MARTHA D. GRAF

RESTORING FEN PLANT COMMUNITIES ON CUTAWAY PEATLANDS OF NORTH AMERICA

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Résumé

En Amérique du Nord, peu de recherches ont été réalisées sur la restauration des fens. De plus en plus, les industries de la tourbe sont appelées à restaurer des tourbières abandonnées après extraction de la tourbe où les conditions pédologiques ressemblent à celles de fens. Le but de ce projet de recherche est de développer une base écologique à la restauration des fens en Amérique du Nord. Dans un premier temps, j'ai examiné les successions végétales dans les tourbières qui ont été exploitées jusqu'aux strates de tourbe minérotrophe afin de déterminer quelles plantes recolonisent les tourbières abandonnées et sous quelles conditions. L'échantillonnage de 28 tourbières abandonnées à travers le Canada et dans l'État du Minnesota aux États-Unis montre que la revégétation spontanée des secteurs avec tourbe à nue diffère de la végétation colonisant les fens naturels des régions adjacentes. Particulièrement, les *Sphagnum* et les *Carex*, qui abondent dans les fens naturels, ne se retrouvent pas dans les fens exploités puis abandonnés par aspirateur. La majorité des fens abandonnés ont vite été recolonisés par des espèces plutôt apparentées aux milieux humides sans tourbe. Dans un deuxième temps j'ai testé des méthodes de réintroduction d'espèces typiques de fens. Une expérience de trois ans sur le terrain montre qu'une méthode de réintroduction par épandage des diaspores provenant d'un site d'emprunt est efficace pour l'établissement des *Carex* et de sphaignes. Jusqu'à maintenant, l'accent a toujours été mis sur les *Carex* et les plantes vasculaires pour la restauration des fens. Afin d'en savoir plus sur les conditions environnementales nécessaires à la régénération des mousses typiques de fens, j'ai effectué des expériences en serre et sur le terrain. Un ombrage jusqu'à 50 % améliore la régénération des mousses. Le niveau d'eau optimal pour la plupart des mousses se situe juste en dessous de la surface et les sphaignes sont les espèces de bryophytes qui se régénèrent le mieux. Tous ces résultats devraient nous permettre de mieux cibler les efforts pour la restauration des fens.

Abstract

In North America, very little research has been carried out on the restoration of fens. Increasingly, peat industries are faced with the task of restoring abandoned, harvested peatlands where the environmental conditions closely resemble a fen. The goal of this research project is to explore techniques for the restoration of fen plant communities on vacuum-extracted peatlands in Canada. The plant succession on abandoned, harvested peatlands where peat has been extracted to the minerotrophic layers was examined to determine which plants frequently colonize these abandoned sites. After surveying 28 abandoned harvested fens across Canada and in Minnesota, USA, the spontaneous vegetation was not similar to the vegetation found on undisturbed fens from the same areas. Specifically, *Sphagnum* and *Carex* species, abundant on undisturbed fens were not found on abandoned, vacuum-harvested fens. However, harvested fens were quickly recolonized by marsh species if they were not actively drained. A field experiment was carried out to test two reintroduction techniques for *Sphagnum* and *Carex* species as well as the use of phosphate fertilizer. The application of donor diaspores, commonly used for dry peatland restoration was effective for reintroducing both *Carex* and *Sphagnum* species. In the past, the focus of fen restoration has been vascular plants. In order to find out more about the environmental conditions necessary for the vegetative regeneration of eight common fen mosses, field and greenhouse experiments were carried out. The presence of shade was shown to greatly improve the regeneration of the mosses. The optimal water level for most species was just under the surface and *Sphagnum* species were shown to be the most successful at regenerating. The findings of this research will aid the development of strategies for the restoration of fens on harvested peatlands.

Preface

This thesis is presented in the form of a series of articles. The first chapter is a general introduction and literature review. The second chapter was submitted to the journal *Wetlands* in September 2006. This article is currently in the final stages of revision by the journal's editor. I am the first author, Dr. Line Rochefort is the second author and Dr. Monique Poulin is the third author. I developed the research hypotheses, Dr. Rochefort and Dr. Poulin helped with the project design. I was responsible for data collection, data analysis and manuscript preparation. Dr. Poulin helped with the data analysis and both Dr. Rochefort and Dr. Poulin assisted in the manuscript preparation with editorial comments.

For the third, fourth and fifth chapters I am the first author and Dr. Line Rochefort is the second author. Chapter three is being prepared for submission to *Écoscience* and chapter four is being prepared for submission to *Applied Vegetation Science.* The fifth chapter was submitted to the journal *Restoration Ecology* in February 2007. For these articles I was responsible for developing the research hypotheses and Dr. Rochefort assisted with the project design. I carried out the data collection, analysis and manuscript preparation. Dr. Rochefort assisted with the manuscript preparation.

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I would like to thank my family for all of the encouragement, love and long-distance support. I would especially like to thank the women in my life, Mirm and Meg, for making me who I am today.

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Table of Contents

List of Tables

List of Figures

LIST OF APPENDICIES

CHAPTER ONE

GENERAL INTRODUCTION

Problem Definition

Peatlands are exceptional ecosystems because of their biodiversity, their importance as global carbon sinks and their contribution to the stabilization of the water cycle. Peatlands are simultaneously viewed as a valuable resource. Peat mining is a common industry in the boreal regions of the Holarctic, especially Finland, Russia and Ireland, where peat is used for fuel (Chapman *et al.* 2003). In North America, peat is primarily used as a growing substrate for horticulture and is a significant industry in Québec and New Brunswick, and, to a limited extent, in Alberta, Michigan, Minnesota and Colorado (Cooper and MacDonald 2000).

Peatland restoration attempts to resolve the conflict between the environmental and economic value of peatlands by allowing the return of ecological functions after peat harvesting. Restoration methods for ombrotrophic peatlands, or *bogs*, have been successfully developed (Rochefort 2001; Rochefort *et al.* 2003). However, in practice, peat harvesting frequently leads to the exposure of the underlying minerotrophic peat and mineral deposits. These sites are richer in minerals and higher in pH than the preexisting bog, thus creating conditions which are sub-optimal for bog community restoration (Wind-Mulder *et al.* 1996; Wind-Mulder and Vitt 2000). Restoration towards a minerotrophic peatland, or *fen*, is more desirable for such sites.

Little research has been carried out on fen restoration in North America (Cooper and MacDonald 2000; Cobbaert *et al.* 2004). Several European countries, most notably England, Germany and the Netherlands, have carried out extensive research on the restoration of fen plant communities (Wheeler and Shaw 1995; Pfadenhauer and Grootjans 1999; Kratz and Pfadenhauer 2001; Lamers *et al.* 2002). European peatlands have a long history of intense use for agriculture, grazing and peat extraction for fuel use. Much of the European fen restoration research is not directly transferable to North America because of different land use and restoration goals. Fen restoration in Europe often aims to return to the historical land use, usually extensive agriculture, (Fojt 1995; Pfadenhauer and Grootjans 1999; Lamers *et al.* 2002), while fen restoration in North America aims to return to the peatland's natural state. It remains unknown which techniques are suitable to reestablish natural conditions of a fen in North America. Therefore, the goal of the present research project is to define target vegetation groups which will aid the return of the North American fen community structure and environmental functions and then to explore restoration strategies which will enable the establishment of these target groups.

ASSEMBLY RULES FRAMEWORK

The framework of this research project is based on the assembly rules approach. This approach was created by community ecologists to understand constraints on a species pool, either biotic or abiotic, which control the distribution and abundance of species in a community (Fox 1999). Assembly rules are a helpful tool in restoration ecology because if the constraints of a system are defined, restoration efforts can focus on manipulating these constraints to steer succession towards the desired community (Temperton *et al.* 2004).

Most literature on community assembly views a community as a series of species pools where species are filtered out through various constraints (Figure 1.1) (Belyea 2004). In such filter models, all species found in the region are represented by the total species pool. Due to environmental and dispersal constraints, only a sub-set of the total species pool, the ecological species pool, actually establishes in a given community. Eventually, some of the species from the ecological species pool will be filtered out due to internal dynamics within the community, such as competition among species. The actual species pool consists of species from the ecological species pool that persist in a community (Figure 1.1) (Belyea 2004).

While the assembly rules approach is an important tool for community and restoration ecology, differences between these areas of ecology make filter models insufficient for restoration ecology. Although filter models provide insight into what limits each pool's species membership and help identify restoration strategies, they provide little information about community structure or ecosystem function (Belyea 2004). However, understanding and targeting the desired structure and ecosystem functions of the degraded system is the crux of restoration ecology (Ehrenfeld and Toth 1997).

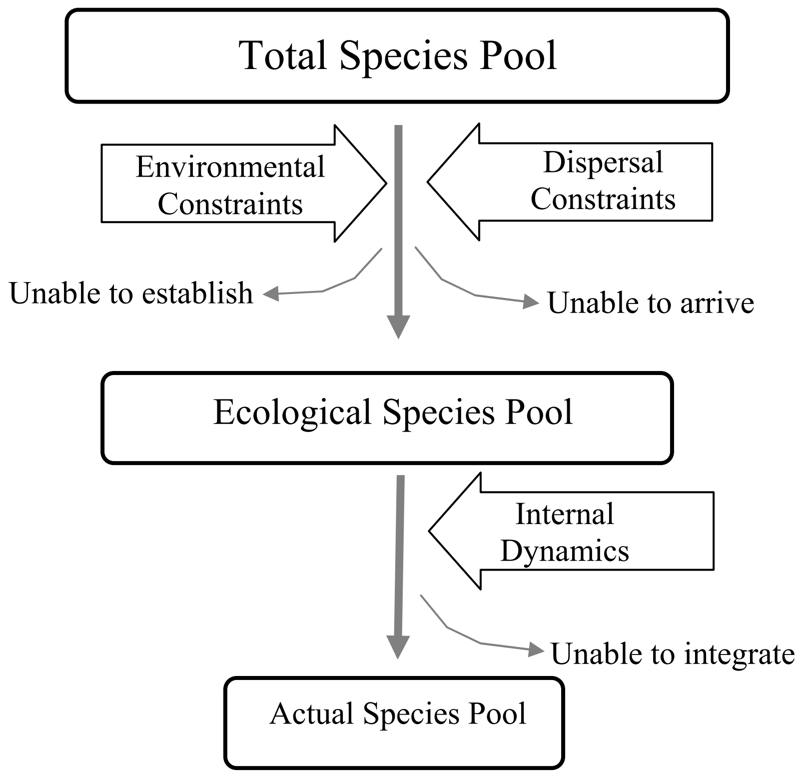

Figure 1.1. A filter model of plant colonization based on the assembly rules approach of changes to a system during stages of colonization (simplified from Belyea 2004). The rectangles represent species pools. The total species pool is the largest as it represents all species in a given region. The ecological species pool consists of species that successfully establish in a community despite environmental and dispersal constraints. The actual species pool consists of the species which persist in the community despite internal dynamics, such as competition. The open arrows represent constraints which limit membership to the species pools located below each arrow.

Another limitation of filter models is that the total species pool is less important in restoration ecology because some target species are no longer found in the region and are therefore not included in the total species pool (Figure 1.1). For restoration, it is important to understand structural and functional differences between degraded and undisturbed sites. Once these differences are understood a target species pool, including all species necessary to the return of the system's structure and/or function, can be identified.

Finally, filter models are static and are ideal for a passive understanding of a system. In contrast, active manipulation of the constraints is needed to achieve restoration. A framework for restoration ecology should include manipulation of the system's constraints.

I propose a new framework inspired by the assembly rules theory, but tailored to restoration ecology. The new model begins with comparing the structure and function of degraded species pools with those of an undisturbed species pools (Figure 1.2). This comparison identifies target restoration species. Once target species have been identified, restoration strategies can be tested to improve environmental and dispersal constraints. The combination of species from the target and degraded species pools represents the novel species pool. In order to ensure that the target species can persist on the restoration site, the internal dynamics between species should be monitored. If aggressive competitors are part of the degraded species pool, they might outcompete the target species. On the other hand, target species establishment may be improved by facilitation. Eventually, the restored species pool, which should be similar in the structure and/or function to the undisturbed species pool, should be reached. Long-term monitoring can verify whether the community structure and environmental functions of the restored site are indeed similar to those found on undisturbed sites. This framework is applicable to any restoration project, but in this research project it is applied to the restoration of a fen community on harvested peatlands in North America.

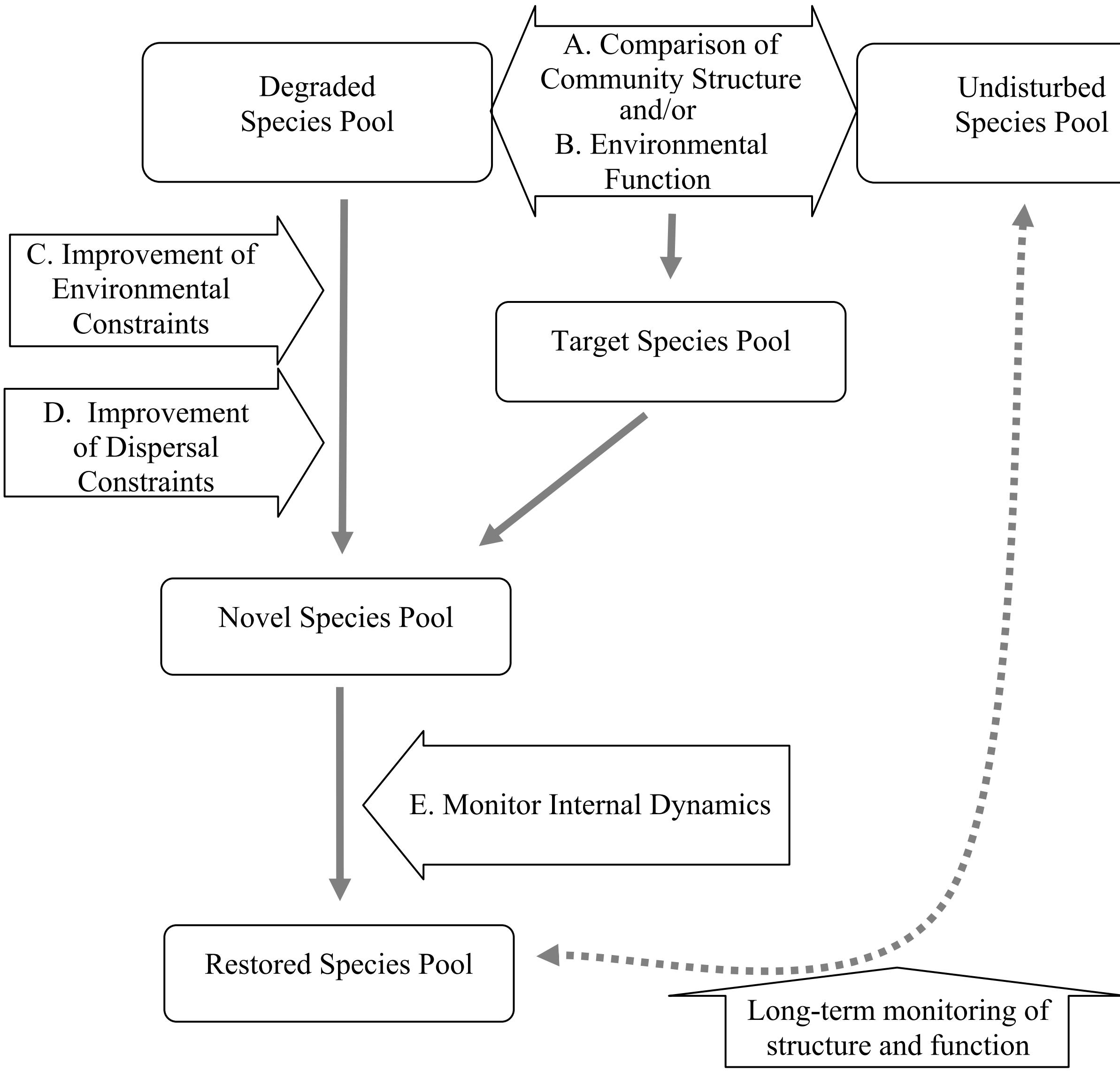

Figure 1.2. A new framework for restoration projects inspired by assembly rules approach. The rectangles represent species pools which are pertinent to restoration. Open arrows represent active measures which should be explored to develop strategies for restoring a degraded system. Solid arrows represent the direction of the species pool development during restoration and the dashed arrow represents similarity between species pools.

The background information included in this chapter is centered on important aspects of the model discussed above (Figure 1.2). First, I define peatlands and describe the structure and function of natural peatlands. Then, I describe the environmental and dispersal constrains acting on harvested peatlands and, finally, I describe the internal dynamics of these sites.

BACKGROUND INFORMATION

PEATLANDS

Peatlands are defined as fresh-water wetlands which accumulate extensive organic matter or peat (Warner and Rubec 1997). Peat is the partially decomposed remains of plants which form where the rate of production exceeds the rate of decomposition (Mitsch and Gosselink 2000). Peatlands are ubiquitous in the cold, wet climates of Northern Europe, Siberia and North America and can also be found in the tropical climates of Asia. *Fens* and *bogs* are the two sub-classes of peatlands and can be differentiated according to hydrology, peat chemistry and plant composition (Table 1.1).

Bogs are extremely acidic peatlands with no significant inflow or outflow of groundwater and are thus 'rain-fed' (ombrogenous). Fens are peatlands which receive runoff from surrounding or underlying mineral soils (geogenous) and are, therefore, less acidic and richer in minerals. Fens, unlike bogs, exhibit a spectrum of pH values and several distinct vegetation communities, depending on the amount of groundwater inflow. Fens can be categorized into three broad groups: poor fens, moderate-rich fens and extreme-rich fens (Vitt and Chee 1990). Poor fens have the least amount of groundwater flow and extreme-rich fens have the most.

Most North American peatlands begin as fens and develop into bogs as the peat gradually accumulates to a thickness where the top layer no longer has contact with groundwater, making precipitation the only water source (Kuhry and Nicholson 1993). Thus, by mining the *Sphagnum* peat layer, the successional clock is set back thousands of years to the peatland's earlier, minerotrophic state.

Table 1.1. The defining hydrological, chemical and vegetation criteria for peatlands.

Peatland Type	Hydrology	Chemistry		Vegetation
		pH	Ca^{2+}	
Bog	Ombrogenous	3.0 to 4.5	<3 mg l^{-1}	*Sphagnum* moss Ericaceous shrubs
Poor Fen	Geogenous	4.5 to 5.7	5 mg l^{-1}	*Sphagnum* Sedges
Moderate-rich fen	Geogenous	5.5 to 7.0	5 to 35 mg l^{-1}	Brown mosses Sedges
Extreme-rich fen	Geogenous	7.0 to 8.5	5 to 35 mg l^{-1}	Brown mosses Sedges

Source: Vitt 2000

PEATLAND COMMUNITY STRUCTURE

Fen community structure (Figure 1.2, point A.) is chararacterized by *Carex* and fen bryophytes. The main floristic difference between bogs and fens is that fens are typically sedge-dominated, while bogs generally lack *Carex* (Table 1.1) (Glaser 1992; Vitt 2000). The microtopography of bogs and fens also differ. The acrotelm (see next section for definition) of bogs is deep and a large percentage of the bog area consists of hummocks. Poor and rich fens have a shallow acrotelm and a higher percentage of area is covered by lawns and carpets (Vitt 1990). However, when bogs, poor fens and rich fens are floristically compared through multivariate analysis, bogs and poor fens are normally more closely related than poor fens and rich fens (Nicholson *et al.* 1996). Bogs and poor fens are dominated by *Sphagnum* mosses, while moderate and rich fens are dominated by 'brown mosses,' which are true mosses largely from the Amblystegiaceae family (Vitt 1990) (Table 1.1).

PEATLAND ENVIRONMENTAL FUNCTION

Peatlands are important ecosystems on a global level due to their role in stabilizing water levels and storing carbon (Figure 1.2, point B.). The diplotelmic structure of peatlands is vital to these functions as it regulates water storage and discharge, thus creating constantly saturated conditions ideal for carbon storage (Price *et al.* 2003). This structure is composed of a two-layered soil structure, the *acrotelm* and the *catotelm*. The acrotelm is the uppermost layer of the peat deposit and is composed of live and slightly decomposed vegetation. It is characterized as having a variable water content, high hydraulic conductivity, periodic aeration and intense biological activity (Ivanov 1981; Ingram 1983). The catotelm, the lower level of more decomposed peat, is characterized by constant water content, very low hydraulic conductivity, and anaerobic conditions. Carbon is sequestered by the submergence of organic matter at the base of the acrotelm, or, as seen from the opposite perspective, by the thickening of the catotelm (Clymo 1984).

The presence of bryophytes is also an important component to the peatland's ecosystem functioning (Vitt 2000). *Sphagnum* is especially important to acrotelm hydroregulation because the loosely woven, expansible surface creates the capacity to store a large amount of water (Clymo 1982). *Sphagnum* mosses and some species of brown mosses possess properties that create an acidic, nutrient poor, heat-insulating, and slowly permeable environment, ideal for peat accumulation (Andrus 1986; Rochefort 2000). Central goals of peatland restoration are the reestablishment of (i) a plant cover dominated by bryophytes and (ii) diplotelmic hydrological layers, which ensure the return of important peatland functions (Rochefort 2000).

Environmental Constraints

Harvested peatlands often become harsh environments where the soil moisture is insufficient for the establishment of typical peatland vegetation (Figure 1.2, point C.) (Larose *et al.* 1997). The low soil moisture is due to the installation of deep drainage ditches around the perimeter and smaller drainage ditches at 30 meter intervals throughout the peatland to enable peat extraction. The live vegetation layer (acrotelm) is removed to expose the more decomposed peat of the catotelm for harvesting. The removal of the acrotelm profoundly affects the water storage capacity, the nature and magnitude of evaporation losses as well as soil processes, including carbon storage (Price *et al.* 2003). Without the attenuating effects of the acrotelm, the water level fluctuates greatly. The drained peat undergoes subsidence in the unsaturated zone and compression in the saturated zone, which leads to a major change in the soil pore structure. The change in pore structure decreases the water storage capacity and hydraulic conductivity which exacerbate the fluctuation of the water table (Price *et al.* 2003). All of these factors create conditions which are unfavorable to the establishment of plants, especially peatland bryophytes.

The bare harvested peatlands are characterized by extreme variation in temperature and soil moisture. Additionally, bare peat can be disturbed by needle-ice formation if the site is rewetted. This creates the phenomenon known as frost heaving, which can kill vascular plants by exposing their roots (Groeneveld and Rochefort 2005). All of the above-mentioned factors create a highly unstable surface substrate and hostile conditions on abandoned, harvested peatland. Lavoie and Rochefort (1996) found that without active restoration measures the structure and function of natural peatlands will not return to harvested peatlands within a reasonable period of time (<25 years).

Hydrological Restoration

An important component of peatland restoration is restoring the natural peatland hydrology. Rewetting techniques used for peatland restoration range from simply blocking drainage canals (LaRose *et al.* 1997; Cooper *et al.* 1998), to creating bunds, polders, retention basins or terracing to retain water (Price *et al.* 2003), to more costly techniques, such as border and pipe irrigation (Richert *et al.* 2000; Rochefort 2001). Blocking ditches, which results in a marked rise in the water table, is an essential step in dry peatland restoration approach (Rochefort 2006). The moisture level of the microclimate on the peat surface can be improved by the use of mulch or nurse plants, which increase the relative humidity near the surface and decrease the evaporation loss compared to a bare peat site (Price *et al.* 2003; Groeneveld and Rochefort 2005).

Dispersion Constraints

Peat extraction in North America is mostly carried out using modern milling machines which vacuum off thin layers of dry peat from the surface (Daigle and Gautreau-Daigle 2001). Because only thin layers can be removed at a time, large areas must be cleared and drained to ensure sufficient supply and profitability. Spontaneous revegetation of these large, barren sites can be exceptionally slow as the residual peat of abandoned sites does not contain a seed bank (Salonen 1987). Furthermore, the surrounding natural areas, typically bogs, contain few to no fen plants (Campbell 2002). One of the major constraints to fen restoration is the availability of suitable propagules (Figure 1.2, point D.). Due to the long distance to natural fens, active introduction of suitable species may be necessary for the return of a fen plant community.

Fen vascular plants

The establishment of *Carex ssp.,* the dominant vascular plant in natural fens, has proven problematic in various restoration efforts (Pfadenhauer and Grootjans 1999; van der Valk *et al.* 1999; Cooper and MacDonald 2000; Patzelt *et al.* 2001). *Carex* and most other fen species spread and maintain themselves through vegetative or clonal growth; therefore, recolonization will be extremely slow or nonexistent if sedge rootstocks have been eliminated from the soil (Cooper and MacDonald 2000; Cronk and Fennessey 2001).

Another important characteristic of vascular fen plants is their need for light. Kotowski (2002) found that the occurrence of fen species in a landscape is directly related to the availability of light, whereas the relationship between fen species occurrence and saturated soil conditions seems to be indirect. Kotowski (2002) stated that fen species are unable to compete with large, dominant plants that grow in richer, unsaturated environments. Thus, if harvested fens are colonized by aggressive, weedy species as has been observed in Europe by Rowlands (2001) and Salonen (1992), perhaps reintroduction measures should be carried out before these ruderal species establish.

Fen Bryophytes

Fen bryophytes are an important component of fen community structure and play a significant role in the peat-accumulating function of fens. However, little research on their regeneration niche has been carried out (Li and Vitt 1994; Mälson and Rydin 2007). Information on the realized niche of fen bryophytes is more prolific (Vitt and Chee 1990; Vitt 1990; Gignac *et al.* 1991; Gignac 1992). The factors that have proven most important in controlling the distribution of peatland bryophytes are four main gradients: wet to dry, ombrotrophic to minerotrophic, mire margin to mire expanse and open to shaded (Gignac and Vitt 1990). Depth to water is often recognized as the most important factor, as it exerts a major influence on the water chemistry and decomposition dynamics (Mulligan and Gignac 2001). Understanding the limiting and optimal environmental conditions for fen bryophyte regeneration is essential to developing restoration strategies which include bryophytes.

Vegetation Reestablishment

Vegetation plays an essential role in the restoration process of peatlands because the ecological functions of the top peat layers depend on the species composition. Therefore, the establishment of the appropriate species is imperative for the return of the ecosystem functions. Due to the poor dispersal abilities of fen plants and the distances between harvested and undisturbed fens, fen plants will probably need to be actively introduced to the restoration sites.

One European fen revegetation technique which is pertinent to the North American context is the *hay transfer* method (Pfadenhauer and Grootjans 1999). This highly mechanized technique is ideal for the restoration of large sites and should be relatively inexpensive. Additionally, this technique has been shown to be effective for reintroducing both vascular plants and bryophytes (Jeschke and Kiehl 2006). The hay transfer method involves mowing a donor site, when the desired seeds are ripe, yet still attached to the stalks, and then transferring the fen "hay" directly onto the restoration site. On experimental plots, 50% to 71% of the fen species were transferred using this method (Patzelt 1998).

In North America, harvested peatlands are often restored with the *Sphagnum* transfer method (Rochefort 2001; Rochefort *et al.* 2003). Preliminary trials have shown some success in restoring fen plant communities using the *Sphagnum* transfer method; however, fen bryophytes did not successfully establish (Cobbaert *et al.* 2004). The *Sphagnum* transfer method involves collecting the first few centimeter of plant material from a donor site, reintroducing these plant fragments in a 1:10 ratio and applying straw mulch as well as phosphate fertilizer (Rochefort *et al.* 2003). This method costs approximately $CAN 1,000 per hectare and, because it uses machinery to collect and spread the vegetation material, is also practical for large restoration sites.

The only other existing research on fen restoration in North America reported in the scientific literature is a study that was carried out on harvested fens in the Rocky Mountains of Colorado (Cooper and MacDonald 2000). In this study, different reintroduction techniques for vascular plants, such as seed sowing and the transplantation of seedlings, rhizomes and willow cuttings, were tested. The estimated cost for this vegetation reintroduction method is between $US 7,000 and $US 12,000 per hectare (David Cooper, 2003, personal communication). Due to the high cost, this technique should be limited to recalcitrant species that do not respond to less expensive vegetation reintroduction techniques.

INTERNAL DYNAMICS

The internal dynamics (Figure 1.2, point E.) among species on a restoration site has a major impact on restoration strategies (Lavoie *et al.* 2003). It is helpful to know, for example, which stage is best for introducing the target restoration species. The ideal reintroduction time minimizes the mortality due to competition with spontaneously established species while minimizing mortality due to adverse abiotic factors (Prach *et al.* 2001).

Unlike abandoned, harvested bogs which can remain void of vegetation for decades (Lavoie and Rochefort 1996), abandoned, harvested fens are rapidly recolonized by vegetation. Famous *et al.* (1991) found that harvested fens revegetated significantly faster than harvested bogs, typically in 3 to 7 years. Famous *et al.* (1991) showed that richer, more humid sites are colonized more quickly than drier, poorer sites. It has been shown on ombrotrophic abandoned sites that spontaneously colonizing plants seem to facilitate the establishment of bog plants (Lavoie *et al.* 2003), but nothing is known about the effects of colonizing plants on fen species establishment.

RESEARCH GOALS AND QUESTIONS

The goal of the present research project is to explore ecological factors which aid the return of fen structure (consisting of sedges and bryophytes) and fen function (peat-accumulation) using the example of harvested peatlands in Canada.

The first research goal is to examine to what extent fen structure and function will return to abandoned, harvested fens without active restoration measures. The main question is whether active restoration measures are necessary. More specifically, will fen species spontaneously recolonize the harvested fens and, if so, which environmental factors are associated with their return? Additionally, the peat-accumulating potential of an abandoned, harvested fen is compared with that of an undisturbed site to see to what extent this function returns to the harvested fens.

The second research goal is to test the nutrient limitations and phenology associtated with reintroduction methods for fen community vegetation. Two reintroduction techniques, two reintroduction times and the use of phosphate fertilizer were tested. I wanted to know which of the two techniques described, (i) the *Sphagnum* transfer and (ii) hay transfer, is more effective for transferring fen plants. Which reintroduction time, spring or mid-summer, will be the most effective for reintroducing plants? Does phosphate fertilization improve the establishment of fen species?

The third research goal is to examine the environmental conditions that aid the regeneration of introduced fen bryophytes. Which species regenerate the best and which environmental conditions (water levels and the presence or absence of shade) improve fen bryophyte regeneration?

ORGANIZATION OF THESIS

This thesis consists of a series of articles which address the research goals and questions listed above. It is structured around the framework shown in Figure 1.2.

Chapter 1 is a general introduction and literature review.

Chapter 2 compares the community structure of of abandoned, harvested fens with undisturbed fens to identify which species do not recolonize harvested fens and should be the focus of reintroduction strategies.

Chapter 3 compares the peat-accumulating function of an abandoned, harvested fen with an undisturbed fen. The decomposition rates of three plants which often recolonize harvested fens were compared with those of three plants which are common to undisturbed fens. The decomposition rates of these plants were measured on a harvested and an undisturbed fen to test the impact of hydrological differences of the two sites on the decomposition rates.

In Chapter 4 several techniques were tested for improving environmental and dispersal constraints on bare peat surfaces. Specifically, two reintroduction methods, the use of phosphate fertilizer and two reintroduction times were tested for fen species reintroduction.

Chapter 5 examines the internal dynamics between spontaneous vegetation of harvested fens and reintroduced fen bryophytes. The regeneration capabilities of nine common fen bryophytes were observed in a greenhouse and field experiment.

Finally, chapter 6 provides general conclusions for this research project. Implications for fen restoration of harvested peatlands and future research avenues are discussed.

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CHAPTER TWO

THE SPONTANEOUS REVEGETATION OF CUTAWAY PEATLANDS OF CANADA AND MINNESOTA, USA[1]

[1] Graf, M.D., L. Rochefort and M. Poulin. 2008. Spontaneous revegetation of cutaway peatlands of North America. Wetlands28:28-39.

ABSTRACT

Modern extraction methods permit peat to be extracted to the minerotrophic layer of ombrotrophic peatlands (bogs). As the environmental conditions of these harvested peatlands are similar to minerotrophic peatlands (fens), such sites should be restored towards a fen system. However, it is not known whether fen species would recolonize such harvested sites on their own. We surveyed vegetation and environmental variables in 28 harvested peatlands with minerotrophic residual peat across Canada and in Minnesota, USA, and compared them to 11 undisturbed fens. Compared to harvested bogs previously studied, the harvested fens sampled in this study revegetated remarkably quickly (50% to 70% vegetation cover) when the hydrological conditions were suitable. However, revegetation was less extensive for sites that were still drained (25% vegetation cover). A high water table and a thin layer of residual peat were the most important factors contributing to rapid recolonization rates. Although the harvested fens were rapidly recolonized, species composition was not the same as observed on undisturbed fens. *Carex* and *Sphagnum*, dominant in undisturbed fens, generally did not recolonize harvested fens. Thus, whether the goal is to increase species richness or to ensure the return of peat-accumulating functions, fen species may have to be actively introduced.

