Régénération des bryophytes dans les tourbières perturbées

Thèse

Mélina Guêné-Nanchen

Doctorat en biologie végétale
Philosophiae doctor (Ph. D.)

Québec, Canada

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Mélina Guêné-Nanchen

Sous la direction de :

Line Rochefort, directrice de recherche

Résumé

La restauration écologique des tourbières se définit comme l'ensemble des procédés permettant d'assister à la régénération d'une tourbière qui a été dégradée, endommagée ou détruite. La gamme des tourbières perturbées qui nécessitent des actions de restauration est très diversifiée. L'étude de la régénération naturelle des écosystèmes perturbés a fréquemment été utilisée pour développer des méthodes de restauration qui sont adaptées aux types spécifiques de ces écosystèmes. Une compréhension plus complète des trajectoires de régénération, des contraintes environnementales et de dispersion, ainsi que des interactions interspécifiques, est directement reliée au développement de méthodes de restauration et à l'amélioration de nos connaissances sur la réponse des espèces et des communautés à des changements environnementaux. Cette thèse étudie la régénération de la végétation, plus spécialement des bryophytes, ainsi que les facteurs influençant leur régénération dans trois cas problématiques de restauration des tourbières perturbées. Premièrement, la régénération des communautés de bryophytes a été étudiée en fonction des conditions environnementales dans 28 tourbières minérotrophes des Territoires du Nord-Ouest et de l'Alberta ayant brûlé il y a un, deux ou cinq ans. Un changement de dominance a été observé entre les bryophytes pionnières (couvert moyen passant de 16 à 11 %) et les bryophytes de succession tardive (3 à 27 %) entre la 2^e^ et la 5^e^ année après le feu. La répartition et l'abondance des espèces de bryophytes semblent être contrôlées par leurs différences de capacité de régénération en lien avec leur stratégie d'histoire de vie, leur niche écologique et l'effet variable de la biomasse carbonisée. L'intégration de la notion de niche écologique chez les bryophytes de succession tardive ainsi que l'utilisation des espèces ayant un fort potentiel de régénération (comme *Aulacomnium palustre* et *Ptychostomum pseudotriquetrum*) devraient être considérées lors de l'élaboration des plans de restauration des tourbières minérotrophes. Deuxièmement, la régénération des sphaignes a été étudiée dans 25 sites donneurs (tourbières ombrotrophes où la végétation de surface a été récoltée pour servir de matériel de réintroduction) sur une chronoséquence de 17 ans en fonction des conditions environnementales et des pratiques de récolte. Les sphaignes dans les sites donneurs se régénèrent en moyenne en 10 ans, quoique des différences mineures dans la composition et l'abondance des espèces ont été observées entre les sites donneurs et les tourbières naturelles. Les espèces pionnières (p. ex., *Eriophorum vaginatum*), compétitives (p. ex., *Sphagnum rubellum*) et préférentielles des microhabitats plus humides (p. ex., *Chamaedaphne calyculata*) étaient plus abondantes dans les sites donneurs. Les pratiques de récolte avaient l'effet le plus important sur la régénération de la végétation, suggérant qu'il est possible d'accélérer la reprise des sphaignes en adoptant des pratiques de récolte appropriées. Des pratiques responsables consistent à éviter les sites donneurs très humides et la récolte durant le milieu de l'été lorsque les mousses ont un plus faible potentiel de régénération et lorsque le risque d'enlisement de la machinerie est élevé. Troisièmement, la régénération et le développement de tapis de sphaignes ont été étudiés dans deux types de tourbières restaurées et colonisées par des plantes pionnières de type graminoïde (Cypéracées). Dans le premier cas, le *Carex aquatilis* dominait un fen modérément riche restauré et formait des communautés denses avec beaucoup de litière. Dans le deuxième cas, l'*Eriophorum angustifolium* était dominant avec un faible couvert de litière dans une tourbière à sphaignes restaurée où la densité de la plante graminoïde avait été contrôlée par coupe répetée. Il a été démontré que l’effet des plantes graminoïdes sur les tapis de sphaignes était déterminé par leur litière plutôt que par la structure de la plante elle-même. En raison de l’ombre créée par la litière compacte, la présence d’une communauté dense d’une plante graminoïde accumulant beaucoup de litière comme *Carex aquatilis* ne semble pas être bénéfique pour développer des tapis de sphaignes productifs. La décision de contrôler les plantes graminoïdes pour accroitre le développement des tapis de sphaignes devrait prendre en considération, bien sûr, le couvert de la plante (non requis si le couvert moyen < 30 %), mais aussi sa forme de croissance (moins essentiel lorsque la plante pousse en tige unique), de même que ses potentiels d’accumulation de litière et d’envahissement (p. ex., *Phragmites australis*, *Scirpus cyperinus*). En somme, en plus de répondre spécifiquement à trois cas problématiques de restauration de tourbières perturbées, cette thèse fournit une compréhension améliorée des processus de régénération naturelle des écosystèmes de tourbières et des facteurs qui les influencent. Les résultats ont un lien direct avec le développement d’outils pour la restauration et avec l’approfondissement de nos connaissances sur les réponses des organismes et des communautés végétales aux changements de l’environnement.

Abstract

The ecological restoration of peatland is defined as all the processes permitting the regeneration of a peatland that has been degraded, damaged or destroyed. The landscape settings and types of peatlands that require restoration actions is very diverse. The study of natural regeneration of disturbed ecosystems has frequently been used to develop restoration methods that are adapted to specific types of ecosystems. A comprehensive assessment of regeneration trajectories and the environmental and dispersal constraints, as well as the interspecific interactions is directly related to the development of restoration methods and the improvement of our knowledge on the response of species and communities to environmental changes. This thesis studies the regeneration of vegetation, especially of bryophytes, and the factors influencing their regeneration in three problematic cases of restoring disturbed peatland. Firstly, the regeneration of bryophyte communities was studied against a range of environmental conditions in 28 minerotrophic peatlands in the Northwest Territories and Alberta that had burned one, two or five years ago. A shift of dominance between pioneer (mean cover from 16 to 11 %) and late successional bryophytes (from 3 to 27 %) was observed between the second and fifth year after the fire. Bryophyte distribution and abundance were controlled by the species difference in terms of regeneration capacity related to their life history strategy, habitat niche, and the variable effect of the burned biomass. The integration of the ecological niche concept for late successional bryophytes and the use of species with a high potential of regeneration (such as *Aulacomnium palustre* and *Ptychostomum pseudotriquetrum*) should be considered during the elaboration of restoration plans of minerotrophic peatlands. Secondly, the regeneration of *Sphagnum* mosses was studied in 25 donor sites (peatlands where surface vegetation was harvested to supply reintroduction material) on a chronosequence of 17 years according to environmental conditions and harvesting practices. It takes on average 10 years for *Sphagnum* mosses in donor sites to recover, though minor differences in the species composition and abundance was observed between donor sites and natural peatlands. Pioneer species (e.g., *Eriophorum vaginatum*), competitive species (e.g., *Sphagnum rubellum*) and preferential species of wet microhabitats (e.g., *Chamaedaphne calyculata*) were more abundant in donor sites. Harvesting practices had the greatest effect on the regeneration of donor sites, suggesting that it is possible to speed up *Sphagnum* regeneration by choosing appropriate management practices. Best practices would be avoiding very wet donor sites and harvesting in the midsummer should be avoided when mosses are at their lowest regeneration potential and when the risk of machinery sinking is high. Thirdly, the regeneration and development of the *Sphagnum* carpets were studied in two experiments conducted in two types of restored peatlands colonized by pioneer graminoid plants (Cyperaceae). In the first experiment, *Carex aquatilis* dominated a moderately rich restored fen and formed dense communities with a lot of litter. In the second experiment, *Eriophorum angustifolium* was dominant with a low cover of litter in a restored cutover *Sphagnum*-dominated bog where the graminoid plant cover was controlled by repeated mowing. It was demonstrated that the effect of graminoid plants on the *Sphagnum* carpet was determined by the litter rather than by the structure of the plant itself. Because of the shade created by the dense litter, the presence of a community of a graminoid plant that accumulates a lot of litter such as *Carex aquatilis* is not beneficial for the formation of productive *Sphagnum* carpets. The decision to control graminoid plants to enhance the growth of *Sphagnum* carpets should consider the cover of the plant (not necessary when mean cover < 30 %), but also its life form (less necessary when the plant grows in unique stem), its litter accumulation and potential for invasion (e.g. *Phragmatis australi*s, *Scirpus cyperinus*). In conclusion, this thesis, in addition to specifically address these three problematic cases, provides a more comprehensive assessment of the processes of natural regeneration of peatland ecosystems and of driving factors. The results have a direct link with the development of tools for the restoration of peatlands and with a deeper understanding of the responses of plants and communities to environmental changes.

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Avant-propos

Cette thèse inclut six chapitres, dont l'introduction générale (chapitre 1) et la conclusion (chapitre 6). Les quatre autres chapitres sont écrits sous forme d'article scientifique, dont je suis la première auteure. Pour chacun de ces articles scientifiques, j'ai élaboré les objectifs et hypothèses de recherche, développé la méthode, récolté les données, effectué les analyses statistiques et rédigé les manuscrits. Chacun des articles scientifiques a été réalisé en collaboration avec ma directrice de recherche, Line Rochefort. Elle a également pris part à chacune des étapes de préparation des manuscrits. De plus, Marie-Claire LeBlanc est coauteure du chapitre 2 et a également collaboré à l'élaboration du projet. Le chapitre 2 sera soumis à la revue scientifique *Journal of Vegetation Science* dans une forme légèrement différente de celle présentée dans cette thèse. Sandrine Hogue-Hugron est coauteure des chapitres 3 et 5; elle a également contribué à l'élaboration des dispositifs expérimentaux de ces chapitres. Le chapitre 3 a été publié dans *Restoration Ecology* en juillet 2018. Le chapitre 5 a été publié dans la revue *Mires and Peat* en septembre 2017. Finalement, Rémy Pouliot est coauteur du chapitre 5 et a aidé à la conception du projet. Des modifications mineures ont été apportées au chapitre 5 entre sa version intégrée dans la thèse et sa version publiée.

