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LE *POLYTRICHUM STRICTUM* COMME STABILISATEUR DE SUBSTRAT ET PLANTE COMPAGNE POUR LES SPHAIGNES DANS LA RESTAURATION DES TOURBIÈRES EXPLOITÉES PAR ASPIRATEUR

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RÉSUMÉ

La végétalisation des tourbières exploitées est limitée par un microclimat rigoureux et un substrat instable. Le polytric (*Polytrichum strictum*) est une mousse pionnière qui pourrait à la fois tempérer le microclimat et stabiliser le substrat, permettant ainsi la croissance des sphaignes et autres plantes. Nous avons déterminé que les sphaignes (*Sphagnum* sp.) croissent davantage en proximité du polytric sur deux sites restaurées. Cette association est expliquée par l'amélioration du microclimat par le polytric. En effet, nous avons démontré que dans un tapis de polytric, la luminosité est réduite, les écarts de température sont diminués et l'humidité des sphaignes est accrue en comparaison avec la tourbe à nue. Le polytric stabilise le substrat en réduisant le soulèvement gélival, favorisant la survie de Sapins baumiers (*Abies balsamea*) transplantés selon un dispositif expérimental. L'utilisation des plantes compagnes est recommandée comme méthode complémentaire pour la restauration des tourbières.

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ABSTRACT

The revegetation of post-harvested peatlands is limited by a harsh microclimate and an instable substrate. Polytric (*Polytrichum strictum*) is a pioneer moss which is thought to ameliorate the microclimate and stabilize the substrate, thus permitting the growth of *Sphagnum* and other peatland plants. We determined that *Sphagnum* grows better in proximity to polytric on two restored peatlands. This association is explained by favorable microclimatic conditions within the polytric carpet. We found that within a polytric carpet, irradiance is reduced, temperature fluctuations are diminished, and the water content of *Sphagnum* within the carpet is increased compared to bare peat. Furthermore, polytric stabilizes the substrate by reducing frost heaving, enhancing the survival of experimentally transplanted fir trees (*Abies balsamea*). The use of companion plants such as polytric is recommended as an aid to peatland restoration.

AVANT PROPOS

L'introduction générale du mémoire inclut une revue de littérature qui a été soumise pour publication à la revue scientifique finlandaise Suo, sous le titre de «Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems». Celle-ci fut rédigée entièrement par moi-même. Line Rochefort, ma directrice de thèse et deuxième auteure, l'a éditée pour publication en enlevant notamment les sections qui font référence aux autres chapitres du mémoire.

J'ai rédigé le premier chapitre sous forme d'article. Line Rochefort, deuxième auteure, l'a revu et corrigé pour publication. J'ai moi-même fait l'installation du dispositif sur le terrain et la collecte des données avec l'aide des assistants de terrain. J'ai traité les données, et j'en ai fait l'analyse. J'ai moi-même préparé les figures.

J'ai rédigé le deuxième chapitre sous forme d'article. J'ai rédigé la première partie de l'article portant sur l'association entre le polytric, la linaigrette et les sphaignes. J'ai moi-même fait la collecte des données avec l'aide des assistants de terrain. J'ai traité les données, et j'en ai fait l'analyse. L'expérience portant sur le microclimat généré par le tapis de polytric a été faite dans le cadre du projet fin de bac d'Ariane Massé, deuxième auteure de cet article, sous ma supervision. J'ai révisé et corrigé les données et j'en ai fait l'analyse statistique. J'ai moi-même préparé les figures. Line Rochefort, troisième auteure, a revu et corrigé cet article pour publication.

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Je voudrais aussi remercier tous mes aides, assistants et conseillers de terrain : Julie Bussières, Bruno Drolet, Patrick Faubert, Christine Groeneveld, Isabelle Jarry, Ian Roul, Robert Rowlands et Olivier Soucy. Particulièrement, je remercie Ariane Massé, assistante de terrain suprême : une personne sympathique, intelligente et travaillante qui a fait de l'été 2000 une saison de terrain agréable et plein de bon souvenirs.

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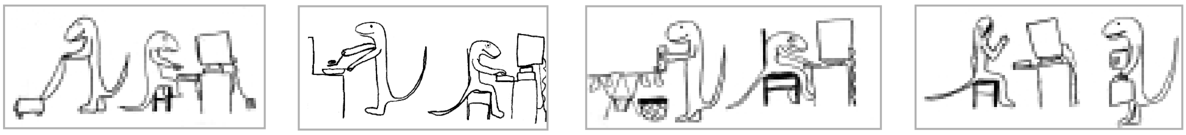

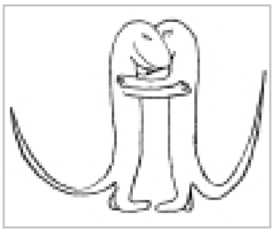

Mais surtout, je désire remercier Jonathan Matthew Olson, mon meilleur ami et mari. Sans son support et sa volonté de faire le ménage, la cuisine, le lavage, et l'épicerie au cours de ces dernières semaines, je n'aurais peut-être jamais terminé.

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INTRODUCTION GÉNÉRALE

NURSING PLANTS IN PEATLAND RESTORATION: ON THEIR POTENTIAL USE TO ALLEVIATE FROST HEAVING PROBLEMS

Introduction to peat bog harvesting and restoration

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* L. 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 canals to dry the site.

When the peat deposit has been exhausted, the site is either abandoned, converted to another used or restored. Even twenty years after abandonment, there is often little natural regeneration of peat mosses for sites (see Fig. 2 in Desrochers *et al.* 1998 for post-vacuum sites). But for sites with less than 30 cm of peat left, a good diversity of vascular plant communities can be found on cutaway peatlands (Rowlands 2000). Reasons for poor peat moss regeneration include: lack of a viable seedbank, inappropriate hydrological regime, harsh microclimate and peat instability (Salonen 1987, Anderson 1997, LaRose 1997, 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 (Rochefort 2000).

The first step in peatland restoration 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. 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 soil moisture on post-harvested bogs. This is accomplished by blocking the drainage canals, which raises the water table (Price 1996).

Water reservoirs may be created to increase water storage and soil moisture (LaRose *et al.* 1997). Reprofiling and microtopography have been considered to enhance soil moisture 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.* submitted) there are sectors and a few peatlands where mire vegetation did not establish and it appears to be largely caused by substrate instability (Quinty & Rochefort 2000, Campbell *et al.* in press). Unforeseen in earlier work on peatland restoration, frost heaving problem is exacerbated by the rewetting of former drained peatlands. Peat substrate instability caused by frost heaving in countries experiencing freezing weather might be among the main factors impeding total success of restoration projects. 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. 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 (Figure 1).
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 typically 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.

Figure 1. Damage to plant seedlings from frost heaving. ***Top:*** *Fir seedling (Abies balsamea* L.*) which died as a result of frost heaving.* **Bottom**: *Eriophorum spissum* var. *vaginatum seedling which died as a result of frost heaving. Note the puckered peat surface in the lower picture, characteristic of frost heaved soils. Both pictures were taken at Premier St-Laurent, Rivière-du-Loup, Québec, on a section of bog which was vacuum harvested then abandoned.*

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 typical atmospheric condition for needle ice formation is a clear night sky favouring maximum 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 down the temperature gradient, towards the soil surface. As long as the water supply to the freezing zone is adequate, and the amount of latent heat released by freezing equals the amount of heat radiated from the soil surface, 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 ≥3% of grains smaller than 0.02mm, and in uniform soils containing ≥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). Figure 2 shows needle ice which formed overnight in the wet, highly organic soil of a vacuum harvested bog in eastern Canada.

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 1958).

The control of frost heaving

Moisture control

The most effective way to control frost heaving is to reduce the water content of the soil. However, reducing moisture is incompatible with the water requirements of *Sphagnum* and other peatland plants. The application of a layer of coarse sand on the soil surface has been used to reduce the frost heaving of newly planted conifer seedlings. Sand is thought to reduce heaving by disrupting the migration of water to the freezing front and the subsequent formation of ice lenses (Rietveld & Heidmann 1976). Ploughing and disking susceptible areas may reduce frost heaving by interrupting the capillary flow of water to the freezing front (Heidmann & Thorud 1976) but these management options are detrimental to *Sphagnum* growth (Price *et al.*1998).

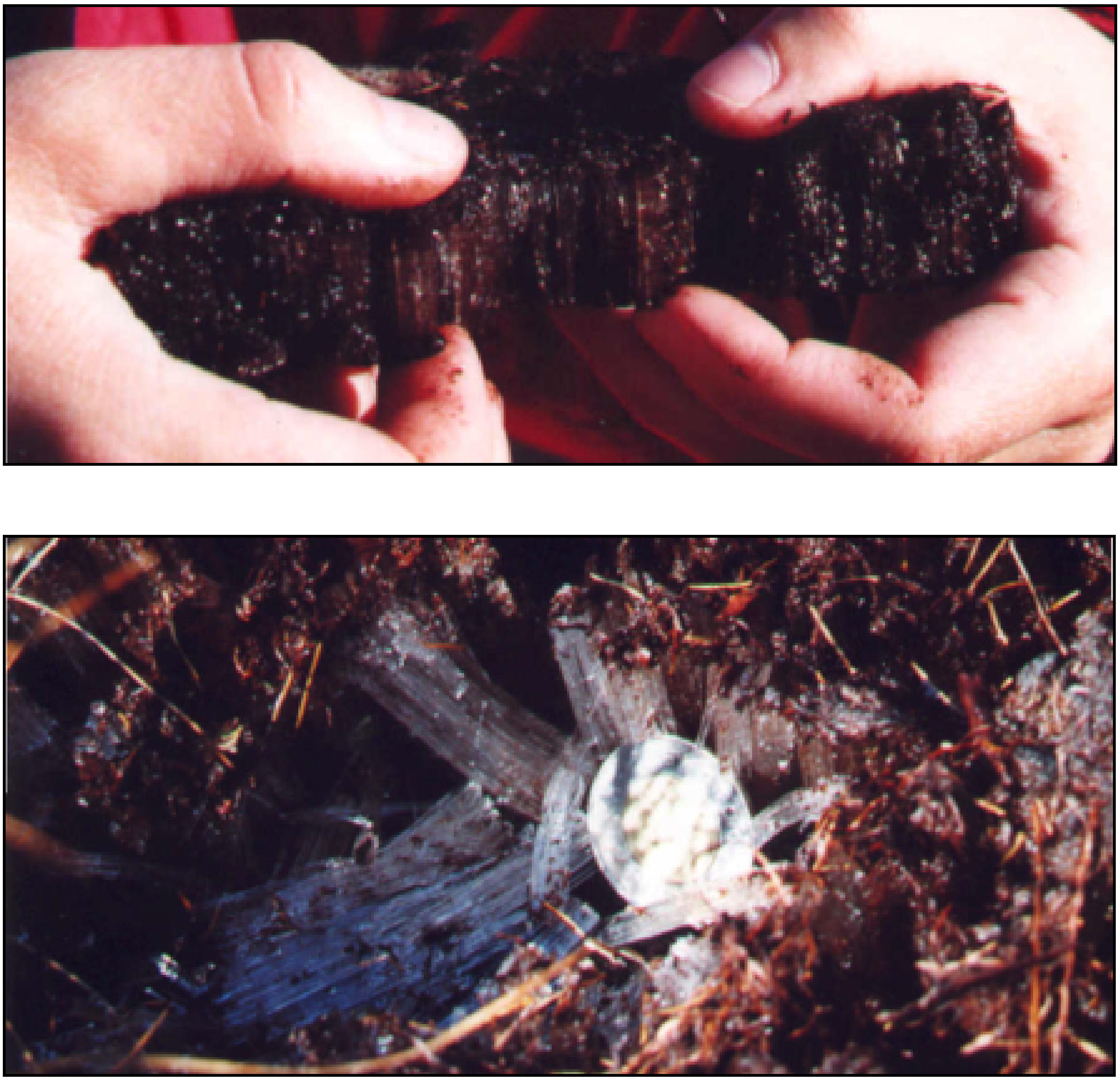

Figure 2. Ice crystals which formed overnight in the wet, peaty soil of a post vacuum harvested peat bog, Rivière-du-Loup, Québec. The coin in the lower picture has a diameter of 27 mm.

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).

In terms of peatland restoration, conventional methods as described previously are often sufficient to reestablish a cover of bog vegetation within a few years. However in some areas restoration efforts fail, and many of these failures appear to be due in part to frost heaving (Figure 3). For example, restoration efforts in the Peak District (United Kingdom) failed due to wind and water erosion, and frost heaving (Anderson 1997). In Miramichi (New-Brunkwick, Canada), a hydro-seeding experiment involving *Eriophorum vaginatum* var. *spissum* failed due to frost heaving (S. Boudreau, personal communication). It is therefore necessary to develop new restoration approaches for sites where frost heaving is problematic. 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

The functions of a nurse plant

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

Figure 3. Restoration effort negatively affected by frost heaving. This picture was taken at the Bois-des-Bel peatland, Cacouna, Québec, one year after the site was restored. The soil surface in the lower two thirds of the picture has been disturbed by frost heaving, severely hampering plant recolonization. The area pictured in the upper third of the picture was barely affected by frost heaving and as a result, plant recolonization is more advanced.

predation whereas under more favorable conditions, competitive interactions dominate (Bertness & Shumway 1993, Hacker & Gaines 1997).

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 (Latheef & 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 (including 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 providing 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 *E. angustifolium* L., than on bare peat. In Finland, Tuittila *et al.* (2000) showed that many peatland species benefited from the sheltering effect of *Eriophorum vaginatum* L. tussocks in cutaway peat fields. In Ireland, tussocks of *Juncus effusus* L. appear to play a similar role as the tussocks of *E. 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 studies such as Grosvernier *et al.* (1995), Buttler *et al.* (1996) and Robert *et al.* (1999) have suggested that the wetland moss polytric (*Polytrichum strictum* Menz. *Ex* Brid.) may be a useful nurse plant in wetland restoration.

Polytric: Pioneer moss and nurse plant on bogs

Pioneer moss

Polytric is a pioneer moss locally abundant on abandoned peatlands (Figure 4). 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) (Figure 5).

One of the most interesting features of polytric, from the viewpoint of peatland restoration, is its tolerance to burial (Faubert & Rochefort, in press) and its binding effect on loose soil. Tolerance is due in part to a high degree of clonal integration. In *P. commune*, nitrogen

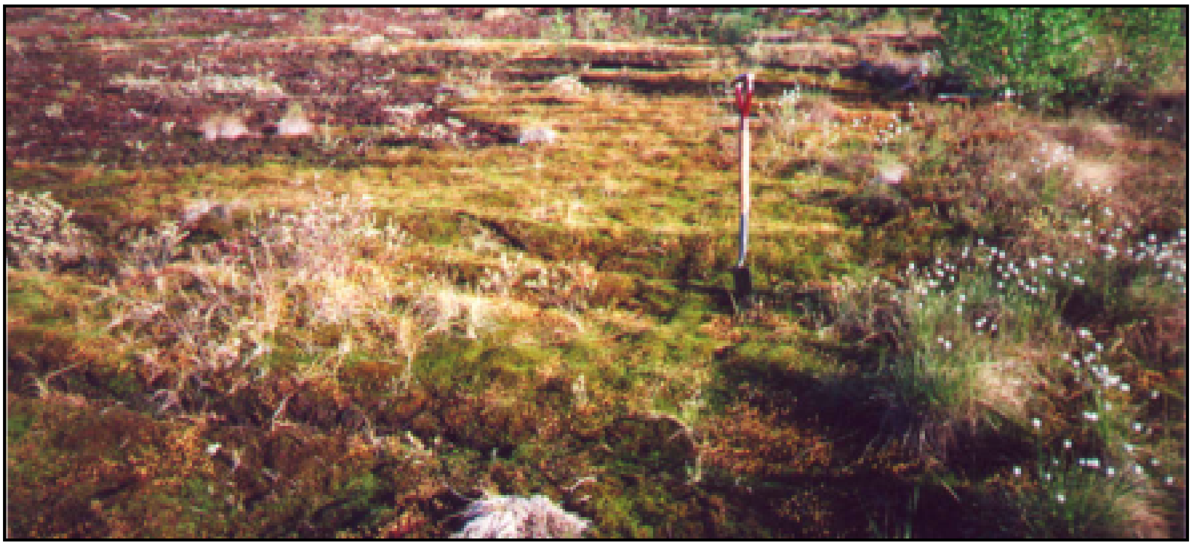

Figure 4. Polytric (Polytrichum strictum). ***Top****: A cut-over peatland colonized by polytric, Ste-Marguerite, Québec.* **Bottom***: A close up view of a polytric carpet.*

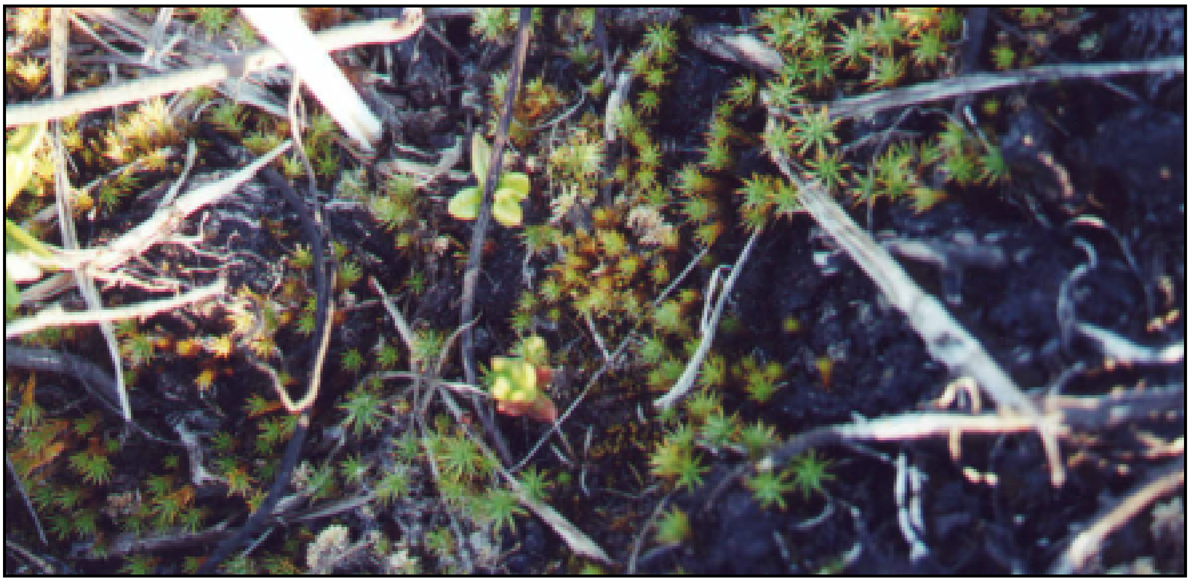

*Figure 5. Polytric, with leaves opened (**top**) and closed (**bottom**) in response to moisture stress, at Sarracénie R97, a post-vacuum harvested site in Rivière-du-Loup, Québec, restored in 1997.*

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 (Figure 6). 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 (D. 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.

Polytrichum as a nurse plant

Due to its high regeneration potential, 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).

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 &

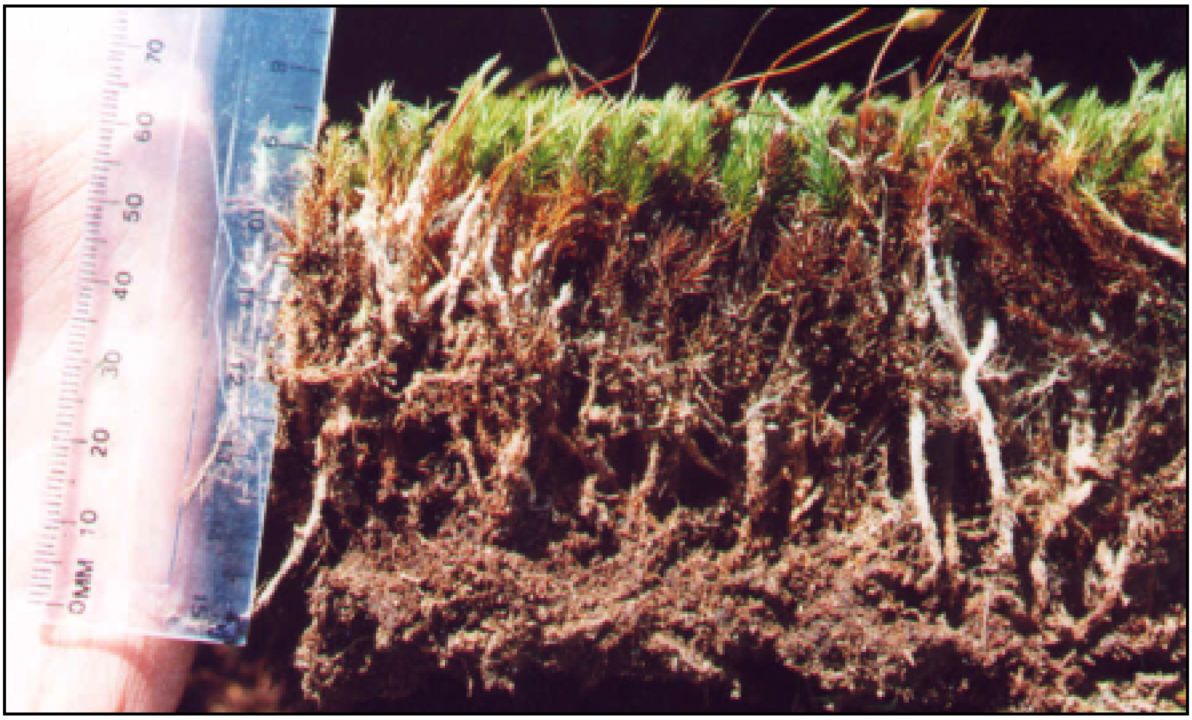

Figure 6. Cross-section of a polytric colony, showing the stems coated with a fuzzy white layer of rhizoids.

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. Studies of *P. pilferum* demonstrated its ability to stabilize sandy slopes 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 polytric 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 polytric. Therefore, it is important to know that *Sphagnum* will displace polytric when it no longer requires nursing.

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 outcompetes the nurse plant, causing its demise (Flores-Martinez *et al.* 1994, 1998, Barnes & Archer 1999). This replacement holds true for *Sphagnum* and polytric. Buttler *et al.* (1996) noted the natural succession from polytric to *Sphagnum* on a dry bog site in Switzerland. From paleoecolgical 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 water 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).

Problems addressed in this thesis

There are many indications that *Polytrichum strictum* has the potential to reduce frost heaving on post-harvested bogs, and to nurse *Sphagnum*. However, neither of these hypotheses have been explicitly tested.

The first objective of this project was to determine if polytric can reduce frost heaving on a post vacuum harvested peat bog (Chapter 1). The effect of a dense polytric carpet on frost heaving was compared to that of other ground cover situations typically found on restored bogs : 1) a layer of moss diaspores spread in a 1 : 10 ratio, 2) a straw mulch applied at 3000 kg ha^{-1} and 3) bare peat. The mechanism by which the three ground covers reduced frost heaving was examined by measurements of temperature, moisture and rates of concrete frost thaw. I also examined the effect of a polytric carpet on the survival of fir seedlings.

The second objective of this project was to determine if polytric is a nurse plant to *Sphagnum* (Chapter 2). Field surveys on restored bogs were used to verify that *Sphagnum* grows better in the presence of polytric. Field experiments were then used to elucidate the nature of the nurse plant effect, in terms of microclimate amelioration. I examined the reduction in irradiance, temperature fluctuations and the changes in water content experienced by *Sphagnum* placed within a polytric carpet, as compared to the other three treatments listed in the preceding paragraph. The ability of a polytric carpet to trap seeds and nurse *Eriophorum* seedlings was also tested. The microclimate experiment data was collected for the third year project of Ariane Masse, as described in the «Avant-propos».

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CHAPITRE 1

POLYTRICHUM STRICTUM AS A SUBSTRATE STABILISER AND COMPANION PLANT TO FIR (*ABIES BALSAMEA*) AND COTTON-GRASS (*ERIOPHORUM VAGINATUM* VAR. *SPISSUM*) ON A POST VACUUM HARVESTED PEATLAND

L'instabilité du substrat est un problème courant sur les tourbières exploitées et abandonnées. Le polytric (*Polytrichum strictum*) est une mousse pionnière bien adaptée pour tolérer les conditions microclimatiques rigoureuses ainsi que l'instabilité des substrats de tourbe résiduelle. Une expérience contrôlée a été menée pour déterminer l'efficacité du polytric en tant que moyen palliatif pour réduire le soulèvement gélival. Des chevilles de bois et des plantules de sapin (*Abies balsamea*) plantées dans un tapis de polytric n'ont subi aucun soulèvement, tandis que le soulèvement sur de la tourbe mise à nue était considérable. Des fragments de polytric appliqués à un ratio de 1 : 10 ont permis une réduction du soulèvement, sans toutefois l'éliminer. Un paillis de paille était efficace contre le soulèvement au cours de l'automne, mais moins efficace durant de dégel printanier en raison de sa décomposition au cours de l'hiver. Le tapis de polytric en combinaison avec le paillis ont réduit le soulèvement en réduisant le nombre de cycles de gel-dégel, en ralentissant le dégel de la tourbe au printemps, et en réduisant le contenu d'eau liquide de la tourbe au printemps. Le polytric peut être qualifié de plante compagne pour le sapin : 16 mois après avoir été planté, les sapins dans les tapis de polytric avaient tendance à être plus en santé (selon un indice) que les sapins sur la tourbe mise à nue. La santé des sapins plantés dans les fragments a été améliorée avec l'ajout d'un paillis de paille, de même que pour les sapins plantés dans la tourbe mise à nue.