RESUMÉ

Les méthodes modernes d'extraction de la tourbe permet l'extraction jusqu'au la couche minérotrophe dans les tourbières ombrotrophes (bogs). Comme les conditions environmentaux de ces tourbières sont semblables aux des tourbières minérotrophe (fens), ces sites devraient être restauré vers un fen. Cependant, ce n'est pas connu, si les espèces de fens coloniseraient ces sites exploités sans réintroduction. Nous avons échantillonné la végétation et les variables environmentaux dans 28 tourbières qui étaient exploitées jusqu'à la couche minérotrophe à travers le Canada et dans l'État du Minnesota aux Etats-Unis. Comparé aux bogs exploités qui étaient déjà étudier, les fens exploités, qui étaient échantillonnés dans cet étude étaient relativement vite re-végété (50% à 70% couver de végétation) quand les condition hydraulique était bonne. Pourtant, la re-végétation était plus bas pour les sites qui étaient encore drainés (25% couvert de végétation). Une nappe phréatique haute et une couche mince de la tourbe résiduelle étaient les facteurs le plus reliés à une vite recolonisation. *Carex* et *Sphagnum*, dominant dans les fens non perturbées, n'ont pas généralement recolonisés les fens exploités. Donc, si le but est de augmenter la richesse en espèces ou d'assurer le retour de la fonction de accumulation de la tourbe, les espèces des fens devraient être réintroduit.

INTRODUCTION

Fen restoration projects on harvested peatlands in North America aim to restore a fen plant community on sites that were previously bogs (Cooper and McDonald 2000, Cobbaert *et al.* 2004). In North America, the dominant succession for peatlands begins with fens (minerotrophic peatlands) and gradually develops into bogs (ombrotrophic peatlands) (Kuhry *et al.* 1993). Thus, when the *Sphagnum* peat layer is completely removed, the successional clock is set back to the peatland's earlier minerotrophic state. Peatlands that have been harvested to the minerotrophic layer are richer in mineral peat content and have a higher pH than bogs, creating conditions that are sub-optimal for bog community restoration (Wind-Mulder *et al.* 1996, Wind-Mulder and Vitt 2000). Restoration towards a fen system is therefore more appriporiate for such sites.

Spontaneous revegetation resulting from natural succession may lead to more stable, better acclimated vegetation communities and cost less than active, imposed restoration strategies (Bradshaw 2000, Prach *et al.* 2001). However, when spontaneous revegetation does not meet restoration objectives, active restoration measures can ‘fill in the gaps’. For example, plants that do not readily recolonize restoration sites can be reintroduced. Several studies have characterized the spontaneous colonization of harvested peatlands with ombrotrophic residual peat (harvested bogs) in northeastern Canada (Lavoie and Rochefort 1996, Girard *et al.* 2002, Lavoie *et al.* 2003, Poulin *et al.* 2005), but little research has addressed abandoned peatlands with minerotrophic residual peat. Such peatlands have been referred to as cutaway bogs with minerotrophic residual peat in Ireland (O’Connell 2000), but will be referred to as harvested fens in this paper. Studies on vacuum-harvested bogs have indicated that the vegetation cover of most vegetation strata was usually < 25%, and that *Sphagnum* moss was rarely present (Salonen 1992, Girard *et al.* 2002, Lanta *et al.* 2004, Poulin *et al.* 2005). Famous *et al.* (1991) found that harvested fens revegetated more rapidly than harvested bogs. Their study showed that 75% of the harvested fens were completely revegetated within seven years; however, the identity of the recolonizing plants was not reported. Harvested fens in Ireland and Finland were mostly colonized by weedy, ruderal species (Salonen 1992, Rowlands 2001).

Abiotic factors such as water table level, residual peat thickness, and pH can strongly influence the succession of harvested fens and bogs (Famous *et al.* 1991, Girard *et al.* 2002). Bulk density and degree of decomposition increase after peatlands are drained and harvested, which, in turn, greatly impacts the hydrology and peat chemistry of the site (Price *et al.* 2003). Harvested peatlands are often phosphate-limited and vascular plants and pioneer mosses recolonize restored bogs more readily if a light phosphate fertilizer is applied (Rochefort *et al.* 2003). In undisturbed fens, variations in pH, electrical conductivity, and calcium, magnesium, and sodium concentrations are mainly responsible for vegetation gradients (Vitt and Chee 1990). Historical factors can also influence the succession of harvested peatlands. Girard *et al.* (2002) explained 44% of the variation of species occurrence with spatio-historical data, such as the duration of extraction activities, the time since abandonment of harvesting activities, the intensity of the harvesting activities, or the distance to the closest unharvested border. More information on the spontaneous recolonization of harvested fens and the environmental conditions associated with their recovery would be useful to tailor fen restoration strategies.

Our research was driven by the following questions: 1) do fen species return to the harvested fen sites spontaneously, 2) if so, which environmental conditions favor their return, and, finally, 3) which vegetation groups, otherwise common in undisturbed sites, are not successful in recolonizing bare surfaces after the abandonment of peat harvesting activities?

MATERIALS AND METHODS

STUDY SITES

Twenty-eight harvested fens and 11 undisturbed fens were sampled between June and August of 2004 and 2005 in the provinces of New Brunswick, Québec, Manitoba, and Alberta, Canada and the state of Minnesota, USA (Figure 2.1). These areas are the centers of peat harvesting in North America. The mean annual temperatures and precipitation, respectively, for the regions sampled are: 4.7°C and 1115 mm in New Brunswick, 3.2°C and 963 mm in Québec, 2.6°C and 514 mm in Manitoba, and 2.4°C and 483 mm in Alberta (Environment Canada 2002), and 3.9°C and 787 mm in Minnesota (National Climatic Data Center 2001). For each potential site, pH and macrofossil data were used to confirm whether the residual peat was minerotrophic and the site could thus be considered a fen.

Peat had been harvested from the sampled peatlands using either the bulldozer or the vacuum-harvesting method. Bulldozed peatlands were drained with small drainage ditches every 30 m across the peatland. When the hydraulic conditions permitted machines to enter the fields, the peat was bulldozed into stockpiles. Since the 1960s, the bulldozer method was largely replaced by the more cost-effective vacuum-harvesting method. For this method peatland hydrology is altered by creating a large drainage canal around the periphery of the peatland and a network of smaller drainage canals (1m x 1m in a "v" shape) every 30 m throughout the peatland (Price *et al.* 2003). The top layers of peat were allowed to air dry thereby eliminating the costly drying process of the bulldozer method. After drying, the top few centimeters were removed with tractor-drawn vacuum machines. For a more detailed description of the vacuum-harvesting method see Poulin *et al.* (2005).

The majority of the harvested fens studied no longer had intact drainage systems because canals usually collapse without active maintenance. The thin residual peat layer remaining on harvested fens is close to the water table, which quickly leads to the deterioration of drainage canals. Because bulldozed sites had been abandoned for a long period, none had intact drainage systems.

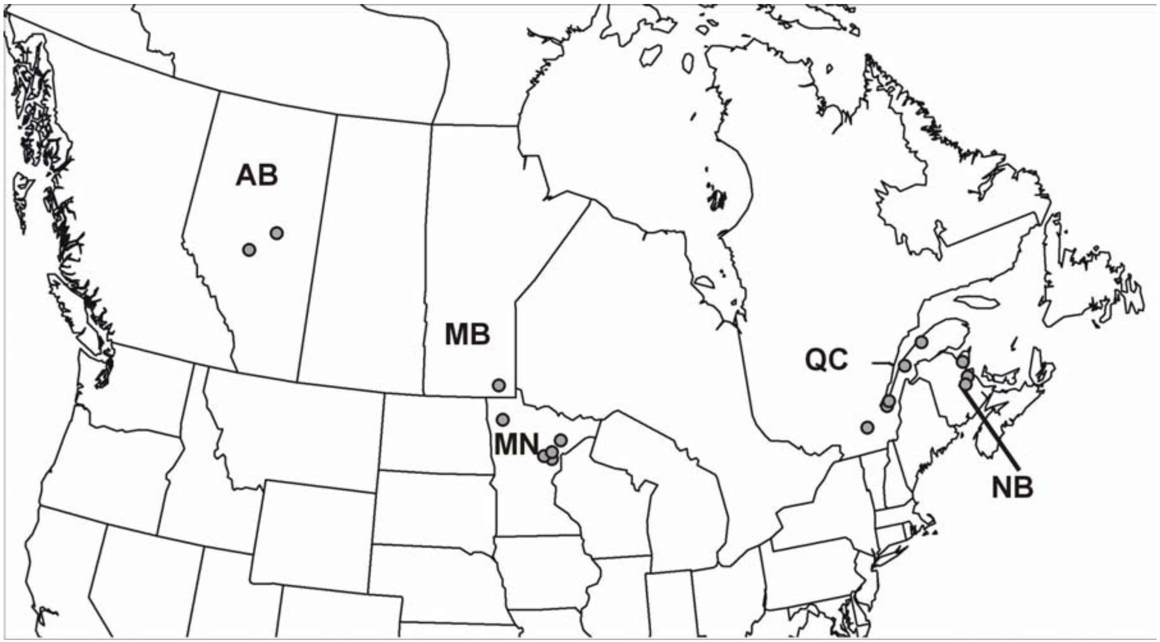

Figure 2.1. Location of the cities (see also Table 2.1) of the studied peatlands in the Canadian provinces of Alberta (AB), Manitoba (MB), Québec (QC) and New Brunswick (NB) as well as the state of Minnesota (MN), USA.

Each of the 28 harvested fens was characterized by the year it had been abandoned, the harvest method, and whether drainage canals were still active. Time since abandonment was determined by asking peatland site managers. The effectiveness of the drainage canals was determined visually by examining whether canals had collapsed or were still actively draining the site. Surveyed fens were grouped into the following disturbance classes: a) undisturbed sites, b) bulldozed sites, c) vacuum-harvested sites with non-functioning drainage canals (or undrained vacuumed), and d) vacuum-harvested sites with functioning drainage canals (or drained vacuumed). In total, 11 undisturbed sites, 6 bulldozed sites, 17 undrained vacuumed, and 5 drained vacuumed sites were sampled (Table 2.1).

SAMPLING DESIGN AND MEASUREMENTS

Between 10 and 25 1-m^2 quadrats, depending on the size of the harvested fen, were equidistantly sampled across each site along transects arranged in a "W", which ensured that borders as well as the center of the fens were sampled. Twenty-five quadrats were sampled for harvested fens > 5 ha, and 10 or 15 quadrats were sampled for sites that were smaller. Eleven undisturbed fens (between 5 and 30 ha in size) were also surveyed with a 'W' transect (10 quadrats per site) to compare the vegetation of undisturbed fens with the spontaneous revegetation of the harvested fens. Each species and its percentage cover (to the nearest 2% for covers less than 10% and to the nearest 5% for covers greater than 10%) were noted within each 1-m^2 quadrat. The nomenclature used for the vegetation follows Scoggan (1978) for vascular plants, Anderson (1990) for *Sphagnum* and, Anderson *et al.* (1990) for other mosses.

Table 2.1. A general description of each abandoned, harvested fen sampled. The abbreviations used to describe the plant composition of the residual peat are the following: *Aln* (*Alnus*), *Aul* (*Aulacomnium*), *Bet* (*Betula*), *Cal* (*Calliergon*), *Cam, (Campylium), Car* (*Carex*), *Cha* (*Chamaedaphne calyculata*), Cyp (Cyperaceae), *Dre* (*Drepanocladus*), *Lar* (*Larix laricina*), lig (ligneous residue), *Pol* (*Polytrichum*), rhi (rhizome), rt (roots and rootlets), *Sci* (*Scirpus*), *Sph* (*Sphagnum)*.

Peat-land	City, Province/State	Location	Disturbance Class	Area (ha)	Year Aban-doned	Plants and % Cover in Residual Peat
1	Inkerman, NB	47 37'N 64 50'W	Drained vacuumed	2	2001	*Sph* 70, lig 20, *Cha* 5, *Lar* 2, rt 2
2	Rexton, NB*	46 38'N 64 53'W	Drained vacuumed	20	1992	*Sph* 45, rt 45, Cyp 5, lig 3, *Aul* 3
3	Kent, NB*	46 37'N 65 08'W	Undrained vacuumed	2	1998	rt 40, *Sph* 35, lig 10, Cyp 10, *Pol* 5
4	St. Fabien, QC	48 18'N 68 52'W	Undrained vacuumed	12	2000	lig 35, *Dre* 35, *Cal* 10, *Lar* 10, rt 5, Cyp 5
5	St. Fabien, QC	48 19'N 68 50'W	Undrained vacuumed	8	1995	rt 40, Cyp 20, lig 15, *Sph* 12, *Sci* 5, *Cha* 2
6	St. Fabien, QC	48 19'N 68 50'W	Undrained vacuumed	7	1998	rt 60, lig 20, *Sph* 10, *Aln* 3
7	St. Fabien, QC	48 18'N 68 51'W	Undrained vacuumed	10	1999	*Sph* 35, rt 30, lig 12, Cyp 12, *Car* 3
8	Rivière-du- Loup, QC*	47 45'N 69 30'W	Undrained vacuumed	6	1988	lig 85, rt 6, Cyp 3, *Car* 3, *Cha* 3
9	Rivière-du-Loup, QC*	47 45'N 69 30'W	Undrained vacuumed	5	1993	lig 50, Cyp 15, rt 12, *Sph* 7, *Dre* 7 , *Lar* 3
10	St. Charles, QC	46 40'N 71 10'W	Undrained vacuumed	5	1999	rt 65, lig 17, Cyp 13, *Car* 7, *Sph* 4
11	St. Henri, QC	46 42'N 71 03'W	Undrained vacuumed	14	1982	rt 50, lig 20, *Car* 17, Cyp 5, *Sph* 4, *Dre* 3, *Lar* 2
12	St. Bonaventure, QC	45 57'N 79 42'W	Bulldozed	12	1984	rt 40, *Car* 20, *Sph* 13, lig 12, Cyp 10, *Bet* 5

13	Cromwell, MN*	46 40'N 92 44'W	Drained vacuumed	16	2002	lig 50, rt 20, *Sph* 20, *Car* 5, *Aul* 3, *Cha* 2
14	Cromwell, MN*	46 40'N 92 46'W	Drained vacuumed	12	2001	lig 45, Cyp 40, rt 15
15	Cromwell, MN*	46 40'N 92 44'W	Undrained vacuumed	20	2002	lig 55, rt 33, Cyp 10, *Sph* 2
16	McGregor, MN*	46 38'N 96 19'W	Undrained vacuumed	4	1998	rt 25, lig 25, Cyp 25, *Car* 10, *Cal* 7, *Dre* 3
17	Central Lakes, MN*	47 17'N 92 28'W	Bulldozed	4	1997	rt 55, lig 12, Cyp 10, rhi 10, *Car* 7, *Sph* 5
18	Central Lakes, MN*	47 17'N 92 28'W	Bulldozed	6	1997	*Sph* 70, lig 15, rt 10, Cyp 5
19	Floodwood, MN*	46 55'N 92 41'W	Bulldozed	4	1975	rt 50, lig 20, rhi 8, *Lar* 8, *Car* 5, *Sph* 5, *Cha* 5
20	Newfolden, MN*	48 24'N 96 10'W	Undrained vacuumed	4	2003	Cyp 40, rt 35, lig 15, *Car* 7, *Aln* 3
21	Newfolden, MN*	48 24'N 96 10'W	Undrained vacuumed	16	2000	lig 45, *Car* 22, rt 15, *Sph* 5, *Cal* 5, *Cam* 7, *Aul* 2
22	Newfolden, MN*	48 24'N 96 10'W	Undrained vacuumed	16	2004	rt 30, lig 25, *Cal* 20, Cyp 15, *Car* 5, *Sph* 5
23	Giroux, MB*	49 35'N 96 30'W	Undrained vacuumed	18	1999	lig 27, rt 25, *Dre* 15, *Cam* 10, Cyp 10, *Cal* 3, *Sph* 2
24	Giroux, MB*	49 35'N 96 30'W	Undrained vacuumed	14	1999	*Sph* 40, Cyp 25, lig 20, rt 13, *Cal* 2
25	Newbrook, AB*	54 20'N 112 55'W	Bulldozed	85	1975	rt 32, *Sph* 23, lig 20, Cyp 12, *Car* 10
26	Newbrook, AB*	54 21'N 112 53'W	Bulldozed	16	1987	*Sph* 65, lig 13, Cyp 7
27	Evansburg, AB*	53 37'N 115 04'W	Undrained vacuumed	28	1993	*Sph* 50, lig 25, rt 12, *Car* 7, Cyp 5
28	Evansburg, AB*	53 38'N 115 06'W	Drained vacuumed	70	1999	lig 37, *Dre* 32, *Sph* 18, rt 10, Cyp 3

* Locations where a natural fen within a 10 km radius was sampled.

Physical variables were measured within or directly adjacent to each quadrat of the harvested fens. The measured variables were depth of peat (using a metal rod), depth to water table (a small hole was dug and the water table was given 15 minutes to stabilize), degree of decomposition of the residual peat using the von Post scale (Malterer *et al.* 1992), and the distance to the closest unharvested vegetated border. As plants can disperse from undisturbed peatland remnants adjacent to harvested peatlands, distance to the closest undisturbed vegetation could be important for recolonization.

A peat sample was taken from the top 5 cm of residual peat within each quadrat after the biological crust (first cm) of peat was removed. These samples were kept cool until analyses could be conducted, which was always within two weeks of collection. Peat samples were analyzed for pH, electrical conductivity, bulk density, and concentrations of Sodium (Na), Calcium (Ca), Magnesium (Mg), and soluble Phosphorus (P_{sol}) (which is the P directly available for plants). An Acumet Model 10 probe was used to measure pH (Fisher Scientific, Pittsburgh, Pennsylvania, USA). Electrical conductivity was measured with an Orion Model 122 conductivity meter (Thermo Electron Corporation Waltham, MA, USA), adjusted to 20°C and corrected for hydrogen ions (Sjörs 1952). These variables were measured in a 4:1 mixture of bi-distilled water and peat. Bulk density was calculated using the difference between the fresh mass and oven-dry mass of a known volume of peat (Hillel 1998). To minimize costs every third peat sample was analyzed for chemistry. P_{sol} was extracted using the Bray 1 method (Bray and Kurtz 1945) and the extract was analyzed using flow injection analysis (Bogren and Hofer 2001). An inductively coupled argon plasma spectrophotometer (ICP-OES Optima 4300DV of Perkin Elmer) was used to determine Na, Ca, and Mg concentrations (Mehlich 1984). For undisturbed sites, a peat sample was taken from the middle of each undisturbed fen to characterize the same suite of chemical variables measured for the harvested fens.

Plant macrofossils of the residual peat were examined for three peat samples from each fen to verify that the peat consisted of fen macrofossils. These samples were chosen at random from the first third, second third, and last third of the peat samples to ensure that all samples were not from the same area of the sites. From each sample, 100 cm^3 of peat was prepared with a KOH solution and washed through a series of sieves (2 mm and 0.5 mm meshes), and then examined for fossils. A guide from Schoch (1988) was used to identify macrofossils.

DATA ANALYSES

Physicochemical and vegetation measurements for each undisturbed and each harvested fen were averaged. Percent cover information was categorized into the following groups: total vegetation, bare peat, Cyperaceae, Gramineae, true mosses and *Sphagnum*. *Carex* and *Scirpus*, as subsets from the Cyperaceae family, were included as additional vegetation subgroups. The physicochemical measurements and grouped vegetation data were compared between disturbance classes (undisturbed, bulldozed, undrained vacuumed, and drained vacuumed) using analyses of variance (ANOVA) and multiple comparison tests (protected LSD). Analyses were conducted using SAS (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, NC, USA). Chemical data and all vegetation groups except total vegetation and bare peat were log transformed to normalize data. Statistical results were considered significant at $\alpha = 0.05$.

A principal components analysis (PCA) was conducted in Canoco (ter Braak and Smilauer, v. 4.5, Biometris - Plant Research International, Wageningen, The Netherlands) using the species data from all quadrats to assess whether species compositions were similar among regions and/or disturbance classes. Two ordination plots were created where sample scores were coded for either region or disturbance class. The environmental variables that had the largest impact on the species composition were determined using redundancy analysis (RDA) in Canoco (ter Braak and Smilauer, v. 4.5, Biometris - Plant Research International, Wageningen, The Netherlands). Only data from vacuum-harvested fens were used for the RDA analysis because future fen restoration projects will likely only deal with such sites. Species data for the PCA and RDA analyses were log transformed to achieve normality. A Hellinger transformation was also applied to the data. This transformation permitted the use of linear models (PCA and RDA) for community composition data with long gradients (Legendre and Gallagher 2001). Sample scores were used to create confidence ellipses for the different regions and disturbance classes using SYSTAT (SYSTAT Software, Inc., Richmond, CA, USA). Each ellipse was centered around the sample mean for each class; the standard deviations of the sample scores from axes 1 and 2 determined the major axes and the sample covariance determined the orientation. Vegetation classes (fen, bog, marsh, and ruderal species) were identified using the habitat descriptions from various plant identification guides (Johnson *et al.* 1995, Marie-Victorin 1995, Newmaster *et al.* 1996).

Species richness (average number of species per 1 m^2 quadrats within each fen) was compared among disturbance classes. The species turnover rate among all quadrats within each fen was calculated as Whittaker's overall β diversity as modified by Harrison *et al.* (1992). This measure ranges from 0 for no turnover to 100 for complete turnover (Magurran 2003). Whittaker's β diversity was chosen as both allow sites with different sample sizes to be compared (Magurran 2003). Mean species richness and mean overall β diversity of each fen were compared using ANOVA and protected LSD procedure in SAS with $\alpha = 0.05$. Beta diversity was log transformed to achieve normality.

RESULTS

ENVIRONMENTAL PARAMETERS

Although harvested fens varied in harvest method or hydrology, only a few environmental variables differed among harvested sites (Table 2.2). The water table for bulldozed sites was higher than both drained and undrained vacuumed sites ($F_{3,24} = 3.48$; $P = 0.031$). The degree of peat decomposition was higher in undrained than drained sites ($F_{3,24} = 3.62$; $P = 0.026$), but did not differ from bulldozed sites (Table 2.2). Finally, time since abandonment of bulldozed sites was longer than for vacuum-harvested sites ($F_{3,24} = 6.11$; $P < 0.001$).

The undisturbed and harvested fens can be considered transitional poor fens due to their peat chemical properties and plant compositions (Tables 2.1 and 2.3) (Gorham and Janssens 1992, Vitt 2006). When macrofossil plant composition was averaged across all sites, residual peat consisted of 27% roots/rootlets, 27% wood, 19% *Sphagnum*, 16%

Cyperacea, and 5% brown mosses. The pH, conductivity, and Ca, Mg, and Na content of peat did not differ among the disturbance classes. P_{sol} concentration of undisturbed sites was higher ($F_{3,37} = 8.17$; $P < 0.001$) than that of harvested sites.

Table 2.2. Environmental parameters (means ± SE) for bulldozed, undrained vacuumed, and drained vacuumed fens in Canada and Minnesota, USA. An ANOVA and protected LSD analysis tested for the differences among disturbance classes. Different lowercase letters in a column indicate significant differences among means ($P < 0.05$). Data for the individual harvested peatlands are reported in Appendix 2.1. Undisturbed fens were not included because variables were not measured.

Disturbance Class	n	Water Table (cm)	Residual Peat Depth (cm)	Degree of Decomposition (von Post scale)	Bulk Density g cm^{-3}	Years since abandonment
Bulldozed	6	-6.7 (± 10.0) a	124.8 (± 32.5) a	6.18 (± 0.09) ab	0.13 (± 0.01) a	21.2 (± 4.1) a
Undrained Vacuumed	17	-23.2 (± 5.9) b	71.4 (± 11.1) a	6.57 (± 0.13) a	0.22 (± 0.03) a	7.4 (± 1.1) b
Drained Vacuumed	5	-41.1 (± 14.4) b	123.0 (± 40.3) a	5.54 (± 0.48) b	0.31 (± 0.11) a	5.4 (± 1.7) b

Table 2.3. Mean peat chemistry data (± SE) of the residual peat for each disturbance class. ANOVA and protected LSD analyses were tested for differences among disturbance classes. Different lowercase letters in a column indicate significant differences among means ($P < 0.05$). Data for the individual harvested peatlands are reported in Appendix 2.1.

Disturbance Class	n	pH	Conductivity (m/cm)	P_{sol} [mg kg^{-1}]	Ca [mg g^{-1}]	Mg [mg g^{-1}]	Na [mg g^{-1}]
Natural	11	5.30 (± 0.9) a	34.5 (± 36.0) a	62.7 (± 8.1) a	6.0 (± 1.5) a	1.1 (± 0.3) a	0.34 (± 0.02) a
Bulldozed	6	4.77 (± 0.4) a	34.7 (± 11.6) a	34.7 (± 5.0) b	6.4 (± 0.9) a	0.9 (± 0.1) a	0.31 (± 0.02) a
Undrained Vacuumed	17	5.30 (± 0.2) a	85.4 (± 26.1) a	27.4 (± 2.4) b	8.1 (± 5.4) a	1.7 (± 0.1) a	0.32 (± 0.02) a
Drained Vacuumed	5	4.46 (± 0.2) a	92.4 (± 66.8) a	28.1 (± 4.3) b	5.8 (± 9.4) a	1.2 (± 0.3) a	0.43 (± 0.08) a

Vegetation Cover

Despite minimal variation in environmental conditions among disturbance classes, revegetation patterns varied greatly (Figure 2.2). Undisturbed sites supported the greatest vegetation cover (close to 100%). Vegetation cover was 70%, 50%, and 25% for bulldozed sites, undrained vacuumed and drained vacuumed sites, respectively. Bare peat showed a complementary picture with the highest percent unvegetated (73 %) recorded for the drained vacuumed sites.

Species of the Cyperaceae and Gramineae families were especially successful in recolonizing undrained harvested sites. Cover of Cyperaceae on undisturbed, bulldozed, and undrained vacuumed sites was similar, but was much lower for drained vacuumed sites (Figure 2.2). Closer examination of the Cyperaceae family shows that undisturbed sites were dominated by *Carex* species (Figure 2.2), while undrained vacuumed sites were dominated by *Scirpus cyperinus* (Appendix 2.1). Bulldozed sites were mainly recolonized by *Rhynchospora alba* and *Carex* species (Appendix 2.1).

Bryophytes were much less successful at recolonizing vacuumed sites. The percentage of *Sphagnum* was high on undisturbed and bulldozed sites (30% and 20%, respectively), but *Sphagnum* was virtually absent from drained and undrained vacuumed sites (Figure 2.2). The percent cover of true mosses was lower for both classes of vacuumed sites than for undisturbed or bulldozed sites (Figure 2.2). However, percent cover of true mosses was relatively low even on undisturbed and bulldozed sites (8% cover).

Plant Species Richness

Species richness was greater in undisturbed and bulldozed sites than vacuum-harvested sites (Figure 2.3). No difference in β diversity could be detected among the disturbance classes (Figure 2.3). As sampling effort of the undisturbed fens was smaller than that of harvested fens, diversity estimates for undisturbed fens are conservative.

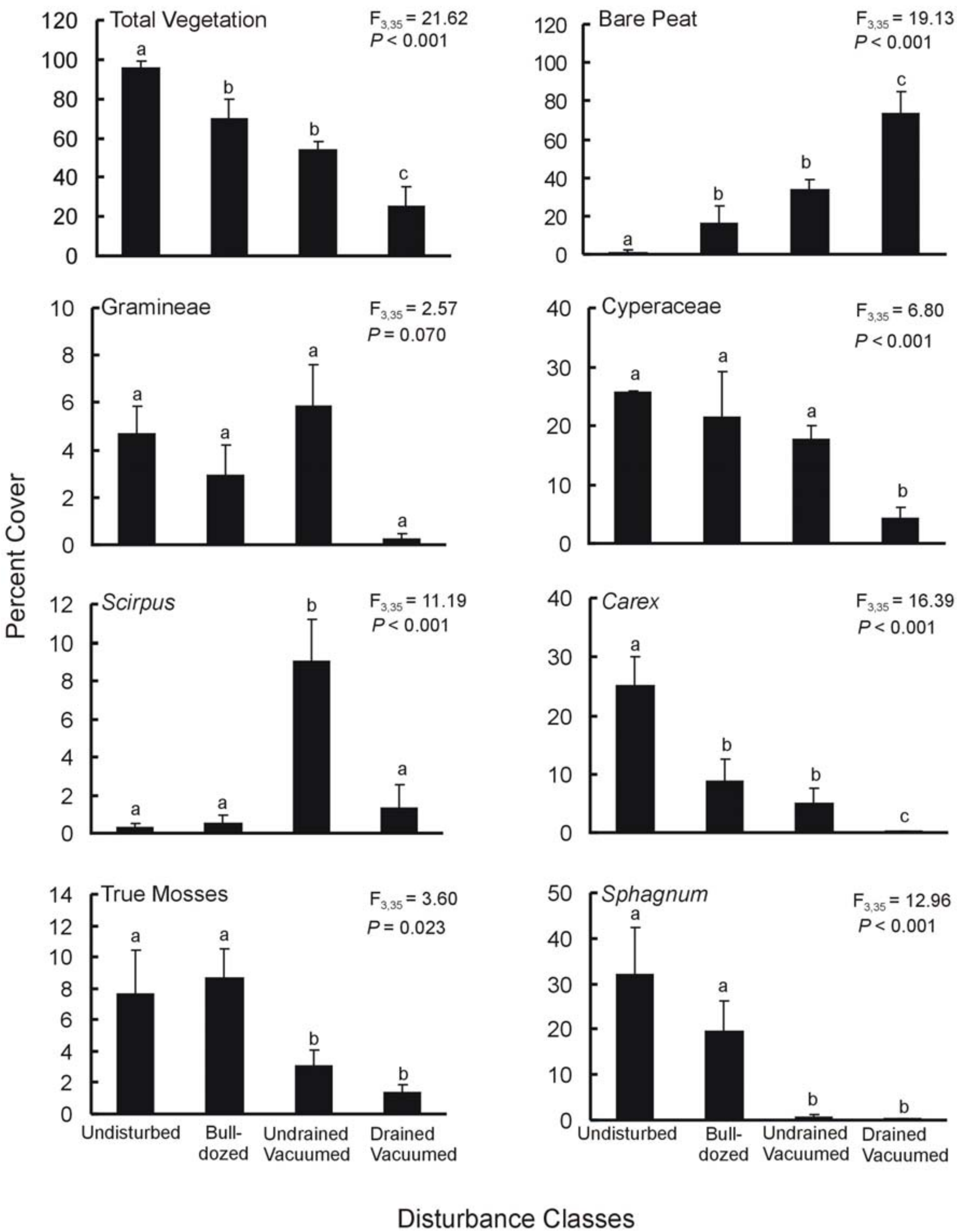

Figure 2.2. Mean vegetation cover, bare peat and various vegetation groups for 28 harvested and 11 undisturbed fens. Lowercase letters show significant differences (α = 0.05) among disturbance classes as revealed by ANOVAs.

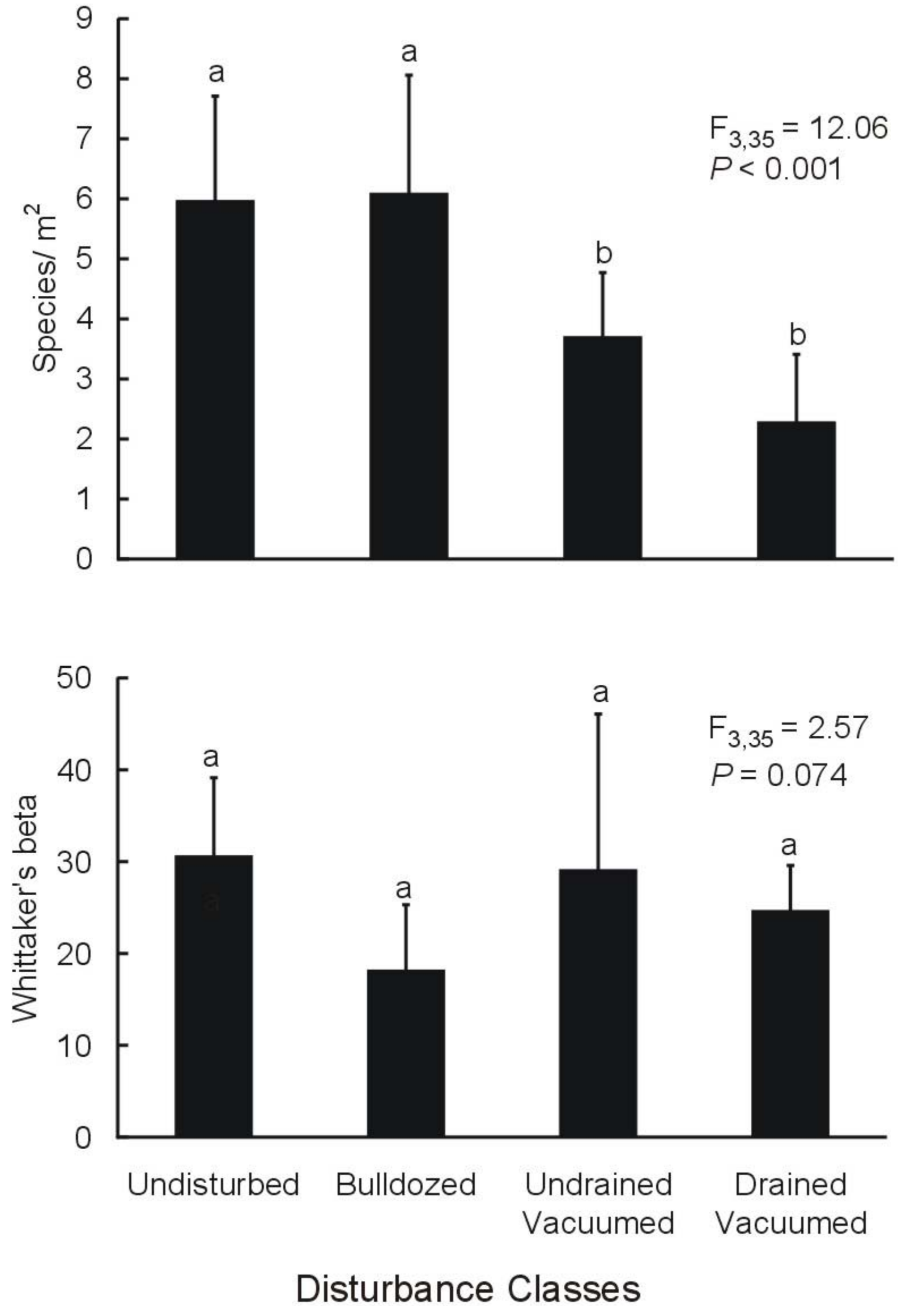

Figure 2.3. Mean species richness per quadrat and Whittaker's β are shown for each disturbance class of fens. The lowercase letters show significant differences ($\alpha = 0.05$) among classes as shown by ANOVAs.