Chapitre 2 : Guêné-Nanchen, M., M.-C. LeBlanc et L. Rochefort. Post-fire regeneration of minerotrophic peatlands – insights for their restoration?

Chapitre 3 (publié le 2 juillet 2018) : Guêné-Nanchen, M., S. Hugron et L. Rochefort. Harvesting surface vegetation does not impede self-recovery of *Sphagnum* peatlands. Restoration Ecology, doi:10.1111/rec.12834

Chapitre 4 : Guêné-Nanchen, M. et L. Rochefort. Is the presence of graminoid plants beneficial to moss carpet development in a restored fen?

Chapitre 5 (publié le 11 septembre 2017) : Guêné-Nanchen, M., R. Pouliot, S. Hugron, et L. Rochefort. 2017. Effect of repeated mowing to reduce graminoid plant cover on the moss carpet at a *Sphagnum* farm in North America. Mires and Peat 20(06):1–12; doi: 10.19189/MaP.2016.OMB.250. (Prix J. Stan Rowe de l'Association canadienne de botanique (ABC) pour le meilleur article en écologie végétale de l'année)

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- 24e symposium du Groupe de recherche en écologie des tourbières (GRET), Université Laval, Québec, Québec, 15 février 2018 (prix pour la meilleure présentation orale)
- Symposium Tourbières et Milieux humides au Canada Atlantique, Institut de recherche sur les zones côtières, Shippagan, Nouveau-Brunswick, 6 et 7 juin 2017
- 23e symposium du Groupe de recherche en écologie des tourbières (GRET), Université Laval, Québec, Québec, 21 février 2017
- Colloque du Centre d'études nordiques (CEN), Université Laval, Québec, Québec, 16 février 2017
- VI International Meeting on the Biology of *Sphagnum*, Yugra State University, Khanty-Mansiïsk, Russie, 15 au 24 aout 2016
- 22e symposium du Groupe de recherche en écologie des tourbières (GRET), Université McGill, Montréal, Québec, 2 mars 2016
- Colloque du Centre d'études nordiques (CEN), Université du Québec à Trois-Rivières, Trois-Rivières, Québec, 11 février 2016
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Chapitre 1

Introduction générale

Problématique

Les tourbières sont des écosystèmes saturés en eau où le taux de production de matière organique est supérieur à son taux de décomposition (Payette 2001). Les tourbières à sphaignes – ou tourbières ombrotrophes (bogs) et tourbières minérotrophes pauvres (fen pauvres) – sont alimentées seulement par l’eau de pluie et de la fonte des neiges. Le plus souvent, celles-ci se développent par succession végétale sur des stades plus jeunes de tourbières (tourbières minérotrophes riches) dont la source d’alimentation en éléments minéraux a été coupée, par exemple, par la croissance en hauteur du massif de tourbe. Les tourbières minérotrophes riches – ou fens riches – sont influencées par une source d’eau souterraine ou de surface enrichissant le milieu en éléments minéraux et leur permettant de supporter un cortège de plantes plus diversifié que celui des tourbières à sphaignes (Rydin et Jeglum 2013). En milieu boréal, dans ces deux types de tourbières, les communautés végétales dominées par les bryophytes (comme les sphaignes et autres mousses) sont responsables des plus grands taux d’accumulation de matière organique (Vitt 2000).

Les tourbières couvrent seulement 3 % de la surface planétaire et pourtant, elles stockent le tiers du carbone emmagasiné dans les écosystèmes terrestres (Turunen et coll. 2002). Elles sont donc d’une importance majeure dans le cycle mondial du carbone et leur altération, notamment en raison des changements climatiques, est inquiétante (Tarnocai 2006). Les tourbières ont été considérablement perturbées par diverses activités anthropiques. Elles ont été drainées, entre autres, pour l’agriculture et la foresterie, pour en extraire la tourbe pour utilisation comme combustible ou comme substrat horticole (Vasander 2003; Pellerin et Poulin 2013). Globalement, il est estimé que 16 % de la surface totale des tourbières a été détruite par les activités humaines (Joosten et Clarke 2002).

Des méthodes de restauration sont généralement nécessaires pour rétablir les communautés végétales typiques et les fonctions écologiques des tourbières (Rochefort et coll. 2003; Graf et coll. 2008). La restauration écologique des tourbières se définit comme l’ensemble des procédés permettant d’assister à la régénération d’une tourbière qui a été dégradée, endommagée ou détruite (SERI 2004). Au Canada, la recherche sur la restauration des tourbières est relativement jeune et certaines problématiques de restauration demeurent. Notamment, la recherche sur les méthodes de restauration s’est largement centrée sur les tourbières ombrotrophes utilisées par l’industrie de la tourbe horticole (Chimner et coll. 2017). Cependant, la gamme de tourbières perturbées qui nécessitent des actions de restauration est très diversifiée. Dans plusieurs cas, l’utilisation de la méthode de restauration développée pour les tourbières à sphaignes perturbées par l'extraction de la tourbe n'est pas adaptée et est peu efficace pour ces autres écosystèmes de tourbières. Ceci correspondrait à vouloir appliquer une même recette à différents types de tourbières et illustre le mythe du livre de recettes, comme présenté par Hilderbrand et coll. (2005). D'après ces auteurs, les techniques de restauration cherchant à imiter le caractère et les processus de régénération naturels des écosystèmes ont beaucoup de chance d'avoir du succès.

L'étude de la régénération naturelle des écosystèmes perturbés a en effet fréquemment été utilisée pour développer des méthodes de restauration pour plusieurs écosystèmes (Higgs 2003; Hobbs et Suding 2009). Une compréhension plus complète des trajectoires de régénération et des interactions avec l'environnement biotique et abiotique est directement reliée au développement de techniques de restauration et à l'amélioration de nos connaissances sur la réponse des espèces et communautés à des changements environnementaux (Brooker et coll. 2008). Il existe donc un besoin d'approfondir nos connaissances sur les processus de régénération de la végétation, plus spécialement ceux des bryophytes dans les tourbières perturbées, afin d'en favoriser la restauration.

Ce projet de doctorat se penchera sur trois problématiques spécifiques dont chacune abordera la régénération naturelle des bryophytes dans différents types de tourbières perturbées, ainsi que l'influence des conditions abiotiques et biotiques sur leur régénération. Plus précisément, nous nous intéresserons aux contraintes face à la régénération des bryophytes, soit les filtres environnementaux, les contraintes de dispersion des espèces et les interactions interspécifiques. En premier lieu, cette étude examinera la régénération naturelle de tourbières minérotrophes riches perturbées par le feu afin de mieux connaitre les trajectoires de régénération de ces milieux et d'améliorer les méthodes de restauration pour les fens riches perturbés. Ensuite, la régénération végétale des tourbières ombrotrophes ayant été perturbées par le prélèvement de végétation de surface sera détaillée selon diverses méthodes de récolte et de conditions environnementales afin de recommander des pratiques de récolte responsables. Finalement, les effets des plantes graminoïdes pionnières sur l'établissement et la structuration des tapis de bryophytes seront étudiés dans des tourbières où des tapis de sphaignes ont été réintroduits par une méthode de restauration. Ce projet doctoral, en plus de répondre à ces trois problématiques spécifiques sur la restauration et la gestion des tourbières, propose d'améliorer les connaissances fondamentales sur la régénération des tapis de bryophytes dans les tourbières perturbées.

Une approche basée sur les règles d’assemblages

L’utilisation des règles d’assemblage peut s’avérer utile pour orienter la recherche sur la régénération des communautés végétales dans les milieux perturbés. Selon cette approche, la composition d’un écosystème est influencée par une série de filtres qui déterminent les espèces qui réussiront à les franchir et qui coloniseront le milieu (Keddy 1992). De plus, selon différents auteurs, tous les facteurs ayant une influence, qu’ils soient abiotiques ou biotiques, doivent être pris en compte dans la structuration des écosystèmes (Weiher et Keddy 2001). Notamment, pour déterminer les espèces qui réussiront à se régénérer et à s’établir, il faut prendre en considération les contraintes de dispersion des espèces (liées principalement à leur stratégie d’histoire de vie), de même que les interactions entre les espèces. Comme les méthodes de restauration consistent à manipuler les filtres abiotiques et biotiques afin d’arriver à la composition d’espèces ou à l’état de l’écosystème désiré, l’identification de ces filtres est un facteur clé pour développer des méthodes de restauration adaptées. Plus spécifiquement, ceci est primordial lorsque les méthodes de restauration cherchent à imiter les processus de régénération naturels.

La Figure 1.1 présente le schéma conceptuel du projet, selon lequel l’étude de la régénération naturelle des écosystèmes perturbés et de leur trajectoire de régénération peut être utile à leur restauration. En effet, l’étude de l’influence des contraintes à la régénération de la végétation, plus précisément des filtres environnementaux, des contraintes de dispersion et des interactions interspécifiques, est directement reliée au développement ou à l’amélioration des méthodes de restauration. L’amélioration des contraintes à la régénération lors de la restauration vise à accélérer la reprise de communautés végétales, que représente le raccourci de la restauration. Chacun des aspects du schéma conceptuel sera abordé dans l’introduction, soit : les perturbations environnementales étudiées et les contraintes à la régénération de la végétation (filtres environnementaux, contraintes de dispersion, interactions interspécifiques).