1.1 Abstract

Substrate instability is a common problem on post vacuum harvested peatlands. Polytric (*Polytrichum strictum*) is a pioneer moss well adapted to tolerate the harsh microclimatic conditions and peat instability on these sites. A controlled field experiment was used to determine the effectiveness of polytric against frost heaving. Wooden dowels and fir trees placed in a polytric carpet experienced almost no frost heaving, whereas heaving was severe on bare peat. Polytric fragments spread in a 1 : 10 ratio reduced but did not eliminate frost heaving. Straw mulch effectively reduced heaving in the fall, but was less effective in the spring because it had partially decomposed. The polytric carpet in combination with mulch reduced frost heaving by reducing the number of freeze-thaw cycles, by slowing the rate of ground thaw in the spring and reducing the unfrozen water content of the peat during the spring thaw. Polytric can be qualified as a nurse plant to fir trees : after 16 months, fir trees planted in the polytric carpet were healthier (according to an index) than trees planted in the bare peat. This difference was borderline significant. Trees planted in fragments fared better when also covered with straw, as did trees planted in bare peat.

1.2 Introduction

Cutover peatfields where peat is extracted by modern methods of milling peat are not easily recolonized by wetland plants or any plant at all compared to the pre-mechanization methods of block-cutting the peat (Lavoie & Rochefort 1996, Desrochers *et al.* 1998, Antonella *et al.* 1999, Robert, Rochefort & Garneau 1999), especially when residual peat depth is more than 50 cm. Reasons for this include a lack of a viable seedbank, inappropriate hydrological regime, harsh microclimate and peat instability (Salonen 1987, LaRose 1997, Price *et al*. 1998, Rochefort 2000, Campbell *et al.* 2002, in press). In light of the difficult conditions on post-harvested sites, human intervention is necessary to restore a functional peatland ecosystem within a time frame of decades (Rochefort 2000).

The North American approach to restore cutover peatlands is often sufficient to re-establish a cover of bog vegetation within a few years (Rochefort *et al.* submitted). However, some restoration efforts fail, and many of these failures are due in part to the instability of the surface (Quinty & Rochefort 2000). Similarly, a restoration attempt of eroded blanket mire in the United Kingdom failed due to wind erosion, water erosion and frost heaving (Anderson 1997). Quinty & Rochefort (2000) believe that the rewetting step of the restoration process exacerbates problems related to frost heaving. In addition to damaging plants, recent work in summit peats on the fells in Finnish Lapland have shown that frost action, especially needle ice formation, destroys the structure of the surface peat and activates the process of deflation (Luoto & Seppälä 2000). We must therefore develop new restoration techniques for sites where instability, and particularly frost heaving, is a problem.

Frost heaving occurs when soil water freezes into ice crystals or lenses near the surface of the soil. Soil water is attracted to the freezing front, promoting the growth in length of the ice crystals, which may raise a crust of soil by several cm in a single night (detailed in the introduction of this thesis). Reducing the moisture content of the soil is an effective way to control frost heaving. However, this is incompatible with existing restoration techniques and the moisture requirements of *Sphagnum* and other peatland plants. A series of methods to reduce frost heaving is discussed in the general introduction of this thesis. Among them are the uses of chemicals, mulch, snow pack, shade and plant cover. In this study we focus on the use of plant cover as a means to alleviate frost heaving. Plants modify the moisture content and the heat transfer between the soil and the air, as well as the soil temperature (Belotelkin 1941, Anderson 1947). A dense and uniform plant cover is the most effective (Decker & Ronningen 1957). Plants such as alfalfa, mosses, trees and grasses have been shown to reduce frost heaving in a variety of environments (Jones & Peace 1939, Larson 1960, Krumbach & White).

Polytrichum strictum (polytric) is a pioneer moss present in and typical to *S. fuscum* dominated bogs which are considered as a climax of mire development (Reinikainen 1964, Salonen 1992, Buttler *et al.* 1996, Tuittila *et al.* 2000). It also grows spontaneously and abundantly on post harvested peat bogs (L. Rochefort & F. Quinty, Université Laval, personal communication). The dense and uniform cover provided by this plant could potentially reduce frost heaving. An internal water conducting system and specialized leaves allow it to photosynthesize under higher light levels and a lower water content than other mosses (Bayfield 1973, Callaghan *et al.* 1978, Silvola 1991). Polytric is highly resistant to burial; following deep burial by sand or volcanic ash, food reserves in the stems provide enough energy for emergence from depths up to 6 cm or more (Birse *et al.* 1957, Collins 1969). One of the most interesting features of polytric, in the context of peatland restoration, is its stabilizing effect on loose soil. A dense coat of rhizoids, covering the lower part of the stem, captures fine wind-born particles, stabilizing the surface (Leach 1931, Collins 1969). We have observed that polytric can have a stabilizing effect on post-harvested bogs. For example a field experiment, established on a post-harvested bog near Rivière-du-Loup, was blown away by the wind twice during installation, and then again after the experiment was completed. In contrast, a second experiment established at the same time and on the same site persisted because the mixed plant material reintroduced allowed the growth of a dense cover of polytric (L. Rochefort, personal communication). Once polytric has established on a site, it can ameliorate the conditions for later succession plants such as conifers, various woody plants and *Sphagnum* (Marsh & Koerner 1972, Buttler *et al.* 1996, Filion & Morin 1996).

This study had two purposes. First, to determine if polytric moss could stabilize the surface of vacuum harvested peatlands by reducing frost heaving. Second, to determine if polytric was a good nurse plant for other peatland plants.

1.3 Methods

1.3.1 Study area

In the spring 2000, eight vacuum harvested peat bogs in Québec and New Brunswick were visited to find a site affected by frost heaving suitable for experimentation. Premier St-Laurent, a site located near Rivière-du-Loup, Québec (47^{-}48’N, 69^{o}28’W), was chosen for several reasons. First, the physical characteristics and sparse vegetation were typical of vacuum harvested sites in Québec. Hundreds of uprooted seedlings were scattered over the peat indicating that frost heaving was a major factor limiting revegetation; the few plants, which survived frost heaving were often severely damaged. The surface of the peat showed the dimpling pattern characteristic of frost heaving.

The average annual temperature is 3.2^{o}C, with average January and July temperature of -12.2^{o}C and 17.8^{o}C, respectively. Local annual precipitation averages 924 mm, of which 73 % falls as rain (Environment Canada, 1993). The peatland is part of a 3 375 ha bog-poor fen complex, classified as a “domed bog” (National Wetlands Working Group 1997). The study site, a 4.4 ha section of the bog, was vacuum harvested for approximately 10 years and then abandoned in 1980 (J. Gagnon, Premier Tech, personal communication). The residual peat layer is more than two meters thick. With time the drainage ditches have partially filled in, but the blockage is incomplete and the site is very dry. During the months of July and August, the water table averaged 66 cm below the surface.

Although 15 years have elapsed since the site was last harvested, vegetation is sparse. Tussocks of *Eriophorum vaginatum* var. *spissum* Fern. are evenly scattered over the site. Ericaceous shrubs such as *Vaccinium angustifolium* Aiton., *Ledum groenlandicum* Oeder., *Kalmia angustifolia* L., *Rhododendron canadense* L. and *Chamaedaphe calyculata* L. are present in small numbers. Also present are small trees such as *Betula papyrifera* Marsh., *Abies balsamea* L., *Larix laricina* (Duroi) K. Koch. and *Picea mariana* (Mill.) B.S.P., and a few other vascular plants, lichens and mosses. *Polytrichum strictum* is the dominant moss, forming large circular colonies especially around the *Eriophorum* tussocks. *Sphagnum* is rare, being sporadically present in or near ditches. Together these plants cover approximately 10% of the total area.

1.3.2 Treatments and experimental design

Three levels of polytric were tested against frost heaving: carpets, fragments and none. The carpet was chosen to represent naturally occurring colonies of polytric. We wondered if the layer of top spit applied during restoration (Rochefort 2001) was sufficient to protect against frost heave. For this reason, a 1 : 10 ratio of polytric fragments was used as a treatment. As straw is already used in restoration to protect moss diaspores from desiccation, and has been shown to reduce frost heaving in an agricultural setting, we tested our three levels of polytric (carpet, fragments and none) in a factorial arrangement, with and without straw (Table 1).

The experiment was initiated in the month of May 2000 and ended in October 2001. A complete randomized block design with six blocks was used. Within each block, each experimental unit (plot) measured 1.5 x 1.5 m, and was separated by at least 1 m from its nearest neighbour. Metal rods (diameter = 1 cm, length = 2 m) were inserted 1.5 m into the peat to delimit the corner of each plot and provide a reference point for frost heave measurements. All existing vegetation and debris were removed from the plots, and the peat surface was smoothed with a garden rake before applying the treatments. The resulting smooth peat surface had the appearance of a freshly abandoned peat field. A small wooden boardwalk was installed between the plots to minimise trampling (Figure 1).

1.3.3 Application of treatments

Straw was applied by hand, at the rate currently used in peatland restoration, 3000 kg ha^{-1} (Quinty & Rocherfort 1997). In plots where there was both polytric and straw, the straw was spread over the polytric. Fine plastic nets with a porosity of 97.5% were placed over the straw to prevent it from blowing away.

Table 1. Description of the factorial treatments used in the frost heaving experiment at Premier St-Laurent, Rivière-du-Loup, Québec.

	Main effects	
Name of treatment[1]	Polytric	Straw
Carpet	Carpet	Absent
Carpet + straw	Carpet	Present
Fragments	Fragments	Absent
Fragments + straw	Fragments	Present
Bare peat	Absent	Absent
Straw	Absent	Present

[1] Each treatment is referred to by this name in the text.

Figure 1. Experimental set-up at Premier St-Laurent, Rivière-du-Loup, Québec. One block (out of six) is shown. Treatments (clockwise, starting at the front left) : 1) Carpet + straw, 2) Control, 3) Straw, 4) Fragments + straw, 5) Fragments, 6) Control, 7) Bare peat, 8) Carpet.

Because polytric is a nurse plant, there are often other plants growing within the carpet. It was locally difficult to find the 27 m^2 of pure polytric carpet required for this experiment. For this reason, Ste-Marguerite-Marie peatland located in the Lac-St-Jean region of Québec (48°47'N, 72°10'W) was used as a donor site. The polytric carpet was transplanted in squares measuring 25 x 25 cm. The average length of the polytric stems was 2.6 cm. An average of 2.3 cm of peat was left under each square to hold the carpet together. In each plot at the experimental site, the top 2 cm of peat was raked aside to compensate for the thickness of peat adhering to the carpets. Nine squares of polytric were planted per plot in these raked areas so as to recreate the appearance of a natural moss carpet.

Polytric fragments were also obtained from the Ste-Marguerite-Marie peatland. A lush carpet of polytric was selected, and the stems were clipped flush with the peat surface. The average fragment length was 7.9 cm. These fragments were spread over the plots in a 1:10 ratio. This is a ratio commonly used in the North American method of peatland restoration (Quinty & Rochefort 1997, Rochefort 2001)

1.3.4 Estimation of frost heave

Fir seedlings and wooden dowels were used to estimate the frost heaving. In each plot, 8 small fir trees (*Abies balsamea*) were planted in the peat. Fir trees were chosen because seedlings were abundant on the site and easy to transplant. They were also clearly susceptible to frost heaving damage. Trees with only one shoot (no branches) and not more than two brown needles were transplanted. The average shoot length was 4.2 ± 0.6 cm, the average root length 9.9 ± 2.8 cm. To plant the fir trees in bare peat, we dug a little hole, gently placed in a tree and refilled the hole. To plant in the carpet, we dug out a plug of polytric, placed the tree in the resulting hole and pushed the plug back in place. Although we were as gentle as possible, this plug planting method evidently caused trauma to the seedlings. In addition to the fir trees, sixteen wooden dowels, 0.64 cm in diameter and 14.8 cm in length were inserted 10 cm into the peat in each plot. To measure the vertical displacement due to frost heaving, a straight metal bar was clamped to the corner rods 10 cm above the peat surface. The distance between the top of each fir seedling and dowel and the metal bar was measured with a ruler, on 24

August 2000, before any frost heaving occurred. This distance was re-measured on 7 November 2000 during the fall heaving season, and again on 29 May 2001, after all heaving was over the following spring. The method described is similar to that of Decker and Ronningen (1957) and Portz (1967).

One hundred and fifty kg ha^{-1} of phosphorus fertiliser were applied to enhance the establishment of the polytric carpet, fragments and fir seedlings. This is the same amount currently recommended for the restoration of peat bogs (Rochefort 2001). All plots with polytric were watered with 56 L of bog water during the first two weeks after they were planted; the other plots received 24 L over the same time period.

1.3.5 Polytric as a nurse plant to fir seedlings

The fir seedlings were used to evaluate the nurse plant effects of polytric. On the 24th August 2000 and 29 May 2001, two and eleven months after planting, seedling health was evaluated on a scale of 1 to 3, where 1 = healthy, 2 = almost dead, and 3 = dead. A final rating was given on 16 October 2001, 16 months after the seedlings had been planted. On this date a scale of 1 to 5 was used, with 1 = perfectly healthy, all leaves bright green, 2 = almost healthy, only a few chlorotic or dead leaves, 3 = half dead, all leaves chlorotic or many leaves dead, 4 = almost dead, only a few living needles, and 5 = dead. Trees which were missing but had been noted as dead on a prior sampling date were considered dead; all other missing trees were excluded from the analysis.

1.3.6 Environmental variables

Temperature was monitored in four treatments : carpet, fragments, bare peat and straw. Soil temperature was measured using a StowAway® datalogger (Onset Computer Corporation, USA) with an external sensor buried 1.3 cm below the peat surface. Measurements were taken every half-hour from the 19 to 30 October 2000 and every hour from 26 April to 11 May 2001. Air temperature was measured every hour with a foil-covered external sensor placed just above the ground from 26 April to 28 May 2001. Between three and five replicates were used for each treatment.

Unfrozen volumetric soil moisture was measured using time domain reflectometry (s), after sundown on 29 April 2001. TDR works by measuring the transmission time of an electrical pulse along two (or more) waveguides that are inserted into the peat. In each plot, TDR probes with two 30-cm-long parallel waveguides were inserted for their full length angled from the peat surface to the thaw line, to obtain an average unfrozen soil moisture reading for each plot. Soil moisture values were read directly from the display of a Campbell Scientific 21X Micrologger (Campbell Scientific, Inc.). Three readings were taken from different locations in each plot, the average being used for the analysis.

Depth to the thaw line was measured in the evening of 25 April 2001, a few days after the snow cover had melted, and the in the early morning hours of 30 April 2001. A slender rod was pushed vertically into the unfrozen peat until the thaw line was reached and the depth was recorded (Rydén & Kostov 1980). Cracks in the thaw line were avoided. Five depths were taken per plot, the average being used for the analysis.

1.3.7 Statistical analyses

Vertical movement of dowels and fir seedlings, health of fir seedlings, volumetric soil moisture and depth to the thaw line were analysed with an analysis of variance (ANOVA), using the GLM procedure of SAS (SAS Institute Inc. 1988). Where there was no interaction between the main effects, a Tukey multiple comparison test was done on the means of each factor averaged over all the levels of the other factor (Sokal & Rohlf 1981). Where there was an interaction between the main effects, the Tukey multiple comparison test was limited to comparing the means of one factor within each level of the other factor. The Tukey multiple comparison test was chosen because it is relatively severe test which minimizes type I error. The data for the frost heaving of fir seedlings in the spring was log transformed to reduce heterogeneity of variances. All tests were considered significant at $P \leq 0.05$

On 24 August 2000, three plots were randomly chosen, and the position of each dowel and fir was re-measured. The average of the absolute value of the difference between the first and second measure was calculated. This value, 0.36 cm for the dowels, and 0.39 cm for the fir seedlings, is considered the measurement error. Any frost heaving value between ± 0.36 cm for the dowels and ± 0.39 cm for the fir seedlings is therefore considered to be zero.

Tables of the ANOVA results for each analysis are presented in Appendix A.

1.4 Results

1.4.1 Appearance of the treatments 11 months after planting

On 30 May 2001, 11 months after the treatments were applied the straw had partially decomposed over the winter and no longer covered as much of the peat as it did in the fall. In some of the straw-covered plots there were minute polytric plants growing under the straw. Microscope observations revealed masses of polytric protonema, from which new plants were sprouting. In the polytric carpets many new shoots were visible. The carpets covered by straw were greener and appeared to be growing more vigorously than those not covered by straw. Fragments covered with straw produced some new polytric shoots. Masses of rhizoids growing out from new shoots were growing 4 to 5 mm down into the peat; if the plants were pulled up, a clump of peat gripped by the rhizoids came with the plant. Fragments not covered with straw were generally brown and looked dead, although some individuals produced new shoots.

1.4.2 Heaving of dowels and fir in the fall

In the fall, a significant interaction was found between straw and polytric (Figure 2a). This is because the dowels did not heave in any of the plots covered with straw, whereas in the plots without any straw, the dowels heaved when in bare peat or fragments, but not when planted in the carpet.

Frost heaving results in the fall are the same for the fir seedlings, except that on average they heaved less than the dowels (average heaving of dowels = 2.80 cm, average heaving of fir seedlings = 1.96 cm) (Figure 2b).

In some cases, especially on the bare peat, dowels and fir trees heaved completely out of the peat. As further frost action after the dowels and firs were expulsed was not measured, the values recorded are considered to be minimal values.

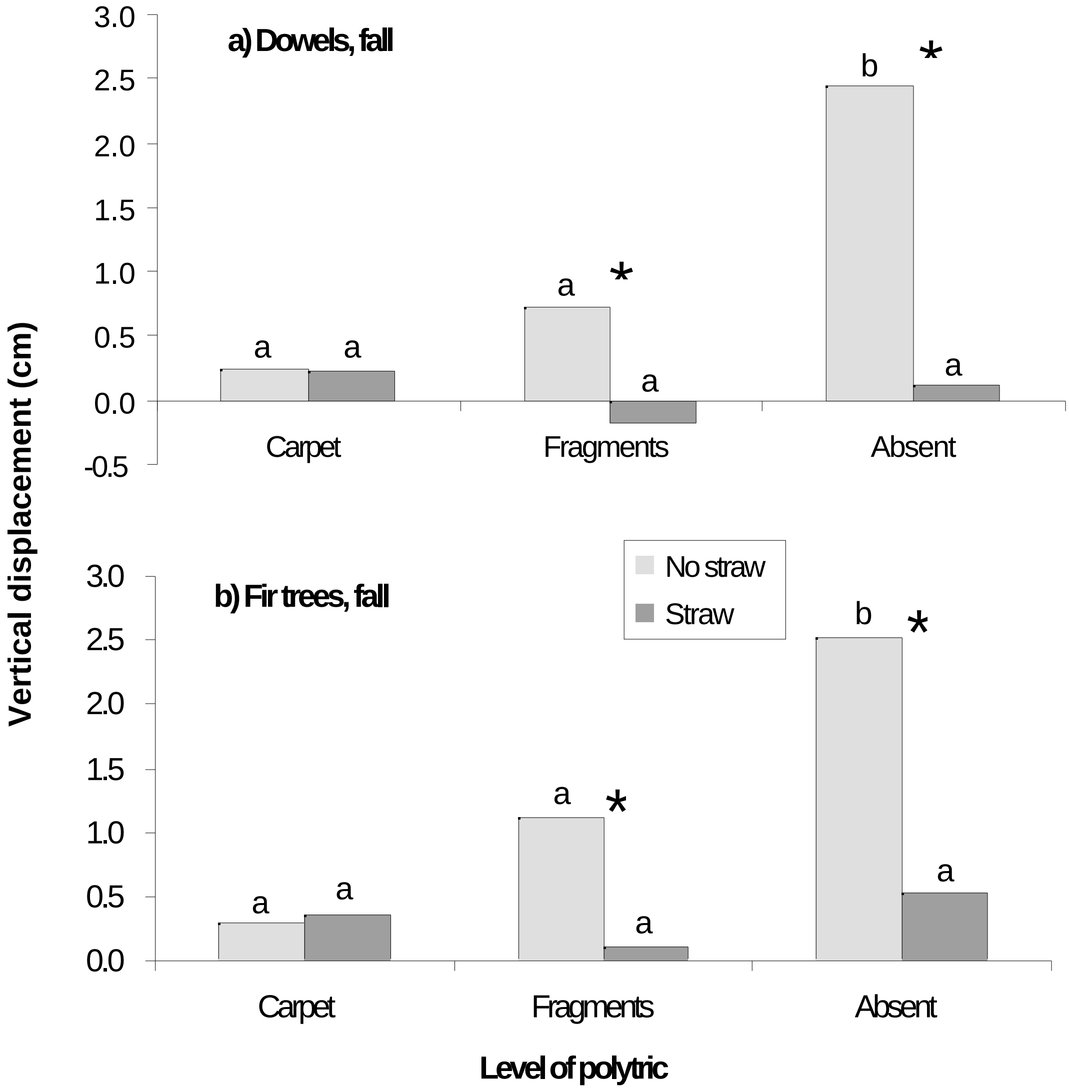

Figure 2. Vertical displacement of dowels and fir trees in fall 2000 (cumulative frost heave from 24 August to 7 November) due to frost heaving on an abandoned vacuum harvested bog, at Premier-St-Laurent, Rivière-du-Loup, Québec. ***a)*** *Dowel heave in the fall. $ANOVA_{Straw*Polytric}$ df=2, F=16.43, p<0.0001.* ***b)*** *Fir tree heave in the fall. $ANOVA_{Straw*Polytric}$ df=2, F=13.85, p<0.0001. Values followed by different letters are significantly different at $p \leq 0.05$ by the Tukey test, within a level of straw. Asterisk (*) indicates a significant difference between levels of straw.*

1.4.3 Heaving of dowels and fir in the spring

By the end of the frost heaving period in the spring, virtually all the dowels, except those planted in the polytric carpet, had heaved (Figure 3a). As in the fall, a significant interaction was found between straw and polytric. This is because the dowels planted in bare peat or fragments and covered with straw heaved the same amount: between 2.5 and 3 cm. However, when they were not covered with straw, the dowels planted in the bare peat heaved a lot more than those planted in the fragments.

By the end of the same period, more than half of the fir trees planted in treatments other than the polytric carpet had heaved so much that their roots were pushed completely or partially out of the peat. None of the fir trees planted in the carpet suffered roots exposure. Fir trees in the polytric carpet did not heave; there was more heaving in the fragments, and the most heaving was observed in absence of polytric where 75% of the seedlings heaved so much that their roots were visible. These three treatments differed significantly from each other. Fir trees planted in straw heaved half the amount of fir trees planted without straw, a significant difference (Figure 3b).

1.4.4 Health of fir trees

Shortly after planting, we noticed that trees growing in the polytric carpet (health index = 1.1, where 1=healthy and 3=dead) were significantly less healthy than trees growing in the bare peat (1.0), regardless of the presence of straw (Figure 4a). This is likely due to the planting method. The health of trees planted in the fragments was intermediate (1.1), and did not differ significantly from either. Straw had no significant effect on fir health (present=1.1, absent=1.1). As the experiment progressed, this negative planting effect appeared to be overridden by other factors, and had disappeared by the next sampling date (29 may 2001).

Eleven months after they were planted, fir seedling health and survival was somewhat affected by the ground cover (Figure 4b). Fir seedlings were significantly healthier and less likely to die when planted in straw (1.3) compared to when there was no straw (1.6).