VEGETATION COMPOSITION

The ordination plots generated from PCA axis scores did not generate strong patterns when samples were coded by region (Figure 2.4), despite the immense geographic distance between some regions (Figure 2.1). When samples were coded by drainage and harvest method, a much stronger pattern emerged (Figure 2.5). Undisturbed fens exhibited the tightest grouping. Undisturbed and drained vacuum-harvested sites were markedly different due to the high percentage of bare peat at drained vacuumed sites (Figures 2.2 and 2.6). The vegetation of bulldozed sites most resembled that of undisturbed sites (Figure 2.5), with both being dominated by typical fen species (Figure 2.6). The samples from undrained vacuumed sites were the most variable in terms of species composition as shown by the large ellipses on the ordination plots (Figures 2.5 and 2.6). In general, most undrained vacuumed sites were dominated by bare peat, *Scirpus cyperinus* and, to a lesser extent, other common wetland plants (i.e., *Juncus tenuis*, *Juncus effusus*, *Solidago graminifolia* and *Spiraea latifolia*) (Figure 2.6).

The recolonization of marsh and fen species was correlated with high water tables (Figure 2.7). Fen species were associated with long abandonment times whereas marsh species were associated with high pH and higher peat decomposition. Several ruderal species were correlated with high electrical conductivity, medium to high pH values, and high Ca and Mg concentrations. Bog species were correlated with a thick residual peat layer and low pH values. The occurrence of bare peat on vacuum harvested sites was associated with a thick residual peat layer, dry conditions (deeper water tables) and a short time since abandonment.

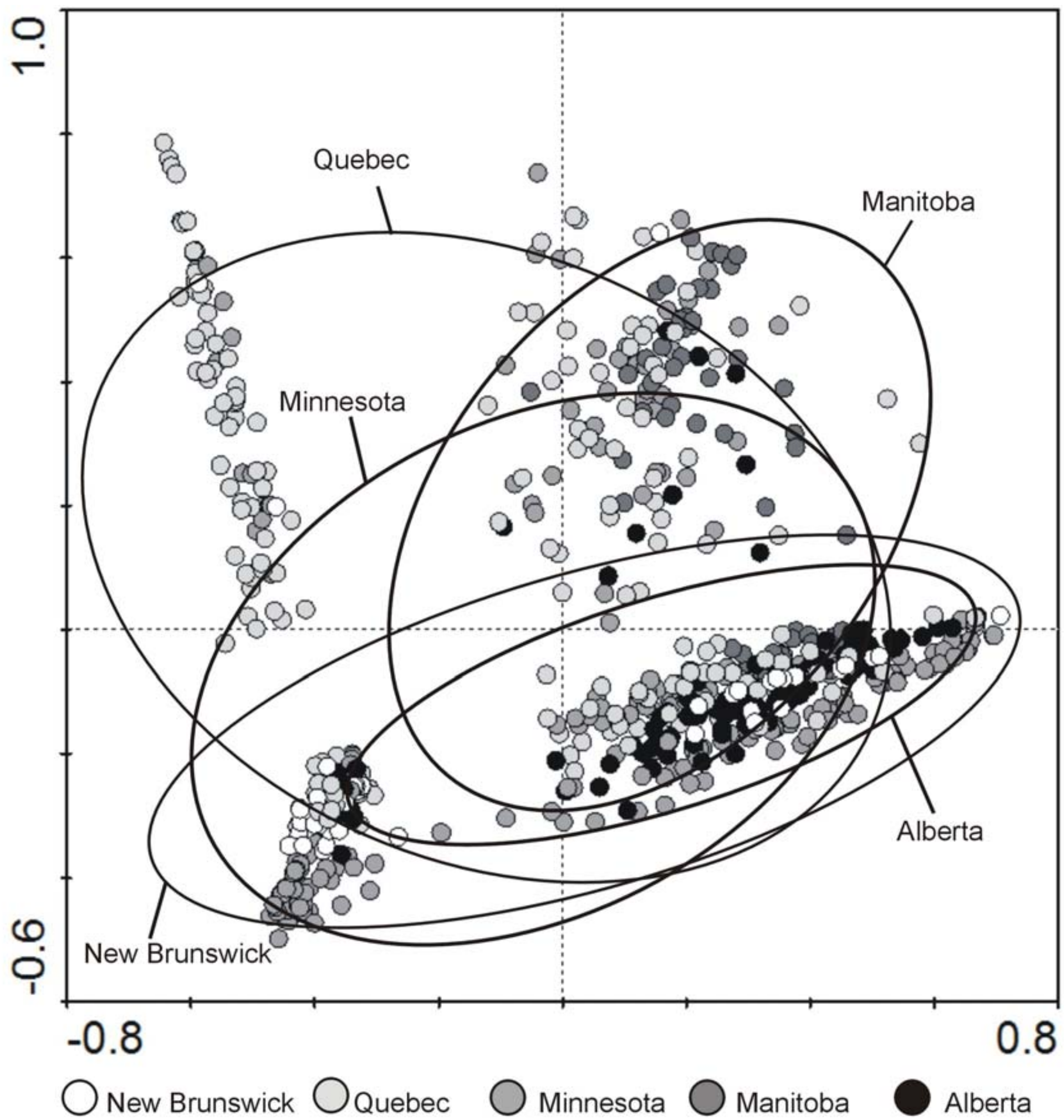

Figure 2.4. Principal Components Analysis (PCA) ordination plot of site scores for vegetation recorded in 1 m^2 quadrats of 28 harvested and 11 undisturbed fens coded according to the region. Confidence ellipses are shown for the sample scores from each region. Each confidence ellipse is centered around the sample mean, the standard deviations determine the major axes and the sample covariances the orientation.

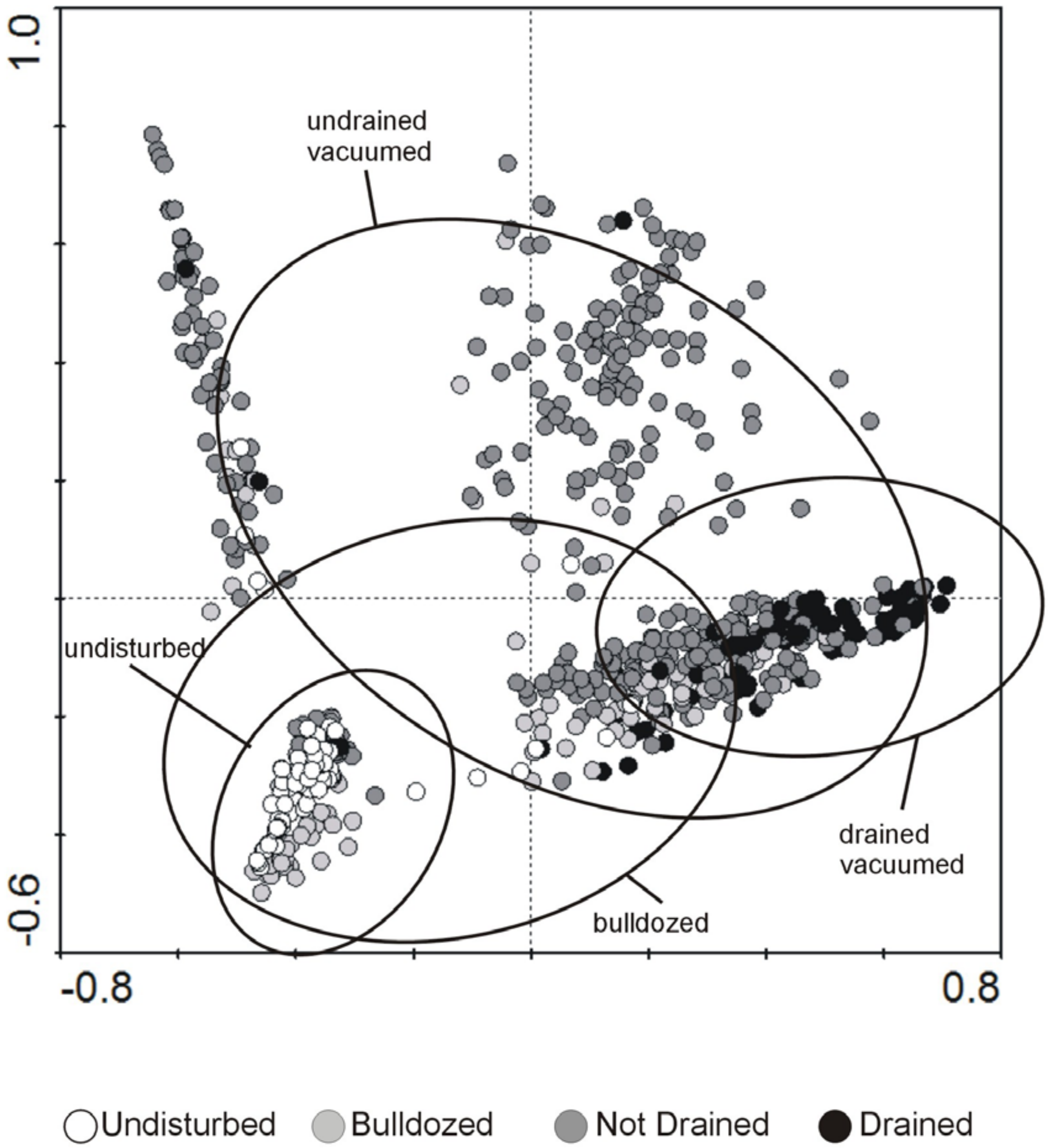

Figure 2.5. PCA ordination plot of site scores for vegetation recorded in 1 m^2 quadrats from 28 harvested and 11 undisturbed fens coded according to the disturbance class (harvesting type and drainage). Confidence ellipses are shown for the sample scores from each region. Each confidence ellipse is centered around the sample mean, the standard deviations determine the major axes and the sample covariances the orientation.

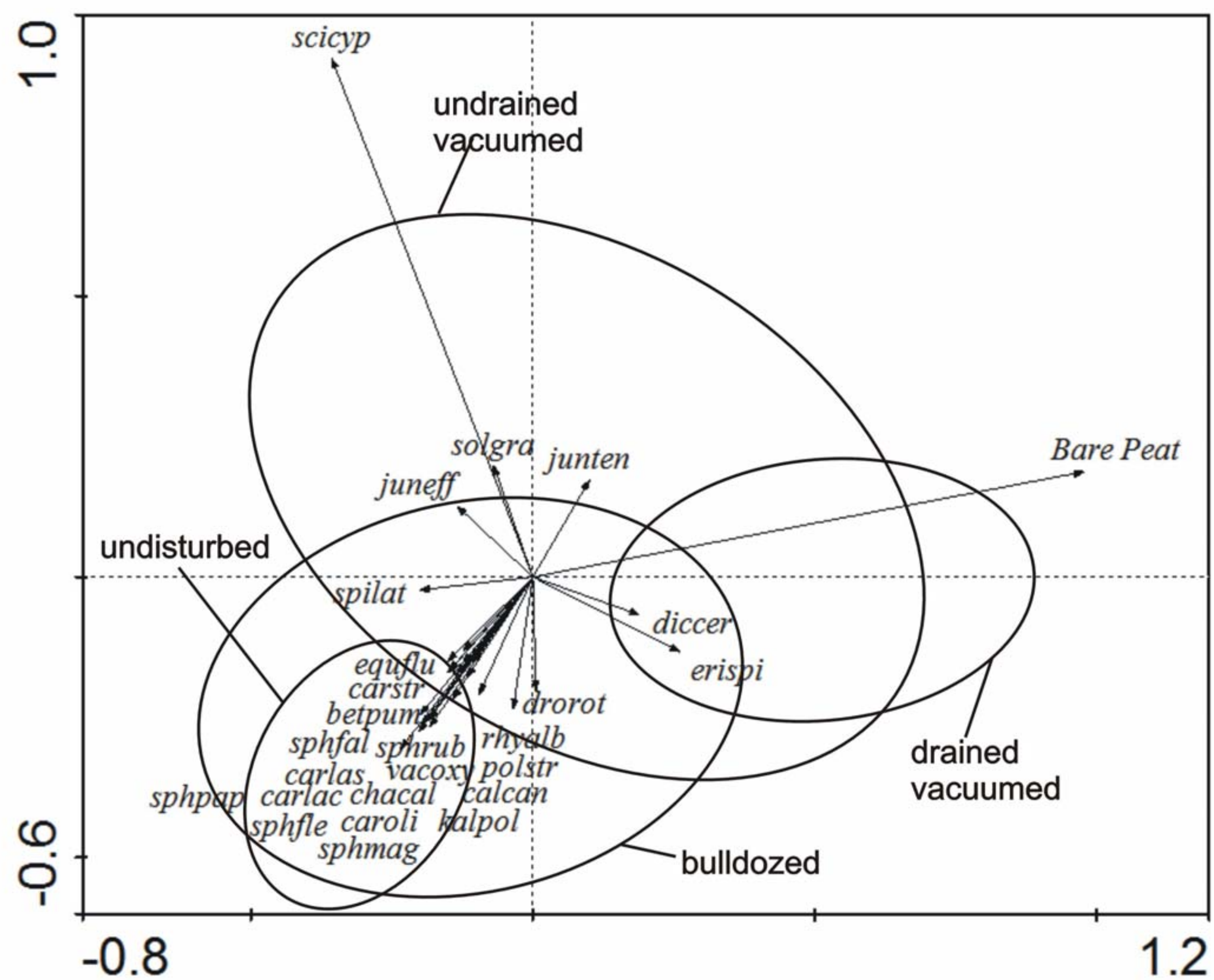

Figure 2.6. PCA ordination plot of species scores for all vegetation samples from 28 harvested and 11 undisturbed fens with the confidence ellipses for the disturbance classes shown in Figure 2.5 inserted. The species abbreviations are the first three letters of the genus and species names of each species; the full names are shown in Appendix 2.3.

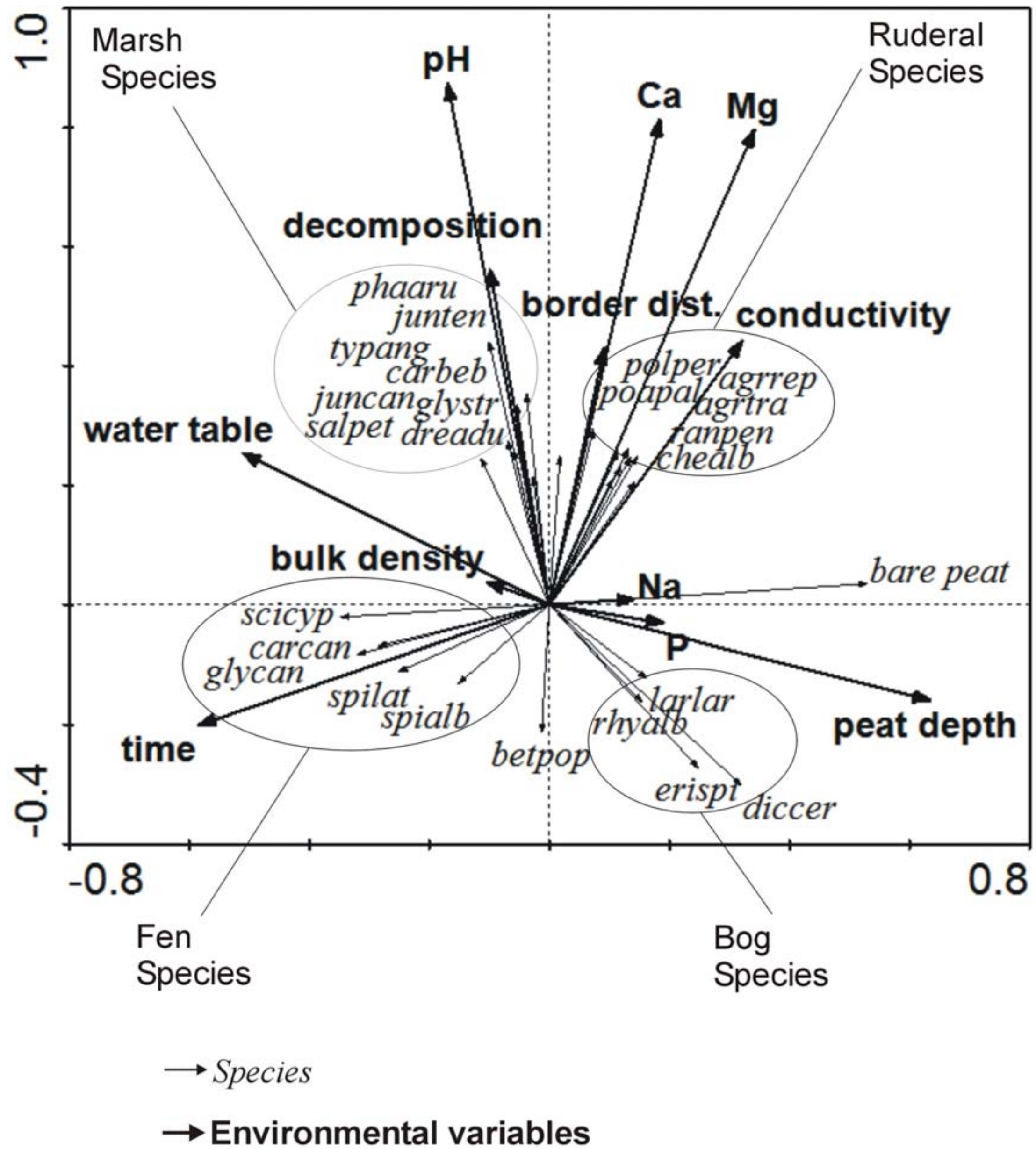

Figure 2.7. Redundancy analysis (RDA) biplot for samples from the vacuumed-harvested sites where drainage canals were no longer functioning. The species abbreviations are the first three letters of the genus and species names; the full names are listed in Appendix 2.3. The environmental variable 'time' refers to the time since abandonment of peat harvesting and 'border dist.' refers to the distance between the sampled quadrat and the closest unharvested, vegetated border. Environmental variables explained 16.6% of total variation in species data with 7.4% by Axis 1 and 2.4% by Axis 2.

DISCUSSION

Cutaway peatlands with residual minerotrophic peat, or harvested fens, were quickly recolonized by vegetation. Despite a short time since abandonment, 5 to 7 years on average, vacuum-harvested fens in this study showed relatively high percentages of vegetation cover when compared to vacuum-harvested bogs of Eastern Canada (Poulin *et al.* 2005). We found that harvested fens supported a vegetation cover between 25% and 60%, whereas other studies show that harvested bogs usually supported vegetation cover below 25% cover for most vascular plant groups (Famous *et al.* 1991, Poulin *et al.* 2005). The hydrology of the sites we sampled played a crucial role in revegetation success; sites where drainage canals had collapsed revegetated to a greater extent with wetland plants than sites with active drainage canals. Thus, this study shows that recolonization of harvested fens is not limited by dispersal for many, but not all, wetland species. However, environmental conditions for species establishment and survival need to be met for rapid colonization.

Vegetation composition varied considerably among disturbance classes even though few differences were observed in environmental conditions. Only available P concentration was higher in undisturbed sites compared to harvested sites, as has also been observed when comparing harvested and undisturbed bogs (Andersen *et al.* 2006). Thus, recolonization may be limited by the availability of resources for plant establishment.

The bulldozed sites supported vegetation that most resembled that of the undisturbed fens. This could be because the hydraulic conditions of bulldozed sites most resembled natural conditions and because bulldozed sites were older, allowing for a longer recovery time. *Sphagnum* species were especially successful at recolonizing bulldozed sites, a pattern also observed in trenches of harvested block-cut peatlands (Poulin *et al.* 2005). The successful recolonization of the bulldozed sites is of secondary importance from a restoration perspective, as this peat harvesting method is no longer used and will most likely not be used in the future due to its costly drying process. For the remainder of this discussion, we will focus on the spontaneous revegetation of the vacuum-harvested fens because future restoration projects will mitigate this type of harvested peatland.

Vascular plants were more successful than bryophytes at recolonizing vacuum-harvested fens (Figure 2). In particular, *Scirpus cyperinus* was very successful presumably due to its easily dispersed seeds. Although *Scirpus* species are found on undisturbed fens, *Carex* is generally the dominant genus. In European fen restoration projects, *Carex* species are reintroduced because they are generally dispersal limited and because undisturbed remnants, which could serve as diaspore sources, are scarce (van Duren *et al.* 1998, Roth *et al.* 1999, Patzelt *et al.* 2001). Because harvested fens were originally bogs, the undisturbed remnants adjacent to the harvested surface are unlikely to be fens. Therefore, the local species pool may not even contain *Carex* species. Thus, while the harvested fens were quickly colonized, the lack of some genera suggests that the chances of spontaneous colonization of some key fen species are limited. However, the success of *Scirpus* and other wetland plants is a good indication that the conditions should be adequate for reintroducing fen species.

Bryophytes, especially *Sphagnum*, were virtually absent from the vacuum-harvested sites, despite *Sphagnum* diaspores being present in nearby undisturbed bog remnants. *Sphagnum* species establish on bare peat surfaces much more effectively if vegetative propagules are reintroduced and a mulch layer is spread for protection during the first few years (Rochefort *et al.* 2003). We expect the same is true for true mosses, which may explain why bryophyte colonization was a rare event at our study sites.

Similar to observations by Soro *et al.* (1999), the drained and undrained vacuumed sites supported fewer species per square meter than the undisturbed sites even though the sampling effort of undisturbed sites was smaller than for harvested sites. However, the turnover rate was similar among all disturbance classes because fewer species observed on the drained and undrained vacuumed sites increased the chance that turnover rate would be high. The average time since abandonment was very short for the vacuum-harvested sites. Thus, with time, vacuum-harvested sites will probably become more diverse. However, even after 50 years the vegetation of harvested bogs had not yet recovered to its original composition (Soro *et al.* 1999). Reintroducing species is an option to accelerate community recovery.

In vacuum-harvested sites, recolonization rates were higher when residual peat layers were thin. A similar trend was observed on block-cut, harvested bogs where *Sphagnum* recolonization was higher in trenches with a thin residual peat layer than those with a thick residual peat layer (Poulin *et al.* 2005). Vacuum-harvested fens with a thick residual peat layer were drier, as was also found for the trenches of harvested, block-cut peatlands (Poulin *et al.* 2005). The relationships among a thin residual peat depth, improved hydrology, and higher cover of spontaneous revegetation could have implications not only for fen restoration, but also for bog restoration. In cases of bog restoration where recreation of the proper hydrology is impossible, one option might be to remove more of the residual peat layer. The removal of the *Sphagnum* residual peat layer has been suggested to improve the hydrology of a harvested peatland in Germany (Sliva and Pfadenhauer 1999). As radical as this might seem, removing peat to create better hydrological conditions might be an interesting alternative. Thus, when bog restoration is not an option, the creation of a fen or a marsh will increase landscape diversity and create a better habitat for wildlife than forest plantations or berry farms, which are other proposed land use alternatives for harvested peatlands.

CONCLUSIONS

This research suggests that reintroducing fen species would increase the biological value of harvested peatlands with minerotrophic residual peat. However, it is not known which vegetation groups should be emphasized because the goals of fen restoration largely remain undefined. Rochefort (2000) defines the goals of peatland restoration in North America as focusing on the return of ecosystem function, especially peat accumulation. If this is the goal, the return of *Sphagnum* species, which inhabit transitional and poor fens, should be emphasized (Rochefort 2000). Sliva (1997) and Wind-Mulder (1996) both advocate the reintroduction of *Sphagnum* species to direct and accelerate the succession towards a bog condition.

The question remains whether the return of fen ecosystem functioning should be the goal of fen restoration or whether it might be beneficial to put more emphasis on their possible contribution to regional diversity. Fens are notorious as 'hot spots' of diversity (Bedford and Godwin 2003) and are rare in southeastern Canada (Kuhry *et al.* 1993). The reintroduction of fen species to cutaway peatlands with minerotrophic residual peat could create a biological gem out of lackluster non-restored sites, dominated by a few, ubiquitous species.

To date, North American fen restoration research has focused entirely on reintroducing vascular plants (Cooper and McDonald 2000, Cobbaert et. al. 2004). By including bryophytes in restoration projects the diversity and perhaps the peat-accumulating function of the restored peatlands would be improved. Before target vegetation communities for fen restoration can be identified, more research is needed to understand the respective roles of mosses and vascular plants in the ecosystem functions of restored fens.

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App.2.1. Mean physicochemical data (±SE) of peat for each harvested site. Peatland numbers correspond to those in table 2.1.

Peat-land	n	Water Table (cm)	Peat Depth (cm)	Degree of Decompos-ition	Bulk Density (g cm^{-3})	pH	Electrical Conductivity (μS cm^{-1})	P_{sol} (mg kg^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	Na (mg g^{-1})
1	15	-24.8 (10.51)	40.1 (2.4)	5.1 (0.1)	0.52 (0.01)	4.61 (0.07)	13.1 (1.5)	No data	3.0 (0.9)	1.1 (0.1)	0.20 (0.03)
2	25	-132.1 (12.45)	22.9 (2.5)	6.2 (0.1)	0.64 (0.01)	4.33 (0.10)	18.7 (2.6)	No data	0.5 (0.1)	0.3 (0.1)	0.20 (0.03)
3	10	-30.6 (6.81)	30.3 (1.9)	7.3 (0.2)	0.59 (0.00)	4.15 (0.02)	11.7 (1.2)	No data	0.5 (0.1)	0.4 (0.1)	0.12 (0.02)
4	25	-33.3 (4.05)	33.3 (3.9)	6.1 (0.2)	0.39 (0.01)	4.80 (0.12)	43.4 (9.9)	13.5 (3.9)	4.7 (1.0)	1.1 (0.2)	0.45 (0.05)
5	15	-60.4 (2.92)	48.4 (2.6)	6.9 (0.3)	0.19 (0.01)	5.52 (0.12)	39.9 (5.0)	36.4 (6.4)	4.8 (0.7)	0.9 (0.3)	0.50 (0.22)
6	10	-55.4 (3.92)	42.2 (4.7)	6.9 (0.2)	0.16 (0.01)	5.32 (0.07)	27.7 (3.5)	34.9 (10.6)	5.8 (0.7)	0.9 (0.1)	0.29 (0.01)
7	10	-61.9 (11.41)	21.0 (0.9)	7.1 (0.6)	0.11 (0.01)	6.02 (0.09)	29.1 (4.4)	52.5 (23.0)	10.1 (1.0)	1.6 (0.5)	0.70 (0.10)
8	16	-22.8 (4.72)	50.0 (4.3)	6.6 (0.1)	0.28 (0.05)	4.76 (0.05)	33.1 (14.1)	22.8 (7.6)	3.4 (0.5)	1.2 (0.2)	0.33 (0.08)
9	13	-19.8 (6.40)	72.0 (7.8)	5.9 (0.3)	0.20 (0.01)	4.97 (0.07)	23.9 (2.5)	28.0 (9.0)	5.6 (0.4)	1.5 (0.2)	0.35 (0.03)
10	21	-20.2 (2.41)	26.0 (3.0)	6.0 (0.0)	0.16 (0.01)	4.56 (0.09)	12.0 (1.67)	29.0 (4.6)	2.3 (0.4)	0.6 (0.04)	0.22 (0.01)
11	25	-9.2 (2.10)	49.0 (3.2)	5.3 (0.2)	0.11 (0.01)	5.35 (0.05)	9.3 (0.44)	22.3 (3.9)	6.2 (0.6)	0.6 (0.1)	0.29 (0.01)
12	25	-17.6 (3.26)	96.1 (9.1)	5.9 (0.1)	0.16 (0.01)	4.35 (0.05)	25.2 (2.48)	63.5 (12.3)	4.4 (0.4)	0.4 (0.04)	0.29 (0.02)
13	25	-30.9 (2.96)	233.0 (20.3)	4.2 (0.2)	0.13 (0.01)	4.22 (0.06)	45.9 (6.5)	32.8 (7.1)	2.8 (0.5)	0.5 (0.1)	0.25 (0.02)
14	25	-71.0 (3.29)	180.0 (14.9)	5.2 (0.1)	0.19 (0.01)	3.94 (0.05)	25.6 (2.6)	44.8 (3.4)	3.1 (0.3)	0.4 (0.04)	0.25 (0.01)
15	25	-15.0 (5.13)	128.6 (8.8)	6.0 (0.1)	0.16 (0.01)	4.35 (0.06)	28.8 (5.0)	29.6 (5.4)	5.5 (1.8)	1.0 (0.5)	0.27 (0.01)

App.2.1. Continued.

Peat-land	n	Water Table (cm)	Peat Depth (cm)	Degree of Decompos-ition	Bulk Density (g cm^{-3})	pH	Electrical Conductivity ($\mu S\ cm^{-1}$)	P_{sol} (mg kg^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	Na (mg g^{-1})
16	15	-30.3 (3.38)	95.7 (11.2)	6.5 (0.1)	0.20 (0.02)	4.12 (0.09)	14.4 (4.9)	32.1 (9.0)	3.4 (0.5)	0.3 (0.1)	0.23 (0.01)
17	15	30.5 (7.11)	100.4 (22.8)	6.3 (0.2)	0.29 (0.04)	5.20 (0.10)	18.5 (1.5)	20.7 (4.7)	2.3 (0.3)	0.5 (0.1)	0.23 (0.03)
18	20	-33.3 (3.33)	245.8 (7.9)	6.1 (0.1)	0.13 (0.01)	4.18 (0.02)	12.3 (1.1)	22.8 (2.7)	1.9 (0.2)	0.4 (0.04)	0.27 (0.01)
19	15	-15.5 (3.41)	136.1 (18.8)	6.1 (0.1)	0.13 (0.01)	4.32 (0.09)	17.1 (1.8)	39.6 (4.2)	1.8 (0.8)	0.3 (0.1)	0.24 (0.05)
20	10	-18.4 (10.12)	43.2 (6.7)	7.2 (0.1)	0.21 (0.01)	5.68 (0.05)	273.7 (22.1)	10.6 (1.9)	14.8 (0.9)	1.2 (0.1)	0.24(0.004)
21	25	1.7 (2.88)	62.4 (5.0)	7.0 (0.1)	0.33 (0.12)	6.88 (0.08)	206.7 (26.0)	33.6 (8.5)	13.0 (0.8)	2.5 (0.1)	0.23 (0.01)
22	25	-12.7 (4.48)	55.4 (4.8)	7.1 (0.1)	0.22 (0.01)	6.83 (0.09)	354.9 (40.9)	62.9(10.2)	20.6 (1.3)	3.8 (0.2)	0.24 (0.01)
23	25	-3.4 (0.43)	208.6 (5.88)	6.7 (0.1)	0.12 (0.00)	5.94 (0.07)	60.9 (6.7)	18.0 (3.0)	9.5 (1.0)	3.3 (0.5)	0.38 (0.05)
24	25	7.1 (1.93)	117.4 (5.5)	6.9 (0.1)	0.11 (0.00)	6.07 (0.08)	69.3 (8.0)	9.9 (2.9)	7.8 (0.4)	2.4 (0.2)	0.15 (0.01)
25	25	21.0 (4.47)	65.5 (6.5)	6.5 (0.1)	0.15 (0.01)	6.05 (0.10)	76.3 (6.0)	22.6 (6.3)	6.9 (2.7)	2.2 (0.2)	0.43 (0.05)
26	25	11.4 (4.11)	80.5 (5.2)	6.2 (0.1)	0.10 (0.00)	4.93 (0.06)	42.6 (2.3)	11.5 (2.3)	11.0 (1.7)	1.6 (0.2)	0.36 (0.02)
27	25	-63.1 (5.11)	102.5 (6.3)	6.6 (0.1)	0.11 (0.01)	4.91(0.08)	280.8(65.5)	14.1(8.1)	8.1(0.5)	2.8(0.6)	0.33(0.05)
28	25	-77.2 (10.91)	139.0 (8.5)	7.0 (0.0)	0.10 (0.01)	5.19(0.07)	358.9(69.4)	9.6 (2.5)	9.7(1.2)	2.4(0.2)	0.70(0.14)

App.2.2. Species recorded in 1 m^2 quadrats sampled from peatlands in Canada and Minnesota, USA. Species abbreviations are the first three letters of each genus and species name. A full list of the species can be seen in Appendix 2.3. Frequency refers to the number of quadrats in which species were observed; %, the proportion of all quadrats colonized by each species; mean, percent cover of each species averaged among all quadrats. Species which were present in less than 1% of the quadrats were not included.