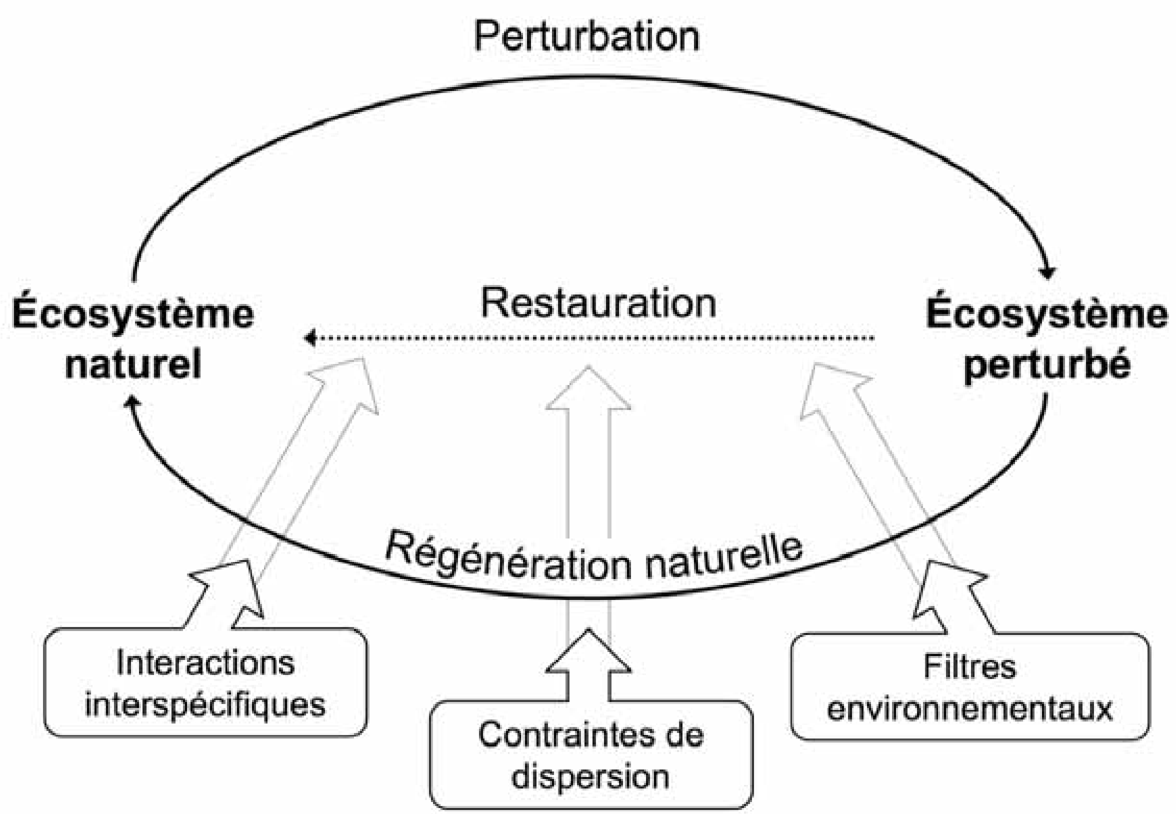

Figure 1.1 Cadre conceptuel pour le développement ou l'adaptation de méthodes de restauration écologique des écosystèmes perturbés. L'ellipse du schéma formée par les lignes pleines représente les processus de régénération naturelle d'un écosystème qui a été perturbé. Les processus de régénération naturelle sont affectés par différents facteurs qui sont représentés par les encadrés avec des larges flèches : les filtres environnementaux, les contraintes de dispersion des espèces et les interactions interspécifiques. Les filtres environnementaux sont d'origines environnementales et sont le reflet direct de la perturbation et des conditions abiotiques auxquelles les espèces se régénérant sont confrontées. Les contraintes de dispersion sont reliées à la capacité des espèces de s'établir et de se propager dans les écosystèmes en régénération. Les interactions interspécifiques réfèrent aux relations entre les espèces se régénérant dans les milieux perturbés, comme la compétition. L'évaluation des processus de régénération naturelle ainsi que des contraintes à la régénération (filtres environnementaux, contraintes de dispersion et interactions interspécifiques) est directement reliée à la restauration des écosystèmes perturbés. Par un transfert des connaissances, représenté ici par les larges flèches grisées, il est possible d'adapter, d'améliorer ou de développer des méthodes de restauration. En effet, la ligne pointillée représente le processus de restauration des écosystèmes perturbés et permettrait donc de court-circuiter les processus naturels, en accélérant la régénération des écosystèmes. Ce cadre conceptuel s'applique aux différents volets de ce projet de doctorat, mais pour lesquels plusieurs aspects changeront entre les volets. Ce cadre conceptuel est inspiré de l'approche des règles d'assemblage (Belyea 2004).

Perturbations environnementales

Les perturbations se définissent comme des évènements distincts dans le temps et l'espace altérant la structure des populations, des communautés et des écosystèmes, et affectant la disponibilité des ressources, du substrat et donc, de l'environnement physique (White et Pickett 1985). Les impacts des perturbations sont très irréguliers, tant sur une échelle spatiale que temporelle, et à tous les niveaux de la communauté. Les perturbations diffèrent grandement en sévérité, causant par le fait même une grande variabilité au niveau de l'héritage écologique (Swanson et Franklin 1992), celui-ci correspondant à toutes les structures vivantes ou non, qu'elles soient affectées ou créées par la perturbation (p. ex., microsites). En raison de cette grande variation de l'héritage écologique, une multitude de trajectoires de régénération existent.

Les perturbations, qu'elles soient d'origine naturelle ou anthropique, modifient la dynamique de la végétation (Johnson et Miyanishi 2010). À une petite échelle spatiale tant que temporelle, ces modifications de la dynamique de la végétation peuvent prendre la forme de fluctuations, soit des changements quantitatifs non directionnels au niveau individuel. Les perturbations peuvent engendrer la disparation ou la mort d'individus ou de population locale à différentes échelles (c.-à-d., *gap dynamics* à petite échelle et *patch dynamics* à large échelle) en raison d'ouverture du paysage (p. ex., trouées) où les changements de la dynamique de la végétation sont davantage qualitatifs que quantitatifs et créent de l'hétérogénéité dans la composition des espèces (van der Maarel 1988). Des processus de succession cyclique se produisent, où une espèce dominante ou un petit nombre d'espèces ont tendance à se remplacer au fil du temps suite à l'ouverture du paysage par une perturbation mineure (Knapp 1974). La succession cyclique se distingue des successions secondaires et primaires qui sont linéaires et directionnels. Des processus de succession secondaire se produisent dans des écosystèmes affectés par une perturbation qui n'a pas totalement éliminé les organismes vivants (p. ex., restes de sol; Horn 1974) alors que des processus de succession primaire ont lieu dans le cas où les perturbations ont complètement dénué les écosystèmes de vie (Walker et del Moral 2003). Dans les deux cas précédents, la succession consiste en un patron de changement dans la composition spécifique d'une communauté, où les espèces pionnières sont remplacées au fil du temps par espèces de succession tardive plus compétitives. D'après Van der Maarel (1996), ces différents types de dynamique de la végétation, c'est-à-dire, les fluctuations, *gap dynamics*, *patch dynamics*, la succession cyclique, secondaire ou primaire, se distinguent par l'intensité et l'étendue spatiale de la perturbation qui engendrent ces phénomènes.

Les perturbations créent donc en premier lieu les conditions initiales à la dynamique et/ou à la succession des espèces. En deuxième lieu, elles induisent les changements internes de la dynamique des espèces, notamment en agissant directement comme filtre, en sélectionnant par exemple, les traits de certaines espèces pouvant s'établir (White et Jentsch 2004). Les études conduites dans le cadre de ce doctorat ne sont pas des études de succession à proprement parler, puisque la période temporelle à l'étude est trop courte. Cependant, des concepts de succession et de dynamique de la végétation doivent être abordés, comme ils s'opèrent à la suite de perturbations, quoique les différents concepts de succession et de dynamique végétale ne soient pas tous mentionnés ici. Les effets spécifiques de chacun des trois types de perturbations étudiées dans cette thèse sur les filtres environnementaux et la dynamique végétale seront détaillés dans la section suivante, soit les effets du feu, de la récolte de végétation et des perturbations suivant la restauration.

Trois cas de perturbations environnementales étudiés

Feux

Le feu est une perturbation importante des écosystèmes boréaux, entre autres dans l'Ouest canadien, où une surface de 1 850 km^2 de tourbières brûle chaque année en moyenne, mais où les superficies brûlées varient selon les années (Turetsky et coll. 2004). Même si les tourbières sont généralement considérées comme résistantes au feu grâce à leurs conditions humides (Kuhry 1994), des études récentes montrent que les feux de tourbières peuvent être intenses et couvrir de grandes superficies (Turetsky et Wieder 2001; Benscoter et coll. 2005). On considère cependant que la végétation des tourbières ombrotrophes est généralement résiliente au feu (Benscoter 2006; Magnan et coll. 2012). La résilience est la capacité d'un écosystème de répondre à une perturbation en retrouvant ses caractéristiques initiales (Holling 1973). En ce qui concerne l'impact des feux sur la succession végétale des tourbières minérotrophes, particulièrement la régénération des communautés de bryophytes, très peu d'études ont été réalisées jusqu'à maintenant selon nos connaissances.

Les évènements de feu amorcent généralement des processus de succession secondaire. Des plantes pionnières s'établissent rapidement après le feu grâce à l'apport de nutriments par la biomasse carbonisée et/ou par l'ouverture du milieu (Clarkson 1997). Les conditions environnementales et les stratégies de reproduction seraient en fait plus importantes que la disponibilité des diaspores pour la régénération végétale après feu (Benscoter 2006). Spécifiquement, les espèces vasculaires pouvant repousser par rhizomes seront favorisées par rapport aux espèces à croissance lente et ne se reproduisant que par graines à faible dispersion (Johnson 2001, Narita et coll. 2015). Les espèces pionnières identifiées en tourbière après feu sont, entre autres, les plantes graminoïdes (p. ex., *Eriophorum vaginatum*; Bret-Harte et coll. 2013) et les bryophytes dont la germination est favorisée par le passage du feu (p. ex., *Ceratodon purpureus* [Narita et coll. 2015] et *Polytrichum strictum* [Benscoter 2006]).