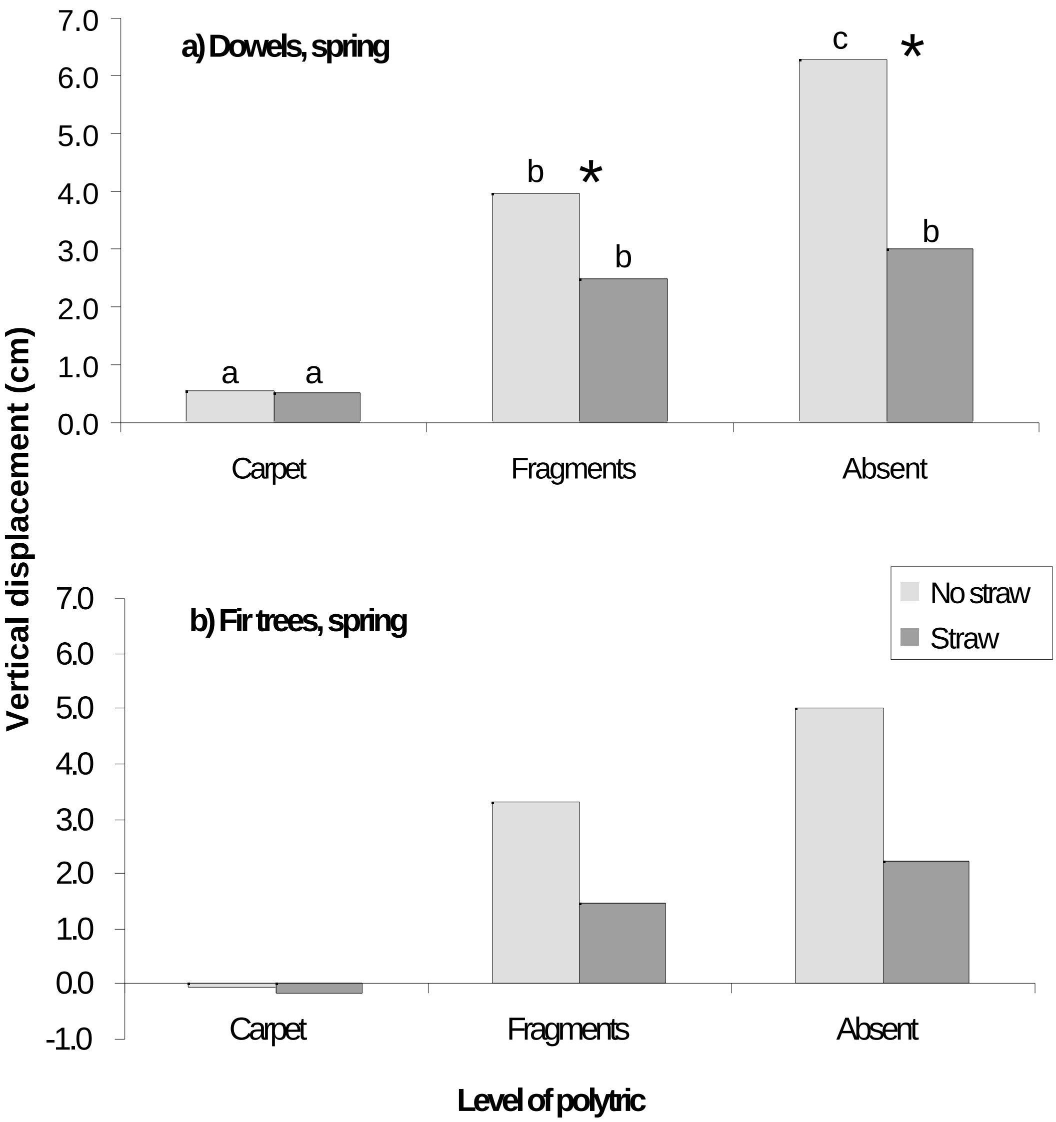

Figure 3. Vertical displacement of dowels and fir trees in the spring 2001 (cumulative frost heave from 24 August 2000 to 29 May 2001) due to frost heaving on an abandoned vacuum harvested bog, Premier-St-Laurent, Rivière-du-Loup, Québec. ***a)*** *Dowel heave in the spring. $ANOVA_{Straw*Polytric}$ df=2, F=18.16, p<0.0001. Statistics presented as in Figure 1.* ***b)*** *Fir tree heave in the spring. $ANOVA_{Straw*Polytric}$, log transformation: df=2, F=2.85, p=0.0769. $ANOVA_{Straw}$ df=1, F=21.48, p<0.0001. $ANOVA_{Polytric}$ df=2, F=128.60, p<0.0001. Tukey, main effects for polytric: Carpet = a, Fragments = b, Absent=c. Straw: Present = a, Absent = b.*

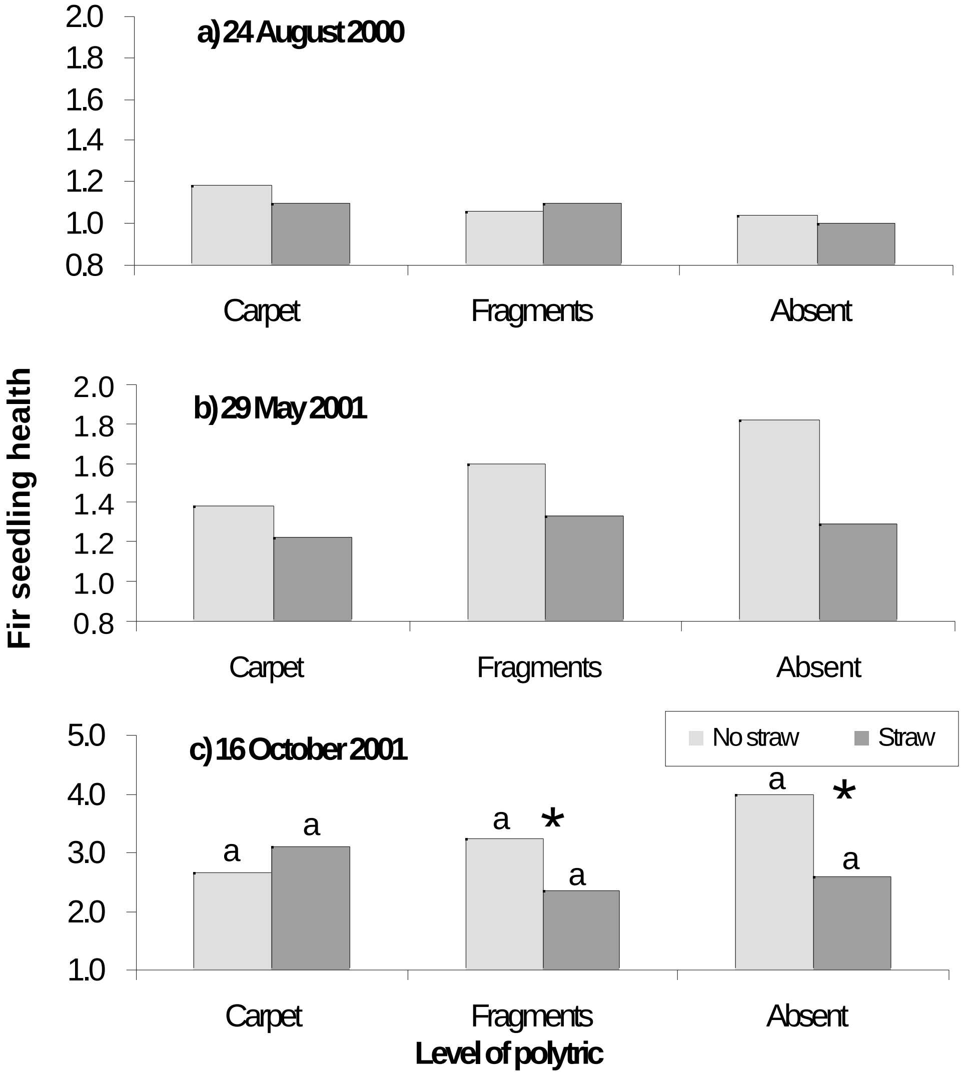

Figure 4. The health of fir seedlings planted at on an abandoned vacuum harvested bog, Premier St-Laurent, Rivière-du-Loup, Québec. ***a)*** *24 August 2000. ANOVA$_{Straw*Polytric}$: df=2, F=0.91, p=0.4149. ANOVA$_{Straw}$ df=1, F=0.73, p=0.4005. ANOVA$_{Polytric}$ df=2, F=3.55 p=0.04149. Tukey, main effects for polytric: Carpet = a, Fragments = ab, Absent = b. Straw: Absent= a, Present= b.* ***b)*** *29 May 2001. ANOVA$_{Straw*Polytric}$: df=2, F=2.15, p=0.138. Tukey, main effects for polytric: Carpet = a, Fragments = a, Absent = a. Straw: Absent= a, Present= b.* ***c)*** *16 October 2001. ANOVA: ANOVA$_{Straw*Polytric}$ df=2, F=4.89, p=0.016. A and B: 1= healthy, 2= almost dead, 3= dead. C: 1= healthy, 2 = almost healthy, 3 = half dead, 4 = almost dead, 5= dead. Statistics presented as in Figure 1.*

Sixteen months after they were planted, fir seedling health and survival was significantly affected by the ground cover; the survival of trees planted in polytric differed depending on the presence of straw (Figure 4c). Straw made no difference to trees planted in the carpet (Carpet=2.7, Carpet + Straw=3.1, where 1=healthy and 5=dead). However, trees planted in fragments fared better when also covered with straw (Fragment=3.3, Fragments + Straw=2.4), as did trees planted in bare peat (Bare peat=4.0, Straw=2.6). In the absence of straw, trees planted in the carpet were healthier than trees planted in the bare peat: this difference was borderline significant (p=0.0543).

1.4.5 Advance of the thaw line

On 17 April 2001 the site was visited for the first time in the new year. All plots were snow-covered, except four where the snow had partially melted. The peat was still completely frozen. By 25 April 2001, all the snow had melted and the concrete frost had begun to thaw.

On 25 April 2001, the average depth to the thaw line was 5.5 cm. That is, there was 5.5 cm of muddy peat overlaying the hard frozen peat. Six days later, on 30 April 2001, the thaw line was on average 7.3 cm below the peat surface. Except for the degree of thawing, results are similar for both dates, so only the second date is further discussed.

There was no significant interaction between polytric and straw, so only the main effects are interpreted. In the plots covered with straw, the peat thawed more slowly than those without straw (Straw=6.2, No straw=7.8 cm of thawed peat. $ANOVA_{Straw}$: df=1, F=12.92, p=0.002). The peat also thawed significantly more slowly in plots covered with polytric carpet (6.6 cm) and polytric fragments (6.4 cm) than plots without any polytric (8.1 cm. $ANOVA_{Polytric}$ df=2, F=5.84 p=0.009).

1.4.6 Unfrozen soil moisture

For this analysis, the two treatments with polytric carpets were eliminated from the data set. The peat beneath the carpet was frozen solid, so it was impossible to properly insert the probe and take a measurement.

There was no significant interaction between polytric and straw, so only the main effects are interpreted. The peat had a higher unfrozen water content when there was no straw (41%) than when there was straw (32%. $ANOVA_{Straw}$: df=1, F=14.91, p=0.002). The water content of the treatments with fragments (32%) tended to be lower than the treatments without polytric (37%) ($ANOVA_{Polytric}$: df=1, F=4.19, p=0.059).

1.4.7 Temperature

In the fall, during the warmer portions of the day (above 7 ºC), soil temperature was generally warmest in the bare peat treatment, followed by fragments, straw and carpet. At night, as the temperature dropped below freezing, the situation was reversed; it was generally warmest under the carpet, followed by straw, fragments and bare peat (Figure 5a).

In the spring, during the warmer portions of the day (above 10 ºC), soil temperature was generally warmest in the peat, followed by the carpet, straw and fragments (Figure 5b). As the temperature dropped to 1 ºC, it was generally warmer under the carpet, followed by the peat, fragments and straw. At the freezing point, there was very little difference between treatments. Below 0ºC, it was warmest under the carpet, followed by fragments, straw and peat.

In the spring, during the warmer portions of the day (above 10 º C), air temperature was generally warmest above the straw, followed fragments, carpet and peat (Figure 5c). As the temperature dropped to freezing, there was little difference between the treatments. Below 0ºC, it was generally warmest above the peat, followed by the fragments, carpet and straw.

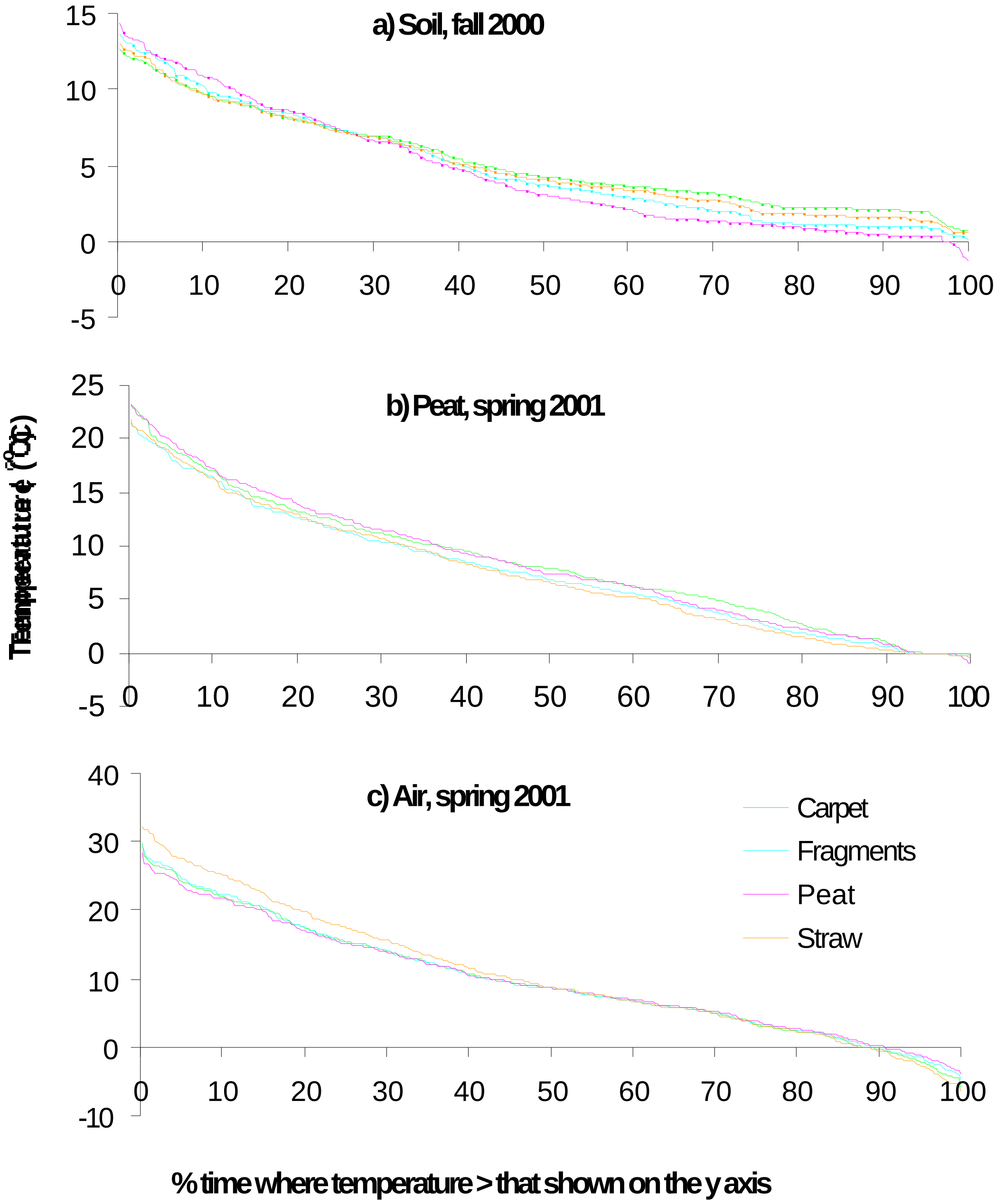

Figure 5. Temperature duration curves for a polytric carpet, fragments, straw and bare peat on an abandoned vacuum harvested bog, Premier St-Laurent, Rivière-du-Loup, Québec. ***a)*** *1.3 cm beneath the peat surface, from 19 to 30 October 2001.* ***b)*** *1.3 cm beneath the peat surface, from 26 April 2001 to 11 May 2001.* ***c)*** *Air temperature just above the ground cover, from 26 April 2001 to 11 May 2001. n = 3 to 5 dataloggers per treatment.*

1.5 Discussion

1.5.1 The control of frost heave on vacuum harvested peatlands

In this study, the carpet of polytric moss was the most effective means of reducing frost heaving. Jones and Peace (1939) found covering bare soil with a layer of moss reduced frost heaving by 95%, compared to bare soil. We found comparable reduction of 92% for the dowels compared to bare peat. Gartner *et al*. (1986) working in the tussock tundra of the arctic found that moss and hepatic mats stabilized soil prone to frost heaving. Once the soil was stabilized, other plants such as *Eriophorum vaginatum* var. *spissum* were able to establish. Marcoux (2000) showed that mature tussocks of *E vaginatum* thesmselves were able to reduce the frost heaving of metal nails by 88% in a post-harvested peatland.

In the study by Jones and Peace (1939), they found it necessary to pin the moss to avoid wind transport, as it was apparently not rooted. The species is not mentioned. Wind transport was not a problem for us as we used polytric moss, which firmly attached to the peat by its rhizoids. New shoots of polytric seemed to have the greatest amount of rhizoids. These rhizoids were tightly bound to the underlying peat. Polytric is well know for its ability to stabilize susceptible soils, although this is the first time, to our knowledge that this has been reported in post-harvested peat bogs. Previous studies have reported on the binding effect of *Polytrichum* on volcanic ash, sand soil and small rocks, in very windy areas of the Antarctic, and in forests following fire (Leach 1931, Collins 1969, Fenton *et al.* 1982, Maltby *et al.* 1990).

Frost heaving was not the only symptom of unstable peat on the study site. Small gullies criss-crossed the bare surface, created by overland flow of water. Although not addressed in this study, there is no doubt that a dense cover of polytric would also reduce wind and water erosion, as vegetation is widely used to prevent wind and water erosion on bare soils (Siddoway & Barnett 1976).

In this study, straw effectively reduced frost heaving. Whereas there was no frost heaving in any of the treatments with straw in the fall, in the spring there was 2.5 to 3.0 cm of dowel heave in the straw and fragments + straw treatments. The straw partially decomposed over the winter and lost some of its protective effect. The polytric, on the other hand, grew, maintaining its protective effect. Field surveys done on a nearby site revealed that three years after restoration, only 9% of the site was still covered by straw, and five years after restoration no straw remained on the site at all (Chapter 2). Straw decomposes very quickly, and unless a plant cover can establish within the first few years following restoration, frost heaving may be a problem after the straw is gone. After one winter outside, Jones and Peace (1939) found that an highly organic mulch, hop manure, decomposed over the winter and thus offered less protection against frost heaving. Woods *et al.* (1978, 1979), working on abandoned coal strip mines, states that the mulch “must remain intact enough for tree seedlings to become well established”. To accomplish this objective, he recommends a heavy straw mulch held together with a “sticker” such as an asphalt emulsion.

The degree of reduction in frost heaving corresponded to the thickness of the ground cover: polytric carpet was the thickest, therefore provided the greatest reduction in frost heaving. Straw, at 3000 kg ha^{-1} was the next best, followed by the fragments spread in a ratio of 1:10. Still, all three ground covers, the carpet, the fragments and the straw reduced frost heaving to varying degrees. At night, these mulches reduced heat loss to the atmosphere, reducing the potential for ice crystal formation. During the daytime, the effect was reversed: temperatures were cooler under the mulches and warmer on the bare peat. This lowered daytime temperature means that ground frozen during the night was less likely to thaw during the day. Soil, which remains frozen during the day, does not heave at night, because there is no liquid water available for needle ice formation (Graber 1971).

Kohnke and Werkhoven (1963) found that straw mulch, applied at 3362 kg ha^{-1} reduced the number of frost heave cycles in a silt loam soil from 22 to less than 7. Other mulches such as forest litter, bark, wood chips, sawdust, cedar shavings, and wood ashes have been found effective against frost heaving (MacKinney 1929, Smagula & Goltz 1988). These 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).

It was clear from field observations that straw was important to the health of the polytric carpet and fragments. On hot summer days, polytric not covered by straw was brown and kept its leaves closed (Figure 6a). Those plants covered by straw, however, were more likely to be green and have their leaves open (Figure 6b), underscoring the importance of the humidifying effect of a straw mulch (Price et al. 1998).

One of the main controls on frost heaving is soil moisture. A wet soil has the potential to heave, a dry soil does not (Higashi 1958, Grant & Saini 1973, Matsuoka 1996). In this study, soils covered with fragments and/or straw had lower moisture content than the bare peat in the spring, most likely alleviating the frost heaving phenomenon.

Once the snow cover had melted, the peat quickly began to thaw, descending on average 0.36 cm per day in the bare peat. When the water in peat melts, the thawing process is promoted because wet peat conducts heat better than frozen peat (Nakano & Brown 1972). Rydén & Kostov (1980) found that wet peat in depressions thawed more quickly than elevated well-drained peat, and attributed this difference to the increased thermal conductivity of wet peat. As the thaw deepens, the volume of water available for needle ice formation increases. Areas with a deeper thaw line, such as the bare peat plots, are therefore more susceptible to heaving. Graber (1971) noted that as the soil on an old field began to thaw from the surface downwards, the concrete frost acted as a drainage barrier, holding the melt water at or near the surface. The result was severe frost heaving and extensive plant damage, as was observed in plots with bare peat in this experiment.

Soils that thaw later are less prone to frost heaving because in the spring the night temperatures quickly rise and stay above freezing. As long as the peat had some sort of covering, be it moss or straw, the thawing process was slowed. The relatively quick thaw on the bare soil at a time where night temperatures dipped below freezing made them susceptible to frost heaving. In this study, the last spring night where soil temperature dipped below

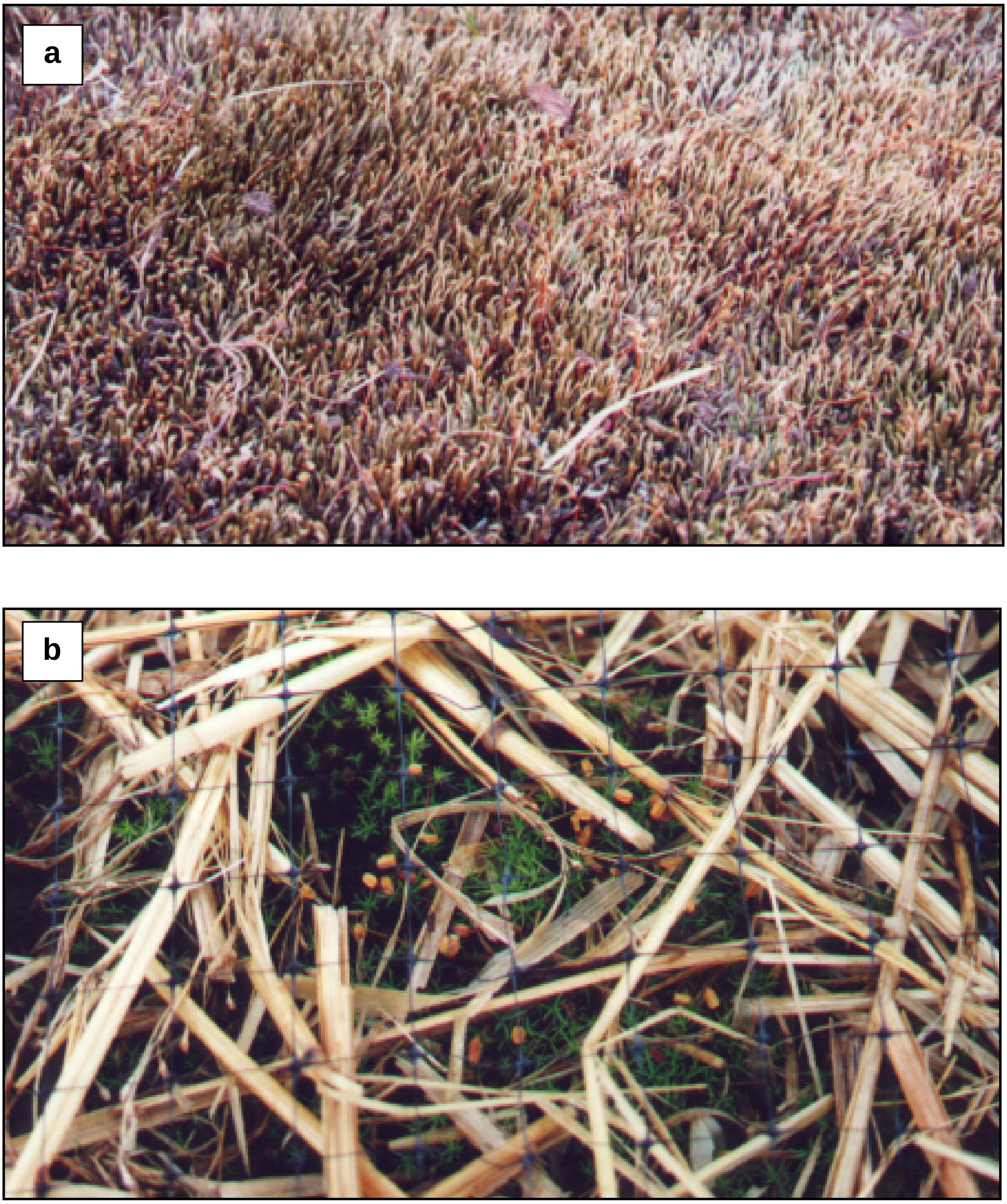

Figure 6. The effect of a straw mulch on Polytrichum strictum. ***a)*** *This carpet was not covered by a straw mulch. During hot and dry periods the leaves closed.* ***b)*** *This carpet was covered by a straw mulch. As a result, the leaves were more likely to remain open.*

freezing was 30 April 2001. So plots that thawed after this time (*e.g.* those covered with straw and/or moss) were not at risk for frost heaving.

As the thaw line reaches a certain depth, cracks in the concrete frost are formed, and the melt water drains away. One of the problems in peatland restoration is maintaining adequate moisture conditions (LaRose *et al.* 1997). In the early spring, moisture is not a problem as the peat is saturated with melt water. However, it quickly dries and moisture becomes limiting. On bare peat, the thaw is quick and early, and the peat rapidly dries. On a peat covered with mulch or plants, the thaw is slower and later, and moisture conditions remain saturated longer.

1.5.2 Polytric as a nurse plant on vacuum harvested peatlands

In this next section we discuss the merits of polytric as a nurse plant in peatland restoration, in terms of reduction in frost heave, amelioration of temperatures extremes or moisture conditions, and reduction of light.

Trees planted in experimental plots of bare peat suffered severe frost heave and high mortality. Frost heaving has long been recognized as a hazard to young tree seedlings (Haasis 1923, Buell *et al.* 1971, Gill & Marks 1991). Schramm (1958) described in detail how 100% of young persimmon, pine and oak seedlings were destroyed by frost heaving on black wastes from anthracite mining operations. Woods *et al*. (1978, 1979) reports that on bare strip-mined soil, up to 69% of conifer transplants heaved during the first year following transplant. Trees growing spontaneously in the soft peat at the experimental site were clearly suffering from frost heaving; the large majority were heaved out and lying on the peat surface, dying or dead. Those that had survived a few years were almost always partially uprooted and stunted (Figure 7a). The exceptions, vigorous and healthy looking trees were invariably growing on stabilized peat, either in an *Eriophorum* tussock or a polytric carpet (Figure 7b).