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	Frequ -ency	%	Mean	Species	Frequ-ency	%	Mean	Species	Frequ-ency	%	Mean	Species	Frequ-ency	%	Mean	Species	Frequ-ency	%	Mean
Mosses and Liverworts																			
polstr	82	11	1.77	aulpal	11	10	2.09	polstr	46	33	5.07	polcom	24	6	0.77	diccer	26	25	4.05
diccer	52	7	0.89	camste	11	10	1.66	warexa	12	9	2.57	polstr	22	6	1.27	polstr	11	11	1.05
polcom	29	4	0.45	dreadu	9	8	1.04	aulpal	9	7	0.36	diccer	20	5	0.49	pohnut	2	2	0.05
aulpal	25	3	0.37	brypse	6	6	0.14	diccer	6	4	0.39	brypse	12	3	0.22	polcom	1	1	0.08
warexa	22	3	0.68	warexa	6	6	0.64	camste	2	1	0.01	pohnut	7	2	0.03	dreadu	1	1	0.29
brypse	19	3	0.14	warflu	6	6	0.76	pohnut	2	1	0.04	dreadu	7	2	0.28				
dreadu	17	2	0.34	drerev	4	4	0.04	polcom	2	1	0.08	mniaff	7	2	0.07				
camste	13	2	0.24	calgig	3	3	0.2	brariv	1	1	0.01	aulpal	5	1	0.02				
pohnut	12	2	0.03	polstr	3	3	0.03	brypse	1	1	0	warexa	4	1	0.2				
mniaff	7	1	0.04	scosco	3	3	0.12	mylano	1	1	0.01	camhis	3	1	0.01				
lopven	6	1	0.06	mnigra	3	3	0.06	lopven	5	4	0.31	brariv	2	1	0				
warflu	6	1	0.11	polcom	2	2	0.05					mylano	2	1	0.01				
drerev	4	1	0.01	tomnit	2	2	0.57					pollon	2	1	0.01				
mylano	4	1	0.01	brywei	1	1	0.01												
				calcus	1	1	0.19												
				pohnut	1	1	0.01												
				mylano	1	1	0.02												

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	**Frequ -ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**
Sphagnum																			
sphrub	41	6	1.49	sphfal	22	21	14.13	sphrub	38	28	7.8	sphcus	6	2	0.25				
sphfal	32	4	2.46	sphfle	17	16	8.09	sphmag	19	14	1.76	sphter	4	1	0.23				
sphmag	28	4	0.6	sphmag	7	7	1.36	sphcen	11	8	2.5	sphcap	3	1	0.03				
sphcus	18	2	0.62	sphcen	5	5	0.74	sphfal	10	7	2.41	sphfim	3	1	0.02				
sphcen	17	2	0.57	sphinu	5	5	1.38	sphpap	9	7	0.74	sphmag	2	1	0.15				
Sphfle	17	2	1.15	sphsqu	5	5	0.3	sphcus	8	6	1.51								
sphpap	11	1	0.29	sphcus	4	4	1.42	sphcap	3	2	0.24								
sphfim	8	1	0.16	sphfim	4	4	0.9	sphfus	3	2	0.18								
sphsqu	7	1	0.04	sphang	3	3	1.93	sphwar	3	2	0.2								
sphwar	7	1	0.08	sphsub	3	3	0.49	sphsqu	1	1	0								
sphcap	6	1	0.06	sphwar	3	3	0.3												
sphter	6	1	0.23	sphmaj	2	2	0.15												
sphinu	5	1	0.2	sphpap	2	2	1.04												
				sphrub	2	2	0.26												
				sphter	2	2	0.75												
Sedges Grasses and Rushes																			
scicyp	234	31	5.36	calcan	29	27	3.08	rhyalb	29	21	5.67	scicyp	204	51	9.25	erivag	31	30	2
erivag	84	11	1.28	carlas	25	24	7.48	calcan	26	19	1.42	phaaru	39	10	1.37	agrsca	10	10	0.08
calcan	74	10	1	carstr	19	18	5.1	caroli	25	18	1.79	erivag	37	9	1.59	rhyalb	7	7	1.37
agrsca	55	7	0.48	carlac	17	16	2.44	caraqu	22	16	2.52	agrsca	35	9	0.69	junbuf	4	4	0.3
rhyalb	53	7	1.98	caraqu	14	13	2.43	scicyp	22	16	1.57	carbeb	31	8	0.78	caline	3	3	0.06
caraqu	48	6	1.04	caroli	11	10	0.92	carcan	19	14	1.56	junten	29	7	0.36	horjub	3	3	0.11
phaaru	45	6	0.82	carhou	10	9	2.16	carutr	16	12	2.03	junbre	25	6	0.69	scicyp	3	3	0.75
carcan	41	6	0.71	carmag	10	9	1.23	erivag	16	12	0.86	carsp	22	6	1.9	caroli	2	2	0.01
caroli	41	6	0.48	glycan	8	8	0.58	phraus	12	9	0.76	calcan	19	5	0.55	caraqu	1	1	0.2
carbeb	31	4	0.42	caline	6	6	0.8	erivir	8	6	0.64	glycan	19	5	0.69	carcan	1	1	0
glycan	31	4	0.54	carlim	5	5	0.49	agrsca	7	5	0.37	carcan	17	4	0.48	eriang	1	1	0.01
junten	29	4	0.19	phaaru	5	5	0.14	caline	4	3	0.55	rhyalb	17	4	1.38	junbre	1	1	0.05
junbre	28	4	0.38	scicyp	5	5	0.17	glycan	4	3	0.47	juncan	15	4	0.35	sciatr	1	1	0

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	**Frequ -ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**
Sedges Grasses and Rushes																			
carlas	25	3	1.07	carsp	4	4	0.13	juneff	3	2	0.06	glystr	13	3	0.76				
caline	24	3	0.42	carutr	4	4	0.94	xyrmon	3	2	0.18	juneff	13	3	0.36				
carstr	23	3	1.06	agrsca	3	3	0.21	eriang	2	1	0.06	junbuf	12	3	0.24				
carutr	20	3	0.51	carang	3	3	0.15	carbru	1	1	0.07	caraqu	11	3	0.38				
juneff	18	2	0.2	carech	3	3	0.22	carsp	1	1	0.02	junnod	10	3	0.09				
carlac	17	2	0.35	carves	3	3	0.41	junbre	1	1	0.04	poapal	10	3	0.41				
junbuf	16	2	0.17	eleery	3	3	0.08	phaaru	1	1	0.36	agrrep	9	2	0.21				
juncan	15	2	0.18	elepal	3	3	0.06	poasp	1	1	0.07	agrtra	7	2	0.59				
phraus	14	2	0.17	carbux	2	2	0.05					horjub	6	2	0.08				
erivir	13	2	0.15	carret	2	2	0.33					scival	6	2	0.06				
glystr	13	2	0.41	juneff	2	2	0.01					carpse	5	1	0.07				
carhou	10	1	0.31	sciacu	2	2	0.07					poasp	5	1	0.05				
carmag	10	1	0.17	carath	1	1	0.28					broine	4	1	0.1				
junnod	10	1	0.05	carbru	1	1	0.03					erivir	4	1	0.05				
poapal	10	1	0.22	carcri	1	1	0					scimic	4	1	0.06				
agrrep	9	1	0.11	cardia	1	1	0.09					carbru	3	1	0.06				
horjub	9	1	0.06	carfla	1	1	0.14					caroli	3	1	0.03				
agrtra	7	1	0.32	carten	1	1	0					eleaci	3	1	0.07				
poasp	6	1	0.04	erivir	1	1	0.01					elepal	3	1	0.04				
scival	6	1	0.03	junbre	1	1	0.04					junpel	3	1	0.15				
carbru	5	1	0.05	junlon	1	1	0					sciatr	3	1	0				
carlim	5	1	0.07	phraus	1	1	0.05					eriang	2	1	0.01				
carpse	5	1	0.04	scimic	1	1	0.08					junart	2	1	0.03				
eriang	5	1	0.02									phraus	2	1	0.06				
scimic	5	1	0.04																
broine	4	1	0.05																
sciatr	4	1	0																

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	Frequ -ency	%	Mean	Species	Freque ncy	%	Mean	Species	Frequ-ency	%	Mean	Species	Frequ-ency	%	Mean	Species	Frequ-ency	%	Mean
Forbs																			
solgra	77	10	0.39	equflu	22	21	0.41	drorot	30	22	0.44	solgra	73	18	0.72	epiang	13	13	0.22
equarv	54	7	1.94	galtri	18	17	0.17	fravir	9	7	1.46	equarv	48	12	3.37	drorot	9	9	0.11
drorot	52	7	0.15	smitri	11	10	0.75	lyster	9	7	0.32	typang	43	11	1.36	lycuni	7	7	0.22
typang	47	6	0.76	trimar	9	8	0.26	utrvul	9	7	0.61	epiang	17	4	0.32	equarv	5	5	0.85
epiang	35	5	0.21	mentri	8	8	1.33	solrug	9	7	0.36	typlat	16	4	0.31	rumace	5	5	0.85
galtri	30	4	0.06	astbor	7	7	0.1	lemmin	6	4	0.12	lycame	15	4	0.12	potgra	5	5	0.06
solrug	24	3	0.16	potpal	6	6	0.14	epiang	5	4	0.04	trifra	15	4	0.06	lepram	3	3	0.03
equflu	22	3	0.06	lycuni	4	4	0.11	vio.sp	4	3	0.23	solrug	14	4	0.17	solpub	2	2	0.05
lycuni	19	3	0.09	typang	4	4	0.26	trifra	4	3	0.07	astumb	13	3	0.1	anamar	1	1	0.02
trifra	19	3	0.05	epilep	3	3	0.02	astnem	3	2	0.2	epilep	13	3	0.04	bidfro	1	1	0
typlat	19	3	0.17	lemmin	3	3	0.1	lycinu	3	2	0.13	ranpen	13	3	0.81	fravir	1	1	0
fravir	17	2	0.32	utrvul	3	3	0.1	hypper	2	1	0.01	drorot	12	3	0.09	galtri	1	1	0.01
epilep	16	2	0.02	solgra	3	3	0.03	typlat	2	1	0.04	hieaur	12	3	0.23	taroff	1	1	0.02
lycame	16	2	0.07	astnem	2	2	0.04	equarv	1	1	0.14	galtri	11	3	0.06				
utrvul	15	2	0.27	calpal	2	2	0.05	lycame	1	1	0.02	hypper	10	3	0.08				
astumb	13	2	0.06	lyster	2	2	0.03	solgra	1	1	0.02	solcan	10	3	0.08				
ranpen	13	2	0.43	myrsp	2	2	0.15	spachl	1	1	0.04	polper	9	2	0.07				
hieaur	12	2	0.12	osmcin	2	2	0.04	rumace	1	1	0.07	euphel	8	2	0.08				
hypper	12	2	0.05	pedlan	2	2	0.03					lycuni	8	2	0.08				
astbor	11	1	0.03	violab	2	2	0.01					chealb	7	2	0.21				
lyster	11	1	0.06	scugal	2	2	0.02					fravir	7	2	0.08				
smitri	11	1	0.11	polamp	2	2	0.02					epigla	6	2	0.04				
lemmin	10	1	0.04	ascinc	1	1	0.03					galtet	6	2	0.06				
solcan	10	1	0.04	cerdem	1	1	0.05					matdis	6	2	0.07				
trimar	9	1	0.04	drorot	1	1	0.03					anamar	5	1	0.02				
polper	9	1	0.04	parpal	1	1	0.02					bidfro	5	1	0.02				
euphel	8	1	0.04	utrint	1	1	0					cirarv	5	1	0.04				
mentri	8	1	0.19	typlat	1	1	0					astbor	4	1	0.03				
vio.sp	8	1	0.06	solrug	1	1	0.01					despin	4	1	0.04				
rumace	8	1	0.13	spaeme	1	1	0.02					galapa	4	1	0.01				

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	Frequ -ency	%	Mean	Species	Freque ncy	%	Mean	Species	Frequ- ency	%	Mean	Species	Frequ- ency	%	Mean	Species	Frequ- ency	%	Mean
Forbs																			
chealb	7	1	0.11	potgra	1	1	0.07					galcir	4	1	0.04				
astnem	7	1	0.05									vio.sp	4	1	0.02				
anamar	6	1	0.01									alipla	3	1	0.03				
bidfro	6	1	0.01									impcap	3	1	0.01				
camapa	6	1	0									utrvul	3	1	0.28				
epigla	6	1	0.02									astnem	2	1	0.01				
galtet	6	1	0.03									cicbul	2	1	0				
matdis	6	1	0.04									galtin	2	1	0.01				
potgra	6	1	0.02									tusfar	2	1	0.11				
potpal	6	1	0.02									spachl	2	1	0.01				
cirarv	5	1	0.02									rumace	2	1	0				
despin	4	1	0.02																
galapa	4	1	0																
galcir	4	1	0.02																
Shrubs																			
spilat	79	11	1.03	chacal	3	30	3.41	spilat	21	15	2.32	spilat	49	12	0.98	saldis	7	7	0.67
saldis	67	9	0.5	vacoxy	1	14	0.66	vacoxy	20	14	1.13	saldis	44	11	0.33	ruball	5	5	0.36
chacal	50	7	0.62	kalpol	1	11	0.3	kalpol	18	13	0.4	salpet	21	5	0.48	salsp	4	4	0.15
vacoxy	35	5	0.3	saldis	1	9	1.04	chacal	15	11	0.49	spialb	17	4	0.09	spialb	4	4	0.18
kalpol	32	4	0.12	spilat	9	8	0.53	salpla	14	10	0.47	salsp	11	3	0.1	chacal	2	2	0.29
salpet	28	4	0.44	salcan	6	6	0.17	rubpub	11	8	2.21	rubida	8	2	0.2	kalpol	2	2	0.01
spialb	25	3	0.1	salped	6	6	0.14	ledgro	10	7	0.17	salbeb	8	2	0.11	kalang	1	1	0.05
salsp	16	2	0.08	andgla	5	5	0.12	rubaca	6	4	0.26	saleri	5	1	0.03	rubida	1	1	0.01
salpla	14	2	0.09	spialb	3	3	0.13	ruball	6	4	0.31	vacang	3	1	0.04	salpet	1	1	0.02
ledgro	12	2	0.05	vacmac	3	3	0.19	saldis	6	4	0.45					vacmyr	1	1	0.15
rubpub	12	2	0.41	rubauc	2	2	0.01	salpet	4	3	0.94								
ruball	11	1	0.11	salpet	2	2	0.08	andgla	2	1	0.01								
salbeb	10	1	0.12	aromel	1	1	0.19	salbeb	2	1	0.33								
rubida	9	1	0.11	ledgro	1	1	0.02	vacang	2	1	0.05								

Total (n=743)				Undisturbed (n=106)				Bulldozed (n=138)				Undrained Vacuumed (n=397)				Drained Vacuumed (n=102)			
Species	**Frequ -ency**	**%**	**Mean**	**Species**	**Freque ncy**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**	**Species**	**Frequ-ency**	**%**	**Mean**
andgla	7	1	0.02	vacang	1	1	0.02	kalang	1	1	0.07								
rubaca	6	1	0.05					salsp	1	1	0.04								
salcan	6	1	0.02																
salped	6	1	0.02																
vacang	6	1	0.03																
saleri	5	1	0.01																
Trees																			
betpop	68	9	1.31	betpum	1	14	1.47	betpop	19	14	2.14	betpop	31	8	0.89	betpop	18	18	3.14
betpap	39	5	0.76	alnrug	6	6	0.63	larlar	6	4	0.12	betpap	18	5	0.55	betpap	16	16	3.12
poptre	27	4	0.18	betgla	1	1	0.08	betpap	5	4	0.22	poptre	17	4	0.27	picmar	9	9	0.06
betpum	21	3	0.23	larlar	1	1	0	betpum	5	4	0.08	picmar	3	1	0.03	poptre	7	7	0.17
picmar	17	2	0.04	picmar	1	1	0.01	picmar	4	3	0.08					larlar	6	6	0.26
larlar	14	2	0.07					acerub	3	2	0.01								
alnrug	6	1	0.09					poptre	3	2	0.09								
acerub	4	1	0																

App. 2.3. List of surveyed species with their botonical authority and associated abbreviations used in tables and figures of thesis.

Mosses and Liverworts	
Aulacomnium palustre (Hedw.)Schwaegr.	aulpal
Brachythecium rivulare Schimp. *in* B.S.G.	brariv
Bryum pseudotriquetrum (Hedw.) Gaertn. *et al.*	brypse
Bryum weigelii Spreng. *in* Biehler	brywei
Calliergonella cuspidata (Hedw.) Loeske	calcus
Calliergon giganteum (Schimp.) Kindb.	calgig
Campylium hispidulum (Brid.) Mitt.	camhis
Campylium stellatum (Hedw.) C. Jens.	camste
Dicranella cerviculata (Hedw.) Schimp.	diccer
Drepanocladus aduncus (Hedw.) Warnst.	dreadu
Drepanocladus revolvens (Sw.) Warnst.	drerev
Lophozia ventricosa (Dicks.) Dum.	lopven
Mnium affine Bland. *ex* Funck	mniaff
Mnium gracile (Kop.) Crum and Anderson	mnigra
Mylia anomala (Hook.) S. Gray	mylano
Pohlia nutans (Hedw.) Lindb.	pohnut
Polytrichum commune Hedw.	polcom
Polytrichum longisetum Brid.	pollon
Polytrichum strictum Brid.	polstr
Scorpidium scorpioides (Hedw.) Limpr.	scosco
Tomenthypnum nitens (Hedw.) Loeske	tomnit
Warnstorfia exannulata (Schimp. in B.S.G.) Loeske	warexa
Warnstorfia fluitans (Hedw.) Loeske	warflu
Sphagnum	
Sphagnum angustifolium (C. Jens. *ex* Russ.) C. Jens. *in* Tolf	sphang
Sphagnum capillifolium (Ehrh.) Hedw.	sphcap
Sphagnum centrale C. Jens. *in* Arnell and C. Jens.	sphcen
Sphagnum cuspidatum Ehrh. ex Hoffm.	sphcus
Sphagnum fallax (Klinggr.) Klinggr.	sphfal
Sphagnum fuscum (Schimp.) Klinggr.	sphfus
Sphagnum fimbriatum Wils. in Wils. and Hook. f. in Hook. f. var. *fimbriatum*	sphfim
Sphagnum flexuosum Dozy and Molk. var. *flexuosum* var. *ramosissimum* Andrus	sphfle
Sphagnum inundatum Russ.	sphinu
Sphagnum magellanicum Brid.	sphmag
Sphagnum majus (Russ.) C. Jens.	sphmaj
Sphagnum papillosum Lindb.	sphpap
Sphagnum rubellum Wils.	sphrub

Sphagnum squarrosum Crome	sphsqu
Sphagnum subsecundum Nees in Sturm var. subsecundum var. andrusii Crum	sphsub
Sphagnum teres (Schimp.) Angstr. in Hartm.	sphter
Sphagnum warnstorfii Russ.	sphwar

Sedges, Rushes and Grasses

Agropyron repens (L.) Beauv.	agrrep
Agropyron trachycaulum (Link) Malte	agrtra
Agrostis scabra Willd.	abrsca
Bromus inermis Leyss.	broine
Calamagrostis canadensis (Mich.) Nutt.	calcan
Calamagrostis inexpansa Gray	calstr
Carex L.	carsp
Carex aquatilis Wahl.	calaqu
Carex atherodes Spreng.	carath
Carex bebbii Olney (Bailey) Fern	carbeb
Carex brunnescens (Pers.) Poir.	carbru
Carex buxbaumii Wahl.	carbux
Carex canescens L.	carcan
Carex crinita Lam.	carcri
Carex diandra Schrank	cardia
Carex echinata Murr.	carech
Carex flava L.	carfla
Carex houghtoniana Torr.	carhou
Carex lacustris Willd.	carlac
Carex lasiocarpa Ehrh.	carlas
Carex limosa L.	carlim
Carex magellanica Lam.	carmag
Carex oligosperma Michx.	caroil
Carex pseudo-cyperus L.	carpse
Carex retrorsa Schw.	carret
Carex stricta Lam.	carstr
Carex tenuiflora Wahl.	carten
Carex utriculata Boott	carutr
Carex vesicaria L.	carves
Eleocharis acicularis (L.) R.andS.	eleaci
Eleocharis erythropoda Steud.	eleery
Eleocharis palustris (L.) R.andS.	elepal
Eriophorum angustifolium Honckeny	eriang
Eriophorum vaginatum L.	erivag
Eriophorum virginicum L.	erivir
Glyceria canadensis (Michx.) Trin.	glycan
Glyceria striata (Lam.) Hitchc.	glystr
Hordeum jubatum L.	horjub
Juncus articulatus L.	junart

Juncus brevicaudatus (Engelm.) Fern.	junbre
Juncus bufonius L.	junbuf
Juncus canadensis Gay	juncan
Juncus effusus L.	juneff
Juncus longistylis Torr.	junlon
Juncus nodosus L.	junnod
Juncus pelocarpus Meyer	junpel
Juncus tenuis Willd.	junten
Phalaris arundinacea L.	phaaru
Phragmites australis (Cav.) Trin.	phraus
Poa L.	poasp
Poa palustris L.	poapal
Rhynchospora alba (L.) Vahl.	rhyalb
Scirpus acutus Mühl.	sciacu
Scirpus atrocinctus Fern.	sciatr
Scirpus cyperinus (L.) Kunth	scicyp
Scirpus microcarpus Presl	scimic
Scirpus validus Vahl	scival
Xyris montana Ries.	xyrmon

Forbs

Alisma plantago-aquatica L.	alipla
Anaphalis margaritacea (L.) Clarke	anamar
Asclepias incarnata L.	ascinc
Aster borealis (T. and G.) Provancher	astbor
Aster nemoralis Ait.	astnem
Aster umbellatus Mill.	astumb
Bidens frondosa L.	bidfro
Calla palustris L.	calpal
Campanula aparinoides Pursh	camapa
Ceratophyllum demersum L.	cerdem
Chenopodium album L.	chealb
Cicuta bulbifera L.	cicbul
Cirsium arvense (L.) Scop.	cirarv
Descurainia pinnata (Walt.) Britt.	despin
Drosera rotundifolia L.	drorot
*Epilobium angustifoliu*m L.	epiang
Epilobium glandulosium Lehm.	epigla
Epilobium leptophyllum Raf.	epilep
Equisetum arvense L.	equarv
Equisetum fluviatile L.	equflu
Euphorbia helioscopia L.	euphel
Fragaria virginiana Dcne.	fravir
Galeopis tetrahit L.	galtet
Galium aparine L.	galapa
Galium circaezans Michx.	calcir

Galium tinctorium (L.) T.andG	galtin
Galium trifidum L.	galtri
Hieracium aurantiacum L.	hieaur
Hypericum perforatum L.	hypper
Impatiens capensis Meerb.	impcap
Lepidium ramosissimum Nels.	lepram
Lycopus americanus Mühl.	lycame
Lycopus uniflorus Michx.	lycuni
Lysimachia terrestris (L.) BSP.	lyster
Lemna minor L.	lemmin
Matricaria discoidea DC.	matdis
Menyanthes trifoliata L.	mentri
Myriophyllum L.	myrsp
Osmunda cinnamomea L.	osmcin
Parnassia palustris L.	parpal
Pedicularis lanceolata Michx.	pedlan
Polygonum amphibium L.	polamp
Polygonum persicaria L.	polper
Potentilla gracilis Dougl.	potgra
Potentilla palustris (L.) Scop.	potpal
Ranunculus pensylvanicus L.f.	ranpen
Rumex acetosa L.	rumace
Scuellaria galericulata L.	scugal
Smilacina trifolia (L.) Desf. (*Maianthemum trifolium*)	smitri
Solidago canadensis L.	solcan
Solidago graminifolia (L.) Salisb.	solgra
Solidago puberula Nutt.	solpub
Solidago rugosa Ait.	solrug
Sparganium chlorocarpum Rydb.	spachl
Sparganium emersum Rehmann	spaeme
Tussilago farfara L.	tusfar
Taraxacum officinale Weber	taroff
Triadenum fraseri Spach	trifra
Triglochin maritima L.	trimar
Typha angustifolia L.	typang
Typha latifolia L.	typlat
Utricularia intermedia Hayne	utrint
Utricularia vulgaris L.	utrvul
Viola labradorica Schrank	violab
Viola L.	viosp

Shrubs

Andromeda glaucophylla Link	andgla
Aronia melanocarpa Michx	aromel
Chamaedaphne calyculata L.	chacal
Kalmia angustifolia L.	kalang

Kalmia polyfolia L.	kalpol
Ledum groenlandicum Oeder (*Rhododendron groenlandicum*)	ledgro
Rubus acaulis Michx.	rubaca
Rubus allegheniensis Porter	ruball
Rubus idaeus L.	rubida
Rubus pubescens Raf.	rubpub
Salix L.	salsp
Salix bebbiana Sarg.	salbeb
Salix candida Flügge	calcan
Salix discolor Mühl	saldis
Salix eriocephala Michx.	saleri
Salix pedicellaris Pursh	salped
Salix petiolaris Sm.	salpet
Salix planifolia (Pursh) Hiitonen	salpla
Spiraea alba Du Roi	spialb
Spiraea latifolia (Ait.) Ahles	spilat
Vaccinium angustifolium Ait.	vacang
Vaccinium macrocarpon Ait.	vacmac
Vaccinium myrtilliodes Michx.	vacmyr
Vaccinium oxycoccos L.	vacoxy

Trees

Acer rubrum L.	acerub
Alnus rugosa (Du Roi) Spreng.	alnrug
Betula glandulosa Michx.	betgla
Betula papyrifera Marsh.	betpap
*Betula populifoli*a Marsh.	betpop
Betula pumila L.	betpum
Larix laricina (Du Roi) Koch	larlar
Picea mariana (Mill.) BSP.	picmar
Populus tremuliodes Michx.	poptre

CHAPTER THREE

EXAMINING THE PEAT-ACCUMULATING POTENTIAL OF FEN VEGETATION IN THE CONTEXT OF FEN RESTORATION OF HARVESTED PEATLANDS[2]

[2] Graf, M. D. and L. Rochefort (article submitted to Écoscience).

ABSTRACT

An important long-term goal for peatland restoration is the return of the system's peat-accumulating function. In order to focus restoration efforts towards specific vegetation groups in fen restoration, knowledge of the peat-accumulating function of dominant fen species is critical. Although many studies have looked at the decomposition and production rates of fen species in undisturbed fens, the altered hydrology and vegetation of the restoration sites will certainly impact peat accumulation. In order to compare the peat-accumulating function of fens under the conditions of restored sites (harvested fen) and undisturbed fens, the decomposition rates of three typical fen species and three species that spontaneously colonize fens were assessed. We found no link between the habitat of the species and their decomposition rates. The average mass loss for all material types was slightly higher (approximately 4%) in the harvested fen than those observed in the undisturbed fen. However, the litter type (leaves, roots/rhizomes or moss fragment) had the largest impact on the decomposition rates. The leaves of vascular plant had the highest mass losses (between 64-48% for all species except *Scirpus cyperinus*) compared to roots/rhizomes (between 43-39%). *Scirpus cyperinus* leaves had mass loss which was slightly lower than the roots/rhizomes (between 34-41%). The two tested bryophytes had significantly lower mass losses (between 20-25% for *Polytrichum strictum* and 11% for *Sphagnum centrale*) than the vascular plant litter. The annual primary production of the tested species was also measured to estimate the peat-accumulating capacity of each species. *Scirpus cyperinus* had an annual primary production which was three times higher (1500 g m^{-2} yr^{-1}) than the other species (between 300 and 550 g m^{-2} yr^{-1}). Due to its low mass loss and high primary production this species should be considered an acceptable replacement to *Carex* species for restoration projects in terms of its peat-accumulating function. Finally, bryophytes should be an important component of fen restoration, due to their superior peat accumulating capacity even on harvested sites.

RÉSUMÉ

Un important but à long terme de la restauration des tourbières est le retour de la fonction d'accumulation de la tourbe. Afin de concentrer les efforts de la restauration des fens vers un groupe spécifique de végétation, il est important d'acquérir de l'information sur le potentiel d'accumulation de la tourbe par les espèces dominantes des fens. Plusieurs études ont déjà examiné les taux de décomposition et de production dans les fens non perturbés. Dans les sites en restauration, l'accumulation de la tourbe risque fort de différer en raison des modifications de l'hydrologie et de la végétation. Ainsi, nous avons estimé le taux de décomposition de trois espèces végétales typiques des fens non perturbés et de trois espèces colonisant les fens résiduels afin d'examiner la fonction d'accumulation de la tourbe dans ces deux types de milieux. Nous n'avons pas trouvé de lien entre l'habitat des espèces et leur taux de décomposition. Pour tous les types de matériel végétal (feuilles, racines/rhizomes ou fragments de mousse), la masse moyenne perdue s'est avérée légèrement plus élevée (approximativement 4 %) dans les fens résiduels que dans les fens non perturbés. C'est le type de matériel qui a eu le plus grand impact sur le taux de décomposition. Les feuilles des plantes vasculaires ont perdu la plus grande masse (entre 64 et 48 % pour toutes les espèces, sauf pour le *Scirpus cyperinus*) par rapport aux racines/rhizomes (entre 43 et 39 %). Les feuilles de *Scirpus cyperinus* ont perdu moins de masse (entre 34 et 41 %) que les racines/rhizomes. La masse perdue par les deux bryophytes étudiés était significativement moins élevée (entre 20 et 25 % pour le *Polytrichum strictum* et 11 % pour le *Sphagnum centrale*) que celle de la litière des plantes vasculaires. La production primaire annuelle des espèces examinées a également été mesurée afin d'estimer la capacité de chaque espèce à se décomposer en tourbe. La production primaire annuelle de *Scirpus cyperinus* s'est avérée trois fois plus élevée (1 500 g m^{-2} an^{-1}) que les autres espèces (entre 300 et 550 g m^{-2} an^{-1}). En raison de sa faible perte de masse et de sa grande production primaire, cette espèce devrait être considérée comme une remplaçante acceptable de *Carex* pour les projets de restauration visant l'accumulation de la tourbe. Finalement, les bryophytes devraient devenir une composante importante de la restauration des fens, en raison de leur capacité supérieure à produire de la tourbe, et ce, même sur les sites résiduels.

INTRODUCTION

Understanding the link between an ecosystem's structure and function is crucial to setting restoration targets and strategies (Naeem 2006). The return of peat-accumulating function has been deemed an important long-term goal in peatland restoration (Rochefort 2000). It is known that species play a major role in the ability of an ecosystem to accumulate peat (Johnson and Damman 1993); however, there is little consensus on which species are most important to peat accumulation in fens. Roth (1999) focused restoration efforts on reeds and sedges because he felt they were important peat-accumulating species. Chimner *et al.* (2002) found 50% of fen peat to consist of structural root material when peat accumulation in fens was simulated. Vitt (2000), on the other hand, found that vascular plant-dominated layers produce less biomass and decompose more readily than the bryophyte-dominated ground layer in fens. Currently, most fen restoration projects focus on restoring vascular plant vegetation (Wheeler and Shaw 1995; van Duren *et al.* 1998; Cooper and MacDonald 2000; Hald and Vinther 2000; Kratz and Pfadenhauer 2001; Tallowin and Smith 2001; Kotowski 2002; Lamers *et al.* 2002).

Historical data do not provide a clear picture of which vegetation groups are mainly responsible for peat accumulation in fens. Paleoecological studies of peatlands in North America show a wide range of plant composition in fen peat. Vitt (2000) examined 341 peatland cores across North America and found that the major component of fen peat was bryophytic: *Sphagnum* in poor fens and brown mosses in rich fens. However, Kubiw *et al.* (1989), Nicholson and Vitt (1990), Lavoie and Richard (2000a) Lavoie and Richard (2000b) all found vascular plants and bryophytes to be equally important components of the peat, while Griffin (1977) Warner *et al.* (1991) and Hu and Davis (1994) found fen peat to be dominated by vascular plants.

The use of historical data to determine restoration goals is often limited because present environmental conditions may differ greatly from those prevalent during the formation of the system. In the case of harvested peatlands, the hydrology of the restoration sites differs substantially from the hydrology of natural peatlands. Abandoned peatlands are characterized by a water table that fluctuates greatly (Price *et al.* 2003), while natural fens are characterized by extremely constant water tables (Bedford and Godwin 2003). To what extent an altered hydrology will affect the decomposition rates and thereby the peat-accumulation rate of plants is unknown.

The vegetation of the restoration sites also differs from the vegetation common to undisturbed fens. Harvested fens which are no longer being actively drained are quickly recolonized by spontaneous vegetation (Famous et al 1991; Chapter 2). The spontaneous vegetation can be characterized as wetland species, dominated by *Scirpus cyperinus*, *Juncus* sp. and other forbs. In contrast, undisturbed fens with chemical properties similar to the harvested fens are dominated by *Carex* and *Sphagnum* species (Chapter 2). Although the community structure and species of the harvested fens is different from undisturbed fens, it is not known whether this dissimilarity also translates to differences in the peat-accumulating potential of the sites.

The goal of this study was to identify which vegetation groups are important in returning the peat-accumulating function of a fen. Specifically, we wanted to know 1) if spontaneously colonizing plants are as efficient in accumulating peat as typical fen species and 2) whether decomposition rates vary greatly between undisturbed and harvested fens. In order to respond to these questions, the decomposition rates of three species which frequently spontaneously recolonize harvested fens were compared with the decomposition rates of three species common to undisturbed fens. The decomposition rates were measured over two growing seasons on both an undisturbed and harvested fen. The annual production of these plants was also measured to approximate the overall peat-accumulation potential of each plant.