Le feu a un effet sur la structure physique de la tourbe et, ainsi indirectement, sur ses propriétés hydrologiques. Le feu lorsqu'il brûle les couches de tourbe de surface, expose les couches de tourbe profonde qui sont plus âgées et caractérisées par plus faible porosité et donc un rendement en eau plus faible (Thompson 2012). Même si le feu n'entraine pas de changement du volume d'eau stockée dans le sol d'après Thompson (2012), cette eau est plus difficilement accessible particulièrement pour les plantes sans système vasculaire conducteur. Le feu augmente le rayonnement solaire atteignant la surface du sol et accroit la température du sol (Norton 2003). En conséquence, les pertes d'eau par évapotranspiration sont plus importantes sur les surfaces brûlées (Thompson et coll. 2014). Au niveau de la physicochimie, le feu entraine une perte de carbone, d'azote et de phosphore total par la biomasse brûlée (Smith et coll. 2001). Une libération des cations échangeables (p. ex., Ca, Mg, K, Na) peut également être observée en surface les premières années suivant le feu (Neff et coll. 2005; Dikici et Yilmaz 2006). Toutefois, il faut savoir que l'effet du feu sur la physicochimie de la tourbe varie grandement entre les études publiées sur le sujet.

L'étude de la régénération naturelle des fens riches brûlés pourrait servir de modèle pour étudier leurs trajectoires, et pour développer et adapter des techniques de restauration pour les fens riches perturbés. La tourbe post-feu présente des conditions pour la repousse des plantes similaires à celles de la tourbe après extraction de la tourbe par aspirateur à des fins horticoles. Par exemple, elles présentent toutes deux une faible variabilité microtopographique (Price et coll. 1998; Benscoter et coll. 2005), des conditions hostiles à la recolonisation végétale (Thompson et coll. 2014; Chimner et coll. 2017) et, selon la sévérité du feu, les banques de graines pourraient être absentes des deux substrats (Salonen 1987; Norton 2003).

Récolte de végétation

Différentes études ont montré la nécessité de réintroduire des diaspores de sphaignes lors de la restauration des tourbières ombrotrophes afin de rétablir la fonction d'accumulation de carbone

(Rochefort 2000; Waddington et coll. 2010). Comme il n'existe pas de pépinières de sphaignes actuellement, les tourbières ombrotrophes naturelles ainsi que des secteurs intacts des tourbières à sphaignes extraites représentent la source de diaspores la plus appropriée (sites donneurs). La récolte des plantes consiste à déchiqueter les dix premiers centimètres de la couche de végétation, puis à la récolter. Le déchiquetage s'effectue avec différents types de machinerie (herse rotative, hacheuse, niveleuse, bouteur, rotoculteur) et à différentes saisons (Quinty et Rochefort 2003).

La récolte de végétation entraine une perturbation au niveau de la structure végétale, de la structure physique et des conditions hydrologiques de la tourbière. À la suite de la récolte de la végétation, des processus de succession secondaire s'enclenchent puisqu'une bonne partie de la couche vivante et active de la végétation (acrotelme) est supprimée. La récolte de matériel végétal laisse généralement sur place les racines et les rhizomes des plantes vasculaires de même que des diaspores muscinales. Cependant, la profondeur de récolte et la présence ou l'absence perturbations physiques causées par la machinerie auront un effet sur la régénération de la végétation (Campeau et Rochefort 1996). L'enlisement de machinerie mélange les diaspores de sphaignes et la tourbe dans une « soupe tourbeuse » limitant leur régénération (Faubert et Rochefort 2002). La machinerie peut également causer des ornières et, en s'enlisant, exposer la tourbe à nu, la rendant sujette à l'érosion et au soulèvement gélival[1] (Groeneveld et Rochefort 2005). De plus, la récolte de matériel végétal abaisse la surface du sol et la rapproche donc de la nappe phréatique, ce qui rend les zones récoltées plus humides que les zones adjacentes non récoltées. La suppression d'une partie de l'acrotelme par la récolte pourrait modifier les conditions physiques et hydrologiques de la tourbe qui est en contact avec la végétation en régénération (p. ex., porosité, conductivité hydraulique, humidité; Letts et coll. 2000). Toutefois, les modifications au niveau de la structure physique et des conditions hydrologiques de la surface récoltée sont nettement moins importantes que celles occasionnées par l'extraction de la tourbe par aspiration à des fins horticoles (Price 1997).

Ainsi, lorsque la récolte des plantes est effectuée de façon adéquate, celle-ci ne cause pas de dommages permanents aux sites donneurs et ne requiert pas de restauration active (Rochefort et Campeau 2002). En effet, l'ajout de paille et de diaspores de sphaignes n'accélère pas la régénération

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[1] Le soulèvement gélival se produit lorsque l'eau contenue dans la tourbe gèle en formant des aiguilles de glace, soulevant le sol de plusieurs centimètres (jusqu'à 12 centimètres par endroits) et rendant ainsi le substrat instable (Groupe de recherche en écologie des tourbières, communications personnelles)

des sites donneurs (Rochefort et coll. 1997). Cependant, d'après des observations de Line Rochefort (professeure-chercheure et directrice du Groupe de recherche en écologie des tourbières), la reprise végétale varie entre les sites donneurs, en fonction entre autres, de la machinerie utilisée et de la saison de récolte. De plus, un intérêt grandissant de l'industrie de la tourbe à utiliser les sites donneurs pour plusieurs récoltes subséquentes existe (L. Rochefort, communications personnelles). Donc, les pratiques de récolte et les facteurs environnementaux permettant d'accélérer la reprise des sites donneurs doivent être identifiés.

Perturbations dans les tourbières restaurées

Même si la restauration des tourbières vise le rétablissement de conditions environnementales favorables au retour de la végétation, ces environnements peuvent demeurer hostiles les premières années suivant les actions de restauration. Entre autres, le niveau de la nappe phréatique reste fluctuant même après le remouillage par le blocage des canaux de drainage, et ce, pendant plusieurs décennies (Price et coll. 2003). De plus, des zones des tourbières restaurées peuvent rester dénuées de végétation suivant les actions de restauration pour diverses raisons (González et Rochefort 2014). La tourbe nue est soumise au soulèvement gélival et est plus susceptible à l'érosion (Campbell et coll. 2002; Groeneveld et Rochefort 2005). Également, les plantes réintroduites le sont sur une tourbe plus vieille (qui se trouvait en profondeur avant la récolte de tourbe); cette tourbe est moins poreuse, avec une conductivité hydraulique plus faible et une rétention en eau élevée, ce qui entraine des problèmes de connectivité hydraulique avec les diaspores de mousses réintroduites (McCarter et Price 2015). Les espèces de bryophytes réintroduites font donc face à certaines conditions adverses à leur établissement et leur développement. D'autre part, lors de la restauration, diverses plantes vasculaires sont réintroduites soit par graines, ou fragments de plantes, ou sont recrutées naturellement. Ainsi, le développement des tapis mousses peut être affecté par des interactions interspécifiques, de façon positive comme négative (voir Interactions interspécifiques).

La réintroduction d'un tapis de sphaignes par une méthode de restauration peut se faire dans le simple but de restaurer la tourbière et ses fonctionnalités, mais peut aussi se faire afin de produire des fibres de sphaignes (culture de sphaignes). En effet, la culture de sphaignes se définit comme la production durable de biomasse de sphaignes sur une base cyclique et renouvelable. Lorsque la restauration vise à rétablir la fonction primaire des tourbières, soit d'emmagasiner du carbone par l'accumulation de la tourbe, le rétablissement des bryophytes est primordial. Plus les tapis de mousses seront productifs, plus de matière organique sera stockée (Vitt 2000; Bérubé 2017). Cette prémisse s'applique également dans le contexte de la culture de sphaignes où la maximisation de la production de biomasse est visée. Ainsi, l'identification des conditions permettant le développement de tapis muscinaux productifs se doit d'être étudiée dans un contexte de réintroduction muscinale par une méthode de restauration, et ce, peu importe le but de leur réintroduction.

Filtres environnementaux

Les filtres environnementaux sont critiques lors de la régénération des écosystèmes perturbés. Ceux-ci déterminent quelles espèces s'y établissent ou non, selon leurs exigences ou leur tolérance en ce qui concerne les facteurs du milieu. Pour le cas des tourbières, les filtres environnementaux sont classifiés dans cette étude en trois catégories, soit le climat, le substrat et le milieu adjacent.

L'influence du **climat** s'évalue à deux échelles, régionale et locale. Les gradients de température et de précipitations à l'échelle régionale auront un effet sur la croissance des espèces et sur leur tolérance aux stress climatiques. À titre d'exemple, les conditions climatiques initiales suivant une perturbation sont plus déterminantes quant à la régénération des sphaignes dans les tourbières ombrotrophes que les conditions climatiques subséquentes (Chirino et coll. 2006). Quoique les filtres climatiques régionaux ne puissent pas être manipulés lors de la restauration, leur importance ne doit pas être négligée pour la régénération de l'écosystème (González et Rochefort 2014). À une échelle locale, les variations du microclimat en termes de température et d'humidité de l'air sont également cruciales, particulièrement pour leurs effets sur la tolérance à la dessiccation des bryophytes (Proctor et coll. 2007). Le microclimat n'est pas seulement influencé par le climat à l'échelle régionale, mais aussi par les microvariations au niveau des communautés végétales et des facteurs abiotiques. Ces microvariations peuvent être manipulées lors de la restauration.