There is no doubt that the reduction in frost heaving of the peat substrate was a major factor influencing the health and survival of fir trees in this study. Trees which have suffered frost

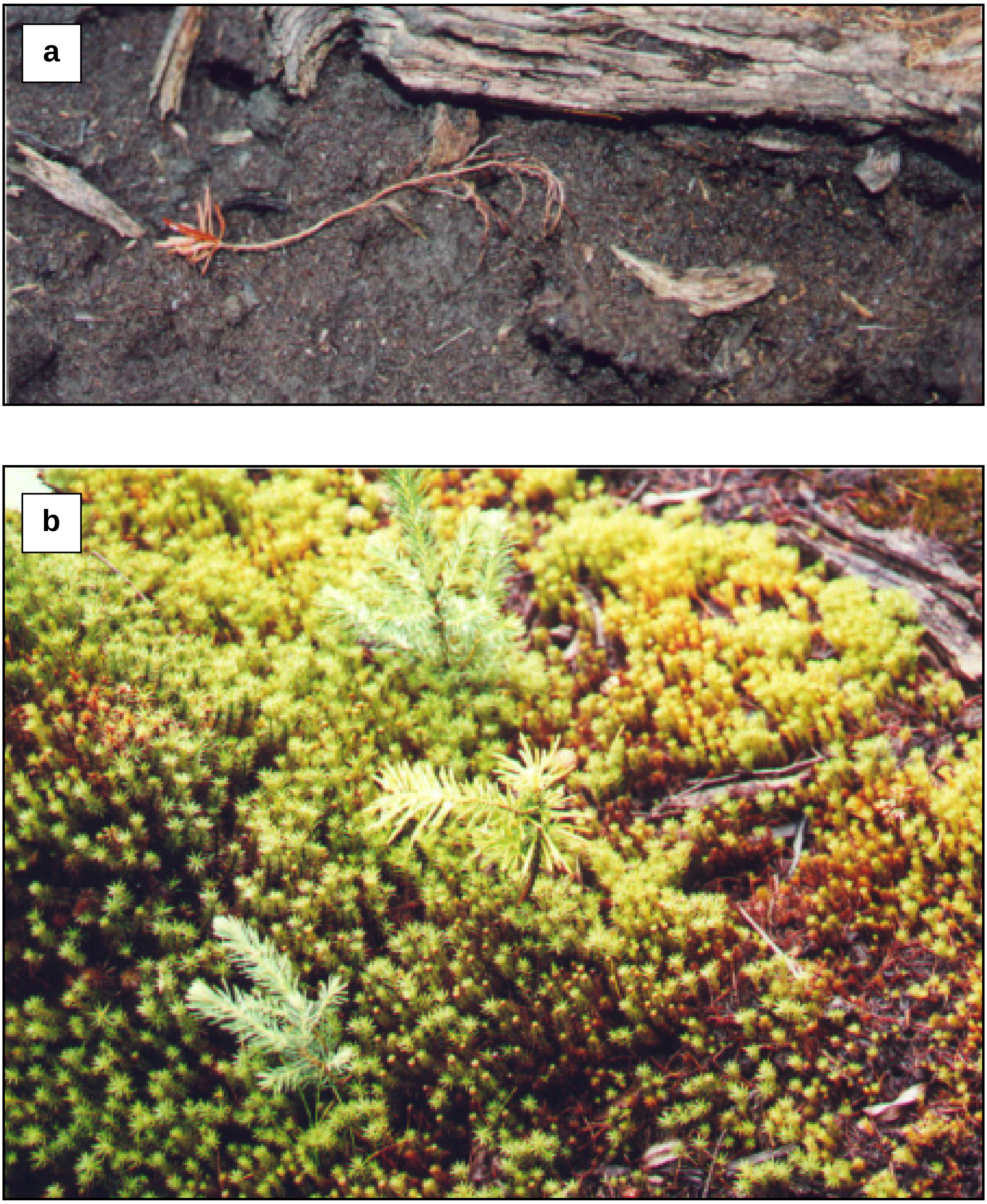

Figure 7. The effect of companion plants on the growth of conifer seedlings on a post vacuum harvested peatland, Premier St-Laurent, Rivière-du-Loup, Québec. ***a)*** *This small conifer was uprooted by frost heaving.* ***b)*** *These conifers grew spontaneously in a naturally occuring polytric carpet and have not been affected by frost heaving.*

heaving damage to their roots are more susceptible to drought damage in the summer (Larson 1 960). Trees growing in the polytric carpet, fragments and straw mulch had a double benefit; they suffered less frost heaving damage over the winter, and were offered a moist microclimate in the summer (Chapter 2).

Dowels and fir trees had similar heaving patterns; this had also been found in other studies (Decker & Ronningen 1957, Portz 1967). The dowels were more readily obtainable, easier to install and monitor for frost heaving than fir trees. The dowels were therefore a good biological model for frost heaving and the study of nursing plant effects.

Surface temperatures from 46 to 54^{o}C can cause heavy fir seedling mortality (Frank 1990). Measures taken during the summer months showed that a maximum of 47^{o}C was reached at the end of July in individual plots for all treatments. However, on average it was cooler under the fragments and straw compared to the bare peat, by as much as 11^{o}C. When temperatures were below 43^{o}C, or when there was sufficient precipitation, polytric offered the same cooling benefits and reduced evaporative demands as the straw and fragments (Chapter 2). Similarly, Gill and Mark (1991), found that an herb canopy eliminated death of tree seedlings by heat stress and desiccation.

Although they will grow in many soils, fir trees prefer a moist soil (Marie-Victorin 1995). On the experimental site, the peat was saturated during the spring and fall, but very dry during the summer, with the water table more than 65 cm below the peat surface during the months of July and August. Any additional source of moisture would therefore be important to the seedlings. Within a polytric carpet, and under straw and fragments, moisture is increased compared to bare peat (Chapter 2). It is therefore no surprise that seedlings growing in the carpet were healthier than seedlings growing on the bare peat. Both Parker *et al.* (1997) and Filion and Morin (1996) attribute improved water relations to enhanced growth of conifer seedlings.

Polytric seemed to be growing faster than the fir trees in some of the carpet plots. However, the resultant light reduction caused by the growing moss is not likely to be a problem, as young balsam firs are very shade-tolerant (Farrar 1995). In fact, it is recommended to give young trees partial shade during their first growing season as they are injured by excessive heat and sunlight (Hartmann *et al* 1990). Photosynthetically active radiation (PAR) measured at the level of the rhizoids in the polytric carpet was found to be 6% (Chapter 2). This is a lot lower than the 50% required for optimum seedling growth (Frank 1990). However, only the trunk of the fir trees was in the rhizoid zone; the needles were at the top or above the carpet surface, where PAR would be closer to the optimum. In some cases, it was clear that the polytric was overgrowing the fir tree; these seedlings did appear etiolated and were therefore rated "2 = almost healthy, or 3 = half dead" during the field survey (Figure 8a). However, when compared to trees in the other treatments, survival and health was still better in the polytric carpet or under straw and fragments than on bare peat (Figure 8b). Other studies have shown that shaded pine seedlings survived much better than lightly shaded seedlings; competition from shading agents (grass and trees) was of secondary importance (Larson 1960).

Nutrient competition could potentially reduce the growth of plants taking shelter in the polytric carpet. Phosphorus is the element most likely to be limiting as it is scarce in post-harvested bogs (Wind-Mulder *et al.* 1996). However, a study by Chapin *et al.* (1987), revealed that the fine roots of spruce situated beneath the moss layer had a higher capacity to absorb phosphate than did *P. commune.* He further showed that *Sphagnum* moss, which may be nursed by polytric, had a much higher rate of phosphate absorption than polytric. Nurse plants can actually increase the amount of nutrients available to the beneficiary (Walker & Chapin 1987, Belsky 1994). For example, a study by Gartner *et al*. (1986) showed that *Eriophorum* seedling growing in the protection of moss mats had higher nitrogen and phosphorus concentrations than seedlings growing in frost boils. As a light phosphorus fertilizer was applied at the beginning of our experiment, nutrient competition is unlikely.

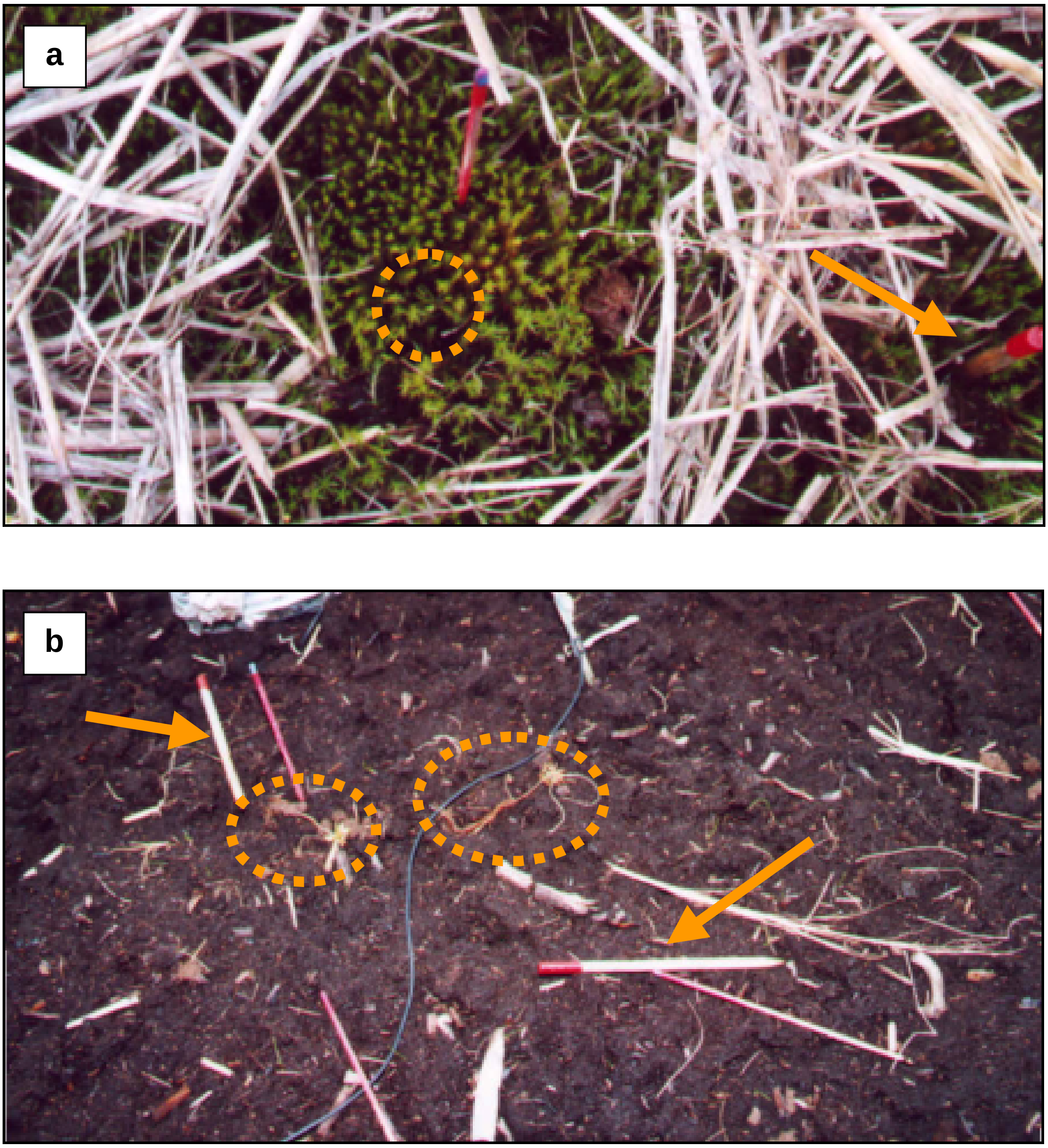

Figure 8. Fir trees planted in an experimental plots at Premier St-Laurent, Rivière-du-Loup, Québec. ***a)*** *This fir tree (circled in orange) was planted in a polytric carpet, and is being overgrown, but is still green and alive. Note the wooden dowel (indicated with an arrow) which has not heaved at all.* ***b)*** *These fir trees (circled in orange) were planted in bare peat and been completely expulsed from the ground following frost heaving. Note the two wooden dowels (indicated with arrows) which have also completely heaved out of the ground, and the foil covered datalogger sensor (top, center).*

1.6 Recommendations for restoration and conclusions

Restoration techniques must be cost effective and simple in application. The establishment of large carpets of polytric must therefore be easily achievable. There has been considerable study on the reproduction of polytric, and opinions are divided when it comes to the success of sexual versus asexual reproduction. Authors such as Miles and Longton (1990) and Hobbs and Pritchard (1987) consider successful establishment from spores impossible or extremely unlikely, whereas other such as Callaghan *et al.* (1978), Johnson (1981), Clement (1985), Innes (1990), and Maltby *et al.* (1990) consider it to be regularly successful, or at least possible though perhaps not common. The masses of protonema and their accompanying young plants observed growing under layers of straw where no polytric had been planted strongly suggests successful reproduction by spores. Some of the plants in the polytric carpet produced spores in their first year, which could easily have been wind-dispersed to adjacent plots. Experiments within our lab revealed that polytric spores germinate massively once a threshold concentration of phosphorus is reached (Isabelle Jarry, unpublished data). As harvested peat bogs are particularly poor in phosphorus (Wind-Mulder *et al.* 1996) the successful sexual reproduction of polytric is likely attributable to the phosphorus fertilization applied at planting, in addition to the protective layer of straw. Therefore, we feel that under restoration conditions, polytric could easily establishs by spores. The use of polytric as a means to reduce frost heaving on post-harvested bog is thus feasible, as little work is required to rapidly produce a carpet.

On sites where peat instability does not appear to be a problem, straw is undoubtedly the best mulch, as it confers the same protection as polytric, at least immediately after application. It has the advantage of providing protection during the hottest times (unlike polytric which closes its leaves), and never competing with beneficiary plants for water or nutrients. In fact, as it decomposes, we suspect that it releases nutrients. As decomposition is rapid, a second application would be necessary if regenerating plants show signs of stress. This is particularly true at sites where optimal rewetting has not be achieved.

However, on those sites where instability is a problem, straw alone is not the best option. It can easily blow away in windswept peat field, and its effect is short term. In these cases, polytric becomes an interesting addition to restoration techniques. Inclusion of some small amount of polytric in the top spit coupled with a light phosphorus fertilizer will assure its rapid spread over the entire site. Straw mulch is still considered necessary, as it takes at least two growing seasons for polytric to reach an appreciable size. It was quite obvious in this study that polytric itself benefited from the straw mulch. If restoration is done in the fall on a site susceptible to frost heaving, we recommend a higher rate of straw application to compensate for decomposition over the winter.

The fragment treatment was designed to mimic the application of top spit to a restoration site. It is clear that a 1:10 ratio will reduce but not prevent frost heaving. This suggests that the top spit all by itself, is insufficient to prevent frost heaving. Fragment cover was uneven; those fir trees in thick patches of fragments heaved less than those in bare spots. This observation underscores the importance of a thick, evenly spread cover. Decker and Ronningen (1957) working in alfalfa fields found that a dense and uniform plant cover offered the best insurance against frost heaving; similarly Brink *et al*. (1964) recommend planting dense seedling stands to reduce frost heaving damage. The thickness of the mulch must be balanced with the needs of regenerating *Sphagnum*; too thick a mulch intercepts too much light, too thin will not offer enough protection (Campeau, Rochefort & Price, submitted).

The extent of competition between polytric and its benefactor plants, especially *Sphagnum*, remains unclear at this time. An interesting question is "Under what conditions does polytric enhance the establishment of *Sphagnum*, and under what conditions does competition negate the positive facilitation?". Further research is needed.

In abandoned post-harvested bogs, where no restoration is done, invading plants cannot choose between straw mulch and a nurse plant. Protection from a nurse plant is their only option, and even if competition exists, the fact remains that without these pioneer nurse plants, the return of a bog to a carbon sequestering ecosystem might simply not occur.

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CHAPITRE 2

POLYTRICHUM STRICTUM AS A COMPANION PLANT TO *SPHAGNUM* ON POST VACUUM HARVESTED PEATLANDS

Les plantes compagnes sont de plus en plus reconnues comme technique complémentaire aux méthodes conventionnelles dans la restauration des écosystèmes dégradés. Le polytric (*Polytrichum strictum*) est une mousse pionnière fréquemment trouvée dans les tourbières exploitées et abandonnées. Le premier objectif de cette étude consiste à détecter l'existence d'une association entre le polytric et les sphaignes (*Sphagnum* sp.) pour deux sites restaurés. Le deuxième objectif vise à expliquer les raisons d'une telle association. Nous avons établi que les sphaignes sont plus abondantes à proximité du polytric sur deux sites restaurés. De plus, à proximité de linaigrettes denses (*Eriophorum vaginatum* var. *spissum*), les sphaignes étaient à la fois plus abondantes et plus longues qu'en absence de plantes compagnes. Le premier tiers extérieur et le troisième tiers central d'un touradon de linaigrette étaient moins propices à la croissance des sphaignes que le deuxième tiers. Des expériences de terrain ont montré des différences microclimatiques entre divers traitements de recouvrement du sol : 1) la présence d'un tapis de polytric ; 2) sous un couvert de fragments de polytric ; 3) sous un couvert de paille, et 4) sur la tourbe mise à nue. En comparaison avec la tourbe mise à nue, les radiations photosynthétiquement actives étaient réduites sous les trois couverts. Les tapis de polytric ont augmenté l'humidité des sphaignes comparés à la tourbe mise à nue, mais cet effet était dépendant des conditions météorologiques. Durant les périodes chaudes et sèches, les sphaignes étaient asséchées de façon uniforme dans tous les traitements. Durant les périodes fraîches et humides, les sphaignes sous les trois couverts avaient une teneur en eau supérieure aux sphaignes sur la tourbe à nue. Les trois couverts ont réduit les écarts de température journaliers avec des températures plus fraîches le jour et plus chaudes la nuit. Cependant, en périodes de chaleur intense, la température était plus élevée dans le tapis de polytric que sur la tourbe à nue. En chambre de croissance, les tapis, les fragments et le paillis de paille ont permis de ralentir la perte en eau chez les sphaignes. Cette réduction était variable entre les répétitions, la durée et les traitements. Dans tous les cas, la perte d'eau était rapide, et après 48 heures, les sphaignes étaient desséchées de façon uniforme dans tous les traitements. Dans certaines situations, un tapis de polytric peut mieux capter des graines de la linaigrette dense que la tourbe à nue. Par contre, moins de plantules de linaigrette ont été observées dans les tapis de polytric que sur la tourbe à nue. L'utilisation des plantes compagnes est recommandée comme méthode complémentaire à la restauration des tourbières.

2.1 Abstract

Nurse plants are increasingly being considered to enhance the restoration of degraded ecosystems. Polytric (*Polytrichum strictum*) is a pioneer plant frequently found on post vacuum harvested peat bogs, and thought to be a nurse plant to *Sphagnum*. The first objective was to determine if a positive association exists between polytric and *Sphagnum*. The second objective was to explain why this association exists. We established that *Sphagnum* had greater cover when growing in proximity to polytric on restored vacuum harvested bogs. *Sphagnum* also had greater cover and was longer when growing in proximity to cotton-grass. The peripheral edge (1/3) and central core (3/3) were less hospitable for *Sphagnum* growth than the intermediate section (2/3) of the circular *Eriophorum* tussocks. Field experiments were performed to detect microclimatic differences between polytric carpets, polytric fragments, straw mulches and bare peat. Compared to bare peat, photosynthetically active irradiation was reduced under the three covers. Polytric carpets were able to keep *Sphagnum* more humid than bare peat, but this effect was weather dependant. During hot dry periods, *Sphagnum* in all treatments was equally dry. During cool wet periods, *Sphagnum* beneath the three covers was more humid than on bare peat. In general, daytime temperatures beneath the three covers were reduced during the day and increased during the night compared to bare peat. However, in the hottest periods it was hotter in the polytric carpet than on the bare peat. The rate of water loss of *Sphagnum* under the three covers and on bare peat was determined in a growth chamber experiment. The rate of water loss varied between trials, over time and between treatments. In all cases, water loss was extremely rapid, and after 48 hours, *Sphagnum* in all treatments was equally dry. Under certain conditions, polytric carpets acted as a “seed trap”, retaining more *Eriophorum* seeds than bare peat. However, fewer *Eriophorum* seedlings were found growing in the carpet than on the bare peat. The use of polytric as a nurse plant in peatland restoration is recommended as a complement to other restoration techniques.

2.2 Introduction

Vacuum harvested peatlands are hostile, barren areas, for the most part devoid of *Sphagnum*, the keystone plant in peatland restoration (Lavoie & Rochefort 1996, Rochefort 2000). Plant colonization is severely curtailed for a myriad of reasons, including the destruction of the seed bank of peatland species (Salonen 1987), and limitation of critical nutrients such as phosphorus (Wind-Mulder *et al.* 1996). In the summer, invading plants must content with poor hydrological conditions (Price & Whitehead 2001), and a harsh microclimate with potentially lethal temperatures (Sagot et Rochefort 1996, Price *et al.* 1998, Boudreau & Rochefort 1999). Although moisture conditions are improved in the spring and fall, the increased moisture and below freezing temperatures lead to frost heaving, which can be devastating for newly established plants (Chapter 1, Rietvald & Heidmann 1976, Gartner *et al* 1986). In addition to frost heave, invading plants suffer from peat instability due to overland flow and windblow (Anderson 1997, Campbell *et al.* 2002, in press).

In spite of these difficult conditions, some tough pioneer plants are commonly found on post-milled sites (Tuitilla *et al.* 2000). Polytric (*Polytrichum* sp.) is a pioneer moss well adapted for growth on post harvested bogs. Specialized leaves and an internal water conduction system allow polytric to photosynthesize at higher light levels and lower water content than other mosses. (Bayfield 1973, Callaghan *et al.* 1978, Silvola 1991). Resistance to burial and frost heave, as well as the ability to stabilize loose soil allows polytric to colonize unstable substrates (Chapter 1, Leach 1931, Birse *et al.* 1957, Collins 1969, Fenton *et al*. 1982).

Once they have established, polytric appears to act as a nurse plant, facilitating the growth of other species including *Sphagnum* (Buttler *et al.* 1996, Robert & Rochefort 1999). Parker *et al.* (1997) demonstrated that *P. commune* increases drought survival of white spruce. In Chapter 1 I demonstrated that polytric dramatically reduced the frost heaving of fir trees and enhanced their survival. Other suggested benefits include facilitation of seed germination, amelioration of the microclimate, and the prevention of crust formation, which could isolate diaspores from the soil water (Marsh & Koerner 1972, Parker *et al*. 1997, Grosvernier *et al*. 1995). However, the microclimate within a polytric carpet has not hitherto been characterized.

Our first objective was to determine if *Sphagnum* does indeed occur and grow better in the presence of two common pioneer species, polytric (*Polytrichum strictum*) and *Eriophorum* (*Eriophorum spissum* var. *vaginatum* Fern.) on recently restored vacuum harvested peat bogs. The second objective was to determine how polytric nurses *Sphagnum*. A field experiment was designed to characterize the microclimate of a polytric carpet, in terms of irradiance, moisture, and temperature, and was compared to the microclimate generated by straw mulch, regenerating polytric fragments and bare peat. The role of polytric as a seed trap and seedbed for *Eriophorum* was also quantified. Following the field experiment, a growth chamber experiment was performed to refine our understanding of the rate of water loss of *Sphagnum* using the same four treatments.

2.3 Materials and methods

2.3.1 Field surveys

The purpose of this field survey was to determine if *Sphagnum* moss occurs and grows better within a polytric or *Eriophorum* community in a restored post-harvested bog. The two sites chosen for field surveys were the first vacuum harvested sites to be restored in Québec by the industry, that is, not for any experimental purpose. These sites were chosen because the growing conditions are extremely harsh and nurse plant associations are thus expected to be more important (Bertness & Shumway 1993, Hacker & Gaines 1997).

a) Site description

Both sites are part of the Chemin du Lac peatland near Rivière-du-Loup, Québec, Canada 47^{o}48’N., 69^{o}30’W) (Figure 1). The average annual temperature at the nearby St-Arsène weather station (47^{o}57’N., 69^{o}23’W) is 3.2^{o}C, with average January and July temperatures of -12.2 and 17.8 ^{o}C, respectively. Local annual precipitation averages 924 mm, of which 73% falls as rain (Environment Canada, 1993).

The study sites are part of a larger 3375 ha bog complex, classified as a “domed bog” (National Wetlands Working Group 1997). As of 1995 approximately 62 % of the surface had been extracted (Desaulniers 2000). Two post-harvested sections of the bog, Droséra R95 and Sarracénie R97, were restored by Premier Tech, the peat extraction company. As these were the first large scale restoration efforts undertaken by a peat company in Canada, the restoration methods and revegetation success are described in detail for both sites. Due to machinery and time constraints, the best or recommended restoration procedure could not always be followed. New restoration techniques have been developed since these sites were restored and are described in Rochefort (2001).