Materials and Methods

Study Species

The decomposition rates and the annual production were measured for six species: four vascular plant species and two bryophytes. *Scirpus cyperinus, Juncus brevicaudatus, Polytrichum strictum* are species which frequently colonize harvested fens (App 2.2). *Carex rostrata, Calamagrostis canadensis* and *Sphagnum centrale* represent genera commonly found in undisturbed moderate-rich fens of the boreal zone of North America (Vitt and Chee 1990; Chapter 2). In total, the decomposition rates of ten litter types were measured: the leaves of the four vascular species, the rhizomes and roots of the same species and the two moss species. Scoggan (1978) for vascular plants, Anderson (1990) for *Sphagnum*, Anderson *et al.* (1990) for other mosses.

STUDY AREA AND SITE DESCRIPTIONS

The decomposition rates of the above-mentioned species were measured on an abandoned, harvested peatland and an undisturbed fen. The harvested fen (47° 45’N 69° 30’W) is located approximately 15 km southeast Rivière-du-Loup, Québec, Canada. This fen site is part of a large complex of bogs interspersed with *Alnus* swamps (Gauthier and Grandtner 1975) and is classified as a low boreal peatlands (National Wetlands Working Group 1988). The particular experimental sector, originally a bog, was mined down to its minerotrophic peat layer and hereafter will be refered to as the harvested fen. The harvested fen was abandoned eight years prior to the start of the experiment and spontaneous recolonization had begun (46% total vegetation cover), dominated by *Equisetum arvense*, *Scirpus cyperinus*, *Juncus brevicaudats* and *Spirea latifolia* (unpublished data). The pH of the harvested fen was 4.97 (± 0.07) and the electrical conductivity was 23.9 $\mu S\ cm^{-1}$ (± 2.5).

The undisturbed fen (47°77’ N 52°83’ W) is located approximately 25 km southwest of the harvested fen. This site was chosen because its environmental parameters are similar to the harvested fen; the pH was 4.97 (± 0.24) and electrical conductivity was 30.9 $\mu S\ cm^{-1}$ (± 7.9). The undisturbed fen can be classified as a poor fen, dominated by *Sphagnum centrale*, *Calamagrostis canadensis, Salix discolor, Carex brunnescens* and *Glyceria canadensis.*

The regional climate is characterized by cold winters and warm summers with January and July mean temperatures of –13 and 18 °C, respectively. The mean annual precipitation is 963 mm, of which 72% falls as rain (Environment Canada 2007).

DECOMPOSITION

Senesced leaf litter (yellow in color), belowground biomass of the tested vascular species and fragments of the tested mosses were collected in early September of 2004. The roots and rhizomes of the vascular plants were extracted by cutting peat cores in a 10 cm diameter around individual plants. The roots and rhizomes were rinsed clean of any remaining peat debris. The root material used for this study was randomly selected from all roots (and rhizomes for *Carex* and *Scirpus*) with a diameter of 3 mm or less. The fragments of the two moss species included the stems, branches and leaves of live, healthy specimens; the capitulum of the *Sphagnum* species was removed.

The plant material was oven-dried at 40° C until constant mass and 1 to 2 g (0.5 g for *Sphagnum* species) of plant material was placed in individual mesh bags (5 cm x 7.5 cm). The litter of fine vegetation (*Sphagnum*, *Polytrichum* and *Juncus* leaves) was placed in pre-weighed nylon mesh bags with a 0.25-mm mesh gauge to minimize loss of plant material. All other litter types were placed in pre-weighed fiberglass mesh bags with 1-mm mesh gauge. Each filled bag was weighted to the nearest 0.001 g.

Within each incubation site (undisturbed and harvested) three transects of 10 m located within 30 m of each other were randomly chosen. Six bags were attached to a bamboo rod every meter. The ten litter types were replicated six times per transect for a total of 60 bags per transect. On each site 180 bags and overall 360 bags were deployed. The bags were inserted vertically at a depth of approximately 5 cm below the surface in mid September 2004. All bags were removed after two growing seasons in mid September 2006. In a laboratory, excess peat and debris were cleaned from the bags by rinsing them in a water bath. Growing roots and other vegetation that had penetrated the bags during the two years of incubation were carefully removed with forceps. The bags were dried at 40° C until a constant mass was reached. Each bag was again weighted to the nearest 0.001 g.

The percent of mass remaining (MR) over two growing seasons was computed for each litter material using the following equation (Rochefort *et al.* 1990):

$$MR = [(X_0 – X)/X_0] \times 100 \quad [1]$$

where X_0 is the initial dry litter mass (g) before decomposition and X is the final dry litter mass (g) after incubation in the field.

PRODUCTION

Mosses

Moss annual primary production (MAPP; in g m^{-2}) was estimated using the following equation (Vitt and Pakarinen 1977):

$$MAPP = [W * G] / [SS * H] \quad [2]$$

where W is moss dry biomass (g), G is mean annual increment (m), SS is the sample surface (m^2) and H is the mean living moss height (m). The mean annual increment (G) of *Sphagnum centrale,* growing in the undisturbed fen, was measured using the Velcro technique (Glime 1984). Thirty Velcro strips were placed just below the capitulum along a hummock-hollow gradient within a 5 m^2 area in May of 2005. In October of the same year 24 of the 30 Velcro strips were found and the growth from the Velcro strip to the capitulum was measured to the nearest mm. The mean annual increment (G) of *Polytrichum strictum* growing on the harvested fen was measured using its innate marker, where the natural growth pattern of this species allows the growth from the previous growing season to be easily distinguished from that of the current season (Russell 1988). The innate markers of twenty stems within a colony of 5 m^2 were measured to the nearest mm. For both moss species, the surface sample (SS) was a 50.24 cm^2 core, removed using an aluminium cylinder with sharp cutting edges. Ten cores were randomly sampled from the colonies (an area of approximately 5 m^2) of each moss species. Only the green, photosynthetic active portions of the mosses were used to calculate the moss layer height (H); three lengths per core were measured. To calculate the moss dry biomass (W) the photosynthetic active moss fragments of each core were dried at 40 °C until a constant mass was achieved and weighed to 0.001 g.

Vascular plants

The annual aboveground biomass production was measured in late August of 2005. Ten quadrats of 50 cm x 50 cm were chosen randomly in colonies (approximate areas of 10

m^2) of the four tested vascular species and all biomass within each quadrat was clipped. Any dead leaves or leaves from other species were removed and the biomass was dried at 40 °C until the mass was constant. The material collected from each quadrat was weighed to the closest 0.01 g.

The production of root biomass was measured over two growing seasons using an ingrowth bag method (Finér and Laine 2000; Steen 1991). The ingrowth bags were mesh bags (mesh size 7 mm) with a diameter of 7 cm and a length of 50 cm. Each bag was filled with fen peat from the harvested fen where no vegetation was growing. A wood cylinder was used to compact the peat in the bags so that it resembled the density of the peat in field conditions. Transects of 5 m were set up in communities of the tested vascular plants where a hand-held auger was used to drill holes of the same diameter as the ingrowth bag every meter along transects. In May 2005 five bags were deployed for each species for a total of 20 bags. We were able to find monocultures (no other species within a 2 m radius of transect) for the *Scirpus cyperinus* and *Calamagrostis canadensis.* Transects for *Juncus brevicaudatus* and *Carex rostrata* did contain some individuals of other plants, although the target species were still dominant species (>80% of vegetation cover).

After two growing seasons (in mid September 2006) the ingrowth bags were removed. Before removal the roots around a bag were cut to a depth of 20 cm. Within 48 hours of removal, the bags were placed in a freezer until they could be further processed. Peat was washed away from the root material using a series of sieves (2 mm and 0.5 mm meshes). Forceps were used to remove the roots from the peat and debris that collected in the 0.5 mm sieve. The root biomass from each ingrowth bag was dried at 40 °C until the mass was constant and was weighed to the closest 0.01 g. The masses measured for each vegetation type were extrapolated to primary production measures of biomass (g $m^{-2}yr^{-2}$).

The peat of the ingrowth bags, the harvested fen and undisturbed fen were compared with chemical analyses and bulk density measurements. One peat sample was taken from the middle of each transect and from the peat used to fill the ingrowth bags. The samples were taken from the surface (top 5 cm) after the biological crust (top 1 cm) was removed. Only one peat sample was taken for the *Juncus* and *Scirpus* communities because the communities were in close proximity (10 m apart). After loss on ignition, the peat ash was analyzed for Ca, Mg, Fe, Cu, Zn, Mn and K concentrations using atomic absorption method (ISO number PHL-LA-WI-030 and 031). Total N content was determined after mineralization through acidic digestion following the Kjeldhal method (ISO number PHL-LA-WI 022). Total P was determined after mineralization (ISO number PHL-LA-WI-033).

After two growing seasons, the bulk density of the surface (top 5 cm) was measured twice for each transect at random locations along the transects and twice for the ingrowth bags of a particular tansect. Bulk density was calculated using the difference between the fresh mass and oven-dry mass of a known volume of peat (Hillel 1998).

Statistical Analyses

ANOVAs and LSD (least squared difference) procedures of SAS (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, NC, U.S.A.) were used to test the differences in the decomposition rates for each litter type. The decomposition rates could not be compared between sites because the main effect (the sites) was not replicated. Therefore, the litter types were analyzed separately for each site.

Results

Peat Properties

The chemical properties of the peat for the in-growth bags were comparable to the peat from the incubation sites. However, the peat from the undisturbed fen sites was slightly richer in some nutrients (Table 3.1). The bulk density of the in-growth bags was slightly higher than that of the surrounding areas for all colonies except *Scirpus* (Table 3.1).

Mass Losses

The averaged two year mass loss for all litter on the undisturbed fen was slightly lower (39% ±3) than those observed on the harvested fen (43% ±3). When the individual litter types were compared the same mass loss patterns were observed on both sites (Figure 3.1). The moss species had significantly lower mass losses than the vascular plants on both sites (Figure 3.1). Between the two moss species, *Sphagnum centrale* had a significantly lower mass loss (11% for the undisturbed and harvested fens) than *Polytrichum strictum* (20% for the undisturbed and 25% for the harvested fen).

Among the vascular plants, the two year mass losses observed for *Carex rostrata, Calamagrostis canadensis* and *Juncus brevicaudatus* leaves which were incubated on the harvested fen were significantly higher than other litter types (from 65% to 55%; Figure 3.1). The mass losses of all root litters and the leaves of *Scirpus cyperinus* that decomposed on the harvested fen did not vary among one another, but were significantly lower than the leaves of *C. rostrata*, *C. canadensis* and *J. brevicaudatus* (approximately 42%; Figure 3.1). The differences between mass losses of material which was incubated on the undisturbed fen were less distinct, but followed the same general pattern as the harvested fen (Figure 3.1). The leaves of *C. rostrata*, *C. canadensis* and *J. brevicaudatus* as well as the roots of *C. canadensis* had significantly higher mass losses (between 56% and 48%) than the leaves of *S. cyperinus* and the roots of *C. rostrata* (40% and 34%, respectively; Figure 3.1). The mass loss of *J. brevicaudatus* (41%) was significantly lower than that of *C. rostrata* leaves but was neither significantly higher nor lower than the mass losses of the other vascular litter types (Figure 3.1). The mass loss of the *S. cyperinus* roots (39%) was significantly lower than that of *C. rostrata* and *C. canadensis* leaves, but did not significantly differ from the other litter types of vascular plants.

Table 3.1. Nutrient concentrations (total elements) and bulk density of the top 5 cm of the peat surface on the study sites and the peat used for the ingrowth bags.

	Ingrowth Bags	Harvested Fen	Undisturbed Fen	
		Juncus brevicaudatus/ Scirpus cyperinus	*Carex rostrata*	*Calamagrostis canadensis*
N (%)	0.23	0.29	0.35	0.20
P (%)	0.02	0.07	0.07	0.04
K (%)	0.04	0.06	0.16	1.41
Ca (%)	0.39	0.61	1.28	1.41
Mg (%)	0.09	0.09	0.16	0.25
Mn (ppm)	32.7	37.7	121.6	42.3
Fe (ppm)	1613.9	1983.6	5176.0	8687.2
Cu (ppm)	5.8	29.3	56.0	28.7
Zn (ppm)	6.5	22.8	26.5	13.9
Bulk density (g cm^{-3}) (± SD)	0.19 (± 0.03)	0.14 (± 0.01) (*Juncus*) 0.20 (± 0.04) (*Scirpus*)	0.10 (± 0.01)	0.12 (± 0.01)

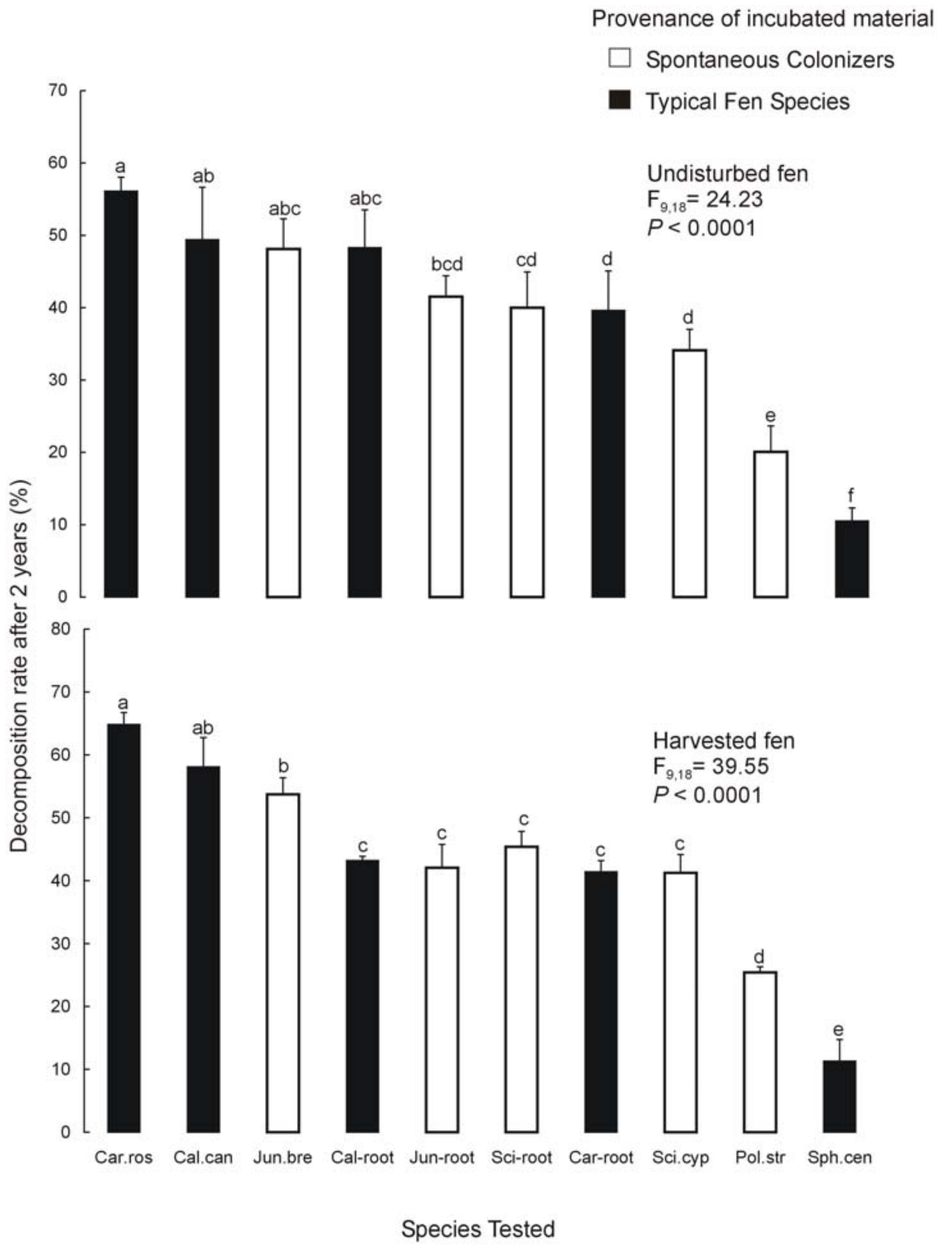

Figure 3.1. The 2-year mass losses are shown for ten tested litter types incubated in an undisturbed and harvested fen. The abbreviations stand for the following plants: *Scirpus cyperinus, Juncus brevicaudatus, Polytrichum strictum*, *Carex rostrata, Calamagrostis canadensis* and *Sphagnum centrale.* For the vascular plants the leaves and roots/rhizomes were incubated seperately. Spontaneous colonizing plants frequently colonize harvested fens and typical fen species correspond to vegetation groups which are common to moderate-rich fens of North America. The lower case letters signify significant differences (α=0.05) between litter types as shown by ANOVA and LSD analysis.

Production

The aboveground biomass production of *Scirpus cyperinus* (1500 g $m^{-2}yr^{-1}$) which grew on the harvested fen was approximately three times higher than the production of the other species (Figure 3.2). The large error bar is due to the fact that harvested fen is an early successional site and biomass production is not homogeneous, varying between bare peat to large *S. cyperinus* tussocks. *Sphagnum centrale* produced the second highest annual biomass (550 g $m^{-2}yr^{-1}$). All other plants had similar annual aboveground primary production rates of approximately 300 g $m^{-2}yr^{-1}$ (Figure 3.2).

In both the undisturbed and harvested fens the belowground annual primary production was substantially lower than the aboveground production of the vascular plants. The belowground production was 178 g $m^{-2}yr^{-1}$ for *Carex rostrata,* 131 g $m^{-2}yr^{-1}$ for *Calamagrostis canadensis,* 121 g $m^{-2}yr^{-1}$ for *Scirpus cyperinus* and 62 g $m^{-2}yr^{-1}$ for *Juncus brevicaudatus*.

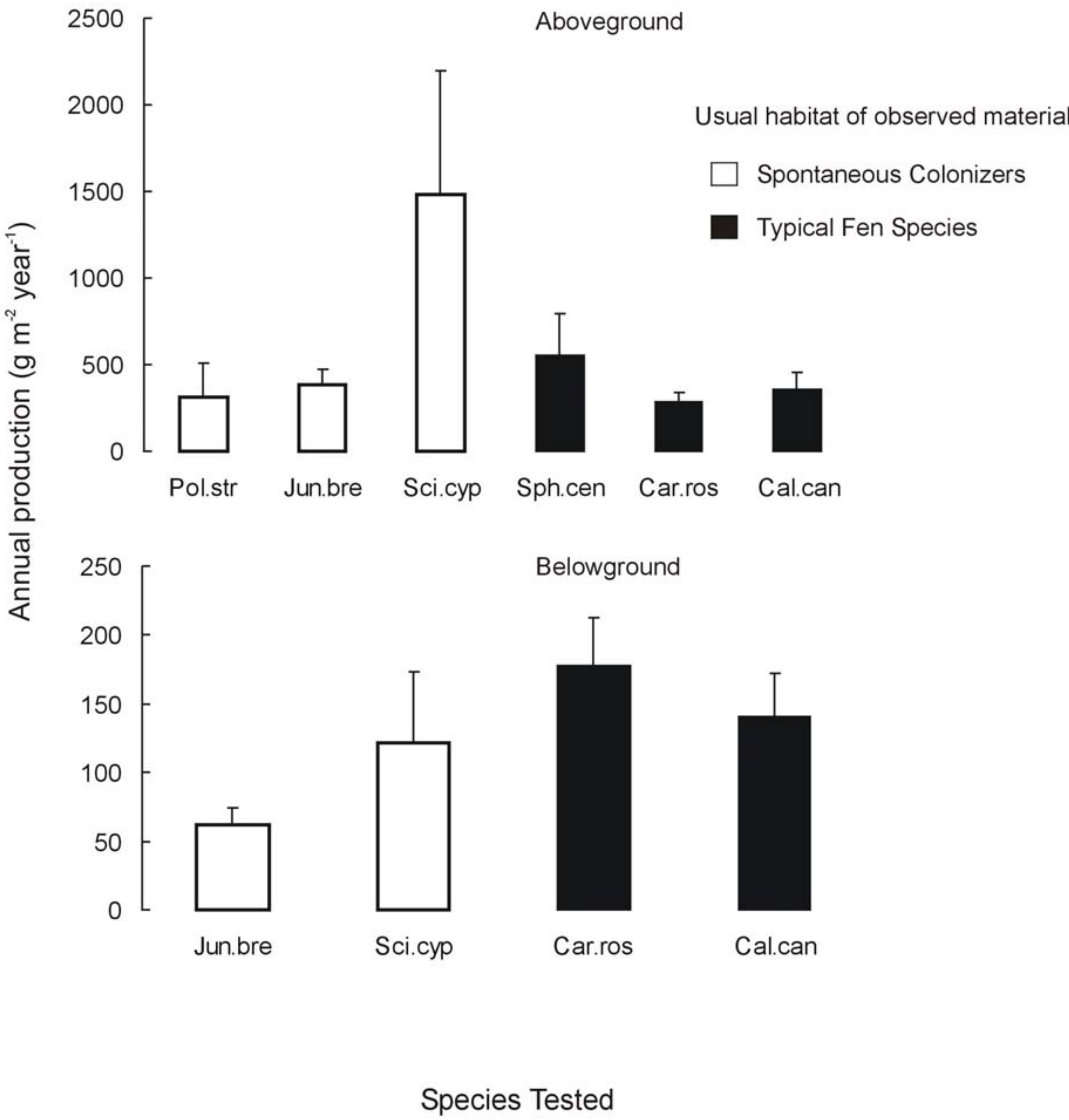

Figure 3.2. The aboveground and belowground annual primary production for the tested species. The abbreviations stand for the first three letters of the genus and species of the following plants: *Scirpus cyperinus, Juncus brevicaudatus, Polytrichum strictum*, *Carex rostrata, Calamagrostis canadensis* and *Sphagnum centrale.* The annual production measurements were for plants which spontaneously colonize harvested fens and vegetation found in undisturbed moderate-rich fens.

DISCUSSION

DECOMPOSITION

This study shows that the mass losses of the bryophytes over two years were substantially lower than the mass losses of aboveground and belowground litter of the vascular plants. The decomposition of *Sphagnum centrale* was substantially lower than all other tested litter material and did not differ between sites (Figure 3.1). This lack of variation shows that the intrinsic litter quality of *Sphagnum* is more important in regulating decomposition than habitat factors, as has been shown in numerous other studies (Clymo 1965; Johnson and Damman 1991; Johnson 1992). However, the mass loss for *S. centrale* observed in this study may not be entirely representative of *Sphagna* found in moderate-rich and poor fens. The decomposition rates of *Sphagnum* are known to vary greatly among species; species that occupy dry hummocks decay more slowly than those that grow in wet hollows (Johnson and Damman 1993). As *S. centrale* is a hummock species in poor fens (Gignac and Vitt 1990), the observed mass losses of this species are probably lower than other *Sphagnum* species found in wetter areas of fen (e.g. *S. fallax* or *S. teres*). Consequently, fens dominated by *Sphagnum* species which grow in wetter habitats will probably have higher mass losses than the mass losses observed for *Sphagnum centrale.*

Although the mass loss of *Polytrichum strictum* was twice that of *Sphagnum centrale*, it was still considerably lower than the mass losses of the vascular litter material. It is difficult to compare this value with values of other true mosses found in fens because most studies on decomposition in fens do not include true mosses (Brinson *et al.* 1981; Moore 1989; Thormann and Bayley 1997). Li and Vitt (1997) compared *Sphagnum* decomposition to brown moss decomposition in hummocks and found that *Sphagnum* decomposition rates are 11% lower, similar to the difference in *Polytrichum* and *Sphagnum* observed in this study. Strangely, fens dominated by non sphagnous mosses accumulate peat as proficiently as *Sphagnum* bogs (Vitt 2000).

The different mesh size of the decomposition bags used for this study likely influenced the decomposition rates of the litter material because vegetation decomposes more slowly in decomposition bags with smaller mesh sizes (Brinson *et al.* 1981; Johnson and

Damman 1993). If the mesh size had had a large impact on the mass losses, then *Juncus brevicaudatus*, *Polytrichum strictum* and *Sphagnum centrale* should all have much lower mass losses than the other litter types. However, *Juncus brevicaudatus* leaves had similar mass losses as the other leaves of vascular plants despite the smaller mesh size used for this litter type. Additionally, the mass loss rates of vascular plant leaves and *Sphagnum centrale* observed in this experiment are largely in agreement with those observed in other experiments (Brinson *et al.* 1981; Johnson and Damman 1993). Therefore, we do not believe that the mesh size greatly altered the data.

Among the litter types of vascular plants, the leaves of the vascular species (except *Scirpus cyperinus*) had the highest mass losses. The mass losses observed for the *Carex* (43%) and *Juncus* (42%) species in this study correspond with the mass losses of the same genus from other studies on northern peatlands (45-74% for *Carex* and 32-37% for *Juncus*) (Brinson *et al.* 1981; Szumigalski and Bayley 1996; Aerts and Caluwe 1997). *S. cyperinus* leaves had a significantly lower mass loss than the leaves of the other vascular plant species. Similarly, in created wetlands *S. cyperinus* was mainly responsible for litter accumulation due to its low mass losses (Atkinson and Cairns 2001).

This study was one of the few to measure belowground decomposition and production in fens, which is strange due to the reported importance of belowground biomass to fen systems (Hartman 1999; Thormann *et al.* 2001). Thormann *et al.* (2001) only included rhizomes in their tested belowground biomass and found that their mass loss was rather high (75%). We included both roots and rhizomes for the *Carex* and *Scirpus* belowground litter to approximate the entire belowground decomposition and found decomposition rates which were much closer to those observed in other fens (Hartmann 1999). Perhaps this indicates that roots are more important than rhizomes to peat accumulation.

PRIMARY PRODUCTION

The annual primary production of *Scirpus cyperinus* (approx. 1500 g $m^{-2}yr^{-1}$) on the harvested fen was 30 times the primary production values from an undisturbed fen in

Alberta (circa 53 g $m^{-2}yr^{-1}$; Szumigalski 1995). Similarly, the primary production of *Juncus* observed in this study was also 30 times the values observed in undisturbed fen (circa 1.9 g $m^{-2}yr^{-1}$; Szumigalski 1995). It is likely that the altered hydrology of the harvested fens as well as lack of competition with other species allowed for higher growth rates. The question remains as to what extent the high primary production of *Scirpus cyperinus* will lead to high peat-accumulation. Several studies have shown that decomposition rates, not production rates are largely responsible for peat-accumulation (Clymo 1965; Vitt 1990).

Belowground primary production has been rarely measured in continental Canada, probably because belowground production is more difficult to measure than aboveground production (Campbell *et al.* 2000). The only study that did measure belowground primary production found great variation in the percentage of net primary production that was made up of belowground plant material (28% to 80% of primary production) (Reader and Stweart 1972). Based on the study by Reader and Stewart (1972), recent studies assumed the belowground primary production to be 50% of the aboveground primary production of continental bogs and fens in North America (Campbell *et al.* 2000; Thormann *et al.* 2001). In our study the belowground primary production was lower than 50% of the net primary production. The belowground NPP estimates of *Scirpus cyperinus, Juncus brevcaudatus, Carex rostrata* and *Calamagrostis canadensis*, species from both undisturbed and harvested fens, were 8%, 14%, 38% and 28% of the NPP, respectively.

Perhaps the difference in the percentage of net primary production attributable to belowground primary production between our study and Reader and Stewart (1972) is due to differing methodologies. Reader and Stewart (1972) excavated 25 cm x 25 cm x 25 cm blocks of peat and removed and weighed all living roots. Therefore, it is difficult to understand how Reader and Stewart (1972) could decipher annual belowground primary production. We believe our estimates to be closer to the true annual belowground primary production because our methodology allowed us to estimate the root growth over a specific period of time.

The disadvantage of the ingrowth bag method is that the peat in the bags differs slightly from the peat on the sites. In our study, the bulk density measurements of the peat from the ingrowth bags were slightly more compact than the peat from the *Juncus brevcaudatus, Carex rostrata* and *Calamagrostis canadensis* communities (Table 3.1). Additionally, the chemistry of the peat from the in-growth bags differed slightly to the peat found on the incubation sites. This certainly affected the root growth in the bags to some extent. More studies which measure belowground NPP in peatlands using modern methodologies (Wallén 1992) would be greatly beneficial to estimating peat accumulation in North American peatlands, as roots are thought to play an important role in the peat accumulation of fens (Chimner *et al.* 2002).

CONCLUSIONS

In this study, decomposition rates were shown to depend mainly on the litter type, not the habitat (undisturbed versus harvested). The leaves of vascular plants had the highest mass losses (except for *Scirpus cyperinus*). The bryophytes had significantly lower mass losses than the vascular plants. This study highlights the importance of re-establishing peat-accumulating species such as bryophytes if one aims to restore this key ecological function of fens. Even if the hydrology of harvested fens is not similar to natural fens, harvested sites will be capable of accumulating peat if they are recolonized by the appropriate species. The water-holding capacity of the fen mosses (Vitt 2000) should create a positive feedback to improve the water-level stability of the peatland with time.

This study also shows that *Scirpus cyperinus*, a plant which dominates harvested fens in North America (Chapter 2), should be considered as functionally similar, perhaps even superior, to *Carex* species in its peat-accumulating capacity. Because of its tussock form, *S. cyperinus* should also be able to create the same structure found in undisturbed fens. Tussocks have been shown to be crucial to creating and maintaining species richness in sedge meadows (Peach and Zedler 2006).

Restoration ecology is a subjective science where humans ultimately decide on the objectives and goals of restoration projects (Higgs 2003). Due to increasing human pressure on landscapes, restoration sites become important landscapes to manipulate so as to maximize the desired ecosystem functions. In the face of climate change, restoring harvested fens should aim to restore species most efficient in producing peat, i.e. bryophytes, especially moderate-rich *Sphagnum* species.

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CHAPTER FOUR

TECHNIQUES FOR RESTORING FEN COMMUNITIES ON CUT-AWAY PEATLANDS IN NORTH AMERICA[3]

[3] Graf, M. D. and L. Rochefort Techniques for restoring fen communities on cut-away peatlands in North America. Applied Vegetation Science, *In press.*

ABSTRACT

Much research on fen restoration techniques has been carried out in Europe, but little can be transferred to the North American context due to differences in goals, desired states and restoration challenges. The goal of this study was to test two reintroduction techniques, two donor: recipient area ratios, two reintroduction times, two different plant communities used for donor sites and phosphate fertilizer. In total, 8 treatments were tested in the field within a completely randomized block design. This study found that *Sphagnum* transfer method, a reintroduction technique commonly used for bog restoration in North America, was effective for establishing *Sphagnum* and *Carex* species. The hay transfer technique, commonly used for fen restoration in Europe, was much less successful, probably due to the questionable viability of the reintroduced seeds. The treatments which included light phosphorus fertilization had a higher *Carex* cover after three growing seasons. The timing of the reintroductions had no impact on the success of revegetation. However, vegetation reintroduction should be carried out in the spring while the ground is still frozen to mimize other ecological impacts. The success of the *Sphagnum* transfer method on small-scale experimental units indicates that a large-scale restoration using this technique is feasible.

RÉSUMÉ

Bien que beaucoup de recherches soient effectuées en Europe sur la restauration des fens, il n'est pas facile de transférer les techniques qui y ont été développées en Amérique du Nord, parce que l'histoire de l'utilisation des terres et les objectifs de restauration sont très différents entre les deux continents. Le but de cette étude était d'expérimenter deux techniques de réintroduction de plantes de fens, deux ratios de réintroduction, deux moments de réintroduction, deux sites d'emprunt, ainsi que l'utilisation de fertilisant pour la restauration des fens. Au total, huit traitements ont été testés au champ dans un dispositif en blocs complètement aléatoires. Ainsi, l'application des diaspores, une technique souvent utilisée pour la restauration des tourbières ombrotrophes en Amérique du Nord, s'est montrée efficace pour l'établissement des espèces de *Sphagnum* et de *Carex*. La technique de transfert du foin, souvent employée pour la restauration des fens en Europe, a eu moins de succès, probablement en raison de la qualité discutable des graines réintroduites. Les traitements ayant bénéficié d'une légère fertilisation de phosphate ont obtenu les plus grands recouvrements en *Carex.* Le temps de réintroduction n'a pas eu d'impact sur le succès de la revégétalisation. La réintroduction de la végétation devrait néanmoins se faire au printemps, alors que la terre est gelée, afin de minimiser les autres impacts écologiques. La technique de réintroduction des diaspores a connu un bon succès à petite échelle, ce qui indique qu'elle pourrait également être utilisée dans le cadre d'une restauration à grande échelle.

INTRODUCTION

Research on restoring bog vegetation in North America is abundant (Ferland and Rochefort 1997; Malterer and Johnson 1998; Price *et al.* 1998; Rochefort 2000; Rochefort *et al.* 2003; Campeau *et al.* 2004; Chirino *et al.* 2006); however, research on restoring fen vegetation has been initiated only recently (Cooper and MacDonald 2000; Cobbaert *et al.* 2004). These projects aim to restore fen vegetation communities on peatlands which have been harvested for horticultural peat. Modern peat harvesting techniques can lead to the exposure of the underlying minerotrophic peat and mineral deposits. Such peatlands are richer in minerals and higher in pH than the preexisting bog, thus creating conditions which are sub-optimal for bog community restoration. Restoration towards a fen ecosystem including *Sphagnum* species common in moderate-rich fens is more desirable for such sites (Wind-Mulder *et al.* 1996).