Le **substrat** agit comme filtre environnemental selon sa structure physique, sa disponibilité en eau, son contenu nutritionnel et sa toxicité. Dans le cas des tourbières perturbées, l'influence de la structure physique de la tourbe est principalement liée à sa stabilité et à son contenu en eau. Par exemple, la faible régénération des sphaignes sur la tourbe nue est majoritairement attribuable à leur incapacité d'extraire l'eau de la tourbe décomposée (caractérisée par une faible conductivité hydraulique; Price 1996), au soulèvement gélival (Groeneveld et Rochefort 2005) et à l'érosion par le vent et l'eau (Faubert et Rochefort 2002). Les bryophytes sont des espèces sans système vasculaire conducteur et leur contenu en eau dépend directement de celui du substrat (Proctor 2000). L'influence du contenu en éléments nutritifs du substrat est reliée aux exigences nutritionnelles spécifiques de chacune des espèces. Les espèces de bryophytes des tourbières à sphaignes sont généralement considérées comme peu exigeantes en éléments nutritifs; de plus, un pH élevé associé à une forte concentration en calcium serait toxique pour les sphaignes (Clymo 1973). À l'inverse, les bryophytes des fens riches seraient davantage exigeantes en ce qui concerne les éléments nutritifs (Vitt et coll. 1995) et plus tolérantes à des concentrations élevées de certains éléments qui seraient toxiques pour des espèces de tourbières à sphaignes (Pouliot et coll. 2013).

Finalement, selon sa nature et sa distance par rapport au milieu perturbé, le **milieu adjacent** à l'écosystème perturbé intervient comme filtre environnemental en influençant la dispersion des espèces. Notamment, la présence ou l'absence de banques de diaspores[2] dans les milieux adjacents, ainsi que la distance de ces banques par rapport aux milieux perturbés influencent la recolonisation végétale dans les tourbières (Campbell et coll. 2003). Le milieu adjacent peut aussi entrainer une pression supplémentaire lorsqu'il est lui-même perturbé. Les sites de tourbières industrielles pour l'extraction de la tourbe constituent de bons exemples de mosaïques de milieux, où on trouve : des tourbières en cours d'extraction, restaurées, non restaurées, naturelles, de même que des forêts… Notamment, la présence de tourbières extraites à proximité des tourbières restaurées menerait plus fréquemment à une faible régénération des bryophytes dans les sites restaurés (González et Rochefort 2014). Il a été proposé que cette faible régénération soit liée à la déposition aérienne de tourbe sur les diaspores muscinales (Faubert et Rochefort 2002) ou à une réserve de propagules très limitée dans ces milieux adjacents (Poulin et coll. 1999).

Contraintes de dispersion

La régénération des bryophytes dans les tourbières perturbées dépend des conditions abiotiques, mais également des caractéristiques de régénération des différentes espèces. La recolonisation des tourbières perturbées peut se réaliser à l'aide de diaspores de source externe, en l'absence ou en présence de diaspores de source interne (p. ex., banque des diaspores). Qu'importe sa source, toute diaspore doit se disséminer, germer dans le cas de graines ou de spores, s'établir et croitre lors de sa régénération. Les trois premiers stades de la régénération, soit la dissémination, la germination et

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[2] Toute partie d'une plante – graine, fruit, fragments, rhizomes, etc. – qui peut donner naissance à un nouvel individu

l'établissement, sont les plus critiques pour la recolonisation d'une communauté végétale dans un milieu perturbé (Grubb 1977).

L'efficacité à laquelle une espèce se dissémine détermine son potentiel de recrutement et est donc cruciale pour déterminer la composition future d'une communauté végétale (Houle 1995; Schupp et Fuentes 1995). Chez les bryophytes, la capacité de dissémination d'une espèce dépend de la taille de ses spores ou de ses diaspores asexuées (p. ex., propagules, gemmules, bulbilles). Des diaspores de petite taille auront une grande capacité de dispersion, mais une plus faible chance de s'établir et une plus faible longévité dans la banque de diaspores, représentant le compromis entre la taille des diaspores et leur survie. Par conséquent, les espèces produisant des petites diaspores en produiront davantage. Une fois disséminée, une diaspore doit être en mesure de germer s'il s'agit d'une graine ou d'une spore ou de se régénérer s'il s'agit d'un fragment de plante, et ce, dès que les conditions environnementales deviennent appropriées. Il est probable que dans les tourbières perturbées, les conditions propices à l'établissement des bryophytes ne soient pas toutes réunies en même temps ou ne persistent pas assez longtemps pour permettre leur établissement (Campbell et coll. 2003). Puis, lorsqu'une plante se rend à maturité dans un milieu perturbé, elle doit se propager de manière végétative ou sexuée et résister à des conditions de stress extrêmes. Selon During (1979), les stratégies de résistances aux stress constituent un compromis entre l'évitement du stress sous forme de spores et la tolérance du stress sous la forme de l'individu établi. Il y aurait aussi un compromis de l'effort reproductif des espèces, soit une balance entre l'espérance de vie d'un individu selon sa reproduction asexuée ou son investissement dans la reproduction sexuée (During 1992).

Selon Noble et Slatyer (1980), la séquence de succession végétale suivant une perturbation peut être prédite en fonction de certains attributs des espèces : son mode de dissémination et de persistance dans un site en régénération, sa capacité à s'établir et croître à maturité dans une communauté végétale en développement et le temps pris par l'espèce pour atteindre certaines étapes de stade de vie. Ces « attributs » constituent des traits d'histoire de vie. Leur combinaison désigne différentes stratégies d'histoire de vie qui ont été sélectionnées pour être adaptées à l'environnement des espèces et qui représentent le patron de survie et de reproduction des espèces.

Le potentiel de recolonisation des espèces végétales dans les milieux perturbés dépend de leur capacité de dispersion, de germination et d'établissement, donc de leurs traits d'histoire de vie. Selon MacArthur et Wilson (1967), il existe deux stratégies généralistes décrivant le patron de reproduction et de survie des espèces, soient les espèces pionnières et les espèces de succession tardive (Tableau 1.1).

Tableau 1.1 Caractéristiques de stratégies d'histoire de vie des espèces végétales pionnières et de succession tardive.

	Espèce pionnière	Espèce de succession tardive
Cycle de vie	Court	Long
Compétitivité	Faible	Élevée
Croissance	Rapide	Lente
Effort reproductif	Élevé	Faible
Amplitude de la niche écologique	Grande	Petite
Habitats de préférence	Tous (espèce opportuniste)	Milieux stables

Les espèces végétales pionnières sont celles qui investissent beaucoup dans la reproduction, qui croissent vite et qui sont en mesure d'exploiter une grande variété d'habitats. Elles sont celles qui amorcent la succession végétale dans les milieux perturbés. Elles survivent un temps grâce à la grande efficacité de leur mode de dissémination. Puis, avec l'amélioration des conditions environnementales, comme elles sont peu compétitives, elles sont remplacées par des espèces qui le sont davantage. Finalement, lorsque l'environnement se stabilise ou atteint son climax, ce sont les espèces de succession tardive qui dominent (Connell et Slatyer 1977). Celles-ci se développent lentement, investissent peu dans la reproduction, mais sont fortement compétitives.

Une espèce végétale peut ne pas correspondre uniquement à l'un ou l'autre de ces types stratégies, mais représenter plutôt un intermédiaire (Stearns 1992). De la même façon, les espèces correspondant à différentes stratégies d'histoire de vie ne se succèdent pas une par une, mais la succession représente plutôt un spectre continu d'espèces qui interagissent entre elles.

Interactions interspécifiques

Dans les premiers stades de colonisation d'une tourbière, la compétition agit principalement entre les plantes pour leur conquête de l'espace limitant où les conditions environnementales sont favorables à leur recolonisation (Salonen et Setälä 1992; Rydin et Jeglum 2013). Dans les tourbières naturelles et perturbées, les plantes vasculaires sont en compétition avec les bryophytes quant à la disponibilité en eau, en nutriments et pour l'accès à la lumière et à l'espace (Rydin et Jeglum 2013). Puis, avec l'ajout de nouvelles communautés végétales, d'autres interactions se mettent en place (p. ex. : tolérance, inhibition, facilitation; Walker et del Moral 2003). Il est connu que les interactions de facilitation positives prédominent dans les milieux ayant des conditions stressantes pour les organismes et que les interactions de compétition négatives prédominent lors de la conquête d'un espace limitant et sous des conditions optimales (Callaway 1995; Callaway et Walker 1997).

Parmi les interactions interspécifiques, la facilitation par des plantes compagnes, qui sont des plantes qui aident la croissance d'autres plantes durant au moins une partie de leur cycle de vie (Hacker et Gaines 1997), est particulièrement intéressante dans le contexte de la restauration. Les plantes compagnes améliorent les conditions abiotiques et la structure de l'environnement. À titre d'exemple, la mousse *Polytrichum strictum* agit comme plante compagne lors de la restauration des tourbières ombrotrophes, car elle réduit le soulèvement gélival, améliore les conditions du microclimat et favorise l'établissement des sphaignes (Groeneveld et Rochefort 2005). Par ailleurs, une relation de facilitation dans les tourbières a été observée de la part des plantes arbustives pour la formation de buttes de sphaignes (Pouliot et coll. 2011). De plus, certaines plantes vasculaires de type graminoïde (Cypéracées; *Eriophorum*, *Carex*, *Scirpus*, etc.) permettraient de modifier les conditions du microhabitat, en réduisant les pertes d'eau par évaporation et la photoinhibition (c.-à-d., inhibition de la photosynthèse par un excès de lumière) chez les sphaignes (Harley et coll. 1989; Bergamini et coll. 2001). Il a aussi été suggéré que les plantes graminoïdes puissent favoriser l'établissement et le développement des tapis de sphaignes après la restauration des tourbières en leur servant d'échafaudage (Pouliot et coll. 2011; Malmer et coll. 1994). Les plantes compagnes sont donc des outils intéressants qui peuvent s'avérer essentiels lors la régénération des écosystèmes dégradés.