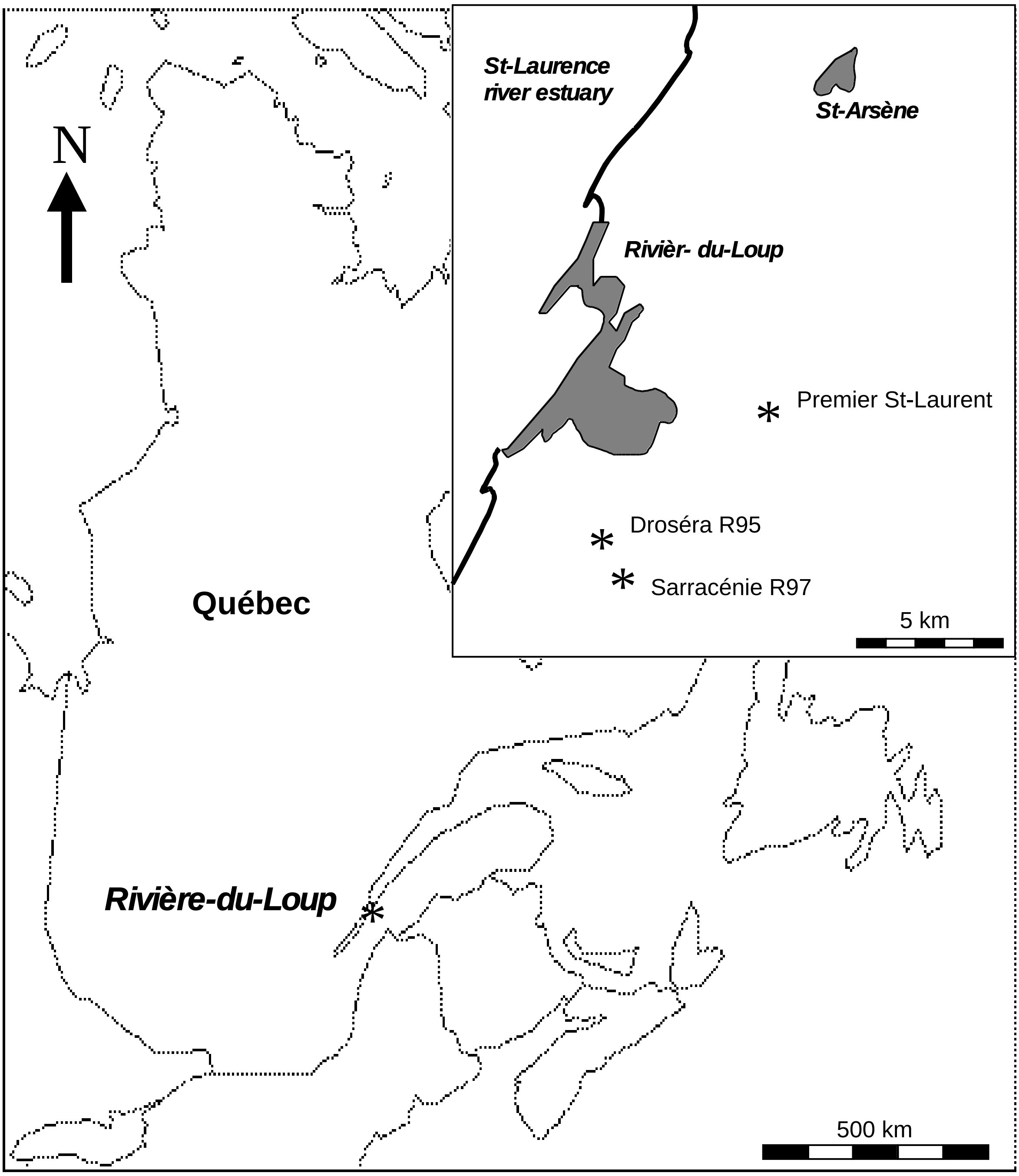

Figure 1. Location of the study area within the province of Québec (Canada). Inset : Location of the peatland study sites: Premier St-Laurent and Chemin-du-Lac (Droséra R95 and Sarracénie R97), in Rivière-du-Loup, Québec. Also indicated is the St-Arsène weather station. Grey color = urban area.

b) <u>Droséra R95</u>

Restoration protocol

This 3.4 ha section of the bog was vacuum harvested for 24 years and then abandoned in 1992. Following abandonment, average residual peat depth ranged from 48 to 80 cm, with a mean of 63 cm. The peat was highly decomposed, being rated H6 –H7 on the von Post scale. In 2000, bulk density was 0.17 g cm^{-3}, and pH was 4.6 (S. Boudreau, unpublished data).

Drainage ditches were blocked at intervals in September 1995. The remaining operations were done in October 1995, except as indicated. Using a screw profiler, each field was reprofiled by pushing the domed center outwards towards the sides. This created a central depression along the length of each field.

The donor site was a small unharvested section of bog at Premier St-Laurent that Premier Tech wished to open for extraction. Because of nearby peat extraction activities, the initial *Sphagnum* cover on the donor site was low, ranging from 50 to 80%. Unfortunately, the top 30 cm of the acrotelm was harvested rather than the recommended 10 cm (Campeau & Rochefort 1996, Quinty & Rochefort 1997), and the resulting top spit was of poor quality.

The top spit was spread with a manure spreader in a ratio of 1 to 10. Because the beginning of the fields near the access roads were drier, less top spit was spread over these areas, whereas more top spit was spread towards the lower ends of the fields. After the first layer of top spit had been spread, the tractor made a second pass to add an additional layer. The heavy machinery left ruts in the fields, and *Sphagnum* matted in the ruts. Protective straw mulch was applied at the rate of 1 to 1 _ tons per ha. The first four fields were covered in October 1995, but the last two fields were not covered until June 1996. In the fall of 1999, 10 to 15 g m^{-2} rock phosphate fertilizer was applied by hand to the areas where no plants were growing.

Revegetation following restoration

In 1999 –2000, the water table varied from 65 to 70 cm below the surface, with an average of –70 cm in July and August 2000 (S. Glatzel, unpublished data). Soon after restoration, the site was massively invaded by *Eriophorum*, which now covers just over 32% of the fields. Ericaceous shrubs cover 14% of the site, while graminoids (excluding *Eriophorum*), trees and other vascular plants cover 9%, 3%, and 2% respectively. Polytric and *Sphagnum* cover 15% and 16% of the fields, respectively. Other mosses cover 3%. The total vegetation cover (both vascular and non-vascular) is 56%. Four years after restoration, no straw remains. Bare peat covers 39% of the fields (E. Groeneveld, unpublished data).

c) Sarracénie R97

Restoration protocol

This 4.7 ha section of the bog was vacuum harvested for 28 years and then abandoned in 1996. Following harvesting, average residual peat depth ranged from 28 to 82 cm, with a mean of 50 cm. In 2000, the peat was less decomposed than Droséra R95, being rated H4 –H5 on the von Post scale. Bulk density was 0.15 g cm^{-3} and pH was 3.74 (S. Boudreau, unpublished data).

In September and October 1996, the ditches were completely filled in. In October 1996, each field was reprofiled by creating multiple depressions along the length of each field, rather than one as in Droséra R95.

The topspit was collected, spread and mulched in June 1997. The donor material was collected from an industrial park to be developed in Rivière-du-Loup and of high quality. The top spit was spread with a manure spreader. Initially, near the drier and more elevated access road, a ratio of 1 to 7 was used. Towards the lower end of the field, the top spit was spread in a thicker layer, ranging from 1:3 to 1:5 because it was drier. A protective straw mulch was applied the same month. In the fall of 1999 rock phosphate fertilizer was applied as in Droséra R95.

Revegetation following restoration

In 1999 –2000, the water table varied from 15 to > 75 cm below the surface, with an average of –58 cm in July and August 2000 (S. Glatzel, unpublished data). Although this section was restored two years later than Droséra R95, plant regrowth 38 months after restoration has been more successful. As in Droséra R95, the site was rapidly invaded by *Eriophorum*, which now covers just over 36% of the fields. Ericaceous shrubs cover 15% of the site, while graminoids (excluding *Eriophorum*), trees and other vascular plants cover 17%, 1%, and 1 % respectively. Polytric and *Sphagnum* cover 27% and 15% of the fields respectively. The cover of other mosses amounts to 3%. The total vegetation cover (both vascular and non-vascular) is 67%. Three years after restoration only 9% of the straw remains. Bare peat covers 27% of the fields (E. Groeneveld, unpublished data).

d) Vegetation surveys

The purpose of this experiment was to determine the effect of polytric and *Eriophorum* on the frequency, length and width of *Sphagnum.*

Point transects were run every 4 meters across the width and every 8 meters along the length of each field for both sites. At each point, a thin stick was touched to the ground and we noted if it touched *Sphagnum*, polytric and/or *Eriophorum*. A small circular quadrat (diameter 2.2 cm) was then centered on the ground around the point, and presence of these three species in the quadrat noted. The length of *Sphagnum* or polytric was measured if either were present at the point or in the quadrat. For approximately half the points in Sarracénie R97, the width of the capitula was also measured for *Sphagnum*. When the point or quadrat fell in an *Eriophorum* tussock, the location of the point relative to the tussock was noted (Figure 2) *i.e.* the outer, middle, or inner third. Also, ground cover at the point was recorded as straw, *Eriophorum* litter, *Eriophorum* seed fluff (for Sarracénie R97 only), other plant litter, wood or bare peat.

Drainage canals were not surveyed in Droséra R95 as they were only blocked at intervals. Drainage canals on Sarracénie R97 had been completely filled with peat during restoration and were surveyed. The first 15 to 20 meters of the fields bordering the roads were not surveyed because little if any top spit had been applied and nothing was growing. In total, 843 points were surveyed on Droséra R95 and 1028 on Sarracénie R97.

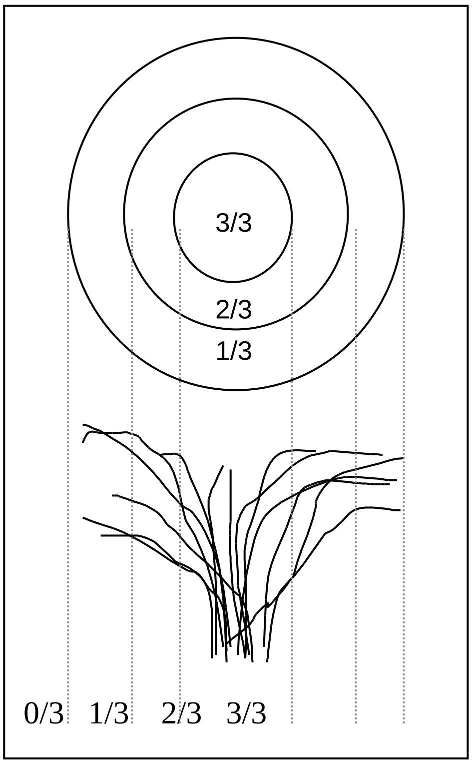

Figure 2. Division of Eriophorum spissum *var.* vaginatum *tussocks into thirds.* ***Top*** *: Looking down on a circular tussock. The outermost ring is the 1/3, the middle ring is the 2/3 and the central ring is the 3/3. All areas beyond the leaves are 0/3 (outside of the tussock).* ***Bottom*** *: Side view of same tussock, showing the same divisions.*

e) Statistical analyses

Spatial autocorrelation

In many nurse plant studies, a non-random positive association between a nurse plant and its beneficiary coupled with differences in microhabitat beneath the nurse plant are interpreted as proof of nurse plant effects (*e.g.* Franco & Nobel 1988, Elba De Pietri 1992, Franco-Pizaña *et al.* 1995, Tewksbury *et al.* 1999). However, this does not take into account the possibility that both species may require similar growing conditions and therefore may occur together due to a pre-existing microhabitat. For this reason, we found it useful to calculate an index of spatial autocorrelation, the I of Moran.

An x, y coordinate was generated for each point at both sites. Data was then imported into MapInfo (version 5.0.1), a GIS software package. Topologic links were generated to the 10th order within a 50 m radius for each data point, for polytric, *Sphagnum* and *Eriophorum*. The Moran's I was then calculated using MapStat (version 1.2, Thériault 1998). For all analysis, Droséra R95 and Sarracénie R97 were analyzed separately.

***Frequency of* Sphagnum**

The purpose of this analyses was to determine if the nurse plants polytric and *Eriophorum* increased the frequency of *Sphagnum*. We used two-way contingency analyses, to test for differences in *Sphagnum* frequency, in the presence and absence of polytric and under the different *Eriophorum* thirds (SAS Institute Inc. 1988). Data from both the point and the small circular quadrat were pooled. The model was :

Presence/Total = Polytric, Third, Polytric x Third

Where Presence = Number of sample points with *Sphagnum*
Total = Total number of sample points
Polytric = Two levels; absent or present
Eriophorum = Four levels; absent, 1/3, 2/3, 3/3.

Where there was no interaction between the main effects, and the analysis indicated a significant difference, the LSMEANS option of PROC GENMOD in SAS was used to locate differences within main effects. When the analysis indicated a significant interaction between main effects, multiple comparisons were used to compare the means of one factor within each level of the other factor, using the same option as above.

***Length and width of* Sphagnum**

The purpose of this analysis was to determine if the presence of polytric, presence and position under the *Eriophorum* tussock had a positive influence on the length and width of *Sphagnum*. We used an analysis of variance with the following model:

Sph = Polytric, Third, Polytric x Third

Where Sph = *Sphagnum* length or width (2 separate analyses)

Polytric = Two levels; absent or present

Eriophorum = Four levels; absent, 1/3, 2/3, 3/3

Data from both the points and quadrats were pooled. Following the ANOVA, A protected LSD was performed using the same criteria as for *Sphagnum* frequency. This test was chosen because it generated a statistic equivalent in severity to that used for the frequency of *Sphagnum* data. Data for *Sphagnum* length was log transformed to reduce residue heterogeneity. All test were considered significant at $p \leq 0.05$.

Tables of the ANOVA results for each analysis are presented in Appendix A

2.3.2 Nursing effect

The objective of this second experiment was to explain the observed polytric- *Sphagnum* association. Although our results clearly showed that *Eriophorum* is also a nurse plant, other studies have already addressed this point (Boudreau & Rochefort 1999, Marcoux 2000, Tuitilla *et al.* 2000). For this reason we chose to only pursue studies with polytric. Three separate experiments were performed: 1) A field experiment designed to characterize the microclimate generated by a polytric carpet, in terms of irradiance, temperature and moisture. 2) A growth chamber experiment to study the rate of water loss of *Sphagnum* in the presence and absence of polytric. 3) A field experiment to determine if polytric can be a seed trap and germination bed for *Eriophorum*.

Both field experiments were performed on the same site as the frost heaving experiments, using the same plots. However, only 4 of the six treatments were used: polytric carpet, polytric fragments, straw and bare peat (Table 1). The growth chamber experiment was done at Laval University.

a) The microclimate in a polytric carpet

Data was collected over a six week period, from 3 July 2000 to 25 August 2000. Irradiance, temperature and water content of *Sphagnum* were measured at the peat-air interface in order to establish the microclimatic conditions generated under the different covers : polytric carpet, polytric fragments, straw and bare peat.

Irradiance

Irradiance measures were taken in each treatment with a photometer (SunScan Analysis System Delta-T Devices LTD, Cambridge). Measures were taken on 14 July and 14 August 2000, under the following conditions: it was midday, there was at least 200 µmol m^{-2} of light and there were no abrupt changes from sunny to cloudy (Potter *et al.* 1996). Six loggers were placed per treatment (one per block), but due to equipment malfunction, the actual n varied from 3 to 6.

In the bare peat treatment, the meter long probe was place on the peat surface across the center of each plot. Where there were fragments and straw, the probe was inserted beneath the ground cover in the center of the plot. For measures in the carpet, a long narrow furrow was cut near the edge of each carpet. When the probe was laid in the furrow, it was at the same height as the rhizoid coat of the polytric stems (where *Sphagnum* is often found growing). The

Table 1. Name, purpose and description of treatments used for field experiments on polytric as a nurse plant at Premier St-Laurent, Rivière-du-Loup, Québec, and growth chamber experiments at Laval University.

Treatment	Purpose of the treatment	Description of the treatment
Polytric carpet	To simulate a dense polytric colony.	Squares of polytric were removed intact from naturally occuring colonies and transplanted into the experimental site.
Polytric fragments	A treatment to simulate the reintroduction of plant material according to the usual North American restoration techniques.	1 m^2 of polytric fragments were clipped even with the ground and spread over 10 m^2 of bare peat.
Straw	To test the effect of a straw mulch as used in peatland restoration.	3000 kg ha^{-1} of straw was evenly spread over bare peat.
Bare peat	To test conditions on a surface left bare after harvesting.	Bare peat, raked, with pieces of wood removed.

surface of the probe was then covered with freshly clipped polytric so as to recreate the appearance of a natural carpet. Although this method is the same used by Keizer *et al.* (1985), the results should be regarded as approximative due to the disruptive nature of the measurement. Within each block, the border of data collection between experimental units was random.

Air temperature

Air temperature was measured every 30 minutes during three periods: 10 to 19 July, 23 July to 3 August, and 8 to 24 August 2000. StowAway® dataloggers (Onset Computer Corporation, USA) with external sensors were placed in each plot. The sensor was placed in the center of each plot within the rhizoids of the polytric carpet, on bare peat, or beneath the fragments or straw. Maximum, minimum and daily averages were then calculated.

***Water content of* Sphagnum**

For the moisture measurements, we wanted a method that directly reflected the amount of water available to *Sphagnum*. *Sphagnum* has no physiological mechanism to prevent water loss and therefore tends to be in equilibrium with its environment. For this reason we chose to use *Sphagnum* moss itself as a method for measuring the moisture in a polytric carpet.

Sphagnum fuscum (Schimp.) Klinggr.was chosen for this measure. It is one of the species used in peatland restoration and was readily available. *Sphagnum* was harvested in the evening preceding its use, cut into 2.5 cm sections then stored for 12 hours at 4^{o}C. Each section had a capitulum. Prior to being inserted in the treatments, the *Sphagnum* sections were saturated with bog water. Ten *Sphagnum* sections per plot were placed at random locations on the bare peat, beneath the straw and polytric fragments. As the fragments were in a 1:10 ratio, the *Sphagnum* sections were not necessarily beneath fragments at every location. In the polytric carpets they were horizontally inserted in the zone where the stem was covered with rhizoids. Each *Sphagnum* section was held in place with a metal bobby pin.

Sphagnum were placed out during the following six intervals: 13 to 17 July, 18 to 20 July, 25 to 28 July, 1 to 4 August, 8 to 11 August and 25 to 27 August 2000. The *Sphagnum* sections were retrieved on rainless days, three to five days following their insertion. The order of retrieval was random within each block. The ten *Sphagnum* were collected, placed in a screw top bottle (one bottle per plot) and stored at 4^oC for a maximum of 24 hours. The wet weight was then measured. Dry weight was determined following 24 hours of oven drying at 105^oC. Percent water content was calculated as (g H_2O / g dry weight) x 100.

b) <u>The rate of water loss in *Sphagnum*</u>

The purpose of this experiment was to determine the effect of a polytric carpet on the rate of water loss of *Sphagnum*, as compared to newly introduced polytric fragments, straw and bare peat. We felt that the controlled environment of the growth chamber would allow us to refine our understanding of water loss in *Sphagnum* over a smaller time scale than was possible in the field.

Polytric carpet, fragments and peat were collected from Premier St-Laurent as for the field experiment, and stored at 4^oC for three weeks prior to use. *Sphagnum* sections were collected from a regenerated bog and prepared as in the field experiment. This experiment was set up 29 October 2000, and data was collected from 8 January 2001 to 24 February 2001.

Experimental design was a split plot, where the main plot was a growth tray (54 cm long x 28 cm wide x 6.6 cm deep) to which each treatment was applied, and the split-plot was the four *Sphagnum* individuals removed for moisture measures at each time. The main plots were arranged in 4 completely randomized blocks. Photoperiod was set to 16 hours. Lighting was provided by fluorescent light placed just above the trays, and averaged 140 µmol m^{-2} s^{-1}. Average daily temperature was 24^oC. Apart from the lights, no additional heat was directed at the growth trays, nor was ventilation provided beyond that already present in the room. The growth trays were watered three times per week using de-ionized water, except during data collection. All trays received the same amount of water.

The growth trays were filled with 6 cm of peat for the fragments, straw and bare peat treatments. The peat was waterlogged. Small lumps were broken by hand. The peat surface was then smoothed by applying pressure with the bottom of an empty tray. This resulted in a surface as uniform as possible. Fragments and straw were then spread as in the field experiment. For the polytric carpet treatment, a 3 cm layer of peat was placed in the bottom of the growth tray. The carpets were then placed on the layer of peat. Each tray thus had the same thickness of peat; 6 cm for fragments, straw, bare peat and polytric carpet (3 cm in the tray + 3 cm attached beneath the polytric carpet).

Sphagnum stem sections were distributed among the treatments, 36 per growth tray, with the capitula 5 cm apart. Before and after depositing the *Sphagnum* stem sections in the treatments, the growth trays were watered with deionized water to imitate field conditions following rain. The various covers were therefore equally wet at the beginning of each observation period.

At each time interval, four randomly chosen *Sphagnum* stem sections were removed from the growth trays and placed in a glass sample flask. The time intervals were 0.5, 1, 2, 4, 6, 8, 16, 24 and 48 hours. The final time interval was used for comparison with the field experiment results. Wet weight was measured on the harvest day; dry weight was taken following 24 hours oven drying at 105^{o}C. Percent water content was calculated as (g H_2O / g dry weight) x 100. The experiment was repeated three times, using the same experimental set-up, but different *Sphagnum* stem sections.

c) Polytric as a seed trap and germination bed

The purpose of this experiment was to determine if polytric carpets act as seed traps as suggested by Parker *et al.* (1997). The experiment was designed with the following assumption : all ground covers receive an equal amount of seed rain. After a given amount of time, more seeds will remain on some substrates than others because the substrates vary in their ability to retain the seeds. The suitability of polytric as a seedbed for *Eriophorum* was tested by counting the number of emergent *Eriophorum* seedlings 11 months after the experiment was set up.

Two different substrates were tested for seed retention : polytric carpet and bare peat. *Eriophorum* seeds were chosen because they are wind-dispersed, easy to handle and were readily available. In the context of this experiment, a seed is defined as : an achene with its seed and the attached perianth bristles.

For a first trial, forty intact seeds (including their bristles) were gently placed in a 50 x 50 cm central subplot of each polytric carpet and bare peat plots. The trial began on 12 July 2000, under a sunny sky with some clouds and a light wind. We quickly realized that natural seeds were not suitable for experimentation because the bristles broke apart making it impossible to distinguish individual seeds. Thus we decided to use another proxy. Furthermore, it was clear from this first trial that seed disappearance occurred within a few hours of deposition. After a few hours, and especially if the seeds got wet, no further seed transport occurred.

A second trial was initiated, using artificial seeds. These were constructed from chicken feather dyed bright red. They were similar in weight and shape to the *Eriophorum* seeds, and had the advantage of being more durable and visible: we could still distinguish individual “seeds” three months later. On the 8 August 2000, a windy day, between 36 and 40 artificial seeds were placed as in the first trial, the design being repeated over three blocks. The number remaining after 1 and 2 hours was counted.

To confirm the results of 8 August 2000, the experiment was repeated on 24 August 2000, a day with light wind and damp peat. Thirty artificial seeds were placed in each block in the early morning. The number remaining after four hours was counted.

Eleven months after the experiment was set up, the number of *Eriophorum* plants growing in the carpet, fragments, straw or bare peat was recorded. These plants are the result of natural seeding from nearby tussocks and possibly the seeds that were planted in the first seed trial. Seedlings from the spring of 2001 were not counted.

d) Statistical analyses

The microclimate in a polytric carpet

All statistical analyses were performed using the GLM procedure of SAS (SAS Institute Inc. 1988). A protected LSD was used to locate differences between treatment means once treatment effects were found significant. All tests were considered significant at $p \leq 0.05$.

For the irradiance, the percent PAR transmitted through each cover was calculated. The average of both sample dates was pooled for the analysis of variance.

For the field experiment on water content of *Sphagnum*, the analysis of variance was performed on the percent moisture of *Sphagnum* stem sections: (wet weight – dry weight)/dry weight * 100, using the appropriate model for complete randomized blocks with time as a split plot factor. A cubic transformation was necessary to reduce variance heterogeneity. Five individual values (out of 144) were removed from the data set because the percent moisture of *Sphagnum* came out negative. Average daily temperature between 6h00 and 18h00 on bare peat was calculated for each experimental period, as was total precipitation. For the experimental period from 18 – 20 July, temperature data was available only for the first two days.

The rate of water loss in Sphagnum

For the growth chamber experiment on the rate of water loss of *Sphagnum*, the analysis of variance was performed on the percent moisture of *Sphagnum* stem sections, using the appropriate model for the split plot design. The three repetitions were analyzed separately. Data for the first and second repetition were square root transformed to reduce variance heterogeneity. Eight individual values (out of 432) were removed from the data set because the percent moisture of *Sphagnum* came out negative.

Polytric as a seed trap and germination bed

For the seed trap experiment, the percent of initial artificial seeds remaining after a stated time period was calculated for each treatment and analyzed with an analysis of variance. Each count was analyzed separately. No multiple comparison test was needed, as only two treatments were being compared at a time.

For the germination bed experiment, data was analyzed with an analysis of variance, followed by a protected LSD.

Tables of the ANOVA results for each analysis are presented in Appendix A.

2.4 Results

2.4.1 Field surveys

a) <u>Spatial autocorrelation</u>

The I of Moran indicates that there is no spatial autocorrelation for polytric, *Sphagnum* or *Eriophorum* on Droséra R95 (Figure 3 a, b, c) at the first neighbour. We do not consider interactions past the first neighbor as it would be inappproprite with the sampling scheme used (Legendre & Fortin 1989). On Sarracénie R97, the I of Moran indicates that there is a weak spatial correlation for all three species that extends past the first neighbour, and up to the 10th for *Eriophorum* and *Sphagnum*. Therefore, there is no realistic probability correction possible to compensate (Upton & Fingleton 1985).

A spatial autocorrelation indicates that the plants are not randomly distributed; *e.g.* the presence of polytric at a given point influences the probability of finding polytric at an adjacent or nearby point. As individual moss plants are very small, polytric plants at adjacent points separated by several meters are unlikely to directly affect each other. Rather, the spatial autocorrelation occurs because of an underlying gradient, such as moisture or nutrient level. The underlying structure of multiple depressions in each field at Sarracénie R97 (rather that the single central depression at Droséra R95) may help explain detected spatial autocorrelation.

In the context of this sampling, it means that any association found between polytric and *Sphagnum*, or *Eriophorum* and *Sphagnum* may be due to shared environmental requirements, rather than nurse plant effects. However, differences in *Sphagnum* presence and length according to its position beneath the *Eriophorum* tussock indicate that the observed association are due to more than spatial gradients. Furthermore, as the detected spatial autocorrelation detected on Sarracénie R97 weak, we chose to pursue classical hypothesis testing, keeping in mind that at least part of the association detected in Sarracénie R97 is due to underlying environmental gradients.