Although much research has been conducted on fen restoration in Europe, little can be transferred to the North American context due to different goals, desired end-states and restoration challenges (Table 4.1). These dissimilarities can be attributed to differences in starting conditions, vegetation types, differing land-use as well as histories population densities and the resulting pressure on the landscape. Due to the paucity of undisturbed fens in Europe, restored fens create important habitats (Kratz and Pfadenhauer 2001). Therefore, often the goal of restoration projects in Europe is high plant diversity and the successful reintroduction of rare species (Wheeler and Shaw 1995; van Duren *et al.*1998; Hald and Vinther 2000; Kratz and Pfadenhauer 2001; Tallowin and Smith 2001; Lamers *et al.* 2002). In contrast, large undisturbed fen systems are abundant in boreal North America (Zoltai and Pollet 1983; Rubec 1998; Vitt *et al.* 2005); therefore, the focus of restoration is on the return of the peatland's ecosystem functions (Rochefort 2000). The great majority of European projects aim to restore intensive agricultural lands to extensively-managed fen meadows, not back to their undisturbed state (Rowell *et al.* 1985; Pfadenhauer 1994; Pfadenhauer and Klötzli 1996; Lamers *et al.* 2002; Jacquemart *et al.* 2003). The restoration of agricultural lands implies challenges (i.e., eutrophication, competition with existing plants, succession towards a forest; succession towards a bog due to altered hydrology) different from those in North America. Abandoned, cut-over peatlands are primary succession sites which are void of vegetation and have no viable seed bank (Campbell *et al.* 2003). Owing to these inherent differences, fen restoration techniques which correspond with the North American context should be developed and tested.

Bryophyte species are largely absent in European fen restoration projects, although they are often an important component in species composition (Mitch and Gosslink 2000; Succow and Joosten 2001) and function of undisturbed fen systems (Longton 1984; Vitt 2000). The exclusion of bryophytes from European restoration projects is probably because of a lack of donor vegetation sources and unsuitable water chemistry caused by eutrophication (H. Joosten, per. comm.). As problems with eutrophication and donor vegetation sources are not as extreme in North America, fen restoration techniques should include bryophytes because they may be essential in the return of the systems' peat-accumulating function (Rochefort 2000).

The existing research projects on fen community restoration in North America have not been successful in introducing bryophytes (Cooper and MacDonald 2000; Cobbaert *et al.* 2004). Bryophytes have been, however, successfully restored on bogs using the application of donor diaspore material (Rochefort *et al.* 2003). This method, called the *Sphagnum* transfer method, involves collecting the first few centimeters of plant diaspores from a donor site, reintroducing these plant fragments in a 1:10 donor to recipient ratio, applying straw mulch and a light dose of phosphate fertilizer (Rochefort *et al.* 2003).

Table 4.1. An overview of the differences between fen restoration approaches in Europe and North America.

	Europe	North America
Goal	High biodiversity [a,b,c,d,e,f] Ecosystem function [b,c]	Ecosystem function [g]
Major Disturbance	Intensive agriculture [a,b,c,d,e,f] Peat extraction [b]	Peat extraction [h,i]
Desired State	Semi-natural fen state (extensive agriculture) [a,b,c,d,e,f]	Natural fen state [h,i]
Problems	Eutrophication [b,c,d] Succession [a,d] Acidification [d] Existing seed bank/vegetation [b,c,d,f] Changes in hydrology [a,b,c,d]	No seed bank [h,i] Changes in hydrology [h,i]
Techniques	Top-soil removal [c,d,f] Mowing/grazing [a,b,c,f,] Liming [d] Hay transfer [c,d,f] Rewetting/restoration of hydrology [b,c,d]	Rhizome transplants [h] *Sphagnum* transfer [i] Rewetting/restoration of hydrology [h,i]

[a] Wheeler and Shaw (1995) [b] Pfadenhauer and Klötzli (1996) [c] Kratz and Pfadenhauer (2001)
[d] Lamers *et al.* (2002) [e] Rowell *et al.* (1985) [f] Patzelt *et al.* (2001)
[g] Rochefort (2000) [h] Cooper and MacDonald (2000) [i] Cobbaert *et al.* (2004)

A European fen revegetation technique which could be pertinent to the North American restoration goals is the hay transfer method (Pfandenhauer and Grootjans 1999). This technique involves mowing the donor site when the desired seeds are ripe, yet still attached to the stalks, and then transferring the fen "hay" directly onto the restoration site. This technique can only be carried out in the summer months when the seeds are ripe. The hay is spread using a donor to recipient area ratio of 1:1 to 5:1, depending on the biomass produced on the donor site and availability of donor hay. Usually, there is not enough fen hay to cover the entire restoration area so small islands are created so that transferred plants, once established, can then disperse over the whole site. This technique has also been shown to be effective in reintroducing bryophytes on calcareous grasslands (Jeschke and Kiehl 2006).

Using fertilization in restoration projects can have positive and harmful effects on the development of the restored site. In some cases fertilization may aid the establishment of aggressive, fast-growing plants that can persist for a long time after invasion (D'Antonio and Chambers 2006). In contrast, fertilization may help recolonization in severe environments. In the case of bog restoration, a light fertilization of phosphate has been shown to increase the cover of vascular plants and pioneer mosses which facilitate the establishment of *Sphagnum* species by stabilizing the microclimate and substrate (Salonen and Laaksonen 1994; Sliva and Pfadenhauer 1999; Groeneveld *et al.* 2007).

We conducted a field experiment to test vegetation reintroduction techniques which are applicable to fen restoration in North America. The goal of this experiment was to respond to the following questions: (a) which technique, diapsore application or hay transfer, is more effective for reintroducing species, (b) does phosphate fertilization increase the establishment of the reintroduced species and (c) what is the best time, early spring or mid-summer, to reintroduce species?

MATERIALS AND METHODS

SITE DESCRIPTION

The field experiment was carried out over three growing seasons on two areas of an abandoned, cut-away peatland (47° 45'N 69° 30'W and 47° 50'N 69° 25'W), ca. 200 km north-east of Québec City, Canada. This 15 km^2 peatland is part of a large complex of ombrotrophic bogs interspersed with *Alnus* swamps (Gauthier and Grandtner 1975) and is classified as low boreal peatlands (National Wetlands Working Group 1988). Different sectors of the peatland were mined to their minerotrophic peat layer and were abandoned four and eight years before the experiment began. The regional climate is characterized by cold winters and warm summers with January and July mean temperatures of –13 and 18 °C, respectively. The mean annual precipitation is 963 mm, of which 72% falls as rain (Environment Canada 2007). The pH of the restoration sectors varied from 5.0 to 5.9 and the electrical conductivity from 24 to 134 (Chapter 2; Cobbaert *et al.* 2004).

The donor sites are approximately 25 km southwest of the restoration site. These donor sites were chosen because the environmental parameters were similar to the restoration sites and because of their complementary vegetation communities. The pH values were 5.5 and 5.8 and electrical conductivity 27 $\mu S\ cm^{-1}$ and 40 $\mu S\ cm^{-1}$for the first and second donor sites, respectively (Cobbaert *et al.* 2004). The first donor site (47°77' N 52°83' W) is a poor fen, dominated by *Sphagnum* species. The dominant species were (in order of decreasing dominance including all species with >2% cover): *Sphagnum centrale*, *Calamagrostis canadensis, Salix discolor, Carex brunnescens, Glyceria canadensis, Polytrichum strictum, Sphagnum fallax, Spiraea latifolia, Aulacomnium palustre, Sphagnum squarrosum, Solidago rugosa, Rubus idaeus, Alnus rugosa, Sphagnum girgensohnii* and *Carex stricta.* The second donor site (48°19' N, 52°81' W) is a moderate to rich fen, dominated by herbaceous plants, especially *Carex* species. The dominant species which had a percent cover > 2% were: *Carex rostrata, Calamagrostis canadensis, Carex utriculata, Glyceria canadensis, Sphagnum warnstorfii, Aulacomnium palustre, Warnstorfia exannulata* and *Scirpus cyperinus.* For more information about the hydrology, environmental conditions and geomorphology of these sites see Cobbaert *et al.* (2004). The nomenclature used for the vegetation follows Scoggan (1978) for vascular plants, Anderson (1990) for *Sphagnum* and Anderson *et al.* (1990) for other mosses.

EXPERIMENTAL DESIGN

The experiment was a randomized block design with five blocks of eight treatments. The aim was to test two reintroduction techniques, two donor: recipient area ratios, two reintroduction times, two different plant communities used for donor sites, the use of straw mulch and phosphate fertilizer (Table 4.2). Because of the large number of tested variables, the experiment design was not factorial; we only included treatments that were logical from a restoration and ecological standpoint. The first treatment was a *Sphagnum* transfer method carried out in early spring (Table 4.2, treatment 1). Three hay-transfer methods were tested: two with a donor: recipient ratio of 1:1 (treatments 2 and 4), and a third with a 1:10 ratio (treatment 3). The 1:1 ratio is the optimal ratio according to Kratz and Pfadenhauer (2001) and the 1:10 ratio is the same ratio used for bog restoration (Quinty and Rochefort 2003). The hay transfer method which uses a 1:1 ratio does not require the use of straw, because the plant stems collected with the seeds serve as mulch. Two donor sites composed of different plant communities were tested for the hay transfer method: the fen dominated by *Sphagnum* (treatment 2) and the fen dominated by *Carex* (treatment 4).

Two *Sphagnum* transfer methods were introduced in mid-summer, at the same time as the hay-transfer introduction, to isolate the effect of the timing. One *Sphagnum* transfer did not include a phosphate fertilizer (Table 4.2, treatment 5) and a second did (treatment 6). The *Sphagnum* transfer method in mid-summer was chosen to test the effects of phosphate fertilizer because it will most likely include the highest variety of vegetation material as it will contain both fresh *Carex* seeds and fen bryophytes. Two control treatments where vegetation was not reintroduced were included in the experiment. The first control was a straw and fertilizer treatment (7) and the second control was just a straw mulch treatment (8).

The five blocks were located on three 30 m x 70 m areas which were scraped and leveled in the early summer of 2004 to homogenize the surface and remove any vegetation that had spontaneously colonized the sites. Each treatment was applied to 5 m x 6 m experimental units during May and early August of 2004. For the *Sphagnum* transfer method, the top 10 cm of diaspore material was collected by hand, manually shredded and applied to the specified experimental units. The material for the hay transfer technique was collected by hand-clipping the aerial vegetation at the ground level. The straw-mulch was manually applied to the corresponding experimental units just to the point that the reintroduced vegetation or bare peat was completely covered. This is consistent with 3000 kg ha^{-1}, which is recommended for bog restoration (Rochefort *et al.* 2003). The straw-mulch exceeded the experimental units by at least 0.5 m to minimize the border effect. A rock phosphorus fertilizer in a dose of 15 g m^{-2} (Quinty and Rochefort 2003) was applied to specified experimental units.

Table 4.2. Treatments tested in a field experiment which tested reintroduction techniques.

Treatment	Vegetation Reintroduction	Donor: Recipient Ratio	Reintroduction Time	Donor Site	Mulch	Fertilization
1	*Sphagnum*-transfer	1:10	Early Spring	*Sphagnum* fen	Straw	Phosphate
2	Hay-transfer	1:1	Mid-summer	*Sphagnum* fen	No Straw	Phosphate
3	Hay-transfer	1:10	Mid-summer	*Sphagnum* fen	Straw	Phosphate
4	Hay-transfer	1:1	Mid-summer	*Carex* fen	No Straw	Phosphate
5	*Sphagnum*-transfer	1:10	Mid-summer	*Sphagnum* fen	Straw	No Phosphate
6	*Sphagnum*-transfer	1:10	Mid-summer	*Sphagnum* fen	Straw	Phosphate
7	None		Mid-summer		Straw	Phosphate
8	None		Mid-summer		Straw	No Phosphate

Site Monitoring

The regional precipitation of the three growing seasons was assessed by comparing the monthly rainfall data (Direction du suivi de l'état de l'environnement, Ministère du Développement durable, de l'Environnement et des Parcs du Québec) to 30 year averages collected nearby at the St. Arsène meteorological station (Environment Canada 2007). The soil-water potential was measured using tensiometers (Soil Measurement Systems, Tucson. AZ, U.S.A.) on 18 experimental units (between 3 and 4 for each block) at 2 cm below the surface to characterize the water available for the bryophytes and at 10 cm below the surface to characterize the root zone for the vascular plants. Additionally, the water level was measured from a total of five wells, one located at the center of each block. The soil-water potential and water levels were measured weekly during the growing season of 2004. Although positive water potentials are possible, zero was the maximum value because measures could not be taken on flooded areas.

The establishment of the reintroduced species was assessed by visually estimating the percent cover of each species as well as total bryophyte, total *Sphagnum,* total of other mosses (mosses other than *Sphagnum*), total vascular plant, total *Carex*, total shrubs and trees and the total vegetation cover for each experimental unit. The bryophytes were estimated by noting species and percent covers observed within twenty 25 cm x 25 cm quadrats equally spaced on each experimental unit. The vascular plants, shrub/tree cover and total vegetation were estimated using ten 50 cm x 50 cm quadrats per experimental unit. All quadrats were placed 0.5 meters inside the plot border to reduce border effects. These vegetation surveys were carried out in September of three consecutive growing seasons in 2004, 2005 and 2006.

Data Analysis

The cover (%) of each vegetation strata, as well as the most important vegetation groups, such as *Sphagnum* and *Carex*, and the species *Scirpus cyperinus* were compared among treatments using the GLM procedure of SAS and *a priori* contrasts (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, NC, U.S.A.). We analyzed the cover of the above-described vegetation strata rather than the total cover of the reintroduced species because simple addition of these species would not be just, due to superimposition. *A priori* contrasts were used because of the strong inherent structure of the treatments, making this analysis is a powerful option (Day and Quinn 1989). Contrary to post priori contrasts, significant contrasts can be considered even when the main treatment effect is not significant.

Seven *a priori* contrasts were designed for this experiment. The contrasts are outlined below:

1. Two reintroduction techniques in their optimal forms (optimal timing and donor: recipient ratio; Table 4.2, treatment 1 vs. 4)
2. Two reintroduction techniques in identical forms (same reintroduction time and donor: recipient ratio; treatment 3 vs. 6)
3. Two reintroduction times of the *Sphagnum* transfer method (treatment 1 vs. 6)
4. The effect of fertilizer for the *Sphagnum* transfer method (treatment 5 vs. 6)
5. The effect of the ratio used for the hay transfer method (treatments 2 and 4 vs. 3)
6. The two donor sites used for the hay transfer method (treatment 2 vs. 4)
7. All the treatments where vegetation was introduced (treatments 1 through 6) vs. two control treatments where no vegetation was reintroduced (treatments 7 and 8).

Five outlier experimental units out of 40 were not included in the analysis because these experimental units were permanently flooded during the growing season. The scraping for site preparation created a depression in one block installed near a stream which flooded heavily in spring. Because constant flooded conditions were not intended and because we did not reintroduce aquatic vegetation, these experimental units were removed as not to bias the analysis.

RESULTS

VEGETATION

Of the treatments tested, only the reintroduction method and fertilizer treatments showed significant differences in vegetation after three growing seasons. No significant differences in vegetation cover were detected among treatments with different donor sites, reintroduction times, and donor: recipient ratios (Table 4.3). The *Sphagnum* transfer method was shown to be a superior method for reintroducing fen vegetation, as the covers of *Sphagnum*, *Carex* and total vegetation were significantly higher for the experimental units with *Sphagnum* transfer method (Table 4.3 and Figure 4.1, contrasts 1 and 2). When all vegetation reintroduction treatments were compared with the control treatments, only *Sphagnum* cover was significantly higher (Table 4.3 and Figure 4.1, contrast 7). The use of phosphate fertilizer for the *Sphagnum* transfer method showed a significantly higher cover of *Carex* species (Table 4.3 and Figure 4.1, contrast 4). Moreover, the species richness was significantly higher where vegetation had been reintroduced (24 ± 3 species per experimental unit) than where vegetation had not been reintroduced (22 ± 2 species per experimental unit) (Table 4.3).

The mean cover of herbaceous plants was similar for all treatments (circa 30%). The covers for non-sphagnous mosses, as well as the trees/shrub strata, were very low for all treatments (2% for mosses and 0.7% for trees/shrubs) and also showed no difference among treatments.

A closer look at the species that established on the experimental units reveals that the majority were wetland species, many of which recolonized spontaneously. *Scirpus cyperinus* had by far the highest cover (13%) and was found on 85% of the experimental units (Table 4.4). The cover of *S. cyperinus* was significantly higher on control units than on units where vegetation was reintroduced (Table 4.3). Its cover was also significantly higher on the hay transfer unit*s* where the donor site was *Carex*-dominated and the reintroduction time was mid-summer than on the diaspore units where the donor site was *Sphagnum*-dominated and the reintroduction time was early spring (Table 4.3, contrast 1).

Table 4.3. ANOVAs and *a priory* contrasts for a field experiment testing the effect of two reintroduction techniques, two reintroduction times, the use of phosphate fertilizer, two donor: recipient area ratios and two donor sites on fen vegetation establishment. Significant *P*-values are in bold. The letters A, B, C and D signify contrasts which are graphically shown in Figure 4.1.

		Sphagnum sp. (log (x+1)		*Carex sp.* (log (x+1)		*Scirpus cyperinus*		Herbaceous Plants		Total Vegetation		Species Richness	
Source	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Blocks	4												
Treatments	7	64.35	**<.0001**	3.79	**0.007**	1.71	0.16	0.75	0.64	3.01	**0.02**	1.43	0.24
Contrasts:													
A. Reintroduction Method (Optimal timing and ratio)	1	149.68	**<.0001**	13.59	**0.001**	4.08	**0.05**	0.01	0.91	7.78	**0.01**	0.01	0.93
B. Reintroduction Method (Identical timing and ratio)	1	85.59	**<.0001**	6.76	**0.02**	0.25	0.62	1.66	0.21	7.65	**0.01**	1.46	0.24
C. Reintroduction Timing	1	1.74	0.2006	0.09	0.76	2.37	0.14	0.39	0.54	0.00	0.97	2.57	0.12
D. Fertilizer	1	3.15	0.09	4.45	**0.05**	0.75	0.39	2.81	0.11	0.41	0.53	0.04	0.84
Ratio of Hay Transfer	1	0.00	0.99	0.11	0.74	0.23	0.64	0.14	0.72	0.04	0.84	0.04	0.83
Hay Transfer Sites	1	0.91	0.35	0.07	0.79	0.28	0.60	0.35	0.56	0.01	0.91	0.29	0.59
Control	1	93.37	**<.0001**	1.02	0.32	4.05	**0.05**	1.19	0.29	0.70	0.41	4.37	**0.05**
Error	23												
Total	34												

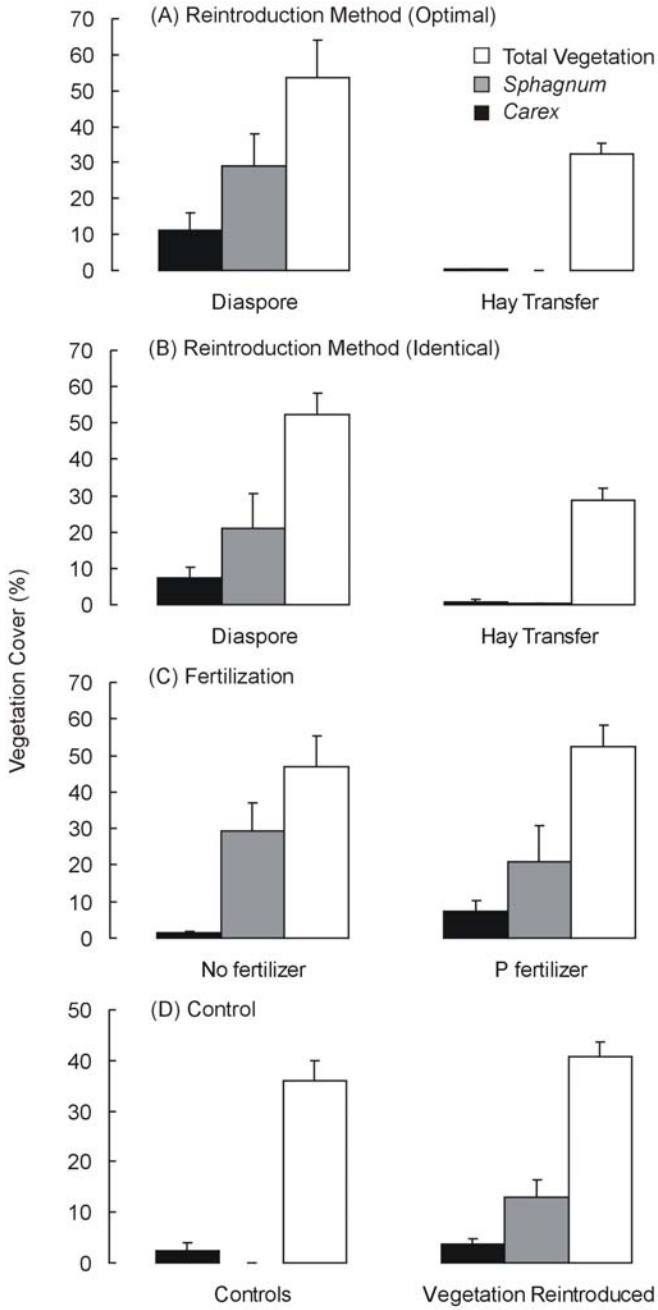

Figure 4.1. Response of *Carex* species, *Sphagnum* mosses and total vegetation (% cover) for different reintroduction techniques. Only the contrasts which showed a significant difference are shown here. A, B, C, and D are the graphic representations of the contrast analyses (Table 4.3) Contrast A "Reintroduction Method (Optimal)" compares a spring *Sphagnum* transfer method in a 1:10 ratio with a summer introduction of the hay transfer method in a 1:1 ratio. Contrast B compares the same reintroduction methods where the reintroduction timing and ratio are identical.

Table 4.4. The frequency, mean total cover of species across all experimental units, provenance and mean cover for units from each reintroduction technique category. The twenty-five most frequent species are shown. The frequency was computed by dividing the number of units where the species was present by the total number of experimental units (n=37). The botanical authority for each species is shown in App. 2.3.

Species	Frequency (%)	Mean Total Cover (%)	Provenance		Cover (%) for treatments		
			Donor Sites	Spontaneous	Diaspore	Hay Transfer	Controls
Scirpus cyperinus	85	13.0	X	X	9.1	15.3	14.9
Solidago gramnifolia	62	2.8	X	X	2.4	3.7	2.8
Agrostis scabra	60	1.4		X	1.0	1.7	1.4
Spiria latifolia	52	0.5	X	X	0.5	0.5	0.5
Dicranella cerviculata	36	0.8		X	0.2	1.6	0.6
Sphagnum centrale	35	7.7	X		21.4	0.2	0.05
Juncus brevicaudatus	34	1.8		X	0.9	0.9	5.0
Polytrichum strictum	31	0.4	X	X	0.5	0.5	0.3
Pohlia nutans	28	0.5	X	X	0.6	0.4	0.3
Lycopus uniflorus	25	0.6		X	0.3	1.0	0.4
Juncus effusus	25	1.9		X	2.0	1.0	3.4
Epilobium leptophyllum	24	0.4		X	0.5	0.4	0.5
Calamagrostis canadensis	23	0.5	X	X	0.6	0.6	0.4
Carex brunnescens	23	1.9	X		5.1	0.2	0.1
Viola palustris	21	0.4	X		1.1	0.1	0.02
Triadenum fraseri	20	0.3		X	0.2	0.2	0.4
Glyceria canadensis	18	1.1	X		2.7	0.3	0.02
Aulacomnium palustre	17	0.2	X		0.2	0.3	0.1
Solidago rugosa	16	0.3		X	0.2	0.2	0.5
Eriophorum spissum	15	1.0		X	0.7	1.3	1.5
Juncus bufonius	13	0.3		X	0.1	0.3	0.03
Equisetum arvense	12	0.4		X	0.3	0.5	0.5
Carex bebbii	12	0.8		X	1.0	0.2	1.2
Salix discolor	11	0.2	X	X	0.3	0.1	0.1
Sphagnum fallax	11	0.1	X		1.4	0.02	0.02

When the covers of the individual species were examined according to the reintroduction method, only *Sphagnum* transfer treatments had species covers which were much higher than the control units (Table 4.4). Only the *Sphagnum* transfer treatments were effective in reintroducing species from the donor sites. The reintroduced species which proved to be the most successful in recolonizing the *Sphagnum* transfer experimental units were *Sphagnum centrale*, *Carex brunnescens, Glyceria canadensis*, *Sphagnum fallax* and *Viola palustris* (Table 4.4).

ENVIRONMENTAL CONDITIONS

The first growing season (2004) was wetter than average. The recorded precipitation was higher than the 30 year averages for the months of June, July, August and September (Direction du suivi de l'état de l'environnement, Ministère du Développement durable, de l'Environnement et des Parcs du Québec; Environnement Canada 2007). The month of August was exceptionally wet with a total precipitation of 186 mm, which is almost double the average of 98 mm. As the first growing season has proven to be critical to the success of *Sphagnum* regeneration (Chirino *et al.* 2006), the wet 2004 season was a good premise for the successful establishment of the *Sphagnum* species. The second growing season (2005) was drier than average with a long dry period in August and the third growing season was average with precipitation evenly spread out throughout the season (Direction du suivi de l'état de l'environnement, Ministère du Développement durable, de l'Environnement et des Parcs du Québec).

The water level and water potential data from the first growing season show that hydrological conditions varied among blocks (Table 4.5). They ranged from near-constant inundation (block A) to the drier conditions (block C and D). The highest *Sphagnum* cover (31% ± 14) was observed for block B where the water level was just under the surface (Table 4.5).

Table 4.5. Water level and soil-water pressure for each block of an experiment on reintroduction techniques.

Block	Water Level (cm)			Water Pressure 2 cm (mbars)			Water Pressure 10 cm (mbars)		
	Mean (±SD)	Max	Min	Mean (±SD)	Max	Min	Mean (±SD)	Max	Min
A	5 (±13)	23	-15	-1 (±2)	0	-5	0 (±0)	0	0
B	-5 (±12)	11	-27	-6 (±9)	0	-23	-6 (±9)	0	-23
C	-29 (±14)	-1	-41	-29 (±24)	-4	-75	-13 (±18)	0	-53
D	-39 (±12)	-16	-68	-44 (±35)	-10	-110	-38 (±41)	0	-104
E	-30 (±17)	-5	-64	-16 (±13)	-3	-45	-9 (±16)	0	-36

DISCUSSION

REINTRODUCTION TECHNIQUES

It was not surprising that the *Sphagnum* cover, and consequently the total vegetation cover, were significantly higher with the *Sphagnum* transfer method because only this technique included large amounts of *Sphagnum* fragments. However, it was surprising that *Carex* percentages were significantly higher on *Sphagnum* transfer units than on hay transfer units. This is surprising because the donor material for one of the hay transfer treatments came from a site where *Carex* was dominant and donor to recipient ratio ten times higher than that used for the *Sphagnum* transfer treatments. Nevertheless, the hay transfer treatment showed a significantly lower cover of *Carex* than the *Sphagnum* transfer treatment (Figure 4.1, Graph A).

Carex species are notorious for being problematic in restoration efforts (Galatowitsch and van der Valk 1996; Pfadenhauer and Grootjans 1999; van der Valk *et al.* 1999; Cooper and MacDonald 2000; Patzelt *et al.* 2001). Seed viability proved to be a major impediment to the establishment of *Carex* species in prairie potholes (van der Valk *et al.* 1999). In controlled conditions, Patzelt *et al.* (2001) *Carex* species showed some of the lowest germination rates found for reintroduced species. Restoration methods which reintroduce rhizomes, not seeds, have shown higher *Carex* establishment (Cooper and MacDonald 2000). The *Sphagnum* transfer method included *Carex* rhizomes which could explain a higher establishment rate, despite a much lower quantity of reintroduced *Carex* material.

The hay transfer technique on our experimental units proved far less successful for reintroducing fen species than was observed in European experiments (Patzelt *et al.* 2001; Tallowin and Smith 2001). Patzelt *et al.* (2001) found that 70% of the donor species were transferred using the hay transfer method. In contrast to our experiment, they introduced seed material from four different donor sites which increased their chances of having viable seeds.

The hay transfer method is highly adapted to European fen management strategies which require mowing in order to prevent succession to shrub land and eventually forests (Table 4.1; Rowell *et al.* 1985; Jacquemart *et al.* 2003). Due to current socio-economic conditions in Europe, there is often no use for this 'hay,' thus it is a perfect source material for restoration. Because of its abundance, it can be collected from several sites and be applied in a donor: recipient ratio of up to 5:1 (Kratz and Pfadenhauer 2001). Conversely, in North America, the fen preservation does not require mowing. Additionally, the intact hydrology of North American fens would require specialized equipment for large-scale mowing in the summer when the seeds are mature. Due to the unpredictability of the germination abilities of the introduced seeds and the logistical challenges of this technique, it seems the *Sphagnum* transfer method is more appropriate to the North American context.

PREVENTIVE CONTROL

The dominance of *Scirpus cyperinus* on our experimental units is not a local phenomenon. This species has been observed on 50% of quadrats sampled from 17 abandoned, vacuum-harvested fens across Canada (Chapter 2). Yet, it is not known whether it should be considered an invasive species, a species that out-competes more desirable species or co-opts the direction of the post-disturbance succession (D'Antonio and Chambers 2006). Or, perhaps *S. cyperinus* is a desirable species which increases species diversity due to an increased micro-topography created by the tussock structure (Peach and Zedler 2006). A dense *Scirpus* cover improved the regeneration of introduced fen bryophytes (Chapter 5).

If *Scirpus cyperinus* proves to be an invasive species, control prior to arrival is the most cost-effective means of managing invasive species (D'Antonio and Chambers 2006). Our experiments showed that this species was significantly higher where no vegetation had been reintroduced. Therefore, reintroducing species directly after peat harvesting has been abandoned might be an effective way to control the spread of this species. Additionally, the diapore application in the spring had a significantly lower cover of *S. cyperinus* than the summer application of the hay transfer treatment. This indicates that a spring application when there are no fresh *S. cyperinus* seeds from a donor site could reduce the spread of this species. Moreover, this species will surely decline on the *Sphagnum*-dominated experimental units as the *Sphagnum* will acidify its environment (van Bremem 1995). The inclusion of *Sphagnum* species will certainly have priority effect on the succession of the restoration site (Menninger and Palmer 2006), steering the succession towards a poor fen.

FERTILIZATION

Fertilization proved to be effective in increasing the percentage of *Carex* species. Fertilization is known to increase vascular plant cover in bog restoration (Rochefort *et al.* 2003). As vascular plants play a more important role in fen systems, using fertilizer should greatly improve the establishment of reintroduced species. Interestingly, no improvement could be discerned for the total herbaceous plant cover for treatments that included fertilizer. This field experiment merely used the same dose as used for bog restoration. More research is needed to see if fen vegetation reestablishment could be improved with a different fertilization mix and/or dose.

REINTRODUCTION TIMING

Our finding of no difference between the vegetation covers of the *Sphagnum* transfer method in the spring and summer, contradicts what has been observed using the same technique for bog restoration (F. Quinty, pers. comm.). The phenology of plants versus restoration success is an area that deserves further investigation.

Even though there were no differences between the vegetation cover for the spring and summer reintroduction times, the logistics of the *Sphagnum* transfer method would make a summer reintroduction more costly and produce more damage to the system. The best option to reduce the disturbance to the donor and restoration sites is to do the majority of the machine work in the early spring when the peatlands are still frozen or have just begun to thaw (Quinty and Rochefort 2003).

ENVIRONMENTAL CONDITIONS

Small changes in hydrology have a profound effect on bryophytes because they capture water mainly through capillary movement and do not have the means to actively extract water from their environment (Rydin and Jeglum 2006). The highest *Sphagnum* covers were observed for units where the mean soil-water potential was just below 0, a fact which has been confirmed in greenhouse experiments (Chapter 5). Additionally, prolonged flooding had a disastrous effect on the establishment of these species. Although greenhouse experiments showed that continuous flooding does not impede *Sphagnum* regeneration (Rochefort *et al.* 2002), physical disturbances in the field, such as erosion and sedimentation, often have a negative effect on regeneration (Quinty and Rochefort 2000).

CONCLUSIONS

This field study showed that the *Sphagnum* transfer method is an effective technique for restoring fen vegetation communities. After three growing seasons *Sphagnum* cover was similar to those observed on undisturbed fens with similar physico-chemical conditions in North America (Chapter 2). In contrast, the cover of *Carex* species on the experimental restoration units was much lower than those observed in undisturbed fens (Chapter 2). However, *Carex* species did establish successfully and perhaps their cover will increase through time through clonal growth.

In this study, the covers of Cyperaceae observed after three growing seasons resembled the cover of Cyperaceae observed in undisturbed fens (Chapter 2). On restored units Cyperaceae cover consisted primarily of *Scirpus cyperinus*, while in undisturbed fens it consisted of various *Carex* species. Therefore, the *Sphagnum* transfer method combined with the spontaneous colonization of *S. cyperinus* should be adequate for a vegetation structure that is similar to undisturbed fens. Nevertheless, the idea of redundant species, those species which can be coarsely classified into the same functional group, has been criticized because the redundancy can change according to ecosystem function and environmental conditions (Naeem 2006). Thus, the presence of several Cyperaceae species, not solely *S. cyperinus* is desirable.