Questions de recherche

Cette thèse vise à répondre à la question : Comment se régénèrent les bryophytes dans les tourbières perturbées et quels sont les effets des différents facteurs qui influencent leur régénération ? Cette question sera abordée en utilisant les concepts suivants des règles d'assemblages : filtres environnementaux, contraintes de dispersion et interactions spécifiques. Les concepts seront étudiés pour trois cas problématiques liés à la restauration des tourbières, qui ont peu ou pas été abordés dans le passé, correspondant aux trois objectifs de la thèse.

Le premier objectif se concentre sur l'étude de la régénération des tapis de bryophytes dans les tourbières minérotrophes brûlées (Figure 1.2). On cherche à répondre aux questions spécifiques suivantes : Quelle est la trajectoire écologique de la régénération des bryophytes des fens riches brûlés, en termes d'abondance, de composition, de stratégie reproductive et de niches écologiques des espèces végétales ? Quelles sont les plantes pionnières et les potentielles plantes compagnes ? Quels sont les effets du passage du feu et de des différentes conditions environnementales sur la régénération des bryophytes ? En parallèle, les concepts étudiés permettront d'identifier des outils éventuels à la restauration de tourbières minérotrophes dégradées. Le chapitre 2 se penchera sur cet objectif.

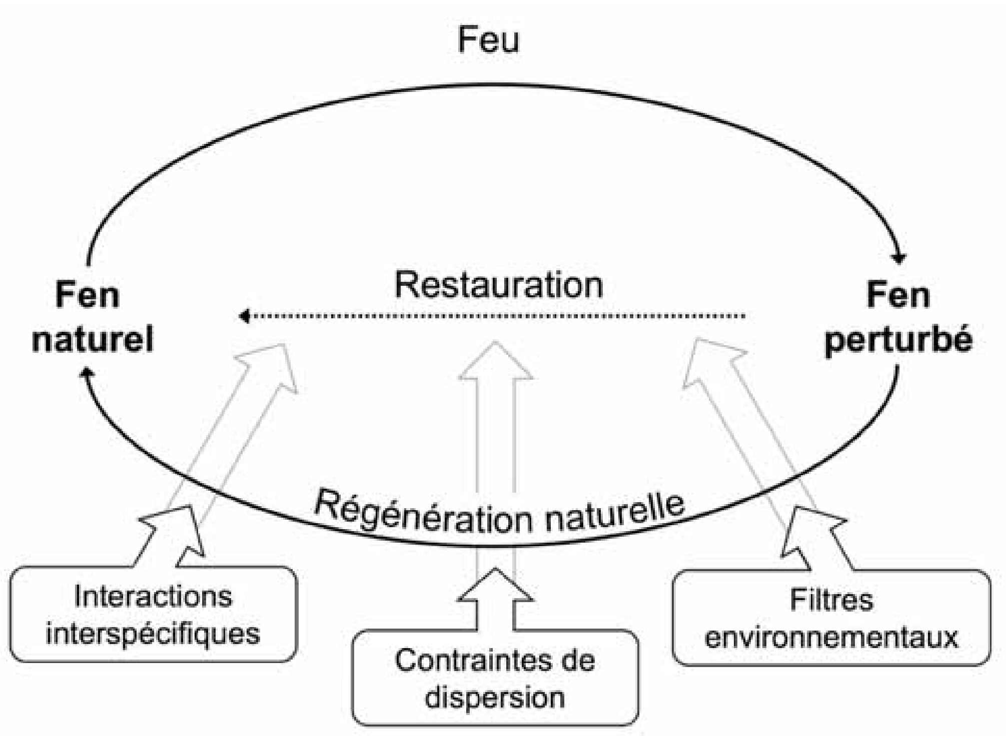

Figure 1.2 Cadre conceptuel du chapitre 2 sur la régénération des bryophytes dans les tourbières minérotrophes riches (fens) brûlées. L'étude des facteurs influençant la régénération naturelle des tapis de bryophytes, soit différents filtres environnementaux, les contraintes de dispersion des espèces et les interactions interspécifiques, est utile au développement et/ou à l'adaptation des méthodes de restauration écologiques des tourbières minérotrophes. La restauration des tourbières minérotrophes à l'aide de méthodes adaptées et adéquates devrait permettre d'accélérer leur régénération (ligne pointillée). Une description complète du cadre conceptuel est disponible à la Figure 1.1.

Le deuxième objectif étudie la régénération des tapis de sphaignes dans les tourbières dont la végétation de surface a été récoltée (sites donneurs) pour la restauration des tourbières ombrotrophes (Figure 1.3). Nous cherchons à répondre aux interrogations spécifiques suivantes : Est-ce que la végétation se régénère dans les sites donneurs, en termes d'abondance et de composition, en portant une attention particulière aux tapis de sphaignes, et ce, en combien de temps ? Est-ce que la régénération varie selon les pratiques de récolte et les conditions environnementales ? Quelles sont les pratiques de récolte les plus appropriées, favorisant une reprise rapide des tapis de sphaignes ? Les connaissances acquises seront intégrées afin de recommander des pratiques de récolte responsables des sites donneurs afin d'optimiser leur reprise. Le chapitre 3 se concentra sur cet objectif.

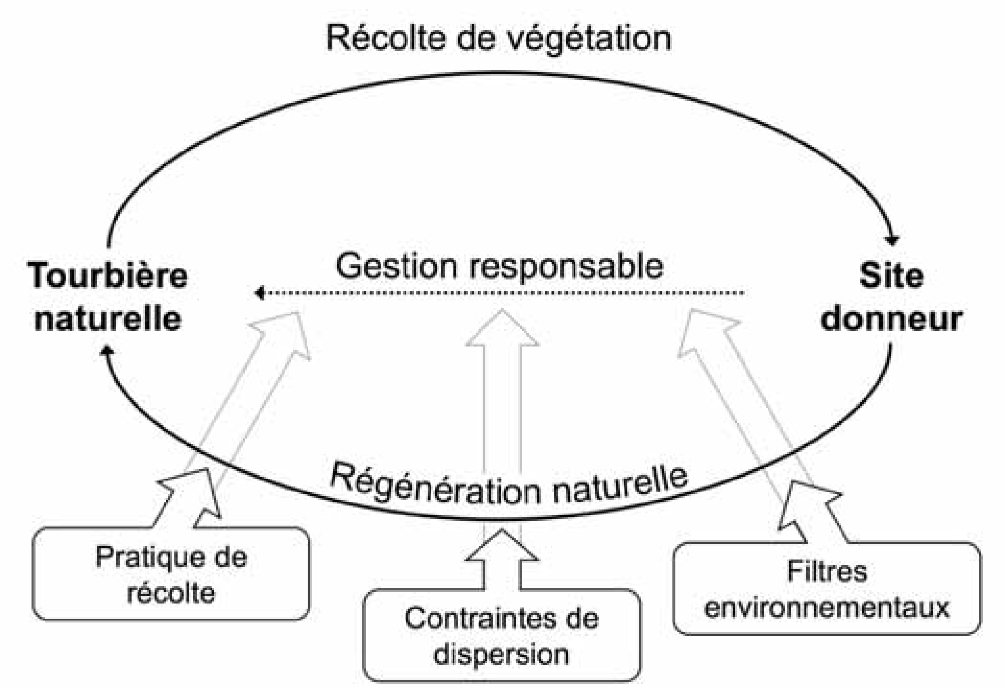

Figure 1.3 Cadre conceptuel du chapitre 3 sur la régénération des sphaignes dans les tourbières perturbées par la récolte de végétation (sites donneurs). L'étude des facteurs qui influencent la régénération naturelle des tapis de sphaignes dans les sites donneurs, soit différents filtres environnementaux, les contraintes de dispersion des espèces et les différentes pratiques de récolte, est utile pour l'amélioration des méthodes de gestion des sites donneurs de matériel végétal pour réintroduction. Des pratiques responsables devraient permettent une régénération plus rapide des sites donneurs (ligne pointillée). Dans ce chapitre, le mot restauration est remplacé par gestion, parce qu'aucune méthode de restauration ne vise à être appliquée sur les sites donneurs. La gestion vise plutôt à l'optimisation des pratiques de récolte et à la minimisation de la perturbation. Une description complète du cadre conceptuel est disponible à la Figure 1.1.

Le troisième objectif examine l'influence des plantes graminoïdes sur les tapis de sphaignes dans des tourbières où ces tapis de sphaignes ont été réintroduits par restauration (Figure 1.4). Cet objectif se divise en deux sous-expériences, une première conduite dans une tourbière minérotrophe restaurée et une deuxième, dans une tourbière à sphaignes restaurée utilisée pour la culture de sphaigne. Les questions spécifiques abordées sont les suivantes : Est-ce que la présence des plantes graminoïdes pionnières favorise le développement des tapis de sphaignes en fournissant des conditions microclimatiques et physiques idéales ? Ou est-ce qu'à l'inverse la densité de ces plantes doit être contrôlée afin de maximiser l'accumulation de biomasse de sphaignes ? Les chapitres 4 et 5 se pencheront sur cet objectif.