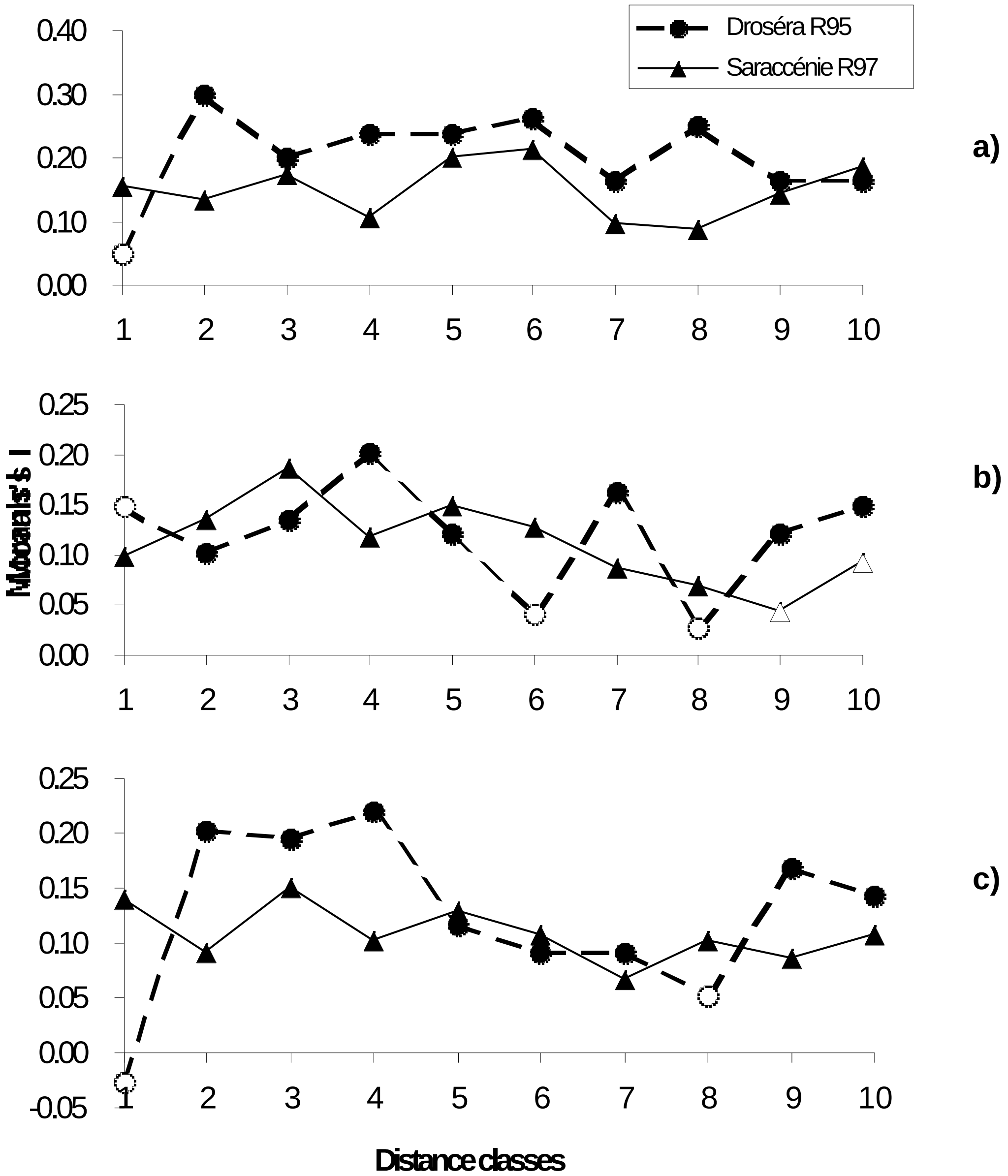

Figure 3. Correlograms of the I of Moran for three species studied at the Chemin du Lac peatland, Rivière-du-Loup, Québec. The width of the distance class varied from 4 to 8 m depending on the proximity to the nearest neighbour. Solid symbols represent the distance classes where the autocorrelation is significant (p ≤ 0.05). Hollow symbols represent non-significant values. ***a)*** Eriophorum vaginatum *var.* spissum, ***b)*** *Polytrichum strictum*, ***c)*** *Sphagnum* sp.

b) Frequency of Sphagnum

On Droséra R95, the presence of either polytric or *Eriophorum* greatly increased the frequency of *Sphagnum* (polytric p = 0.0001, *Eriophorum* p =0.0001) (Figure 4a). *Sphagnum* was much more frequent when polytric was present (frequency = 0.67) than when polytric was absent (0.18). *Sphagnum* was less frequent when there was no *Eriophorum* (0.28), compared to under the 1/3 (0.42), 2/3 (0.53) and 3/3 (0.46). *Sphagnum* tended to be more frequent under the 2/3 than under the 1/3, however this difference was not significant (p=0.0781).

On Sarracénie R97, both polytric and *Eriophorum* had a highly significant effect on *Sphagnum* presence, and there was an interaction between them (polytric*Eriophorum p= 0.0015) (Figure 4b). Where neither companion plant was present, *Sphagnum* was very infrequent (0.12). When only polytric was present, *Sphagnum* was significantly more frequent with polytric (0.44) than without. When only *Eriophorum* was present, *Sphagnum* was more likely to be found growing under the 1/3 (0.41) and 2/3 (0.46) of Eriophorum than under the 3/3 (0.22) or outside of an *Eriophorum* tussock. *Sphagnum* tended to be more frequent where both companion plants were found, compared to points where only *Eriophorum* was found. However, this difference was only significant under the 3/3 (+ polytric = 0.64, - polytric = 0.21)

c) Length and width of *Sphagnum*

On Droséra R95, polytric had no influence on the length of *Sphagnum* (polytric p = 0.301) (Figure 5a). *Sphagnum* was of similar length whether it grew at a point with polytric (1.7 cm) or without (1.6 cm). *Eriophorum* had a highly significant effect on *Sphagnum* length (*Eriophorum* p = 0.0001). *Sphagnum* increased in length with proximity to the center of the *Eriophorum* tussock. The shortest *Sphagnum* was at points without *Eriophorum* (0.80 cm). *Sphagnum* growing under the 1/3 was slightly longer (1.0 cm), but this difference was not significant. *Sphagnum* growing at points without *Eriophorum* or under the 1/3 was significantly shorter than *Sphagnum* growing under the 2/3 (1.8 cm). *Sphagnum* growing in the center of tussocks, the 3/3, was significantly longer than *Sphagnum* growing anywhere else (3.0 cm).

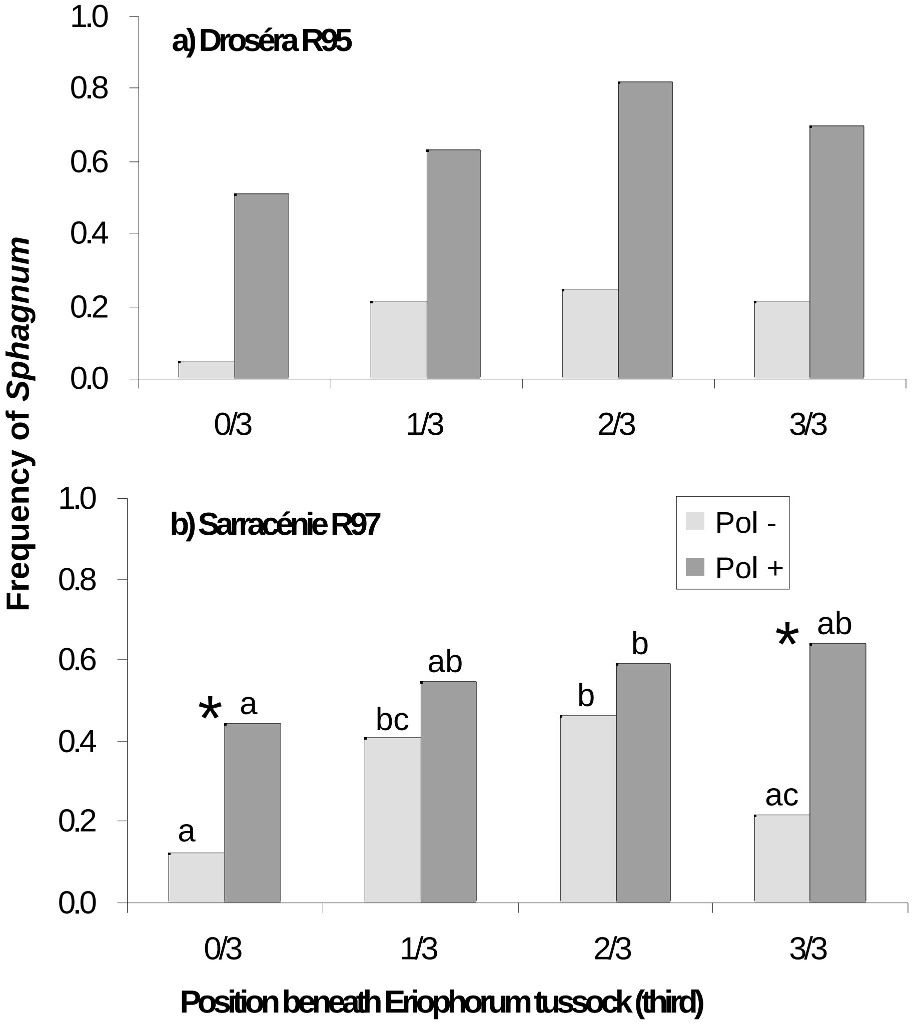

Figure 4a and b. The frequency of Sphagnum *on two restored peatlands, Droséra R95 and Sarracénie R97 located in Rivière-du-Loup, Québec, in relation to the presence or absence of two nurse plants,* Eriophorum vaginatum *var.* spissum *and* Polytrichum strictum. ***a)*** *Droséra R95. No significant interaction, p = 0.1610. Other statistics reported in text.* ***b)*** *Sarracénie R97. Significant interaction, p = 0.0015. Values followed by different letters are significantly different at p ≤ 0.05 by the LSMEANS option of PROC GENMOD in SAS, within a level of polytric. An asterisk (*) indicates a significant difference between levels of polytric.*

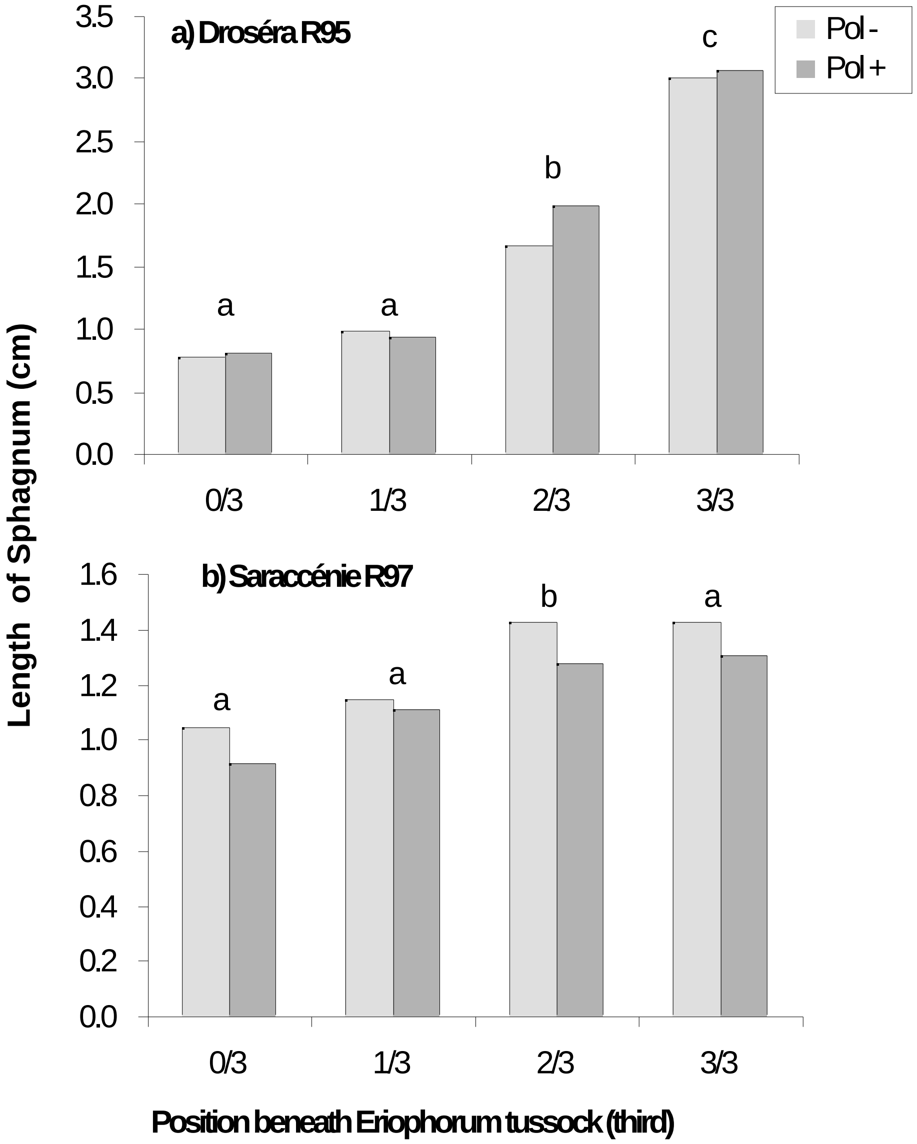

Figure 5a and b. The length of Sphagnum on two restored peatlands, Droséra R95 and Sarracénie R97 located in Rivière-du-Loup, Québec, in relation to the presence or absence of two nurse plants, Eriophorum vaginatum *var.* spissum *and* Polytrichum strictum. ***a)*** *Droséra R95. ANOVA*$_{polytric}$ *df = 1, F = 1.08, p = 0.301. ANOVA*$_{Eriophorum}$ *df = 3, F = 12.62, p = 0.001. ANOVA*$_{polytric*Eriophorum}$ *df = 3, F = 0.29, p = 0.833* ***b)*** *Sarracénie R97. ANOVA*$_{polytric}$ *df = 1, F = 0.59, p = 0.443. ANOVA*$_{Eriophorum}$ *df = 3, F = 3.7, p = 0.012. ANOVA*$_{polytric*Eriophorum}$ *df = 3, F = 0.07, p = 0.977. For both graphs, letters indicate a significant difference at p ≤ 0.05 by the LSD test, between different* Eriophorum *thirds (averaged over the presence and absence of polytric).*

On Sarracénie R97 polytric had no influence on the length of *Sphagnum* (polytric p = 0.4429); *Sphagnum* was the same length whether it grew at a point with polytric (1.2 cm) or without (1.3 cm) (Figure 5b). *Eriophorum* had a significant effect on the length of *Sphagnum*; however this effect was less marked than on Droséra R95 (*Eriophorum* p = 0.012). The shortest *Sphagnum* was at points without *Eriophorum* (1.0 cm). *Sphagnum* growing under the 1/3 was slightly longer (1.1 cm), but this difference was not significant. *Sphagnum* growing under the 2/3 (1.4 cm) and 3/3 (1.4 cm) was significantly longer than *Sphagnum* growing without *Eriophorum*. Overall, *Sphagnum* tended to increase in length with increasing proximity to the center of the *Eriophorum* tussock but there was no significant difference between any of the thirds.

Sphagnum width on Sarracénie R97 was a constant 0.49 cm. It was not affected by polytric (p=0.2358) or *Eriophorum* (p=0.9662).

2.4.2 Nursing effect

a) <u>The microclimate in a polytric carpet</u>

Irradiance

The carpet, fragments and straw reduced the amount of PAR reaching the bare peat (Table 2). The amount of PAR light was 5, 24, 34 and 98% for the carpet, straw, fragments and bare peat respectively. Each treatment differed significantly from all the others. Average photosynthetic photon flux density (PPFD) was 38, 194, 309, 677 and µmol m^{-2} s^{-1} for the carpet, straw, and peat respectively.

Air temperature

The temperature at the surface of the bare peat, and beneath the polytric carpet, fragments and straw are presented in Figure 6. The three graphs have similar trends; above 14 to 19 ^{o}C,

Table 2. Amount of light transmitted within a polytric carpet, polytric fragments and straw, and on the bare peat surface of an abandoned milled bog located in Rivière-du-Loup, Québec. Values presented are the average of two readings taken on 14 July and 14 August 2000. $ANOVA_{Treatment}$: $df = 3$, $F = 228.81$, $p = 0.0001$. Values followed by different letters indicate a significant difference at $p \leq 0.05$ by an LSD.

	Light intensity	
Treatment	PAR (% transmitted)	PPFD (µmol m^{-2} s^{-1})
Carpet	5.1 a	37.6
Fragments	35.0 c	309.1
Straw	25.0 b	194.2
Bare peat	99.9 d	677.4

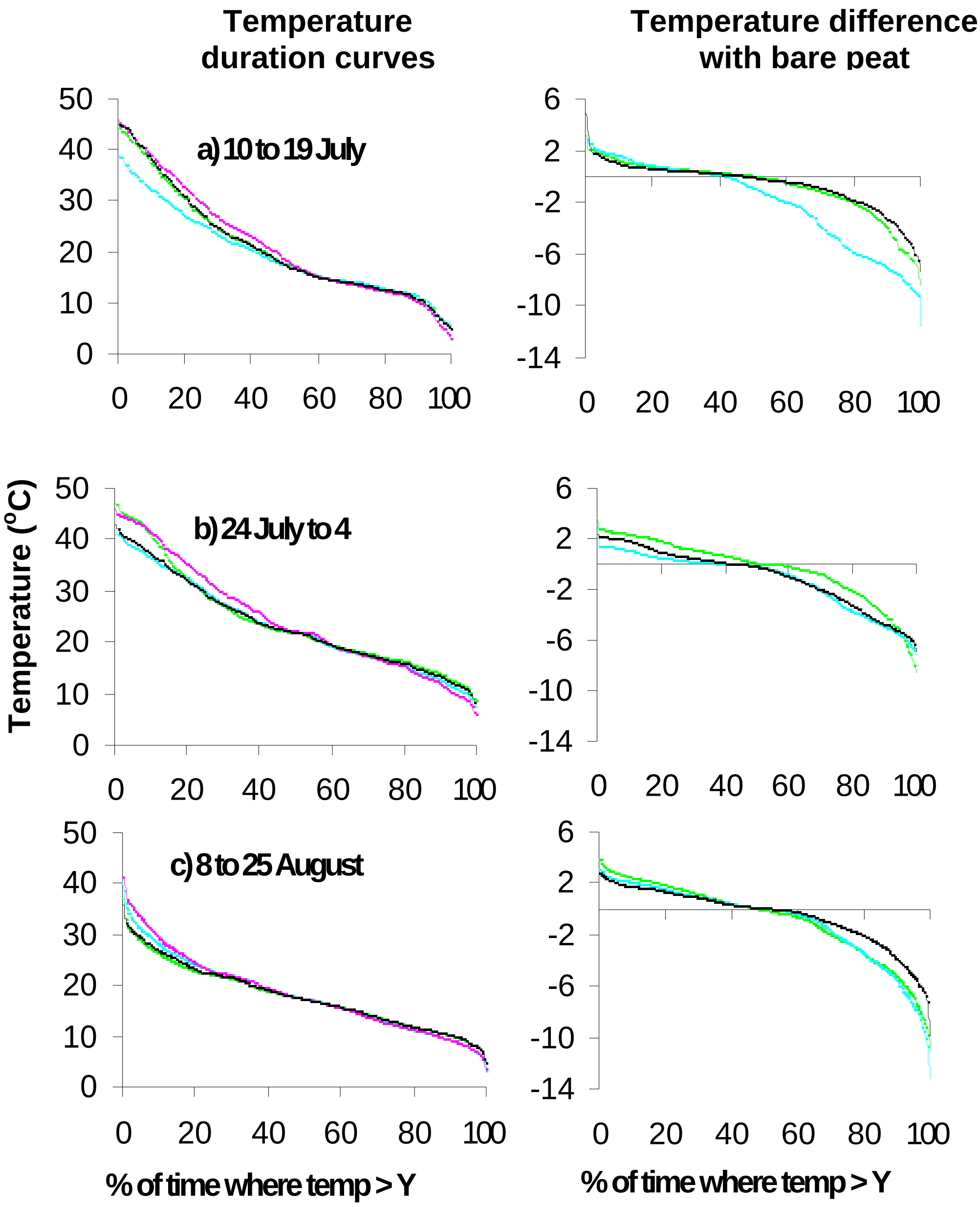

Figure 6a, b, c : Temperature duration curve for surface temperature of bare peat, and beneath a polytric carpet, polytric fragments, and straw on an abandoned vacuum harvested bog located in Rivière-du-Loup, Québec, and temperature duration curves for the difference in degrees C between the three covers and bare peat. Pink = bare peat, green = polytric carpet, blue = polytric fragments, black = straw. Six dataloggers were used per treatment, but because of equipment malfunction, the values presented are the average of n = 3 to 6 dataloggers per treatment.

temperatures under the covers are generally cooler than those observed on bare peat. Below this same range, temperatures are generally warmer than those observed on bare peat. In general, the greatest temperature reduction compared to bare peat was observed at the highest temperatures.

More precisely, from the 10 to 19 July, the average daytime temperature (from 6:00 to 18:00) on the bare peat was 29.0 ^{o}C, the daytime maximum 46.3 ^{o}C and the daytime minimum 8.8 ^{o}C. Precipitation for this period was very low, totalling 0.7 mm (total from 12 to 19 July as precipitation was not measured prior to this date). On average, the polytric carpet reduced the daytime temperature by 1.8 ^{o}C compared to the bare peat, the daytime maximal reduction being 8.4 ^{o}C. Average and maximal daytime reduction beneath the fragments was 4.4 ^{o}C and 11.5 ^{o}C respectively. Average and maximal daytime reduction beneath the straw was 1.4 and 7.4 ^{o}C, respectively.

From the 24 July to 4 August, the average temperature on the bare peat was 31.8 ^{o}C, the daytime maximum 46.1 ^{o}C and the daytime minimum 9.3 ^{o}C. Precipitation for this period was higher totaling 30.6 mm. On average, the polytric carpet reduced the daytime temperature by 1.6 ^{o}C compared to the bare peat, the maximal daytime reduction being 8.6 ^{o}C. Average and maximal daytime reduction beneath the fragments was 3.0 and 7.2 ^{o}C, respectively. When the temperature topped 43 ^{o}C, it was hotter in the carpet than on the bare peat. Average and maximal daytime reduction beneath the straw was 3.0 and 7.0 ^{o}C, respectively.

From the 8 to 25 August, the average daytime temperature on the bare peat was 18.4 ^{o}C, the daytime maximum 42 and the daytime minimum 2.5. Precipitation for this period was highest totaling 52.9 mm. On average, the polytric carpet reduced the daytime temperature by 0.7 ^{o}C compared to the bare peat, the maximal daytime reduction being 11.1 ^{o}C. Average and maximal daytime reduction beneath the fragments was 0.8 and 13.2 ^{o}C, respectively. Average and maximal daytime reduction beneath the straw was 0.4 and 9.9 ^{o}C, respectively.

***Water content of* Sphagnum**

The percent moisture of the *Sphagnum* stem sections measured beneath the different covers shows that the polytric carpet, the fragments and the straw increased humidity at the air peat interface under certain conditions (Figure 7). The effect of the three covers on moisture varied from week to week ($p_{Date*Time}$=0.0021), and was influenced by the temperature and precipitations.

During the first two periods in July, the experimental periods were characterized by elevated temperatures on the bare peat (> 28 ^{o}C) and little precipitation (< 1 mm per period). *Sphagnum* stem sections in all treatments were equally dry, the average water content over both periods for all the treatments being 22%.

During the experimental period beginning 25 July, it was extremely hot, with daily temperatures on the bare peat averaging 35 ^{o}C. Total precipitation amounted to 18.4 mm. We observed the highest moisture beneath the polytric carpet (53%), straw (45%) and fragments (35%). These three treatments did not differ significantly from each other, but *Sphagnum* stem sectionsconserved more moisture than on the bare peat (12%).

During the experimental period beginning 1 August, the daily average temperature on bare peat was 25 ^{o}C, and precipitation totalled 12.2 mm. *Sphagnum* sections in all three covers were significantly more moist than those on bare peat (31%). The highest *Sphagnum* water content was found beneath the straw (165%) and polytric carpet (140%); these two did not differ significantly from each other. *Sphagnum* placed in the polytric fragments had an intermediate water content (95%), which differed significantly from straw, but not from polytric carpet.