The findings of this experiment are limited due to the small size of the units. The success of the *Sphagnum* transfer method at the small-scale level begs a large-scale restoration attempt. Using a combinatorial experiment (Naeem 2006), the effect of the dominant species on the ecosystem function of the fen site could be tested. Such an experiment would have the double benefit of increasing understanding of undisturbed fen systems and allowing the creation of short-term goals for fen restoration that would not be solely dependent on vegetation structure, but also on ecosystem function.

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CHAPTER FIVE

MOSS REGENERATION FOR FEN RESTORATION: FIELD AND GREENHOUSE EXPERIMENTS[4]

[4] Graf, M. and L. Rochefort. Moss regeneration for fen restoration. Restoration Ecology, *In press*.

ABSTRACT

Fen bryophytes are an important component of natural fens and should be included in fen restoration projects. The goal of this study was to examine the regeneration capabilities of nine common bryophytes found in moderate-rich and poor fens in North America. A greenhouse experiment was carried out to examine the limitations and optima for the regeneration of fen bryophytes under different light and water regimes. A field experiment tested these same bryophytes in the presences of three possible 'nurse plants' as well as a straw and control treatment. In the greenhouse experiment, the presence of shade increased regeneration success for eight out of nine species. A water level just under the surface was ideal for the regeneration of the majority of species tested. In the field experiment the highest regeneration was observed under a dense canopy of herbaceous plants. *Sphagnum* species showed the highest regeneration success of the species tested. Fen bryophytes show good potential for use in restoration projects as the tested bryophytes regenerated well from fragments.

RÉSUMÉ

Les bryophytes sont une constituante importante des fens naturels et devraient être inclus dans les projets de restauration des fens résiduels. Le but de cette étude était d'examiner la capacité de régénération de neuf espèces de bryophytes communes dans les fens pauvres et modérément pauvres de l'Amérique du Nord. Une expérience a été menée en serre afin d'examiner les limites et les conditions optimales pour la régénération des bryophytes de fens sous des luminosités et des niveaux d'eau différents. Une expérience au champ a permis d'examiner les mêmes bryophytes en présence de trois possibles « plantes compagnes ». Un autre traitement consistait en l'ajout de paille. Il y avait également un traitement témoin. Au cours de l'expérience en serre, l'ombre a augmenté le succès de la régénération de huit des neuf espèces de bryophytes. Un niveau d'eau juste sous la surface était idéal pour la régénération de la majorité des espèces. Dans l'expérience au champ, la plus forte régénération a été observée sous le couvert des plantes herbacées. Les espèces de *Sphagnum* ont montré le plus grand succès de régénération parmi les bryophytes étudiés. Les bryophytes de fens possèdent donc un potentiel intéressant pour les projets de restauration; en effet, les espèces utilisées se sont bien régénérées à partir des fragments.

INTRODUCTION

Fen restoration is a good example of the subjectivity inherent in restoration (Higgs 2003). Vascular plants have largely been given priority (Patzelt 1998; Pfandenhauer and Grootjans 1999; Cooper and MacDonald 2000; Kratz and Pfadenhauer 2001; Isselstein *et al.* 2002; Kotowski 2002; Lamers *et al.* 2002; Cobbaert *et al.* 2004) even though bryophytes are an equally important element of fen vegetation (Mitsch and Gosselink 2000; Succow and Joosten 2001). Incorporating bryophytes in fen restoration projects will increase species richness and vertical diversity, creating a vegetation structure closer to undisturbed fens. Additionally, bryophytes are important to the ecosystem functioning of fens. They play an important role in water balance, energy flow, nutrient cycling and the creation and modification of habitats occupied by other organisms (Longton 1984). Bryophytes have also been shown to produce more biomass and decompose more slowly than vascular plants in fen systems, contributing greatly to Carbon storage (Vitt 2000). Fen bryophytes play an important role in the species composition and function of fen systems and deserve more attention in fen restoration research.

Many articles have been published on the regeneration capacities of *Sphagnum* mosses common to bogs (Rochefort *et al.* 1995; Campeau and Rochefort 1996; Bugnon *et al.* 1997; Quinty and Rochefort 1997; Buttler *et al.* 1998; Rochefort *et al.* 2002; Tuittila *et al.* 2003); however, few articles have been published on the regeneration capacities of fen bryophytes. Poschlod and Schrag (1990) found six common fen bryophytes were all capable of vegetative reproduction in a Petri dish experiment and that these fragments might be important as diaspores where sexual reproduction is rare. In a greenhouse experiment, Li and Vitt (1994) examined the vegetative regeneration of four moss species from moderate-rich fens and found that nutrient gradients, especially nitrogen, may be a critical attribute in the determination of mature vegetation patterns in peatlands. These articles do not, however, examine the effect of water level and the presences of a protective cover on the regeneration of mosses, factors which are crucial to the success of bryophyte regeneration in the context of restoration (Rochefort and Lode 2006). Mälson and Rydin (2007) examined regeneration capabilities of rich fen bryophytes and found that a protective cover increased recolonization success and that even small changes in hydrology had an effect on biomass growth. Currently, no information exists on the regeneration of bryophytes in the context of moderate-rich to poor fen restoration.

The microclimatic conditions of fen restoration sites can vary greatly, depending on the prior land use and the amount of time since abandonment. On one extreme, restoration sites can be several hundred hectares of bare peat as is the case for cutaway peatlands (Sliva and Pfadenhauer 1999; Cobbaert *et al.* 2004). The bare-peat surface of an abandoned peatland is an extremely harsh environment, where water levels and temperature fluctuate greatly (Price *et al.* 2003). However, if these cutaway peatlands have been abandoned for several years, they are often spontaneously colonized by pioneer vegetation (Famous *et al.* 1991; Salonen *et al.* 1992; Rowlands 2001) creating a more stable microclimate. On the other extreme, fen restoration on former agricultural land will require moss regeneration underneath a dense herbaceous layer (Kratz and Pfadenhauer 2001; Lamers *et al.* 2002).

Microclimate conditions have proven to have a big impact on the success of moss regeneration in bog restoration. The protection of a straw-mulch layer was essential to the regeneration of *Sphagnum* mosses (Rochefort *et al.* 2003). Moreover, the presence of the pioneer moss, *Polytrichum strictum*, stabilizing the substrate and the microclimate, significantly improves the regeneration success of *Sphagnum* bryophytes (Groeneveld *et al.* 2007). The improved establishment of one plant through the presence of a 'nurse plant,' which is usually a pioneer species, has been observed in a variety of harsh environments (Callaway *et al.* 1996; Núñez *et al.* 1999; Bruno *et al.* 2003). As cutaway peatlands with minerotrophic residual peat are quickly colonized by spontaneous vegetation, the 'nursing plant' effect could have a considerable impact on the reintroduction of vegetation.

In this study we examined the regeneration niche of nine fen bryophytes, common to North American poor to moderate-rich fens. Our goal was to learn more about the environmental conditions which enable vegetative regeneration and to examine the effect of microclimate on the bryophyte regeneration. Greenhouse and field experiments were carried out in order to respond to the following questions: (1) What are the optimum and limiting conditions (water level and shading) for the regeneration of nine bryophytes common to North American poor and moderate-rich fens, (2) are there differences in the ability of these species to regenerate vegetatively, and (3) what effect does the nurse plant have on the regeneration success of the tested bryophytes?

MATERIALS AND METHODS

STUDY SPECIES

The nine fen bryophytes species chosen are common to both moderate-rich and poor fens in the boreal North America and represent different realized niches. *Tomenthypnum nitens* Hedw. Loeske and *Sphagnum centrale* C. Jens. *in* Arnell and C. Jens. are found in the dry areas (hummocks) of moderate-rich and rich fens (Gignac *et al.* 1991; Andrus 1986). *Polytrichum strictum* Brid., *Dicranum polysetum* Sw., and *Pleurozium schreberi* (Brid.) Mitt are common to hummocks or dry parts of both fens and bogs (Gauthier 1980; Gignac *et al.* 1991). Although it is known that *Polytrichum strictum* regenerates well (Groeneveld and Rochefort 2005), this species was included in the greenhouse experiment for comparison and to understand its regeneration under controlled conditions. *Dicranum polysetum* is found in similar abundance as *Dicranum undulatum* in peatlands of eastern Canada and because of their similar structure, only one species was tested (Poulin *et al.* 1999; L. Rochefort unpublished data). *Sphagnum fallax* (Klinggr.) Klinggr. is common in wet parts (lawns and hollows) of poor fens and moderate-rich fens (Andrus 1986). *Warnstorfia exannulata* (Schimp. *in* B.S.B) Loeske inhabits the wettest areas of poor fens (Vitt and Chee 1990). *Aulacomnium palustre* (Hedw.) Schwaegr. and *Sphagnum warnstorfii* Russ. are present over a wide range of pH and hydrological conditions (Gignac *et al.* 1991).

GREENHOUSE EXPERIMENT

A greenhouse experiment was carried out over six months from November 2005 through April 2006 at Université Laval, Québec City, Canada. The regeneration capabilities of the above-described bryophytes were assessed in a factorial experiment testing four water levels (at 0 cm, 10 cm, 20 cm and 40 cm below the surface), both with and without shade.

Shade was created using shade nets which blocked 50% of the light (Industries Harnois, St.-Thomas-de-Joliette, QC, Canada), which was chosen because it corresponds to the average total vegetation cover of abandoned fens in North America (unpublished data; see also Table 5.3). The experimental design was a completely random block design with four blocks. The experiment was carried out in plastic containers (61 cm x 47 cm x 50.8 cm). Each container was divided into ten subplots, one for each of the moss species and one was left bare for taking measurements. To control the water level, a small chamber (6 x 3 x 51 cm) within the bare section of each container was created using a plastic cylinder, perforated with small holes and covered with a 1-mm mesh nylon material. This allowed water to move freely between the peat-filled containers and the peat-free chamber. Holes 1-cm in diameter were drilled into the outside wall of the chamber at a specified height to allow the containers to drain to the appropriate water level after watering.

Bryophytes were collected from four natural fens in the area near Quebec City and Rivière-du-Loup in October 2005 and were stored in plastic bags for up to three weeks at 4°C until the experiment was set up. Moss species were randomly assigned to the sub-plots of each container and 25 fragments, each 3 cm in length (including the capitula for Sphagna), were evenly distributed. Each container was watered 20 mm per week (spread evenly over three waterings per week), which corresponds to the average weekly precipitation during the vegetation season in Rivière-du-Loup, Québec. Tap water could not be used as high Calcium concentrations are detrimental to mosses. Therefore, distilled water supplemented with a modified Rudolf solution (Faubert and Rochefort 2002) fivefold diluted to simulate field conditions (rainwater). The temperature was set to 20°C for the fourteen-hour photoperiod and 15°C at night. The relative humidity was 80% and was adjusted to 50% after two months to control the cyanobacteria contamination. Artificial light was supplemented during a 14 hour photoperiod when the natural light was below 300 watts per m^2.

Due to small differences in peat compaction among containers, additional parameters were used to assess water availability. The soil-water potential at 2 cm below the surface was measured, using a tensiometer (Soil Measurement Systems, Tucson. AZ, U.S.A.) and the volumetric water content was measured using a WET sensor (Model 1.2 Delta-T Devices Ltd., Cambridge, U.K.) connected to a moisture meter type HH2 (Model 3.0, Delta-T Devices Ltd.). Both measures were taken weekly from each container for the duration of the experiment.

The temperature of two containers from each block, one with a shade net and the other without, was measured hourly for 60 days during the experiment using StowAway data loggers (Onset Computer Corporation, Pocasset, MA, U.S.A.). The relative humidity of the air 1 cm from the surface of the same two containers per block was measured using a humidity and temperature meter (Melrose, MA, U.S.A.) on three occasions during the experiment.

Peat samples were taken from each block (samples were taken from each container of a block and then mixed). The samples were analyzed for pH, electrical conductivity, and concentrations of Sodium (Na), Iron (Fe), Calcium (Ca), Magnesium (Mg), and total Phosphorus (P) and Nitrogen. An Acumet Model 10 probe was used to measure pH (Fisher Scientific, Pittsburgh, Pennsylvania, USA). Electrical conductivity was measured with an Orion Model 122 conductivity meter (Thermo Electron Corporation Waltham, MA, USA), adjusted to 20°C and corrected for hydrogen ions (Sjörs 1952). These measures were carried out using a 4:1 mixture of bi-distilled water and peat. The P was extracted using the Bray 1 method (Bray and Kurtz 1945) and the extract was analyzed using flow injection analysis (Bogren and Hofer 2001). An inductively coupled argon plasma spectrophotometer (ICP-OES Optima 4300DV of Perkin Elmer) was used to determine Na, Fe, Ca, and Mg concentrations (Mehlich 1984). The N content was determined following the Kjetdhal method (Bremner and Mulvaney, 1982). The peat chemistry (Table 5.1) is characteristic of poor fen peat (Vitt and Chee 1990) and is representative of residual minerotrophic peat from cutaway peatlands in North America (Wind-Mulder and Vitt 2000). The pH and conductivity were tested again at the end of the experiment and had not significantly changed.

The regeneration was estimated by assessing the percentage living cover of each moss species after six months. For the acrocarpous mosses, *Polytrichum strictum, Dicranum polysetum* and *Aulacomnium palustre*, all living bryophytes were the result of new regeneration as the fragment of the main stem served as the foundation of the new growth, but rapidly died. However, the fragments of *Sphagnum* species and the pleurocarpous bryophytes, *Tomenthypnum nitens, Warnstorfia exannulata* and *Pleurozium schreberi*, could continue to grow. Therefore, it was difficult to distinguish new growth from the existing moss. Due to the inherent differences in the morphological growing habits of the bryophytes, each moss species was analyzed separately This data was analyzed with an analysis of variance (ANOVA), using the GLM procedure of SAS and a priori polynomial contrasts (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, NC, U.S.A.).

FIELD EXPERIMENT

The field experiment was carried out over 2005 and 2006 on a cutaway peatland near Rivière-du-Loup, Québec (47 45'N 69 30'W), which is located ca. 200 km north-east of Québec City. This site is part of a large complex of ombrotrophic bogs interspersed with *Alnus* swamps (Gauthier and Grandtner 1975) and is classified as a low boreal peatland (National Wetlands Working Group 1988). The regional climate is characterized by cold winters and warm summers with January and July mean temperatures of –13 and 18 °C, respectively. The mean annual precipitation is 963 mm, of which 72% falls as rain (Environment Canada 2002). The first growing season of the experiment was unseasonably dry during the month of August where during the first 29 days only 44 mm of precipitation fell, compared with the a monthly average of 98 mm. The second season was more temperate. Although the total precipitation was lower, the rainfall was more evenly spread out without any long dry periods (Direction du suivi de l'état de l'environnement, Ministère du Développement durable, de l'Environnement et des Parcs du Québec).

The experiments were set up on two formerly harvested fields (30 m x 70 m) which had been mined to their minerotrophic peat layer, approximately 150 m apart on the same peatland. The chemical analyses were carried out using the same methodology as was used for the greenhouse peat. The peat characteristics can be seen in Table 5.1.

The field experiment was a randomized block, split-plot design with nursing plant treatments as the main factor and the bryophytes species as the sub-plot factor. The nursing plant treatments were: (a) *Scirpus cyperinus* (L.) Kunth, (b) *Equisetum arvense* L, (c) *Polytrichum strictum,* (d) straw mulch cover and (e) control. The first three treatments are plants which frequently spontaneously colonize cutaway minerotrophic peatlands in Canada (unpublished data). These plants additionally represent three distinct vegetation structures: *Scirpus cyperinus* exhibits a large tussock-forming structure, *Equisetum arvense* is a small, early successional plant and *Polytrichum strictum* is a pioneer moss species. The nursing plant treatments were repeated five times for a total of 25 plots, measuring 5 m by 6 m with a 2 m buffer between plots.

During the growing season prior to the start of the experiment, the nurse plant treatments were established. The experimental areas were scraped and leveled in the early summer of 2004 to homogenize the surface and remove any vegetation that had spontaneously colonized the site. In June of 2004 monocultures of *Scirpus cyperinus*, *Equisetum arvense* and *Polytrichum strictum* were established. Mature *Scirpus* tussocks (ca. 1.5 m high) were transplanted to the designated plots from colonies no more than 50 m away on the same abandoned peatland. *Equisetum* was transplanted using rhizomes also collected on site. *Polytrichum* plots were created by introducing moss fragments in a 1:5 donor to recipient ratio. The *Polytrichum* plots were covered with straw to improve their regeneration (Groeneveld and Rochefort 2005) and all plots where plants were introduced were lightly fertilized with rock phosphate (15 g m^{-2}) to aid their establishment (Rochefort *et al.* 2003).

Table 5.1. The means (±SE) for the chemical properties of the peat from the greenhouse and field regeneration experiments.

	Ca	Mg	Fe	Na	P	N-NO_3^-	N-NH_4^+	Conductivity	pH
				mg g^{-1}				µS cm^{-1}	
Greenhouse	3.8	1.15	0.5	0.82	44.4	3.4	148.7	30.0	4.64
	(±0.1)	(±0.02)	(±0.03)	(±0.01)	(±0.9)	(±0.4)	(±7)	(±4.8)	(±0.02)
Field	5.6	1.16	ND*	0.31	28.0	ND*	ND*	23.9	4.97
	(±0.4)	(±0.2)		(±0.08)	(±9.0)			(±2.5)	(±0.07)

*ND: Data not available

In May of 2005 fragments of the study species, excluding *Polytrichum*, were introduced in a 1:10 donor to recipient ratio onto eight sub-plots of 1.5 m x 1.5 m. The sub-plots were located in the center of the main plots with a buffer zone of at least 1 m to the edge of the main plot to ensure similar nursing plant treatments for all tested bryophytes.

The soil-water potential was measured using the same tensiometer as was used for the greenhouse experiment on 10 plots at 2 cm below the surface every 14 days during the growing season of 2005 and the volumetric water content was measured on four areas of each plot on June 28th and August 18th of 2005 using the same WET sensor as was used for the greenhouse experiment. The temperature for each treatment was measured every six hours from the 29th of June to the 19th of July of 2005.

The regeneration of each moss was assessed by estimating the percent cover of each moss (using two 25 cm x 25 cm quadrats per sub-plot) in mid-September of 2005 and 2006. At the same time, the percent cover of the nursing-plant treatments, spontaneous vegetation and the total vegetation was assessed with 16 quadrats of 50 cm x 50 cm for each main plot. Eight of these quadrats were within in the sub-plots and eight were outside of the subplots. This information was used to assess the success of each nursing plant's establishment. Three outliers, main plots that had an exceptionally low or high percentage cover of the nurse plant or spontaneous vegetation, were eliminated for the analysis (for more information see the Nurse Plant Establishment section of the Results). The regeneration (% cover) of the bryophytes was compared among moss species and among nursing plant treatment. For the field experiment, the regeneration of the moss species could be compared because the mosses were reintroduced using the same donor to restoration site ratio, not a specific number of fragments. Also, in the field experiment, there were fewer factors being tested. The presence of an interaction between the two factors was tested. The analysis was carried out using the MIXED and LSD procedures of SAS (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, NC, U.S.A.). The MIXED procedure was used because it is recommended for the analysis of split plot designs.

Additionally, a regression analysis was carried out in order to detect a possible relationship between the regeneration of the introduced bryophytes and the vegetation cover. The average cover of all introduced bryophytes was compared with both the cover of the total vascular plants and the cover of the nursing plant by itself. The average cover of all introduced mosses was used because of the great variation between the regeneration of bryophyte species. For this analysis the outliers were included because the variation between treatments is accounted for. The soil-water potential and the volumetric water content for each main treatment were compared using an ANOVA and protected LSD procedure of the SAS version 9.1.

RESULTS

GREENHOUSE EXPERIMENT

All bryophytes were capable of regenerating vegetatively; however, some had more specific requirement than others. All species, except *Polytrichum strictum*, showed a significantly higher regeneration under shade (Figure 5.1; Table 5.2). Most species, except *Polytrichum strictum*, had the highest cover for the wettest treatments (Table 5.2). The highest cover for *Polytrichum strictum* was observed for a drier treatment (-20 cm) (Figure 5.1). Water levels did not significantly affect the regeneration success of two species, *Warnstorfia exannulata* and *Sphagnum centrale* (Table 5.2).

Although almost all species had a higher regeneration cover under shade, *Pleurozium schreberi* and *Warnstorfia exannulata* strictly required shade for regeneration; their covers were close to zero for all treatments in full light (Figure 5.1). *Aulacomnium palustre* also showed a much higher percentage cover for the shaded, wet treatments (0 cm and -10 cm water levels). However, unlike *Pleurozium schreberi* and *Warnstorfia exannulata*, *Aulacomnium palustre* did successfully regenerate in full-light conditions, even if the percentages were lower (Figure 5.1). Two species, *Dicranum polysetum* and *Tomenthypnum nitens*, were capable of regenerating in a variety of conditions, but, at the end of six months, their covers were relatively low, especially for dry treatments.

The *Sphagnum* species were the most successful in regeneration; each had covers close to 100% for the shaded treatments with water levels at 0 cm and -10 cm (Figure 5.1). Although the percentage covers were higher for the three *Sphagnum* species under shaded conditions, their percentage covers were also relatively high in full-light conditions. In particular, *Sphagnum centrale* had an exceptionally high cover (42%) even for the harshest treatment (full light with -40 cm water level).

The temperatures of the treatments in full-light proved to be noticeably higher compared to those with shade nets. Fifty percent of the time the daily maximum temperature was equal to or greater than 27°C for the shaded treatments, compared to 31°C for the full-light treatments (Figure 5.2). There was also a clear difference between the air humidity underneath shade nets (72% ±3) and where there were no shade nets (65% ±3). The higher regeneration for the wetter treatments was indeed due to greater water availability. The water potential (± SE) was -4.3 (±0.3), -8.6 (±0.5), -16.4 (±0.7) and -33.7 (±0.9) for the water levels 0 cm, -10 cm, -20 cm and -40 cm, respectively. Volumetric water content showed no difference in the 0 cm and -10 cm water levels (both were 74%). Probably the difference was smaller than measurement errors. The -20 cm corresponded to 65% volumetric water content and -40 cm to 44%.

Table 5.2. ANOVAs which compare the regeneration success (% cover) of treatments of a factorial design which tested effects of shade (no shade and 50% shade) and four water levels (0, -10, -20 and -40) for nine fen bryophytes species tested in a greenhouse experiment. Significant *P*-values are in bold.

		Aulacomnium palustre		*Polytrichum strictum*		*Dicranum polysetum* (log (x+1))		*Tomenthypnum nitens*		*Pleurozium schreberi* (log (x+1))	
Source	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Blocks	3										
Water Level	3	8.82	**0.0006**	7.55	**0.001**	18.61	**<.0001**	5.22	**0.008**	10.10	**0.0003**
Shade	1	29.34	<**.0001**	0.69	0.42	7.73	**0.01**	14.45	**0.001**	14.19	**0.001**
Water Level*Shade	3	5.59	**0.006**	2.37	0.10	0.70	0.56	2.32	0.10	2.82	0.06
Error	21										
Total	31										
Contrasts:											
Linear effect (WL)	1	14.62	**0.001**	0.00	**0.99**	55.72	**<.0001**	15.65	**0.0007**	24.03	**<.0001**
Quadratic effect (WL)	1	0.00	0.99	20.16	0.13	0.09	0.77	0.02	0.90	1.21	0.28
Cubic effect (WL)	1	11.84	**0.002**	2.48	0.44	0.01	0.94	0.00	0.97	5.05	0.04
Linear effect (WL)*shade	1	8.98	**0.007**	4.60	0.87	0.77	0.39	6.91	0.02	6.96	0.02
Quadratic effect (WL) *shad	1	1.24	0.27	0.03	0.13	0.52	0.48	0.01	0.93	0.07	0.79
Cubic effect (WL)*shade	1	6.55	0.02	2.48		0.81	0.38	0.03	0.87	1.44	0.24

Table 5.2. continued

		Warnstorfia exannulata		*Sphagnum warnstorfii* (log (x+1))		*Sphagnum fallax* (log (x+1))		*Sphagnum centrale*	
Source	d.f.	F	*P*	F	F	*P*	*P*	F	*P*
Blocks	3								
Water Level	3	2.89	0.06	25.86	**<.0001**	23.16	**<.0001**	2.32	0.10
Shade	1	30.60	**<.0001**	12.83	**0.0018**	**18.22**	**0.0003**	11.12	**0.003**
Water Level*Shade	3	2.79	0.07	0.96	0.43	0.72	0.55	0.62	0.61
Error	21								
Total	31								
Linear effect (WL)*shade	1	0.01	0.94	0.01	0.92	0.38	0.55	0.16	0.69
Quadratic effect (WL) *shad	1	3.16	0.09	0.30	0.59	0.02	0.88	0.01	0.93
Cubic effect (WL)*shade	1	5.20	0.03	2.57	0.12	1.78	0.20	1.70	0.21
Contrasts:									
Linear effect (WL)	1	0.50	0.49	73.91	**<.0001**	59.43	**<.0001**	2.07	0.16
Quadratic effect (WL)	1	7.23	0.014	2.67	0.12	6.58	**0.018**	3.92	0.06
Cubic effect (WL)	1	0.93	0.35	1.02	0.33	3.47	0.08	0.97	0.34

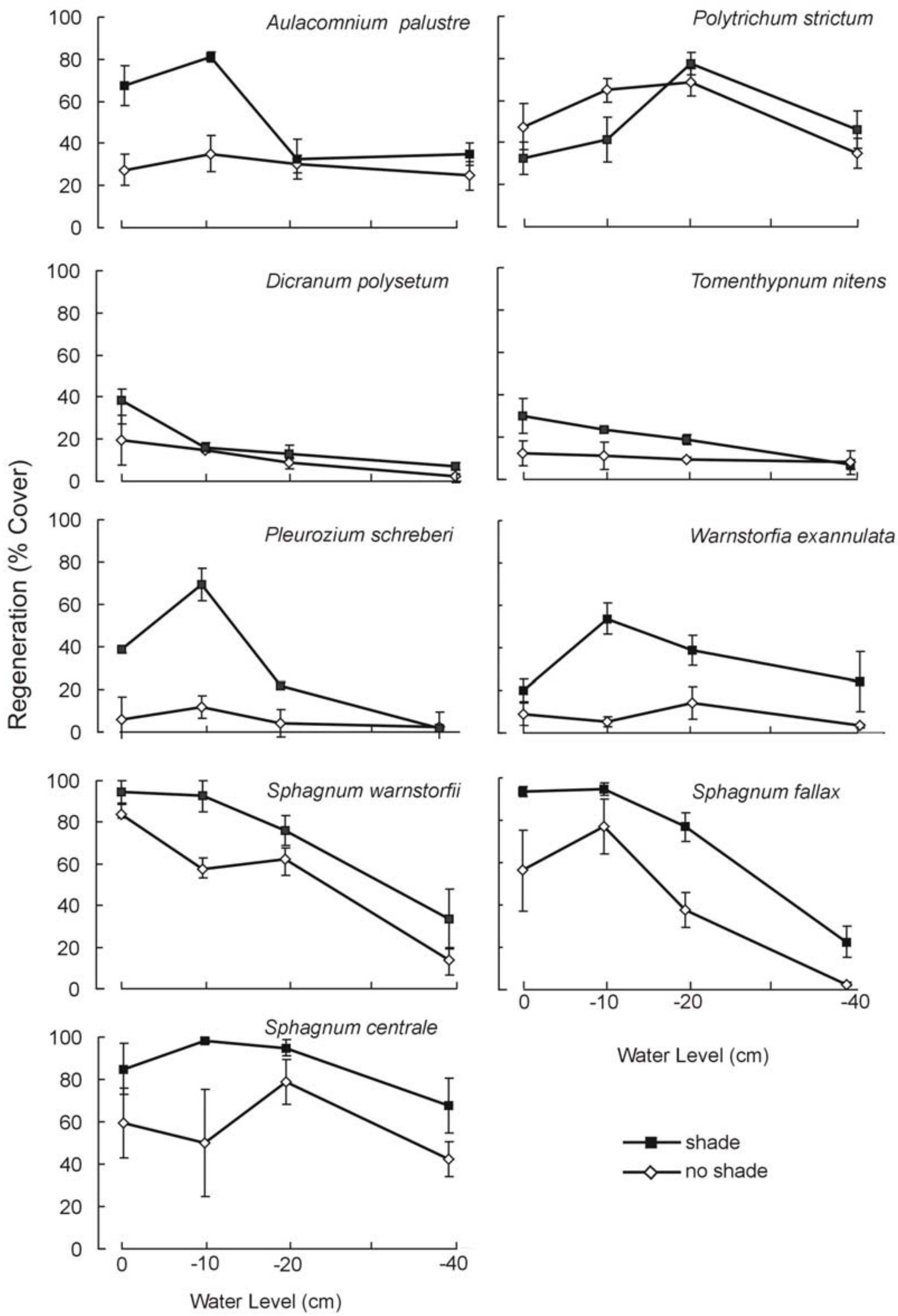

Figure 5.1. The regeneration (% cover) of the nine fen bryophytes tested in a greenhouse experiment. The factorial design tested four water levels in full-light and shade conditions (50% shade).

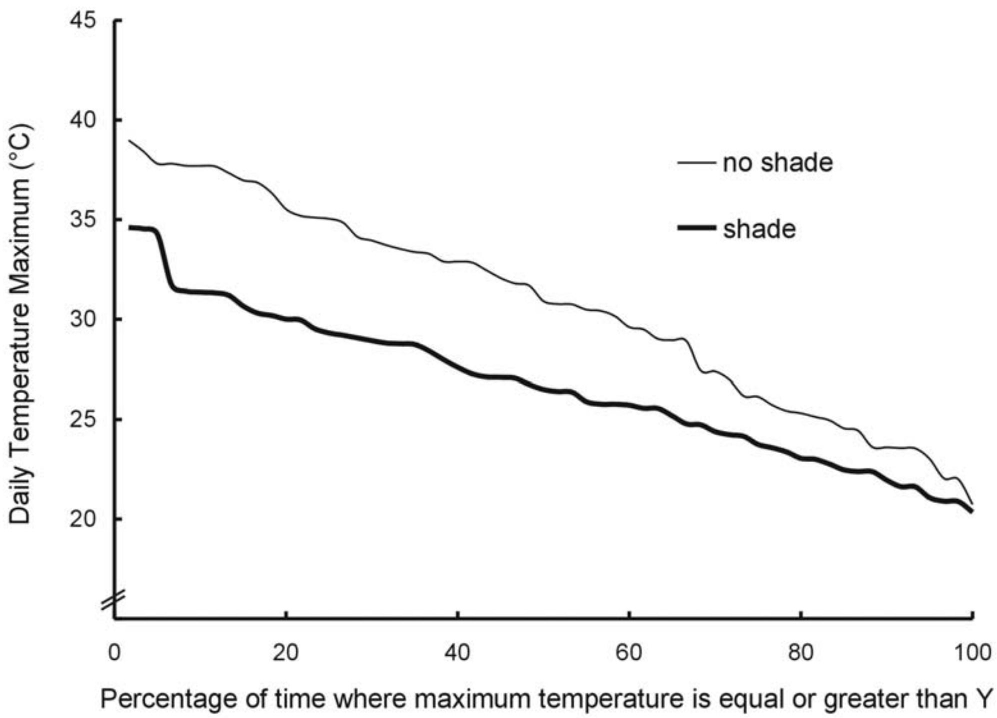

Figure 5.2. A comparison of temperatures measured over a 60 day period under the shade nets (50% shade) and in full-light conditions for the greenhouse experiment.

Field Experiment

Nursing plant establishment

Because the nursing plant treatments are biotic treatments, there was a certain amount of variation among the same treatments, depending on how well a particular nursing plant grew on a particular plot. In order to homogenize the treatments, outlier nursing treatment plots were eliminated. Outlier plots were those in which the cover was greater or lower than the mean plus or minus standard deviation. Spontaneous vegetation also increased variation among the same treatments. Any plot where the spontaneous vegetation was much greater than the others of the same treatment (those with a cover greater than the mean plus the standard deviation) was removed. In the end, three main plots, one *Polytrichum,* one *Scirpus* and one *straw* treatment, were eliminated following these criteria.

After two growing seasons, *Scirpus* showed the highest percent cover (ca. 50%) followed by *Equisetum* and *Polytrichum* (20% and 9%, respectively; Table 5.3). The control plots experienced the highest invasion by spontaneous vegetation (Table 5.3). The *Equisetum* and *Polytrichum* treatments showed comparable covers for spontaneous vegetation, while the *Scirpus* and straw treatments were less colonized by spontaneous vegetation. The spontaneous vegetation was dominated by *Euthamia graminifolia* (L.) Nuttall, *Agrostis scabra* Willd., *Epilobium angustifolium* L. and *Betula populifolia* Marsh.

Moss regeneration

After one growing season the moss covers were modest with a cover of 2%; however the bryophytes grew considerably during the second season bringing the average cover to 8%. After two growing seasons there was significantly higher moss regeneration under the canopy of *Scirpus* than other treatments (Figure 5.3a). There was no difference in moss cover among the straw, control, *Polytrichum* or *Equisetum* treatments. No interaction was detected between the nursing-plant treatment and the introduced bryophytes (Table 5.4), meaning that the same regeneration patterns were observed for bryophyte species for all the nurse plant treatments.

