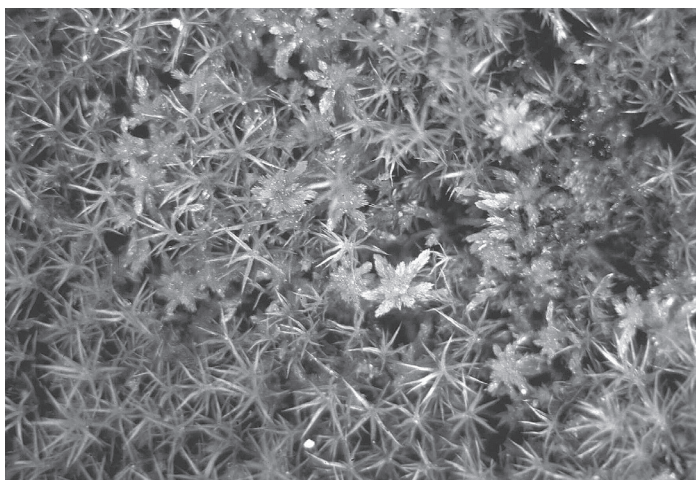


Fig. 2: *Sphagnum* mosses growing among the nursing polytric mat. The photo was taken on a peatland four years after restoration.

outcompetes the nurse plant, causing its demise (Flores-Martinez et al. 1998, 1994, Barnes & Archer 1999). This replacement holds true for *Sphagnum* and polytric. Buttler et al. (1996), for example, noted the natural succession from polytric to *Sphagnum* on a dry bog site in Switzerland. From paleoecological records, we can see that after a disturbance such as peat cutting or fire, there is an initial spread of *Polytrichum*, but after some time has elapsed, the dominance shifts in favor of *Sphagnum* (Jasieniuk & Johnson 1982, Foster 1984, Kuhry 1994, Roderfeld et al. 1996, Robert et al. 1999).

Reasons for this shift are unclear. According to Vitt (1990), polytric is limited by either phosphorus or nitrogen. Harvested peat bogs are slightly nitrogen enriched and polytric is very efficient at retaining nitrogen. Phosphorus, on the other hand, is highly limiting in bogs (Bowden 1991, Wind-Mulder et al. 1996). A study by Chapin et al. (1987) revealed that *Sphagnum subsecundum* can absorb up to 21 times more phosphorus than *Polytrichum commune*. It is possible that over time, *Sphagnum* outcompetes polytric for phosphorus thus gaining dominance. *Sphagnum* is known to modify the environment to its own advantage. As it grows under the shelter of the polytric, it may eventually shift the environment to favor its own growth by raising the water table and lowering the pH (van Breemen 1995). As *Sphagnum* grows and the acrotelm regains function, the wetter conditions may help in

reducing polytric cover, as polytric is generally found in the drier parts of the bog and flooding its leaves reduces photosynthetic capacity (Clayton-Greene et al. 1985, Vitt 1988, Thomas et al. 1996).

Conclusion

As we have gained more experience with the rewetting of cutover peatlands for their eventual restoration back to a peat accumulating system, problems associated with frost heaving have become more apparent because of the higher moisture content of the peat. Nurse plants are an interesting option to solve the problem of frost heaving in peatland restoration. It is clear that *Polytrichum strictum* has the potential to nurse *Sphagnum* (Fig. 2). However, this has not been conclusively demonstrated, nor is the facilitative mechanism known. The authors have discussed more in depth the case of *Polytrichum strictum* because in our geographical context for experimentation, it appears the easiest plant to work with at a large scale. But the concept should be adapted to local possibilities. For example, the relatively new introduced moss in Ireland, *Campylopus introflexus*, could be a potential good nurse plant. Would it nurse other peatland plant during their establishment only during the cracking and disintegrating phase of the moss carpet? More research should also be done with clonal

vascular plants to evaluate if they can function as nursing plants. Some species known to occur naturally on cutaway peatlands include: *Agrostis stolonifera*, *Carex rostrata*, *Eriophorum angustifolium*, *Phragmites australis* and *Triglochin palustris*. These pioneer species are often found by themselves, monospecifically, colonizing and stabilizing bare peat areas. In the end, the success of restoring a cutover or cutaway peatland back to a peat accumulating ecosystem might not be by establishing the key peat-forming species first but by favoring the establishment of nurse plants.

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