The experimental period beginning 8 August was the coolest and wettest, with an average daily temperature of 11 ^{o}C on the bare peat, and a total of 23.0 mm precipitations. During this period, we observed the highest water content in *Sphagnum* for all treatments (> 400%), compared to the other dates. The highest *Sphagnum* water content was observed in the polytric carpet (740%) and beneath the straw (725%). The effect of these covers is significantly

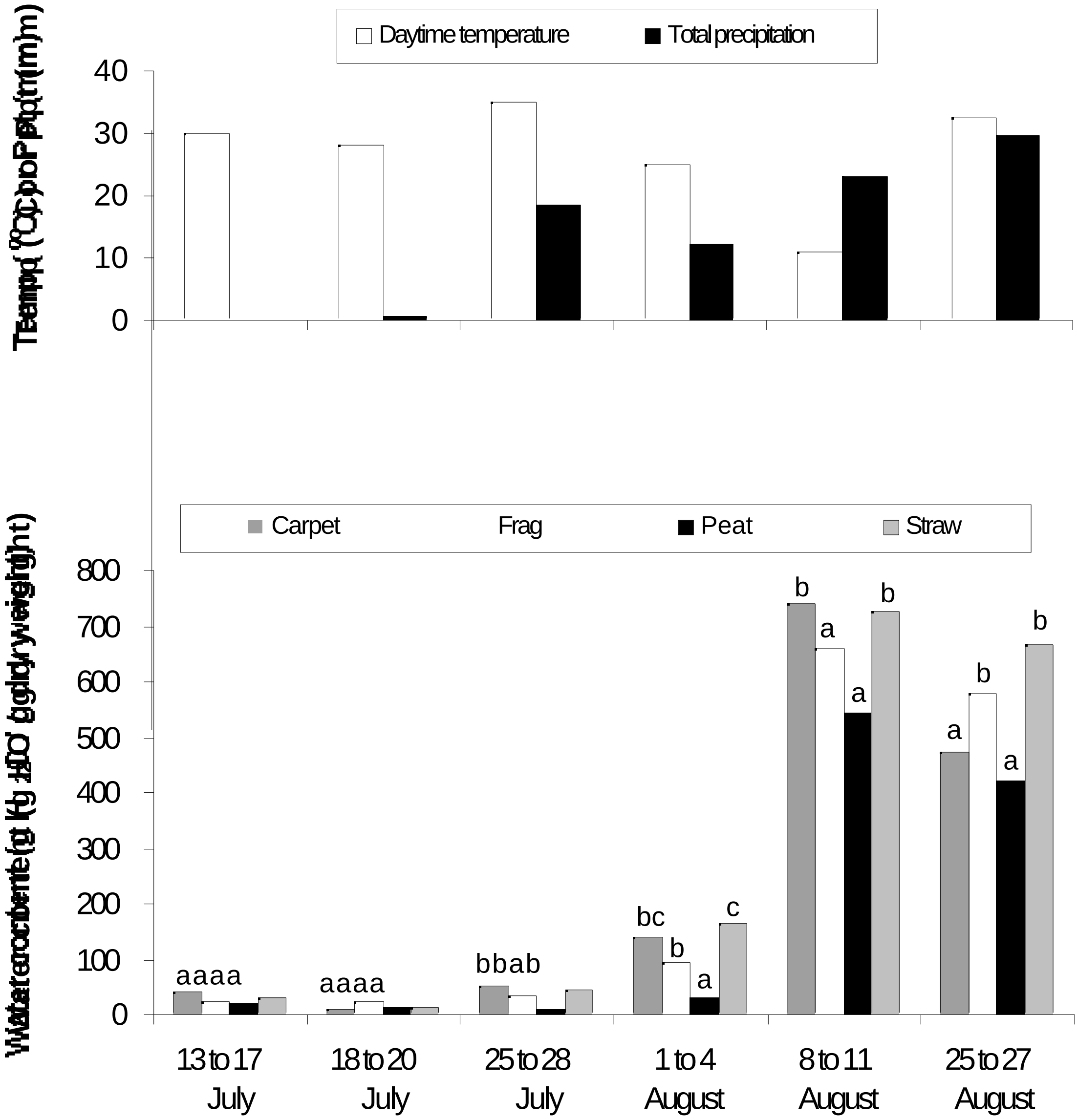

Figure 7. Average daily temperature (from 6:00 to 18:00) and total precipitation, and water content of stem sections of Sphagnum *moss (*Sphagnum fuscum*) placed in a polytric carpet, fragments, and straw, or on the bare peat surface of an abandoned vacuum harvested bog located in Rivière-du-Loup, Québec, during 6 measurement periods (no precipitation data for 1st period). ANOVA$_{Date*Treatment}$: df = 15, F = 456.9, p = 0.002. Within each experimental period, different letters indicate a significant difference at p ≤ 0.05 by an LSD.*

different than that which is observed on the bare peat (543%). The water content of *Sphagnum* in the polytric fragments (661%) was intermediate and did not differ from any other treatment.

The experimental period beginning 23 August was characterized by high daily temperatures on the bare peat (32 ^{o}C) and the most abundant precipitation (29.8 mm total). The highest *Sphagnum* water content was observed beneath the straw (668%) and polytric fragments (580%); these did not differ. *Sphagnum* on the bare peat (419%) was drier than in the carpet (473%), but this difference was not significant.

b) <u>Rate of water loss in Sphagnum</u>

In the first trial, *Sphagnum* sections rapidly and continuously lost water over 48 hours (Figure 8a). There was no difference in *Sphagnum* water content between treatments (treatment p = 0.3383), at any of the sample times (Treatment*Time p =0.1928). Drying was most rapid during the first hour, with an average reduction in water content of 1002% per hour for all treatments. During the second hour, Sphagnum lost an average of 131% water per hour. From two to six hours, water loss averaged 66% per hour. After 8 hours water loss gradually slowed, diminishing to 5% loss per hour between 24 and 48 hours.

Results for the second trial are difficult to explain, as *Sphagnum* stem sections placed under straw cover became wetter by over 300% between the 1st and 2nd hour, rather than losing water as in the other two repetitions (Figure 8b). Percent water content was very variable between blocks, and no significant difference was found between treatments (p=0.1711), at any of the sample times (Treament*Time=0.3980). Overall, the pattern of water loss in the second week was similar to that of the third trial.

In the third trial, a significant difference in *Sphagnum* stem section water content was found between certain treatments and specific times (Treatment*Time p = 0.0008) (Figure 8c). In the first two hours after being placed in the treatments, *Sphagnum* sections dried rapidly in all treatments, losing about 200% water. Between 4 and 16 hours, *Sphagnum* sections retained

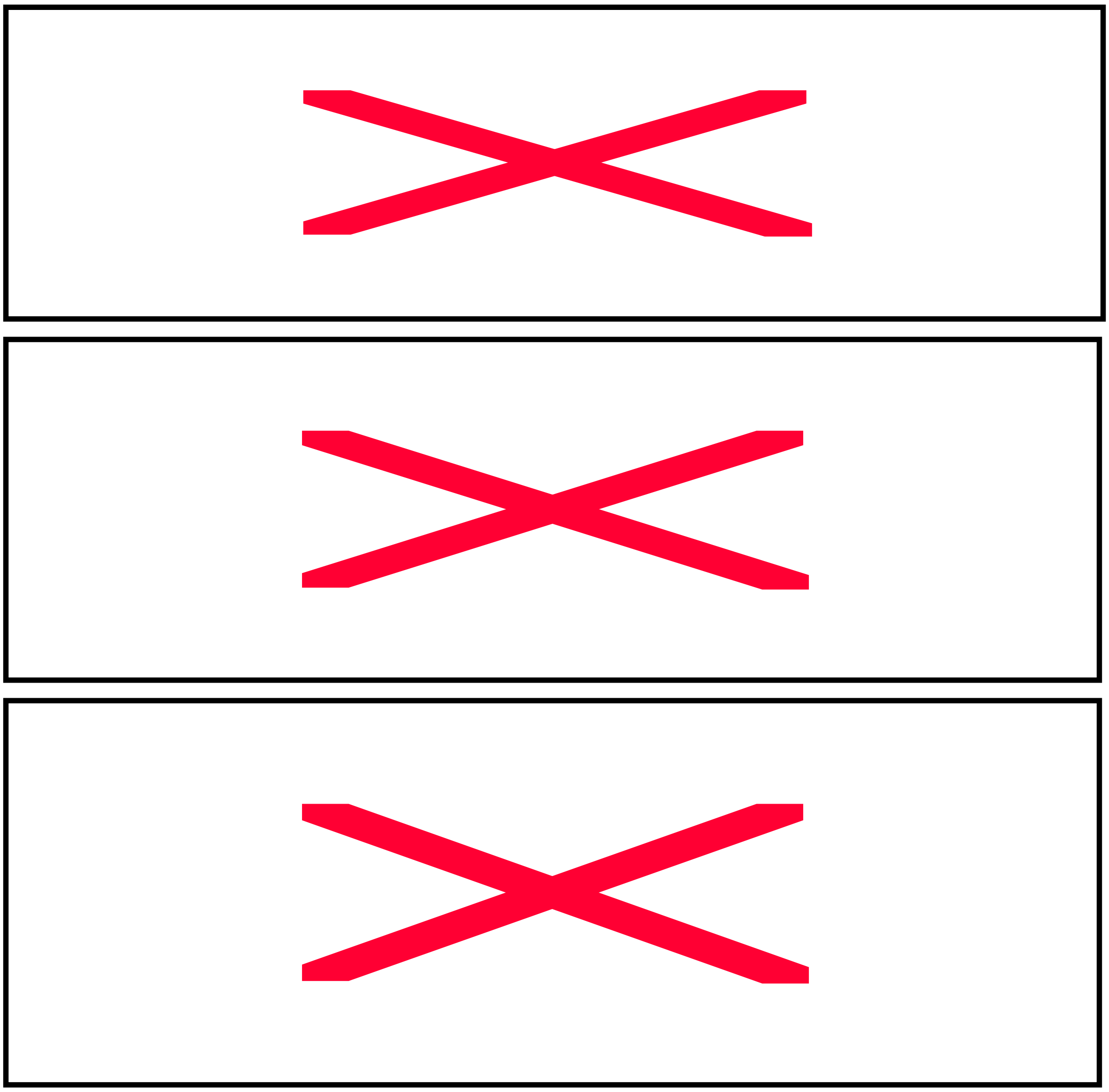

Figure 8a, b, c. Rate of water loss in Sphagnum *stem sections (*Sphagnum fuscum*) placed within a polytric carpet, polytric fragments and straw, and on a bare peat surface over 48 hours in a growth chamber, for three different trials. A star (*) indicates a significant difference between treatments within a given time, where the Treatment*Time interaction was significant. Letters for trial 3 indicate significant differences as indicated by an LSD ($p \leq 0.05$), where c = carpet, f = fragments, s = straw, p = peat.* ***a)*** *Trial 1.* $ANOVA_{Time}$*: df =8, F = 529.13, p = 0.0001.* $ANOVA_{Treatment}$*: df= 3, F = 0.98, p = 0.4066.* $ANOVA_{Treatment*Time}$*: df = 24, F = 1.29, p = 0.1928.* ***b)*** *Trial 2.* $ANOVA_{Time}$*: df =8, F = 95.86, p = 0.0001.* $ANOVA_{Treatment}$*: df= 3, F = 2.10, p = 0.1711.* $ANOVA_{Treatment*Time}$*: df = 24, F = 1.06, p = 0.3980.* ***c)*** *Trial 3.* $ANOVA_{Treatment*Time}$*: df = 24, F = 2.55, p = 0.0008.*

more water when placed under the straw, than in the polytric carpet or on bare peat. Between 6 and 8 hours, *Sphagnum* stem sections retained more water under the fragments than under the polytric carpet and bare peat. The same tended to be true at 4 and 16 hours as well, but this difference was not significant. After 24 hours, the *Sphagnum* sections were very dry in all the treatments, having diminished on average from 1285 to 12% water content over 48 hours, and there was no longer any significant difference between any of them.

c) <u>Polytric as a seed trap and germination bed</u>

For the seed retention test on 8 August 2000, after 1 hour significantly more seeds were retained on the carpet (94%) than the bare peat (52%) (p=0.0201) (Figure 9a). After two hours, the difference was even greater, with 90% retention on the carpet and 43% retention on the bare peat (p=0.0099). When the trial was repeated on 24 August 2000, after 4 hours 94% of the seeds were retained on the carpet, and 86% were retained on the bare peat (Figure 9 b). This difference was not significant (p=0.098).

The number of Eriophorum seedlings growing in the carpet, fragments, straw and bare peat differed significantly 12 months after the experiment was installed (p=0.0375) (Figure 10). Polytric carpet had significantly fewer seedlings (0.8) than fragments (5.3) and bare peat (5.2). The number of seedlings on straw (4.0) was intermediate, and not significantly different from any other treatment.

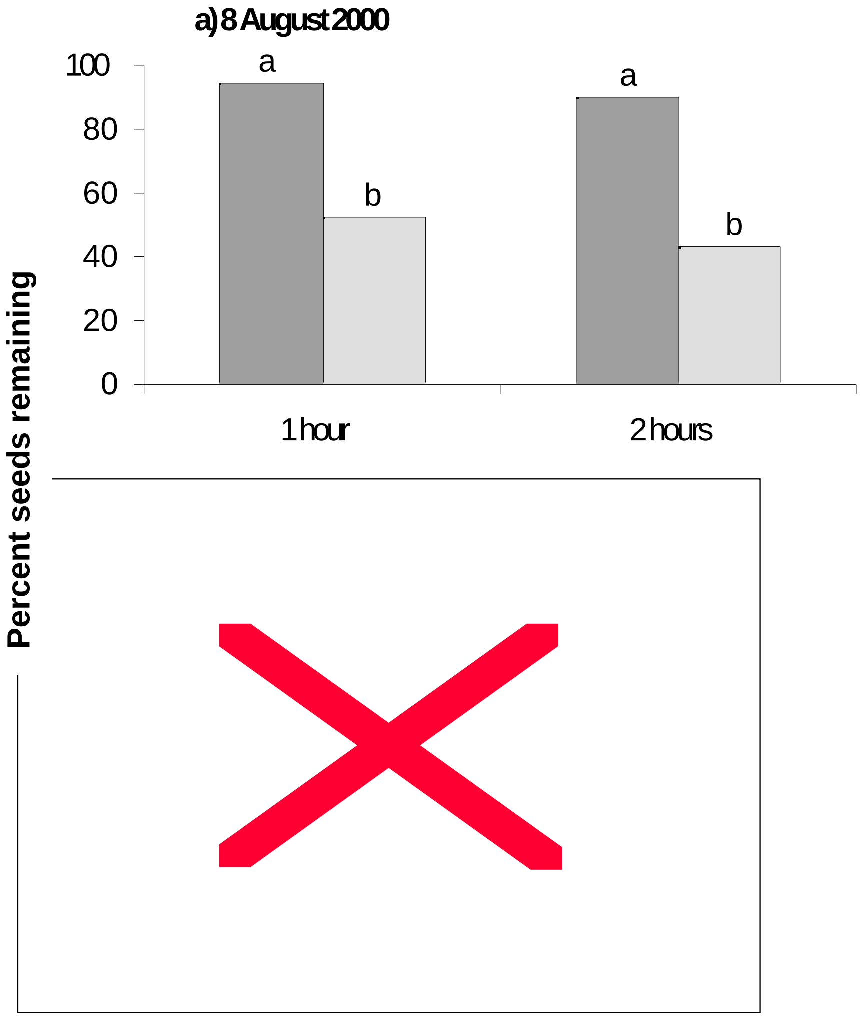

Figure 9a, b : Seed retention on a polytric carpet and on the bare peat surface of an abandoned vacuum harvested bog located in Rivière-du-Loup, Québec. Letters above each bar show significant differences as indicated by the ANOVA ($p \leq 0.05$), for each measurement time. a) 8 August 2000. b) 24 August 2000.

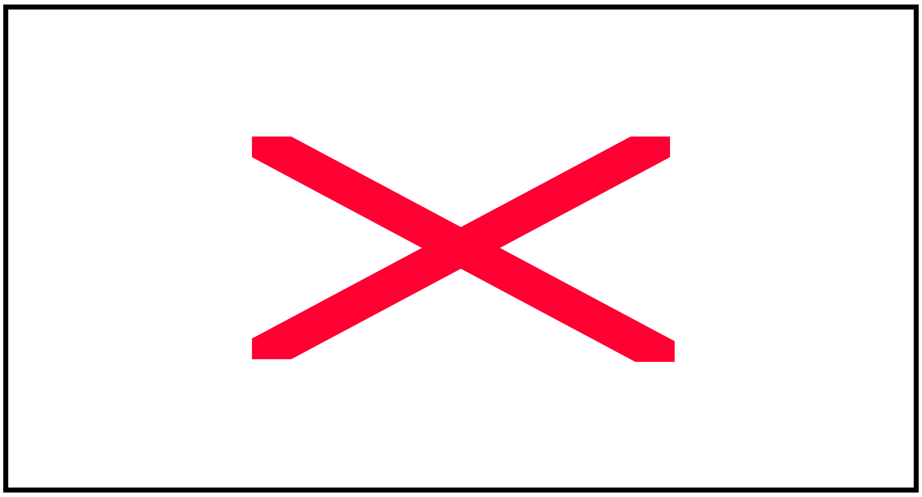

Figure 10: Number of 1 year Eriophorum spissum *var.* vaginatum *growing in a polytric carpet, fragments, straw and bare peat on 30 May 2000, at an abandoned vacuum harvested bog located in Rivière-du-Loup, Québec. Values followed by different letters indicate a significant difference at* $p \leq 0.05$ *by an LSD.* $ANOVA_{Treatment}$ *df = 3, F = 3.64, p = 0.0375.*

2.5 Discussion

2.5.1 Field surveys : Establishing an association

We determined that a positive association existed between the nurse plants polytric and *Eriophorum*, and the beneficiary *Sphagnum*. As stated in the results sections, we must bear in mind that at least part of the association detected in Sarracénie R97 is due to underlying environmental gradients. There are two ways in which a companion plant can increase the biomass of beneficiaries: first, increase the mass of individual plants, and second, increase the overall cover. We used length as an indicator of biomass, as *Sphagnum* width was invariable, assuming that longer *Sphagnum* individuals weigh more than shorter *Sphagnum* individuals of equal width.

a) Cover of *Sphagnum*

On both Droséra R95 and Sarracénie R97, we found that either polytric or *Eriophorum* alone will increase the cover of *Sphagnum*, but when both companion plants are present, the effect on *Sphagnum* cover is even greater. Since both point and quadrat data were pooled, the actual percent cover of *Sphagnum* in the field is proportional to, but less than, frequency.

The effects of nurse plants were more marked at Droséra R95 than Sarracénie R97. For example, polytric always increased the frequency of *Sphagnum* at R95, whereas on R97, polytric only significantly increased the frequency when *Eriophorum* was absent, or at the 3/3. Conditions at Droséra R95 are not the same as those on Sarracénie R97: restoration techniques were not as ideal, rewetting was not as successful and the site is two years older. The stronger nurse plant associations on Droséra R95 could therefore be due to the harsher conditions (Bertness & Shumway 1993, Hacker & Gaines 1997) than those of Sarracénie R97. It is also possible that nurse plant effects increase over time, and may become more evident on Sarracénie R97 after a few more growing season have passed.

The lower *Sphagnum* cover observed under the 3/3 could be due to two reasons. First, there is less room to grow because in this third the tussock is rooted to the ground, in contrast with the

1/3 and 2/3, where the leaves overhang the ground without being rooted. Second, light may be limiting. This is discussed at the end of the next section.

b) Length of Sphagnum

We expected *Sphagnum* to be longer when growing near polytric. Although polytric was longer than *Sphagnum* at more than 85% of the points, and could thus potentially offer shelter, we were surprised to discover that *Sphagnum* growing with polytric was not longer at either site.

In spite of ditch blockage at both sites, the peat remained very dry in the summer. With the exception of early morning and rainy days, polytric kept its leaves folded against its stem to reduce water loss (Bayfield 1973). With closed leaves, it offered less protection to *Sphagnum*, which could explain the lack of effect on *Sphagnum* length. We have observed that on other sites with more humid conditions, which permits polytric’s leaves to remain open, *Sphagnum* length was significantly correlated to polytric length (E. Groeneveld, unpublished data).

The effect of *Eriophorum* on *Sphagnum* length was clearest at Droséra R95. *Sphagnum* grew significantly longer with increasing proximity to the center of the tussocks. The same trend was visible in Sarracénie R97, but there were no significant differences between the thirds: 1/3 = 2/3 = 3/3. On average, *Sphagnum* was 0.45 cm shorter at Sarracénie R97 than Droséra R95. The weaker trend in Sarracénie R97 may simply be due to the fact that the plant have had two growing seasons less than the other site.

We wondered if *Sphagnum* was growing longer with increasing proximity to the *Eriophorum* tussock simply because it was etiolated. We determined that 2% of the PAR was transmitted beneath the 3/3 (14% under the 2/3 and 48% under the 1/3). Other studies have shown that *Sphagnum* can grow when light is reduced by 97 to 98%, although it may be severely reduced (Sonesson *et al.* 1980, Riis & Sand-Jensen 1997). However, the capitula width was invariable beneath the 2/3 and 3/3 and were the same size as those beneath the 1/3 or without *Eriophorum*, so it is unclear if the biomass was actually reduced. Even if the *Sphagnum* was competing with *Eriophorum* for light, the fact remains that without the protection of a companion plant, *Sphagnum* had very little chance of surviving. Other studies have shown that while negative nurse plant interactions exist, they are outweighed by the positive benefits (Nobel 1989, Franco & Nobel 1990, Callaway *et al.* 1996).

Nurse plant interactions, such as those found at the Chemin du Lac Peatlands, are common in harsh environments with extreme conditions (Hacker & Gaines 1997). Nurse plants offer many benefits to the beneficiaries, including reduction of temperature extremes, amelioration of light conditions, improved moisture availability, soil stabilization, increased nutrient availability and predator protection (Latheef & Ortiz 1984, Gill & Marks 1990, Valiente-Banuet & Ezcurra 1991, Callaway 1992, Belsky 1994, Suzán *et al*. 1996, Martinez & Moreno-Casasola 1998, Raffaele & Veblen 1998). In the second experiment, discussed in the following section, we examine some of the factors which could explain the nurse plant association found on Droséra R95 and Sarracénie R97.

2.5.2 Nursing effect

a) The microclimate in a polytric carpet

Irradiance

The amount of PAR transmitted beneath the polytric carpet, fragments and peat was reduced compared to the bare peat. This reduction in light could explain, in part, the association found between *Sphagnum* and polytric at the Chemin du Lac peatland. A reduction in light, ranging from 38 to 80% has been found to increase *Sphagnum* growth (Sonesson *et al.* 1980, Murray *et al.* 1989a, Rochefort & Bastien 1998, Rochefort 2001).

Although *Sphagnum* requires a certain minimum of light to grow, exposure to high light levels can reduce the photosynthetic capacity (Harley *et al.* 1989, Murray *et al.* 1993). As long as the light compensation point is reached, *Sphagnum* will be able to grow in the shade. The light compensation point varies widely by species and environmental conditions. Values of 7.3 to 30 µmol m^{-2} s^{-1} have been reported for aquatic *Sphagnum subsecudum*, with light saturation occurring between 120 and 180 µmol m^{-2} s^{-1} (Riis & Sand-Jensen 1997). Field grown *Sphagnum angustifolium*, average light compensation at 20^{o}C was 127 µmol m^{-2} s^{-1}, with light saturation occurring at approximately 500 µmol m^{-2} s^{-1} (Harley *et al.* 1989). The light compensation point of forest grown *Sphagnum subsecundum* varied from 10 to 600 µmol m^{-2} s^{-1} (average = 171) during summer months, whereas light saturation varied from 200 to 1000 µmol m^{-2} s^{-1} (average = 552) over the same period (Skre & Oechel 1981). Based on these literature values, *Sphagnum* may be light limited in the polytric carpet, where only 5% PAR (38 µmol m^{-2} s^{-1}) was transmitted. In the fragments and straw, irradiance conditions appear ideal; generally above the light compensation point, but below levels of light saturation. On the bare peat, PAR will often be above light saturation levels, causing photoinhibitation.

Levels of light reported for the polytric carpet may not be representative of the light conditions experienced by *Sphagnum* growing in a carpet. Although we tried to place the sensor where *Sphagnum* capitula have been observed growing, once the moss was put back in place, the sensor was no longer visible, whereas *Sphagnum* capitula in a moss carpet are. In a study using similar measurement methods, PAR was reduced to less than 10% in a moss carpet (Keizer *et al.* 1985).

At least two studies have shown that shading favors an increase in length rather than biomass (Clymo 1973, Hayward & Clymo 1983). However, in both these studies the water table was never lower than 14 cm; PPFD is not reported, and may have been below the amount required for photoinhibition. It is also possible that under the drier and harsher conditions of our field site, the reduction in light would be more than compensated for by an increase in water content.

Air temperature

Our results demonstrate that the polytric carpet, fragments and straw covers are able to create a cooler microclimate for the *Sphagnum*. Knowing that high temperatures may limit the growth of *Sphagnum* by increasing evapotranspiration and respiration, reducing photosynthesis and destroying plant cells, polytric can play an important role as companion to *Sphagnum* by keeping it cooler (Harley *et al.* 1989, Balagurova *et al.* 1996, Sagot & Rochefort

1996, Riis & Sand-Jensen 1997). Many studies have shown that nurse plants can promote the establishment of beneficiary species by reducing soil temperatures. For example, on highly disturbed bare pit heaps, Richardson (1958) describes how a layer of moss and lichens nursed a graminoid by decreasing the soil temperature up to 10^{o}C. This effect has also been documented in peat bogs, the Sonoran Desert and sand dunes (Franco & Nobel 1988, Franco & Nobel 1989, Nobel 1989, Suzán *et al.* 1996, Martinez & Moreno-Casasola 1998, Boudreau & Rochefort 1999, Marcoux 2000).

Peat is warmer than polytric carpet or straw because it is dark brown, and therefore experiences a higher maximum temperature during the day (Ludwig & Harper 1958). Mulches such as straw, shade cloths and artificial nurse plants have been found to reduce surface temperatures by as much as 9.2 ^{o}C, as compared to bare peat (Price *et al.* 1998, Rochefort & Bastien 1998, Salonen 1992). Straw mulches are more resistant to heat penetration, and thus keep the soil cooler during the day (Price *et al.* 1998). Incidentally, as we worked at the Chemin du Lac site, we noticed that in many places on Sarracénie R97 the ground was blanketed with *Eriophorum* seed fluff. The moss growing under this fluff appeared greener than moss exposed to the sun (Figure 11). We hypothesize that the seed fluff of *Eriophorum*, released in large quantities during the hottest and driest part of the summer, is yet another facet of the protection provided by *Eriophorum* to beneficiary plants.

The greatest daytime temperature reduction (13.2 ^{o}C) was measured beneath the fragments of polytric. This is surprising, as we expected a greater temperature reduction beneath the straw, which was denser. An unintentional bias was created when positioning the sensor within each block; it was completely hidden beneath a clump of fragments. Because of this bias, we limit the remaining discussion to straw, polytric carpet and bare peat.