The difference between the percentage covers of the different moss species was highly significant after two growing seasons (Figure 5.3b). *Sphagnum warnstorfii* and *Tomenthypnum nitens* had the highest cover (Figure 5.3b); however, even these species showed rather low covers after two growing seasons (ca. 15%). *Sphagnum centrale, Dicranum polysetum* and *Aulacomnium palustre* were slightly less successful at regeneration with cover of ca. 10%. *Sphagnum fallax* had a relatively low cover (ca. 5%) and two species, *Pleurozium schreberi* and *Warnstorfia exannulata*, had extremely low covers 2% and 3%, respectively (Figure 5.3b).

A regression analysis was carried out in order to see whether the higher moss regeneration under a *Scirpus* canopy was due to simply higher vascular plant cover or specifically the structure of *Scirpus*. There was no relationship (R^2=0.05) between the cover of the introduced bryophytes and the total cover of vegetation, which included the nursing plants and the spontaneous vegetation. Additionally, there was no relationship between the total vegetation cover and the cover of the introduced bryophytes when we examined the *Scirpus* treatment alone (R^2 = 0.06). However, when we examined the relationship between the introduced moss species and the percentage cover of *Scirpus* plant cover only, the correlation is much stronger (R^2 = 0.50). The other nursing plant treatments *Equisetum* and *Polytrichum* showed no relationship between their covers and the moss covers (Figure 5.4).

Table 5.3. Percentage covers of the nurse plant treatments, spontaneous and total vascular plant for first and second growing season. The total vascular plant is the nurse plant and the spontaneous vegetation cover, which is not entirely the sum of the two due to superimposition. The outliers have been removed from the values for second growing.

	First Growing Season			Second Growing Season		
Nurse Plant Treatments	Nurse plant % (±SE)	Spontaneous vegetation % (±SE)	Total vascular plant % (±SE)	Nurse plant % (±SE)	Spontaneous vegetation % (±SE)	Total vascular plant % (±SE)
Control	N/A	12 (±3)	12 (±3)	N/A	48 (±3)	48 (±8)
Equisetum	5 (±2)	21 (±5)	23 (±5)	23 (±2)	32 (±3)	54 (±6)
Polytrichum	6 (±1)	7 (±2)	12 (±2)	9 (±0.7)[a]	36 (±6)	47 (±9)
Scirpus	16 (±4)	5 (±1)	19 (±2)	48 (±2)[b]	18 (±2)	64 (±7)
Straw	N/A	8 (±4)	8 (±4)	N/A	20 (±3)[c]	20 (±3)

The mean before the outliers were removed were: [a] 16 (±2), [b] 42 (±2) and [c] 27 (±3).

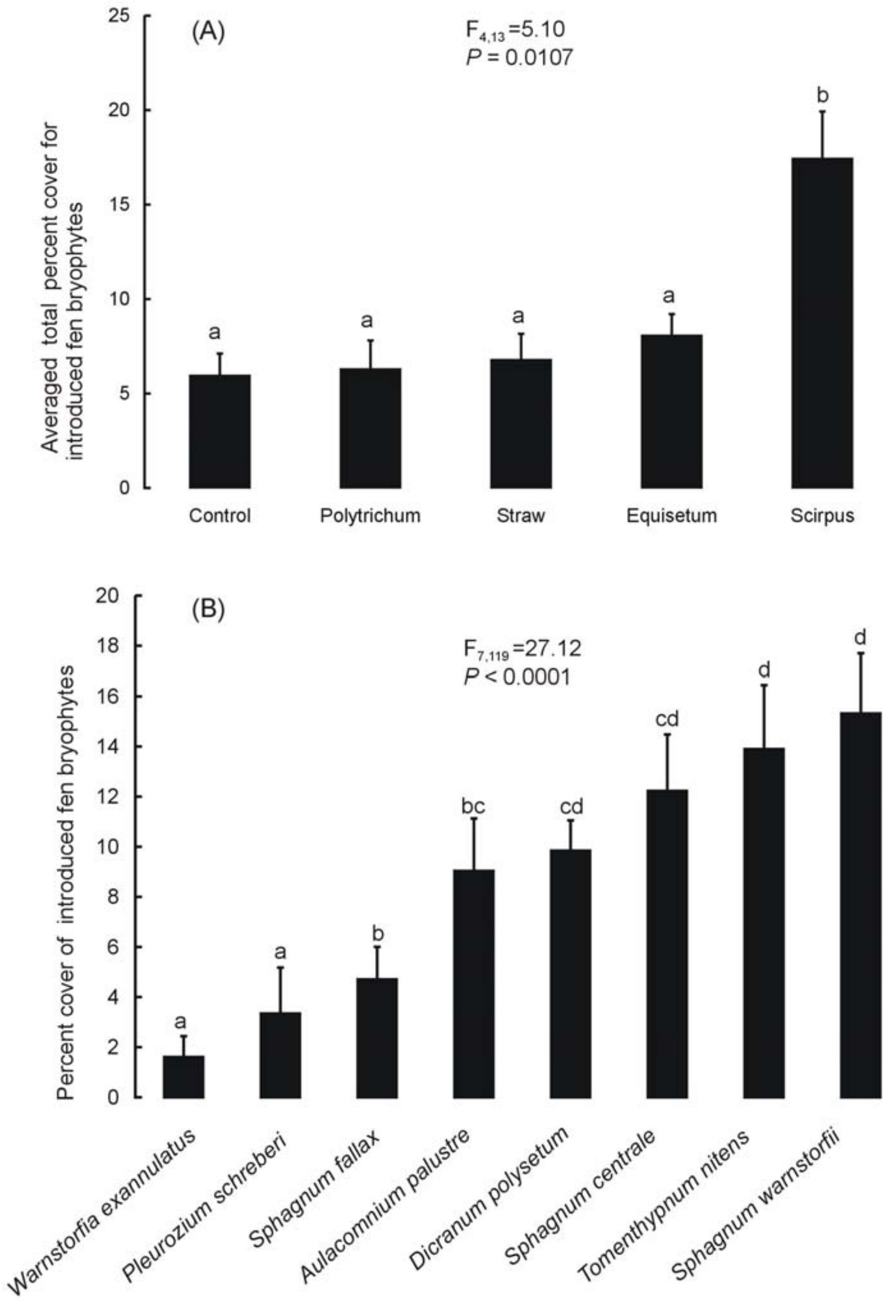

Figure 5.3. The regeneration of eight fen bryophytes in a field experiment is shown. Because there was no significant interaction between the nurse plant treatments (main plots) and the species (sub-plot), the data can be summarized with two graphs. The moss regeneration of all introduced moss species averaged under the canopy of three nurse plant treatments as well as a control and a straw treatment is shown (A). Additionally, the average percent cover of each species for all treatments confounded is shown after two growing season (B).

Table 5.4. ANOVA for the second growing season of a field experiment on the regeneration of eight fen bryophytes species. The regeneration success (% cover) of the introduced moss species were compared among nurse plant treatments (*Scirpus cyperinus, Equisetum arvense, Polytrichum strictum*, straw and control). The percentage covers were also compared between introduced moss species. Significant *P*-values are in bold.

Source	d.f.	F	*P*
Block	4		
Nurse Plant	4	5.16	**0.01**
Error a	13		
Introduced Bryophytes	7	26.35	**<0.0001**
Bryophytes* Nurse Plant	28	1.17	0.12
Error b	119		
Total	175		

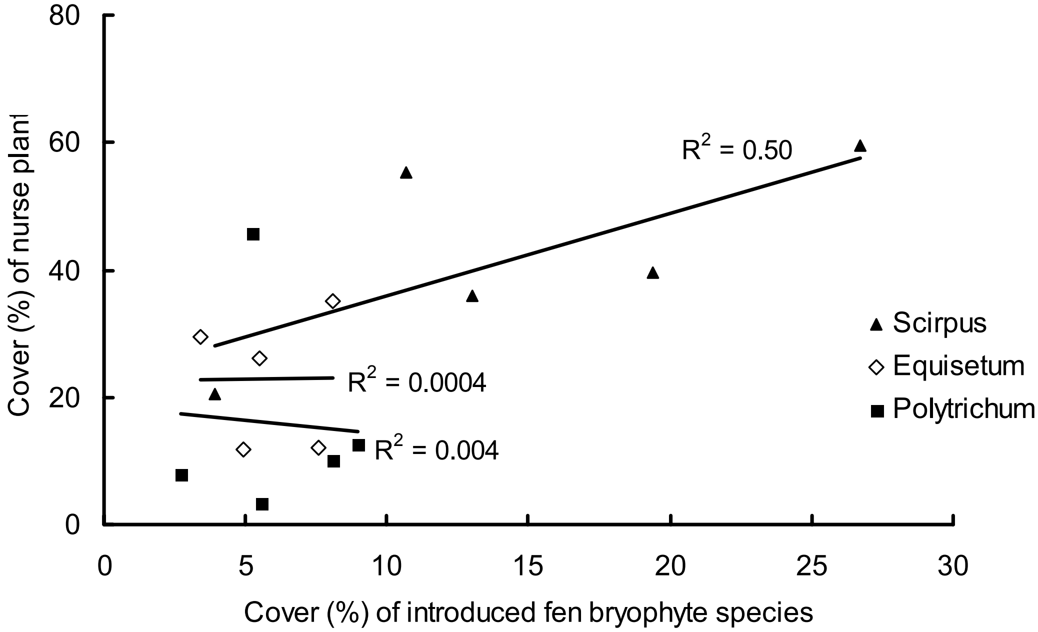

Figure 5.4. A regression showing the relationship between the nurse plant cover (%) and the regeneration (% cover) of introduced bryophytes (average of all species conbined) per plot.

Environmental Variables

The low regeneration rates of the bryophytes are likely due to the extremely harsh conditions during the first growing season. The soil-water potential dipped during this dry period of August 2005 from -50 mbar to -170 mbar (Figure 5.5). The volumetric water content also showed a striking difference between the average June reading of 63% (± 0.01) and the average mid-August reading of 36% (± 0.009). There was no significant difference in the soil-water potential or the volumetric water content among the nursing plant treatments. There was, however, a marked difference in the temperatures measured for each treatment. The control plot showed the highest daily maximum temperatures. Most of the time the control plots were 5°C warmer than straw and *Equisetum* treatments and 10°C warmer than *Scirpus* and *Polytrichum* treatments (Figure 5.6). Although the cover of *Polytrichum* was not as high as the *Scirpus* cover (Table 5.3), straw mulch was added during the *Polytrichum* establishment, greatly increasing the protective cover of this treatment.

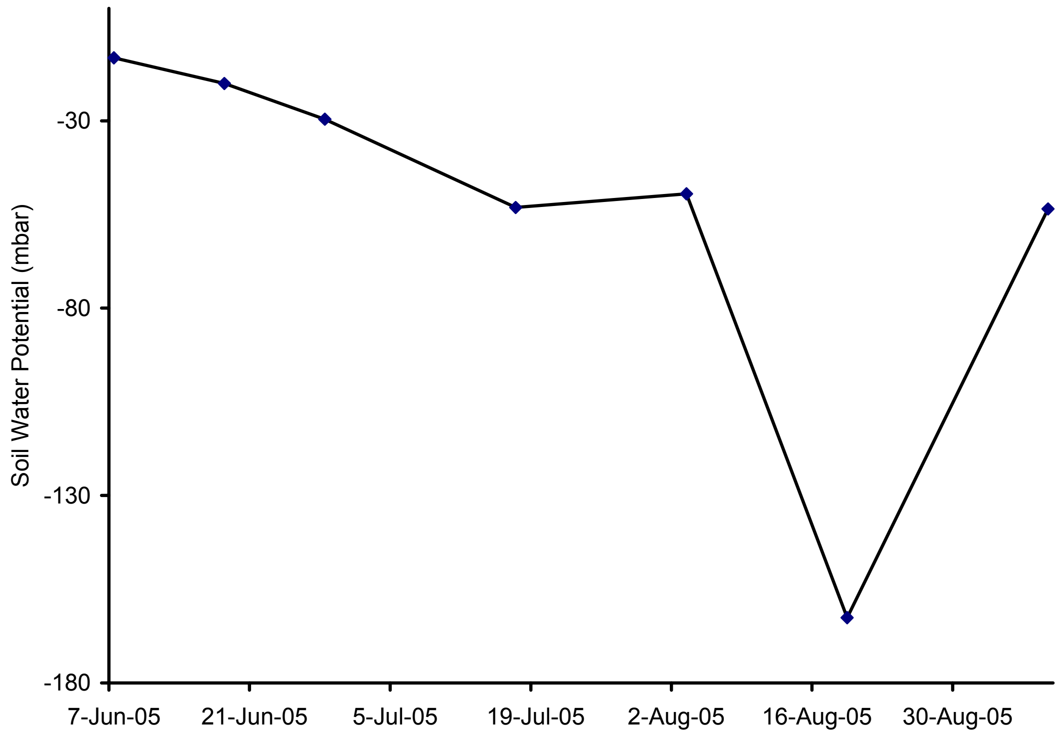

Figure 5.5. The soil-water potential is shown for the first growing season where the summer was very dry and the water potential dipped late in the season.

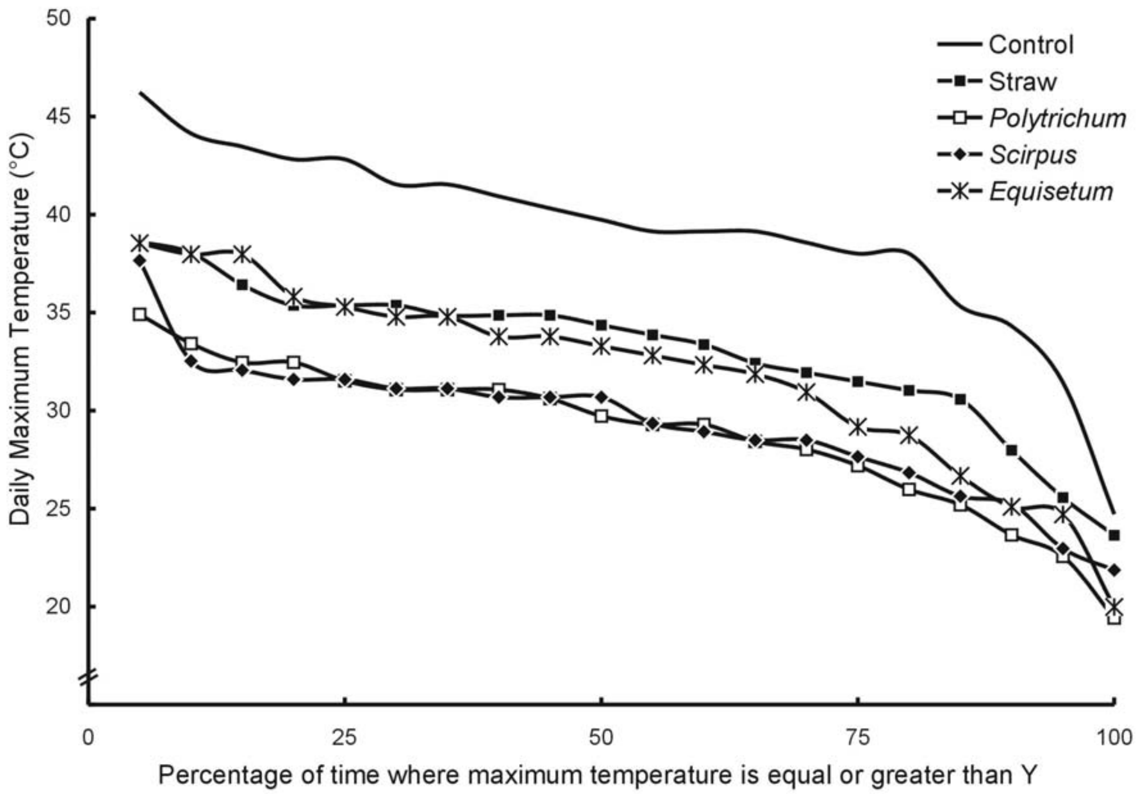

Figure 5.6. A comparison of temperatures measured for the field experiment. Each nurse plant treatment was measured for 38 days in the summer of 2005 (the first growing season).

DISCUSSION

THE EFFECT OF SHADING

This experiment showed that all bryophytes (with the exception of *Polytrichum strictum*) had significantly higher regeneration under dense shade either through shade nets in the greenhouse experiment or under large herbaceous plants (*Scirpus*) in the field. The ability of the moss species to regenerate better under shade is not solely due to photoinhibition (Murray *et al.* 1993), but also to a moderate microclimate and moister substrate conditions. The presence of a protective cover has been shown to improve the moisture content of the substrate (Groeneveld *et al.* 2007).

The regression analysis showed that the presence and density of *Scirpus* was strongly related to successful moss regeneration. One confounding factor is that, due to the presence of *Scirpus* large tussocks, the introduced mosses were applied in a greater density to the areas between tussocks on these plots. However, we believe that the higher regeneration is indeed due to the microclimate created by *Scirpus* because the difference between treatments was only detected after the second growing season. If the higher fragment density had created a bias, it would have been evident after the first growing season. Similarly, in calcareous grasslands the water holding capacity of herbaceous litter allowed for higher growth of bryophytes (Rincon 1988). Shade improved regeneration (except for *Polytrichum strictum*) even for the wettest greenhouse treatments, where water was not a limiting factor. Perhaps this is an indication that air humidity is more important to moss growth than substrate humidity.

Apart from a higher regeneration of fen bryophytes under the *Scirpus* canopy, there was no difference in the bryophytes' regeneration among other nurse plant treatments. It is odd that the control treatment showed similar regeneration rates as the other treatments, considering the temperatures were much higher. This could be explained by spontaneous revegetation. The temperatures were measured early in the first experimental season when there was little spontaneous regeneration. However, by the end of the second year the total vascular plants cover on plots where no nursing plants were reintroduced was similar to the other treatments where plants had been reintroduced. Therefore, the conditions of the control plots were similar to the other treatments during the second growing season. On the other hand, the low daily maximum temperature measured on the *Polytrichum* plots should have translated to higher moss regeneration. In similar studies for bog restoration *Polytrichum* indeed improved moss regeneration (Groeneveld and Rochefort 2002). It seems the tall, dense structure of *Scirpus* creates a more humid microclimate than the small structure of the *Polytrichum* moss. Possibly relative humidity would have been a better parameter to characterize the microclimate for moss regeneration than temperature.

REGENERATION IN RELATION TO WATER AVAILABILITY

This study confirmed that optimal water contents for moss growth are generally lower than saturation values as was also observed by Busby and Whitfield (1977). In the greenhouse experiment, the highest regeneration for bryophytes was often observed at a water level 10 cm under the surface. *Sphagnum* species, for example, are subject to cyanobacteria contamination when constantly saturated (L. Rochefort, personal observations), as we observed in our greenhouse experiment. .In the field, lengthy flooding inhibited the growth of bryophytes mainly due to physical disturbance, such as erosion and sedimentation (Quinty and Rochefort 2000; Rochefort *et al.* 2002). Therefore, fen restoration sites where the water level just below the surface should show the highest moss regeneration, at least for non-aquatic bryophytes.

THE REGENERATION CAPABILITIES OF THE TESTED MOSSES

In both the greenhouse and the field experiments the *Sphagnum* species were among the most successful species in regenerating. *Sphagnum* mosses are better competitors and generally more productive than most non-sphagnous species when relative humidity at the air-peat surface is not limiting (Vitt 1990; Gignac 1992).

Polytrichum strictum showed different regeneration preferences than other tested mosses. This comes as no surprise as it is one of the most ‘developed’ bryophytes, with a water conducing system which allow it to direct water under dry conditions (Bayfield 1973). Its leaves are also sun leaves, adapted for photosynthesis under drier conditions and greater light intensities than other bryophytes (Clayton-Greene *et al.* 1985).

Pleurozium schreberi had minimal regeneration success in the field and in all full-light greenhouse treatments even though it inhabits dry areas and is an aggressive competitor in forest environments (Frego 1994). *P. schreberi* has a narrow fundamental niche and prefers shaded areas (Busby and Whitfield 1977; Mulligan and Gignac 2001) and this study showed that shade is indeed crucial for the regeneration of this species. As this species is dominant in boreal forest, this could prove an important consideration for forest restoration after clear-cutting.

CONCLUSIONS

If the emphasis of fen restoration is the return of the peat-accumulating function, *Sphagnum* species which tolerate slightly minerotrophic conditions should be favored to jump-start the succession towards a bog (Wind-Mulder and Vitt 2000). *Sphagnum* species are considered the keystone of bog restoration due to their ability to alter the chemistry and hydrology of their environment as well as the great capacity to accumulate peat (Rochefort 2000). Some studies have suggested that even non-sphagnous bryophytes, such as *Tomenthypnum nitens*, *Drepanocladus revolvens* and *Campylium stellatum* also have the ability to acidify their environment and likely influence peatland succession (Glime *et al.* 1982; Karlin and Bliss 1984). If fen bryophytes are capable of altering their environment should they be considered the keystone species of fen restoration? A great amount of research has been carried out on the functional role of bryophytes in bogs (Clymo and Hayward 1982), however little is known about their function in fens. More research on the functional roles of vascular plants and bryophytes in fen systems would enable fen restoration projects to focus on a few keystone vegetation groups.

IMPLICATIONS FOR PRACTICE

This study demonstrates that fen bryophytes show good potential for use in fen restoration projects, as all the tested bryophytes were capable of vegetative regeneration.

However, marked differences between the regeneration of the tested species were observed. Specifically, the following conditions improved their regeneration:

- Most species showed the best regeneration with a water level just at or under the surface (0 to -10 cm) in a controlled environment. All species, except *Polytrichum strictum*, had a higher regeneration success under shaded conditions.
- The *Sphagnum* species showed the highest regeneration in both the field and greenhouse experiments.
- The regeneration success of the bryophytes would benefit from the canopy of tall herbaceous plants which create a protected microclimate. Therefore, restoration strategies which include the reintroduction of large, tussock-forming vascular plants, such as plants from the Cyperaceae family, would complement the reintroduction of fen bryophytes.

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CHAPTER SIX

GENERAL CONCLUSIONS

This is the first comprehensive research project on fen restoration in North America. Since new harvesting methods allow peat to be extracted to greater depths, an increasing number of abandoned peatlands will be harvested to the minerotrophic peat layer. Thus, in the future more abandoned peatlands will need to be restored towards a fen vegetation community. The results from this project provide insights for the restoration of harvested fens and will be discussed in the following section

THE ASSEMBLY RULES FRAMEWORK FOR RESTORATION RE-EVALUATED

The assembly rules framework proved to be valuable for pinpointing important research areas for fen restoration of harvested peatlands. A new model for restoration ecology based on the assembly rules approach has been developed and is shown in Figure 6.1. The figure shows how insights gained from the different chapters of this thesis can be used to identify target species and effective methods for fen restoration.

Chapter 2 compares the community structure of degraded species pools from harvested fens with that of undisturbed species pools, showing that *Carex* and fen bryophytes are largely absent from degraded species pools. Chapter 3 examines the peat-accumulating potential of three species from degraded species pools and three species from undisturbed species pools. Of the tested species, bryophytes, especially *Sphagnum*, showed the highest peat accumulating ability due to their low decomposition rates. This result confirms Vitt's (2000) finding that bryophytes decompose more slowly than vascular plants in fen systems. Chapters 2 and 3 indicate that fen bryophytes should be target species for future fen restoration projects as has previously been suggested by Wind-Mulder *et al.* (1996) and Sliva (1997). If the emphasis of the restoration project is put on community structure, a variety of *Carex* species should be included in restoration measures, because results from Chapter 2 indicate that *Carex* are abundant on undisturbed fens and do not recolonize harvested fens.

This project showed that the degraded species pool (Figure 6.1) is more diverse on harvested fens where drainage canals are blocked, showing that hydrology is the major environmental constraint to the revegetation of harvested fens. Abandoned sites which are no longer being drained are quickly recolonized by wetland species (Chapter 2). Among vacuum-harvested sites which are no longer being drained, wetland and fen species are associated with a high water table, a thin residual peat layer and a longer time since abandonment (Chapter 2). Famous *et al.* (1991) also found that wetter sites are recolonized by vegetation more quickly than drier sites.

Another means to improve the environmental constraints (Figure 6.1) acting on the degraded species pool is to apply fertilizer (Chapter 4). *Carex* species showed a higher establishment rate on experimental plots where a light dose of phosphate fertilizer was applied. A higher vascular plant establishment was observed for bog restoration sites where a light phosphate fertilizer was used (Rochefort *et al.* 2003; Sottocornola *et al.* 2007).

While hydrology was found to be the major environmental constraint (Figure 6.1), it was also found that drainage canals on the majority of abandoned harvested fens (23 out of 28) collapsed on their own (Chapter 2). Therefore, active restoration should focus on improving dispersal constraints because the major environmental constraint was overcome without active measures. On harvested fens which are no longer drained, a high revegetation rate of wetland plants was observed (Chapter 2). This suggests that harvested fens would support typical fen vegetation if this vegetation were actively introduced. Dispersal was also found to be a major constraint for fen restoration in Europe (Pfadenhauer and Grootjans 1999; Patzelt *et al.* 2001). This thesis shows that actively reintroducing vegetation would aid the recovery of harvested fens.

Two vegetation reintroduction methods were tested (i) hay transfer and (ii) *Sphagnum* transfer (Chapter 4). The d *Sphagnum* transfer method, commonly used for bog restoration of dry abandoned peatlands (Rochefort *et al.* 2003), proved to be the most effective for reintroducing fen bryophytes (moderate-rich *Sphagnum* species) and *Carex* species (Chapter 4). Due to the wet conditions found on both donor and harvested fens, it is advisable to reintroduce vegetation in spring while the ground is frozen (Chapter 4).

When the internal dynamics of the novel species pool (species from the degraded and target species pool; Figure 6.1) was examined, shade from herbaceous plants was shown to improve the regeneration of bryophytes (Chapter 5). The effect of shade was studied in a field experiment, using a dense herbaceous layer, and in a greenhouse experiment, using shade nets. Both experiments showed that blocking about 50% to 70% of the light allows for a higher regeneration rate for eight of nine tested bryophytes (Chapter 5). This indicates that the spontaneous vegetation, creating a dense herbaceous cover, facilitates the regeneration of introduced bryophytes. Other authors (Callaway *et al.* 1996; Nuñez *et al.* 1999; Bruno 2003) have made similar observations in other harsh environments. Therefore, reintroduction of fen species will be more successful on spontaneously vegetated fens than on bare peat surfaces.

The field plots where the *Sphagnum* transfer method was tested represent the restored species pool (Figure 6.1). After three years, these plots had *Sphagnum* and Cyperaceae (family mainly made up of *Carex*) covers which were similar to surveyed undisturbed sites (Chapters 2 and 4). The success of this method on experimental plots indicates that it should be tested for large-scale restoration projects.

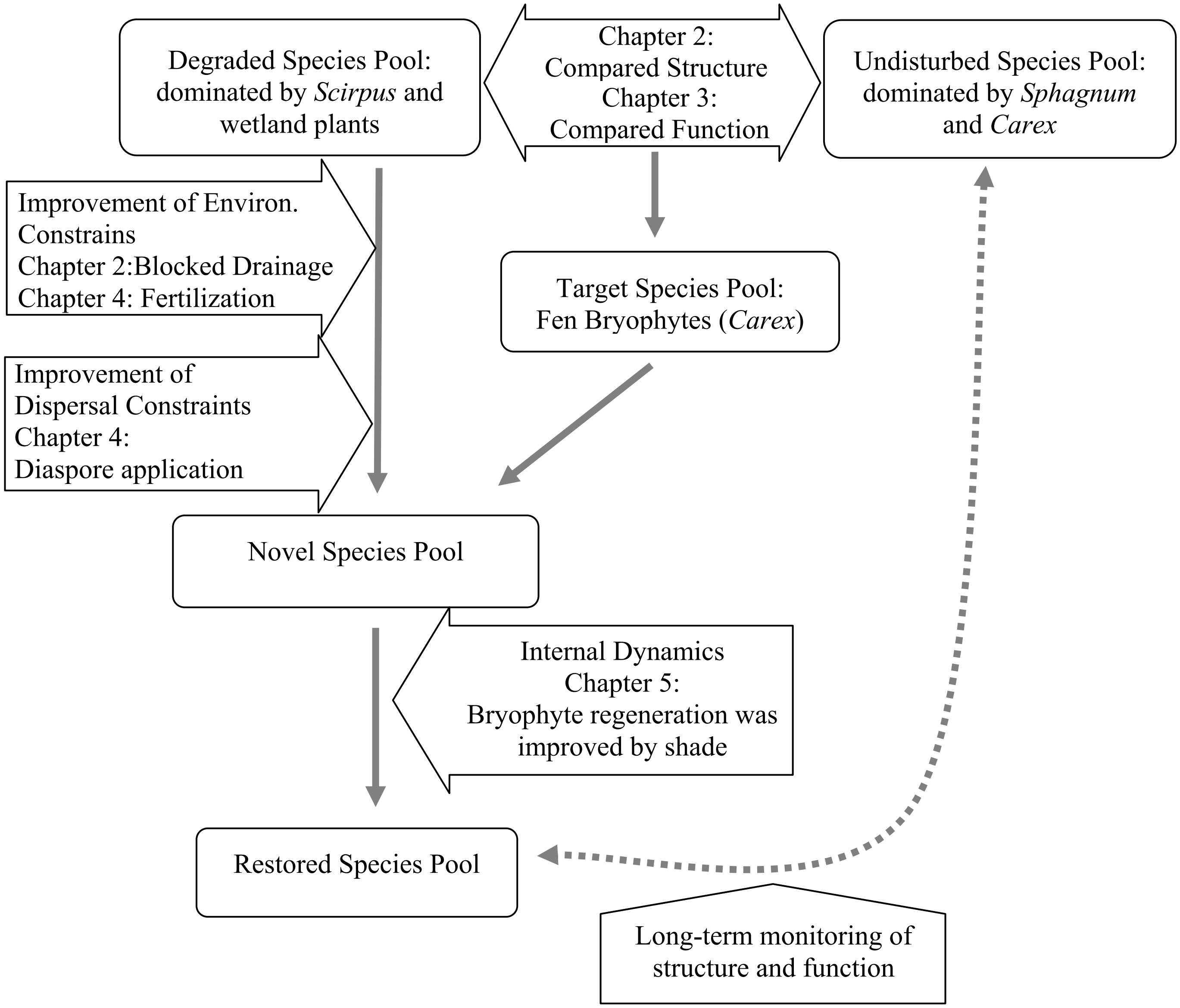

Figure 6.1. A model for restoration projects based on the assembly rules approach. This model has been adapted to include the most important indices for fen restoration of harvested peatlands. The rectangles represent species pools which are pertinent to restoration. Open arrows represent active measures which were explored. Solid arrows represent the direction of the species pool development during restoration and the dashed arrow represents similarity between species pools.

Future Research For Fen Restoration of Harvested Peatlands

This is the first comprehensive research project on fen restoration in North America and it leads to new questions. Adequate hydrological conditions are as important a component to peatland restoration as the return of suitable vegetation (Wheeler and Shaw 1995). Because we know little about the hydrology of abandoned, harvested fens research on the hydrology of these sites would be useful for their restoration. Fens receive runoff from surrounding or underlying mineral soils (Mitch and Gosselink 2000; Figure 6.2a). Although the hydrological conditions of harvested fens allow for the establishment of fen vegetation, it is not known whether fens receive runoff from the surrounding areas. It is probable that the large drainage ditches around harvested peatland siphon off runoff (Figure 6.2b). Future research to characterize the hydrology of harvested fens is essential before a large-scale restoration project can be carried out.

Another important vein of fen restoration is targeting vegetation groups for restoration. A large-scale fen restoration project could test the relationship between various community structures and their ecosystem functions. Are bryophytes really mainly responsible for peat accumulation in all peatlands, including fens as proposed by Vitt (2000)? Do sedge tussocks really increase biodiversity as proposed by Peach and Zedler (2006)? Is there truly a link between structural diversity and functional diversity as proposed by Naeem (2006)? A large-scale restoration project with a combinatorial design (Naeem 2006) could test the effect of the dominant species on the ecosystem function of the fen. Such an experiment would provide both invaluable information about fen systems and enable restoration ecologists to prioritize vegetation groups for fen restoration projects.

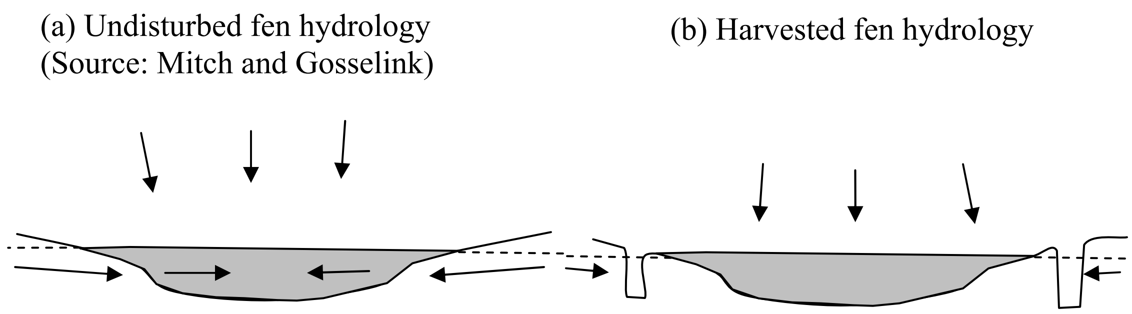

Figure 6.2. Possible differences in hydrology between undisturbed and harvested fens. The arrows represent water input. The undisturbed fen (a) has water input from precipitation and runoff, while perhaps the harvested fen (b) only receives water input from rain. Do active measures need to be taken to restore hydrology?

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