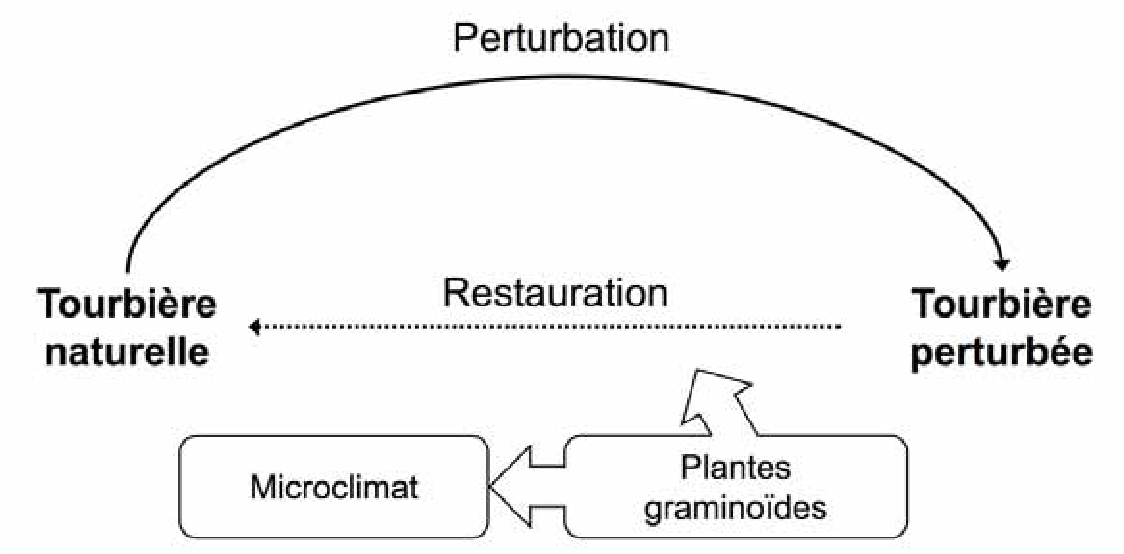

Figure 1.4. Cadre conceptuel des chapitres 4 et 5 sur l'influence des plantes graminoïdes sur le développement des tapis de sphaignes dans des tourbières restaurées. Des connaissances approfondies sur les relations interspécifiques entre les plantes graminoïdes et les sphaignes devraient permettre d'optimiser la productivité des sphaignes et ainsi d'améliorer le succès de la restauration (ligne pointillée). Une description complète du cadre conceptuel est disponible à la Figure 1.1.

Finalement, les contributions et les limites de chacun des chapitres de la thèse seront considérées dans une conclusion générale, correspondant au chapitre 6. Notamment, les potentiels outils pour améliorer les méthodes de gestion et de restauration des tourbières seront identifiés.

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Chapitre 2

Post-fire regeneration of minerotrophic peatlands – insights for their restoration?

Mélina Guêné-Nanchen, Marie-Claire LeBlanc et Line Rochefort

Résumé

Les techniques de réintroduction de la végétation pour la restauration des tourbières minérotrophes riches (fens) ne donnent pas des résultats très concluants pour rétablir des tapis de bryophytes (mousses). L’étude de la régénération naturelle des écosystèmes perturbés offre une opportunité unique afin d’en apprendre davantage sur leur trajectoire de régénération et pour développer et améliorer les méthodes de restauration. Dans cette étude, la régénération des bryophytes a été étudiée dans 28 fens riches qui ont brûlé il y a un, deux ou cinq ans dans l’Ouest canadien. La sévérité du feu variait entre les sites, dans certains seulement la végétation avait brûlé alors que dans d’autres la tourbe avait également brûlé. Les communautés de bryophytes (en termes d’abondance des espèces et de diversité) ont été comparées à celle de 18 fens non brûlés de référence. Le couvert et la diversité des bryophytes dans les fens brûlés se sont partiellement rétablis après cinq ans, mais l’abondance des espèces et leur composition variaient en comparaison aux fens non brûlés de référence. Un changement de dominance entre les bryophytes pionnières (couvert moyen ± $CI_{95\,\%}$ passant de 16 ± 3 % à 11 ± 2 %) et les bryophytes de succession tardive (de 3 ± 1 % à 27 ± 4 %) a été observé entre la deuxième et la cinquième année suivant le feu. La répartition et l’abondance des bryophytes dans les fens brûlés sont principalement contrôlées par leur différence de stratégies d’histoire de vie (pionnière ou de succession tardive) et par les conditions chimiques de la tourbe. Les espèces ayant un fort potentiel de régénération (comme *Aulacomnium palustre* et *Ptychostomum pseudotriquetrum*) devraient faire partie des espèces ciblées à réintroduire. Finalement, nous croyons que cette étude démontre qu’il n’existe pas une approche unique pour la restauration des fens riches, mais que la réintroduction de mousses de fen devrait intégrer la notion de niche écologique.

Abstract

Techniques of ecological restoration of rich minerotrophic peatlands (fens) are not yet optimized for the reestablishment of bryophyte (moss) carpets. The study of natural regeneration of disturbed ecosystems is a unique opportunity to characterize their regeneration trajectories and to develop and improve existing restoration techniques. In this study, we evaluated the regeneration of bryophytes in 28 rich fens that had burned 1, 2 or 5 years ago in western Canada. The fire severity varied between sites, in some only aboveground vegetation burned while in others the peat also burned. Bryophyte communities (in terms of species abundance and diversity) were compared to 18 unburned reference rich fens. Bryophyte cover and diversity of burned fens partly recovered after 5 years but species abundance and composition still differed in comparison to unburned reference fens. A shift in dominance between pioneer (16 ± 3% (mean cover ± $CI_{95\%}$) to 11 ± 2%) and late successional bryophytes (3 ± 1% to 27 ± 4%) was observed between the second and fifth year post-fire. The distribution and abundance of bryophytes in burned fens were mainly controlled by their differences in life history strategy (pioneer or late successional) as well as by the peat chemical conditions. Species with high regeneration potential (such as *Aulacomnium palustre* and *Ptychostomum pseudotriquetrum*) should be part of the targeted species to reintroduce in restored sites. We conclude that there is no single approach for the ecological restoration of rich fens, but that the reintroduction of fen mosses should integrate the notion of habitat niche.

Introduction

In North America, peat extraction activities to produce horticultural substrates mostly occur on ombrotrophic peatlands (i.e., *Sphagnum*-dominated bogs). Because the Canadian horticultural peat industry has been concerned by the responsible management of peatlands, research on ecological restoration of disturbed peatlands has largely focused on *Sphagnum*-dominated peatlands in North America (Chimner et al. 2017). The restoration method, the Moss Layer Transfer Technique (MLTT; see Graf et al. 2012 for a detailed description of the method) is successful at reintroducing *Sphagnum* mosses on ombrotrophic peat if all steps are carried out (Quinty & Rochefort 2003; González & Rochefort 2014). However, *Sphagnum*-bog peat is sometimes extracted down to the underlying older layers of peat (Rochefort et al. 2016). The typical acid-loving *Sphagnum* mosses considered suitable for commercial peat extraction cannot re-establish when the exposed peat is characteristic of rich minerotrophic peatlands (hereinafter referred as fens; pH > 6.0 [Wheeler & Proctor 2000]) because it is not their optimal habitat (Gorham & Janssens 1992). A restoration approach adapted specifically to fen ecosystems is essential where appropriate vegetation should be reintroduced (fen vegetation) (Graf & Rochefort 2008).

The reestablishment of fen mosses is essential in fen restoration considering that they accumulate more carbon than other types of fen vegetation (Vitt 2000; Bérubé 2017; Emsens et al. 2018). This corroborates with the North American goal of ecological restoration which is to bring back the peat-accumulating function of the ecosystem (Graf & Rochefort 2008). Although bryophytes are a main component of vegetation in fens and responsible for the optimization of the carbon-accumulating function, only a few studies focused on their establishment during restoration. Furthermore, these few studies usually obtained low establishment rate of the fen mosses (Gauthier 2014; Rochefort et al. 2016), proving that restoration methods need to be improved.

Restoration methods are often inspired by how ecosystems naturally regenerate (Mitsch & Wilson 1996; Higgs 2003; Hobbs et al. 2006). For example, a paleoecological study provided a reconstruction of the history of plant communities in a *Sphagnum*-dominated bog after several events such as natural fires (Lavoie et al. 2001). After a fire, *Polytrichum strictum* established rapidly and its decline was synchronized with the increase of *Sphagnum* mosses (Lavoie et al. 2001) suggesting that the same could happen on restored bogs if conditions to the expansion of *P. strictum* were recreated. Indeed, the addition of phosphorus fertilizer during *Sphagnum*-dominated bog restoration mimics the fertilizing effect of the burned biomass and facilitates *P. strictum* spore germination (Pouliot et al. 2015). This moss is now considered as a nurse plant because its rhizoids stabilize the soil and therefore, help *Sphagnum* mosses to establish during restoration and provide a more humid safe site for diaspore survival and development (Groeneveld et al. 2007).

Studying the natural regeneration process of fens will be beneficial to advance research in the field of ecological restoration, by identifying pioneer and nurse plants (i.e., plants that help other plants to establish and/or grow), and the trajectory of plant succession (Brooker et al. 2008). However, to the best of our knowledge, no research has been conducted so far about the successional trajectory of burned fens. Opportunities to study fen natural regeneration after a major disturbance are scarce. Natural recolonization of fen mosses in non-restored peat-extracted fens is almost nonexistent because of the harsh conditions present in these sites (e.g., erosion, water table level and substrate temperature fluctuations; Graf et al. 2008). However, it has been shown that the improvement of some regeneration constraints, such as environmental conditions and interspecific interactions, favored fen moss establishment. For example, in fen restoration projects, most fen mosses regenerated better when the water table was stable and close to the soil surface (-5 cm) (Mälson & Rydin 2007), and under a protective cover (Graf & Rochefort 2010; Borkenhagen & Cooper 2016). Fertilization with phosphorus improved the establishment of fen moss diaspores in a fen restoration study (Rochefort et al. 2016). But research on fen restoration is still at an early stage and more research is required, especially on bryophyte regeneration trajectory and interspecific relationships.