The optimal temperature for *Sphagnum* photosynthesis varies by species and climatic conditions. According to Skre and Oechel (1981), the optimum for *S. subsecundum* ranges from 6 to 18 ^{o}C. The optimal temperature for *S. squarrosum*, *S. angustifolium* and *S. warnstorfii* was near 20 ^{o}C; between approximately 13 to 30 ^{o}C, at least 75% of maximal this

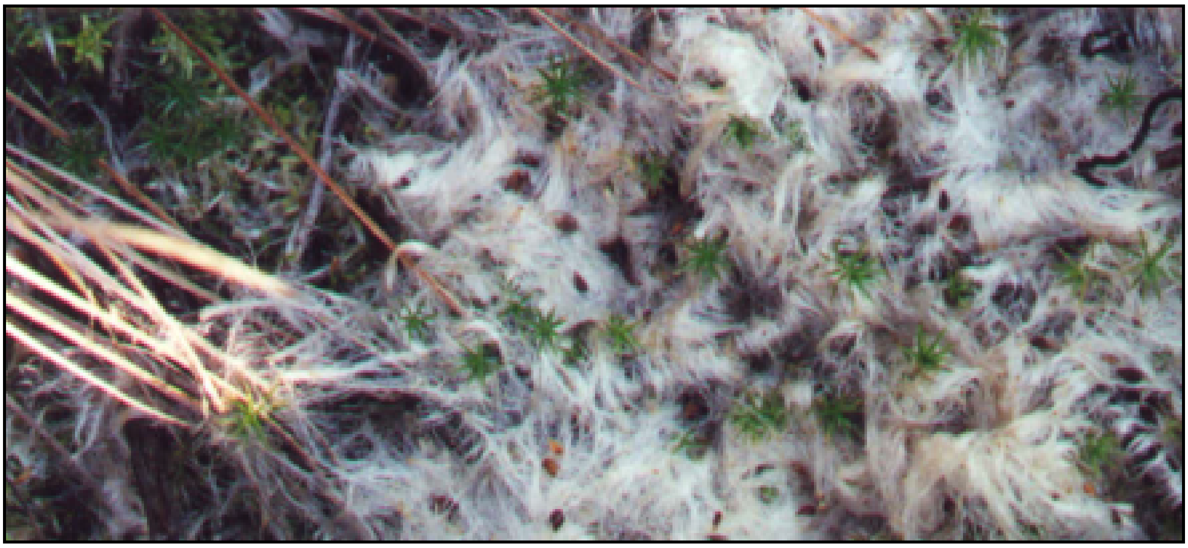

Figure 11. The protective effect of Eriophorum vaginatum *var.* spissum *seed fluff (the seed and its attached perianth bristles) on polytric at Sarracénie R97, a restored vacuum harvested peatland, Rivière-du-Loup, Québec. Polytric and* Sphagnum *covered with* Eriophorum *seed fluff. Note the bright green moss colour and open leaves. 27 July 2000.*

photosynthesis was maintained (Harley *et al.* 1989). According to Kurets *et al.* (1993), the rate of optimal photosynthesis for *S. balticum* was between 3.5 to 14.5 ^{o}C; 9 to 19 ^{o}C for *S. magellanicum*; 2 to 15.5 ^{o}C for *S. flexuosum*; and 8.5 to 16 ^{o}C for *S. fuscum*. Above 30 ^{o}C, the carbon balance for *S. fuscum* became negative. In this study, the polytric carpet and straw mulch reduced maximum temperatures during the day, and increased minimum temperatures at night. *Sphagnum* growing in these covers would thus spend more time in the ideal temperature window than *Sphagnum* growing on bare peat.

During all three experimental periods, there was little temperature difference between polytric carpet, straw and bare peat when temperatures were around 14 to 19 ^{o}C. As these temperatures are mostly within the ranges reported for optimal photosynthesis, the absence of differences between the treatments does not matter.

The degree of temperature reduction depended on climatic conditions. The greatest daytime temperature reduction, 11.1 ^{o}C in the carpet and 9.9 ^{o}C in the straw, occurred during the 8 to 24 August, when it was cool and wet. During the daytime when the temperature on bare peat ranged between 30 and 42 ^{o}C, it was 6.3 ^{o}C cooler on average in the polytric carpet than on the bare peat, a greater difference than that observed during the other two experimental periods. Even at 42 ^{o}C, is was more than 9 degrees cooler under the polytric than on the bare peat. We hypothesize that the abundant rainfall permitted polytric to remain with open leaves, thus reducing daytime temperatures compared to bare peat.

Polytric carpet and straw reduce the temperature compared to bare peat in a similar manner. The exception is at the end of July, where daytime temperatures on the bare peat exceeded 43 ^{o}C, reaching a maximum of 46 ^{o}C. During this time, it was on average 4.0 ^{o}C cooler under the straw than on the bare peat, but hotter in the carpet than on the bare peat, by as much as 2.7 ^{o}C. Our results for this period may be explained by the manner in which polytric reacts to hot dry periods. Polytric changes the arrangement of its leaves, folding them up along the stem to reduce water loss (Bayfield 1973). In this way, the polytric carpet decreases in density during hot and dry periods, which increases the exposure of *Sphagnum*, or in this case, the temperature sensor, to elevated temperatures.

In all covers, the temperature surpassed 42 ^{o}C on at least one occasion. However, these periods were interspersed with cooler and more humid periods at night, which could permit the survival of *Sphagnum* (Sagot & Rochefort 1996).

At night, temperatures were on average higher beneath the covers than on bare peat (except for the period from 8 to 25 August 2000). The maximal nightly increase was 3.8 ^{o}C in the polytric carpet and 2.8 ^{o}C in the straw. The covers increase the night-time temperatures by reducing radiative and convective heat loss. Even in hot dry periods at the end of July, polytric carpet remained effective at night. Because of lower night-time temperatures and possibly dew formation (Skre *et al.* 1983), polytric would not be in a situation of hydric stress and could thus keep its leaves open.

***Water content of* Sphagnum**

Sphagnum plants must remain hydrated to photosynthesize (Skre & Oechel 1981). The effects of complete desiccation on photosynthesis are severe. In as little as 2-4 days, plants may die following complete desiccation. Plants which survive may regain photosynthetic function, but at a much reduced rate (Skre & Oechel 1981, Schipperges & Rydin 1998). Our results confirm the existence of a moister microclimate in the polytric carpet, fragments and straw. The presence and amplitude of this microclimate depends on the temperature and precipitation.

A minimum of precipitation was necessary for the different covers to create an environment more moist than the bare peat. In the almost complete absence of precipitations with high temperatures (13 and 18 July), none of the covers offered an environment more moist than the bare peat. Estimates of the compensation water content, below which the net carbon exchange is negative, vary from 62 to 225% (Skre & Oechel 1981, Schipperges & Rydin 1998), depending on both species and environmental conditions. In mid-July the water content was well below 62%, the lowest moisture compensation point cited in literature. This leads us to conclude that mulch or companion plants, by themselves without any hydrological remediation cannot supply sufficient moisture to *Sphagnum* in drought conditions. This is different from Buttler *et al.* (1998) who determined that a plastic mulch could compensate for a low water table. However, their lowest water table was –40 cm, compared to minimum of –69 cm in our study.

With lower temperatures and higher precipitation towards the end of July and beginning of August, *Sphagnum* had a significantly higher water content in the carpet, straw and fragments. The amount of water required for optimal photosynthesis of *Sphagnum* varies by species and environmental conditions. Murray *et al.* (1998b) found that the optimal range for photosynthesis in *Sphagnum* moss is 600 to 1000%. Other authors have found optimal ranges of 400 to 2500% for various species (Schipperges & Rydin 1998), 725% for *Sphagnum subsecundum* (Skre & Oechel 1981), and 600 to 1000% for *Sphagnum fuscum* (Silvola & Aaltonen 1984). In this study, beneath the carpet fragments and straw, *Sphagnum* was within its optimal range for photosynthesis more often than on bare peat. Companion plants have been found to increase soil moisture many environments including: harvested peatlands, shrub-lands, deserts and disturbed bare pit heaps (Richardson 1958, Valiente-Banuet & Ezcurra 1991, Salonen 1992, Raffaele & Veblen 1998). Many studies have shown that the more humid conditions beneath vegetation or other protective covers were favourable to the growth of *Sphagnum* (Salonen 1992, Buttler *et al*. 1996, Rochefort & Bastien 1998, Price *et al*. 1998, Boudreau & Rochefort 1999).

It is clear that both temperature and precipitation influenced the water content of *Sphagnum*. For example, on the 25 July, daily average temperature was 35 ^{o}C, and total precipitation was 18.4 mm; *Sphagnum* averaged 36% water content. On the 8 August, although precipitation only increased by 25%, temperatures plummeted to 11 ^{o}C. Consequently *Sphagnum* water content averaged 668%, more than 17 times greater.

In general, the polytric carpet and straw provided similar moisture. The exception is 23 August, where *Sphagnum* in the polytric carpet was much drier than the straw. This may be explain by the physiology of polytric. When it is wet, polytric hold its leaves in a horizontal position to optimize photosynthesis. When it is very dry, polytric folds its leaves up along its stem to reduce evapotranspiration (Bayfield 1973). We hypothesize that under wet conditions at the end of August, polytric held its leaves horizontal to maximize photosynthesis. However, the extremely hot daytime temperatures promoted extensive evapotranspiration from the carpet, drying the *Sphagnum*. In a similar manner, Franco and Nobel (1990) found the nurse plant *Hilaria rigida* could either increase or reduce water uptake of the beneficiary, *Agave deseri*, depending on the precipitation pattern. Under conditions of high precipitation and high temperatures, polytric may therefore compete with *Sphagnum* for water. However, the water content of *Sphagnum* in the carpet was above 400%, well within the moisture range required by *Sphagnum*.

b) <u>Rate of water loss in Sphagnum</u>

Although conditions were supposed to be identical over the three trials, the effect of four treatments, carpet, fragments, straw and bare peat on the water content of *Sphagnum* differed considerably between trial. In the first trial, water loss was extremely rapid: 50% of the moisture was lost within the first 4 hours. Conditions were so drying that no cover was able to afford any protection to the *Sphagnum*. This rate of water loss is even greater than that reported by Skre *et al.* (1983), who found a 50% loss of diurnal leaf water content in about 16 hours.

In the second trial data was very variable. Variations of over 800% water content for *Sphagnum* stem sections in a same block clearly demonstrate the very small scale of microclimatic protection. The variation may also have been caused by differences in the initial water content of sphagnum stem sections.

In the third trial, the covers were able to reduce water loss of *Sphagnum*. After 48 hours, the *Sphagnum* was equally dry in all treatments, comparable in water content to the *Sphagnum* in the field on the 13 and 18 July. However, the rate of water loss was not equal in all treatments. Using 400% as optimal for *Sphagnum* growth (Schipperges & Rydin 1998), and 62% as the compensation water content (Skre & Oechel 1981), we see that *Sphagnum* water content was over 400% for approximately 15 hours in the straw, 13 hours in the fragments, 8 hours in the peat, and 7 hours in the carpet. *Sphagnum* was above 62% for approximately 40 hours in the carpet, fragments and straw, and 24 hours on the bare peat.

Similar to the pattern observed in the field on 23 August, when initial water conditions were saturated and temperatures high, polytric competed with *Sphagnum* for water. However, as moisture dropped, polytric likely closed its leaves to reduce water loss, thus providing more moisture for *Sphagnum* compared to the bare peat, and maintaining the water content of *Sphagnum* above the critical moisture point. This switch occurred between 16 and 24 hours.

c) <u>Polytric as a seed trap and germination bed</u>

Parker et al. (1997) suggests that *Polytrichum commune* may help other plants establish by capturing their seeds and allowing them to germinate. In this study we present evidence that a polytric carpet captures more seeds than bare soil. Tooren (1988) determined that the bryophyte layer in a chalk grassland acted as a seed trap, accumulating large numbers of seeds. Mallik et al. (1984) showed that bryophyte layers in heathlands can contain large numbers of viable seeds. Other nurse plants with a flat, cushion growth form have been noted as seed traps for wind-dispersed seeds (Griggs 1956, Kikvidze 1993). Welden (1985) explains how nurse plants reduce wind velocity, thus allowing the deposition of fine wind-born materials, which presumably would include seeds. In contrast, Equihua and Usher (1993) found that the *Calluna vulgaris* seedbank from a moss carpet was either smaller, or had a more limited response to favorable watering conditions than that of bare soil. However, these seeds were not wind-dispersed.

Once the seeds have been trapped by a nurse plant, they are offered a protected environment in which to germinate and grow. However, not all plants grow better in a bryophyte carpet. In this study, although *Eriophorum* seeds were captured by a polytric carpet, very few germinated and survived more than a year, whereas on the bare peat, where up to 46% fewer seeds were retained, there were more than 6 times the number of one year *Eriophorum* plants. *Polytrichum commune* has been found to inhibit the growth of other heathland plants (Corradini & Clément 1999). *Polytrichum formosum* has been shown to reduce soil mineralisation, probably caused by an allelopathic effect (Rozé 1987). It is possible *Eriophorum* seedlings were subject to an allelopathic agent in the polytric carpet.

Groeneveld (Chapter 1) showed that fir seedlings planted in polytric carpets survived much better than those planted in bare peat. Other researchers have found reduced emergence of seed in bryophyte carpets, although those which managed to emerge had increased survival and/or biomass, and with one species (*Calluna vulgaris*) producing about 10 times more reproductive biomass than seedlings growing on bare ground (Johnson & Thomas 1978, Keizer *et al*. 1985, Equihua & Usher 1993). Other species however show opposite tendencies: high emergence in bryophyte layers, followed by severe mortality, possibly due to reduced rooting capacity (Tooren 1988). It is safe to say that a polytric carpet will be detrimental to the growth of some species, such as *Eriophorum*, while enhancing the survival of other species, such as *Abies balsamea*. Reduced light within a bryophyte carpet may limit seed germination (Equihua & Usher 1993). Fir can germinate under very low light (Frank 1990). *Eriophorum*, on the other hand, has a drastically reduced or no germination in the dark (Bliss 1958, Wein & MacLean 1973). Being a pioneer plant, *Eriophorum* does not require nursing to establish. Fir, on the other hand, is a late succession species, requiring shading and protecting during its early years. This is perfectly demonstrated at the study site, where the bare peat is dotted with living *Eriophorum* tussocks but littered with dead fir seedlings.

2.6 Conclusions and recommendations

Many authors have recently suggested that nurse plants may hasten the re-establishment of a typical peatland flora (Buttler *et al.* 1996, Boudreau & Rochefort 1999, Robert *et al.* 1999, Marcoux 2000, Tuitilla *et al.* 2000). In this paper we demonstrate that: 1) *Sphagnum* grows better in the presence of the nurse plants *Eriophorum* and polytric on two restored peatlands, and 2) A polytric carpet can generate microclimatic conditions favorable for the proliferation of *Sphagnum*. A straw mulch, and to a lesser degree polytric fragments, also generate microclimatic conditions more favorable than those found on bare peat.

As discussed in the companion paper on polytric and peat stability (Chapter 1), straw may be the best option for protecting *Sphagnum* as it does not compete for water and may release nutrients as it decomposes. However it degrades rapidly (within a few years), and on windy sites it may blow away. On sites where peat instability is a problem and longer term protection of *Sphagnum* is needed, the facilitation by a polytric carpet is an interesting aid to restoration.

Establishing a polytric carpet is simple. In fact, with current restoration methods, it may be impossible to avoid. Simply spreading topspit collected from a bog where polytric is present, naturally occurring among the *Sphagnum* layer, lightly fertilizing with phosphorus and covering with a straw mulch is sufficient to ensure a continuous polytric carpet within a year (personal observations).

Polytric giving way to *Sphagnum* is a natural succession (Johnson 1982, Foster 1984, Jasieniuk &, Kuhry 1994, Robert *et al.* 1999). As nuclei *Sphagnum* colonies expand in size and coalesce to form a carpet, we expect that it will displace the polytric and form a new acrotelm. Several large scale restoration projects currently underway will allow us to test this prediction.

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CONCLUSION

Plusieurs auteurs ont récemment suggéré que les plantes compagnes peuvent accélérer la revégétation des tourbières abandonnées suite à l'exploitation, par une flore typique de tourbière (Buttler *et al.* 1996, Boudreau & Rochefort 1999, Robert *et al.* 1999, Marcoux 2000, Tuitilla *et al.* 2000) . Une attention particulière a été portée dans ce mémoire aux moyens par lesquels le polytric, une plante compagne, peut faciliter le rétablissement des sphaignes, des plantes clés pour restaurer les fonctions de tourbières. Deux grandes lignes de recherche ont été poursuivies : la stabilisation du substrat et l'amélioration du microclimat par le polytric.

Cette étude a permis de confirmer que : 1) Les sphaignes croissent davantage en présence de deux plantes compagnes, le polytric et la linaigrette dense, sur deux sites de tourbières restaurés. 2) Un tapis de polytric génère des conditions microclimatiques favorables à la croissance des sphaignes. Un paillis de paille, et à moindre effet des fragments de polytric, génèrent aussi des conditions microclimatiques supérieures à celles présentes sur la tourbe mise à nue par exploitation. 3) Un tapis de polytric stabilise le substrat, notamment en réduisant le soulèvement gélival, améliorant ainsi la croissance de plantes telles que le sapin baumier.

Sur les sites où l'instabilité du substrat ne pose aucun problème, la paille est sans doute le meilleur paillis, car elle confère les mêmes avantages que le tapis de polytric, du moins immédiatement après épandage. Contrairement au tapis de polytric, la paille a l'avantage d'offrir une protection aux moments les plus chauds et secs de l'année, et ne risque jamais de faire concurrence avec les sphaignes pour l'eau ni pour les nutriments. Au contraire, durant sa décomposition elle pourrait libérer des éléments nutritifs.

Par contre la paille se décompose rapidement et après seulement 2 ou 3 ans elle n'est plus en mesure d'offrir une protection aux sphaignes, même si celles-ci en ont encore besoin. Sur les sites sujets à de forts vents, la paille s'envole facilement perdant de sa densité, et réduisant par ce fait son effet protecteur. Dans de telles situations, le polytric pourrait être utilisé avec la paille pour augmenter la protection offerte aux sphaignes, car les clones de polytric ne s’envolent pas au vent. Contrairement à la paille, le polytric se propage rapidement et augmente en efficacité avec le passage du temps.

Les techniques de restauration doivent être peu coûteuses et simples en application. Pour être utile à grande échelle, l’établissement d’un tapis de polytric doit donc être facile. En effet, avec les techniques courantes de restauration, il semble assez facile de promouvoir la formation d’un tapis de polytric. Le polytric est trouvé de façon systématique dans les tourbières ombrotrophes naturelles. L’inclusion d’une petite quantité dans le matériel à répandre (topspit), jumelé avec une dose minimale de fertilisant de phosphore en assure la multiplication rapide à la grandeur du site. Un paillis de paille reste essentiel, car le polytric requiert au moins deux saisons de croissance pour atteindre une taille appréciable. Il était très évident dans cette étude que le polytric lui-même bénéficiait de la protection offerte par la paille.

L’importance de la compétition entre le polytric et la sphaigne demeure inconnue. Une question intéressante est : «Sous quelles conditions est-ce que la compétition entre le polytric et les sphaignes annule les bénéfices de l’association?». Des recherches approfondies sur ce sujet sont nécessaires.

La succession polytric → sphaignes est tout à fait naturelle (Jasieniuk et Johnson 1982, Foster 1984, Kuhry 1994, Robert *et al.* 1999). Ainsi, avec le temps, nous nous attendons à ce que les colonies de sphaignes nucléaires se réfugiant dans les clones de polytric prennent de l’expansion pour se fusionner et former un tapis continu. Graduellement, avec la formation d’un acrotelme, les sphaignes pourraient supplanter le polytric. Des projets en cours sur la restauration à grande échelle nous permettront de tester ces prédictions.

Dans les tourbières exploitées, abandonnées et non restaurées, les plantes qui désirent s’y installer ne peuvent choisir entre le polytric et un paillis de paille. La protection par une plante compagne est leur seul recours : même s’il existe de la compétition entre les sphaignes et le polytric, le retour des sites abandonnés vers des systèmes accumulateurs de tourbe serait peut être impossible sans la présence de plantes compagnes pionnières.

Références citées dans la conclusion

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ANNEXE A : Tableaux d'ANOVA

Table 1. Vertical movement of dowels to 7 November 2000.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	2.45	0.49	2.00	0.1143
STRAW	1	10.33	10.33	42.01	0.0001
POL	2	8.44	4.22	17.16	0.0001
STRAW*POL	2	8.08	4.04	16.43	0.0001

Table 2. Vertical movement of fir to 7 November 2000.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	4.60	0.92	4.05	0.0079
STRAW	1	8.50	8.50	37.44	0.0001
POL	2	9.35	4.67	20.58	0.0001
STRAW*POL	2	6.29	3.14	13.85	0.0001

Table 3. Vertical movement of dowels to 29 May 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	8.40	1.68	3.94	0.0090
STRAW	1	23.04	23.04	54.08	0.0001
POL	2	105.31	52.65	123.60	0.0001
STRAW*POL	2	15.85	7.93	18.60	0.0001

Table 4. Vertical movement of fir to 29 May 2001. Data has been log transformed.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	0.54	0.11	7.29	0.0002
STRAW	1	0.32	0.32	21.48	0.0001
POL	2	3.84	1.92	128.60	0.0001
STRAW*POL	2	0.08	0.04	2.85	0.0769

Table 5. Health of fir seedlings on 24 August 2000.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	0.08	0.02	1.20	0.3372
STRAW	1	0.01	0.01	0.73	0.4005
POL	2	0.09	0.05	3.55	0.0441
STRAW*POL	2	0.02	0.01	0.91	0.4149

Table 6. Health of fir seedlings on 29 May 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	0.73	0.15	1.51	0.2237
STRAW	1	0.89	0.89	9.20	0.0056
POL	2	0.41	0.21	2.15	0.1380
STRAW*POL	2	0.21	0.10	1.07	0.3568

Table 7. Health of fir seedlings on 16 October 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	5.70	1.14	1.99	0.1149
STRAW	1	3.35	3.35	5.85	0.0232
POL	2	1.60	0.80	1.40	0.2664
STRAW*POL	2	5.60	2.80	4.89	0.0161

Table 8. Percent soil moisture on 29 April 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	0.04	0.01	1.78	0.1773
STRAW	1	0.06	0.06	14.91	0.0015
POL	1	0.02	0.02	4.19	0.0586
STRAW*POL	1	0.00	0.00	1.19	0.2922

Table 9. Distance to frost line to 25 April 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	4.05	0.81	1.10	0.3854
STRAW	1	5.71	5.71	7.76	0.0100
POL	2	14.02	7.01	9.53	0.0008
STRAW*POL	2	12.37	6.18	8.41	0.0016

Table 10. Distance to frost line to 30 April 2001.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	1.20	0.24	0.13	0.9830
STRAW	1	23.16	23.16	12.92	0.0015
POL	2	20.93	10.46	5.84	0.0086
STRAW*POL	2	5.79	2.90	1.62	0.2197

Table 11. Length of *Sphagnum* at Droséra R95.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
POL	1	0.75	0.75	1.08	0.3010
ERI	3	26.49	8.83	12.62	0.0001
POL*ERI	3	0.61	0.20	0.29	0.8331

Table 12. Length of *Sphagnum* at Sarracénie R97.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
POL	1	0.34	0.34	0.59	0.4429
ERI	3	6.39	2.13	3.70	0.0120
POL*ERI	3	0.12	0.04	0.07	0.9773

Table 13. Width of *Sphagnum* at Sarracénie R97.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
POL	1	0.08	0.08	1.42	0.2358
ERI	2	0.00	0.00	0.03	0.9662
POL*ERI	2	0.12	0.06	1.03	0.3585

Table 14. Water content of *Sphagnum* sections in the field. Data has undergone a cubic transformation. Tests of Hypotheses using the Type III MS for BLOC*TRT as an error term.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	1.94	0.39	0.84	0.5430
TRT	3	19.41	6.47	13.99	0.0001
BLOC*TRT	15	6.94	0.46	1.24	0.2599
DATE	5	845.82	169.16	451.61	0.0001
DATE*TRT	15	14.95	1.00	2.66	0.0021

Table 15. Irradiance in the field.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	5	0.04	0.01	1.29	0.2826
TRT	3	7.06	2.35	361.97	0.0001

Table 16. Trial 1. Water loss of *Sphagnum* in growth chamber. Data has undergone a square root transformation. Tests of Hypotheses using the Type III MS for BLOC*TRT as an error term.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	3	113.47	37.82	13.51	0.0011
TRT	3	10.77	3.59	1.28	0.3383
BLOC*TRT	9	25.20	2.80	0.76	0.6508
TIME	8	15411.76	1926.47	524.89	0.0001
TRT*TIME	24	113.70	4.74	1.29	0.1928

Table 17. Trial 2. Water loss of *Sphagnum* in growth chamber. Data has undergone a square root transformation. Tests of Hypotheses using the Type III MS for BLOC*TRT as an error term.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	3	420.95	140.32	3.70	0.0552
TRT	3	238.23	79.41	2.10	0.1711
BLOC*TRT	9	341.06	37.90	1.91	0.0597
TIME	8	15208.55	1901.07	95.86	0.0001
TRT*TIME	24	506.90	21.12	1.06	0.3980

Table 18. Trial 3. Water loss of *Sphagnum* in growth chamber. Tests of Hypotheses using the Type III MS for BLOC*TRT as an error term.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	3	44994.31	14998.10	1.95	0.1917
TRT	3	273202.37	91067.46	11.86	0.0018
BLOC*TRT	9	69121.48	7680.16	1.11	0.3616
TIME	8	26947242.77	3368405.35	488.27	0.0001
TRT*TIME	24	422276.15	17594.84	2.55	0.0008

Table 19. *Eriophorum* seed retention on 8 August 2000. Count after one hour.

Source	df	Sums of Squares	Mean Square	F Value	Pr > F
BLOC	2	110.86	55.43	1.03	0.4920
TRT	1	2591.68	2591.68	48.28	0.0201

Table 20. *Eriophorum* seed retention on 8 August 2000. Count after two hours.

Source	**df**	**Sums of Squares**	**Mean Square**	**F Value**	**Pr > F**
BLOC	2	187.61	93.81	2.86	0.2591
TRT	1	3280.68	3280.68	100.00	0.0099

Table 21. *Eriophorum* seed retention on 24 August 2000.

Source	**df**	**Sums of Squares**	**Mean Square**	**F Value**	**Pr > F**
BLOC	5	637.49	127.50	2.52	0.1662
TRT	1	208.33	208.33	4.12	0.0980

Table 22. Number of 1 year *Eriophorum* seedlings on 30 May 2001.

Source	**df**	**Sums of Squares**	**Mean Square**	**F Value**	**Pr > F**
BLOC	5	39.33	7.87	1.10	0.4027
TRT	3	78.33	26.11	3.64	0.0375

ANNEXE B

Thème de L'été 2000