Burned fens could serve as a study model since post-fire bare peat conditions are comparable to extracted peat surfaces (by aspiration). For example, both present low microtopographic variability (Price et al. 1998; Benscoter et al. 2005), harsh environmental conditions (Thompson et al. 2014; Chimner et al. 2017) and depending on fire severity, diaspore banks can be absent from both organic substrates (Salonen 1987; Norton & De Lange 2003). Fires are known to have complex effects on both vegetation and abiotic conditions of ecosystems, which depend on the fire severity, its timing during the year, and on the landscape within which it occurs (Menges & Hawkes 1998). For example, the fire severity in peatlands that could be defined as the depth of peat combustion (depth of burn [DOB]; Mack et al. 2011) is influenced by the water retention capacity of the surface vegetation and peat (Benscoter et al. 2011). The peat water availability could be, after the fire, reduced by altered peat properties (Lukenbach et al. 2015). Fires by burning the surface vegetation and exposing the bare substrate increase the surface radiation and daytime soil temperature (Norton & De Lange 2003). While this may impede the recolonization of certain plant species, this may favor the expansion of disturbance-adapted species (Bret-Harte et al. 2013) by the opening of the canopy and/or the enrichment of the peat substrate (Thomas et al. 1994). As commonly proposed by many studies, patterns of vegetation recovery post-fire are influenced by species life-history and their morphological attributes (Kirkman & Sharitz 1994; Menges & Hawkes 1998; Norton & De Lange 2003). This study is the first to present the trajectory of bryophyte regeneration in burned rich fens. It is based on unique data from 28 burned fens in the Northwest Territories and Alberta. We aimed to (1) describe bryophyte (mosses and liverworts) regeneration after fire in terms of composition and abundance, (2) identify pioneer species and potential nurse plants among bryophytes and (3) evaluate the influence of fire and environmental conditions on the regeneration of bryophytes. We predict that pioneer bryophytes will colonize burned fens rapidly because of their high potential of sexual and asexual reproduction. Hydrologic conditions of the site and fire intensity are predicted to be the major driver influencing bryophyte regeneration.

Methods

Study area

The study sites were selected in the southern Northwest Territories (NWT) (60–62°N, 116°W) and northern Alberta (AB) (55–56°N, 111–115°W) in Canada (Figure 2.1) and included 28 minerotrophic peatlands (fens) that burned in either 2011 (NWT = 3 sites, AB = 7 sites), 2014 (NWT = 14 sites) or 2015 (NWT = 4 sites) and 18 unburned regionally associated reference sites (NWT = 10 sites, AB = 8 sites). These regions were chosen because of their accessibility, high density of fens, shortness of fire cycle (35–120 years; Bernier et al. 2016) and occurrence of recent fires. The sites are located in two climatic regions, the Mackenzie District in the Northwest Territories and the Northwestern Forest in Alberta (Environment and Climate Change Canada 2016). The total cumulative precipitation in the southern Northwest Territories is 336 mm, of which 65% falls as rain. The minimum temperature is approximately -26 ºC in January and the maximum is 21 ºC in July (Environment Canada 2018) (station Hay River; 60° 50’ 23” N, 115° 46’ 58” W). In northern Alberta, the cumulative precipitation totals 474 mm, of which 72% falls as rain. The minimum monthly temperature is about -19 ºC in January and the maximum is 22 ºC in July (Environment Canada 2018) (station Ballater; 55º 34’ 41” N, 117º 12’ 34” W).

Burned peatlands and unburned sites (natural reference) were selected by photo interpretation using Google Earth satellite images. Site selection was field-validated during the summers of 2015 and 2016. Fire perimeters were obtained from the Canadian National Fire Database (Canadian Forest Service 2018). During field validation, burned peatlands were examined to confirm the passage of fire (charcoal of shrubs or trees), the presence of remnant structures of fen mosses (Amblystegiaceae and Calliergonaceae families) and surface peat conditions within ranges of moderate or extreme-rich fens (ESRD 2015). The peat pH of the burned peatlands varied from 6.2 to 7.6 (0.3) (minimum and maximum value [standard deviation]) and the corrected electrical conductivity between 225 to 1,988 μS/cm (369). Burned fens were selected to represent a variety of fire severity, vegetation regeneration and wetness. The fires had burned only aboveground vegetation in some sites while some peat thickness had burned in others.

To serve as a reference, 18 unburned sites from the two regions were included in this study for a total of 46 study sites. Selection criteria for the natural reference sites were: to have not burned in the last 35 years (confirmed with fire perimeters and field-validated) and to be moderate or extreme-rich fens dominated by mosses (e.g., *Tomentypnum nitens*, *Campylium stellatum*, *Scorpidium cossonii* and *Aulacomnium palustre*), graminoid plants (e.g., *Carex aquatilis*) and shrubs (e.g., *Dasiphora fruticosa*, *Myrica gale* and *Salix maccalliana*). The pH of the reference fens ranged from 6.5 to 7.7 (0.3) and the corrected electrical conductivity varied from 301 to 1,303 μS/cm (263).

During the summer of 2016, the 46 peatlands were surveyed to document their composition in terms of their bryophyte communities. The number of years since the fire was used to name the sites: 5 years post-fire (2011), 2 years post-fire (2014), 1 year post-fire (2015) and unburned reference sites.

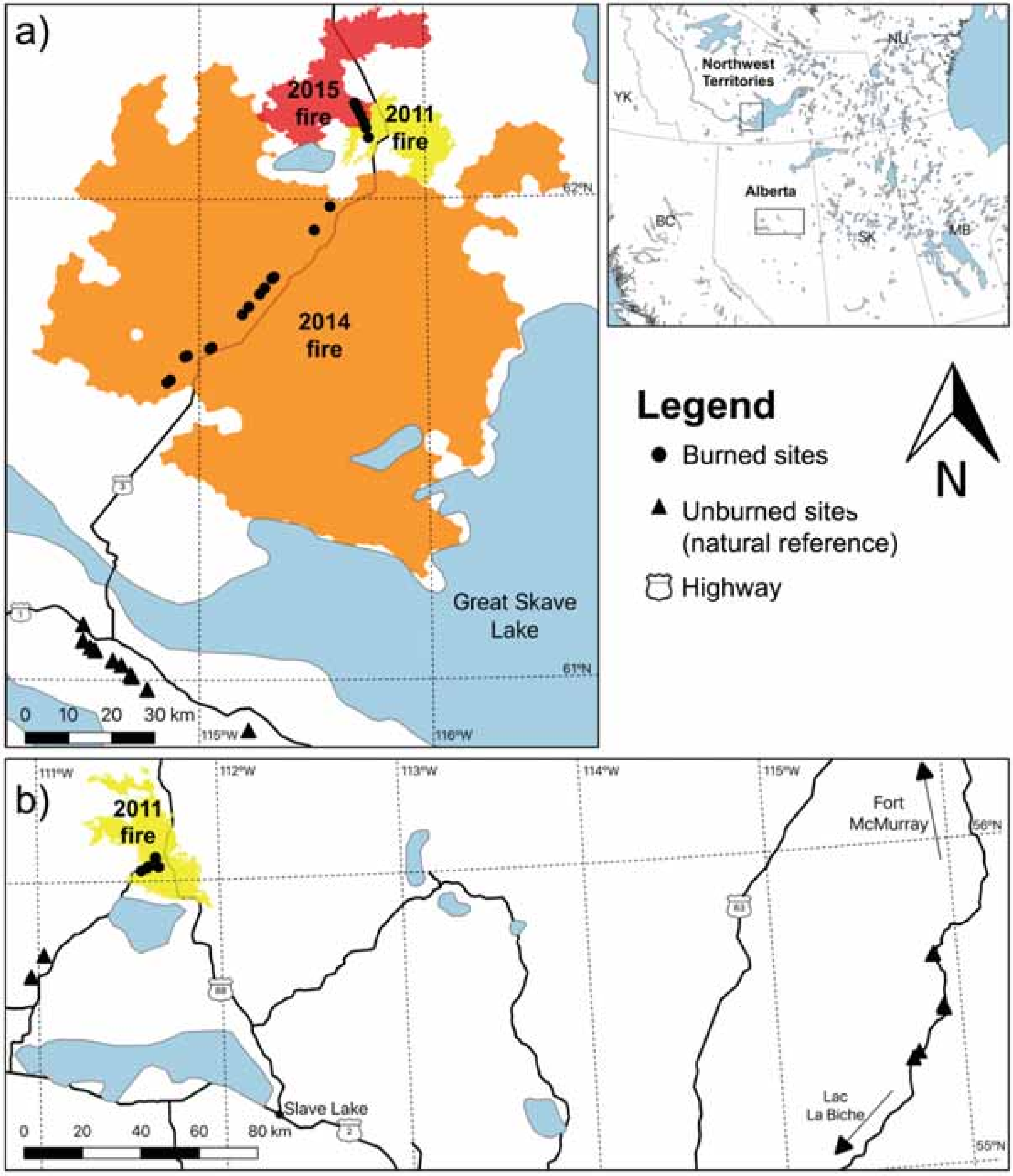

Figure 2.1 Location of the study sites (burned sites and unburned sites used as natural reference ecosystems) in a) the Northwest Territories and b) Alberta.

Inventory approach

Bryophyte regeneration

Circular plots (6 or 12 per site, depending on the size of the site) were surveyed on each site, for a total of 516 plots (Appendix 2.1). Half of the plots within a site were positioned on hummocks and the other half on hollows. Surveys were carried out first in a circular plot (2-m diameter) by evaluating the cover of the following categories: all bryophytes, bare peat and charcoal, and aboveground water. In a smaller circular subplot (70-cm diameter) centered within the larger one, the cover of each bryophyte species was estimated individually. All covers were measured by estimating the surface occupied by the vertical projection of each category or species on the ground. Bryophytes were differentiated in two categories (pioneer and late successional bryophytes) according to their life history strategies (life span, reproductive effort and ecology; During 1992) (Table 2.1 for the full list of bryophytes). Pioneer bryophytes included mosses and liverworts investing high effort into sexual reproduction and mostly found in disturbed environments. Late successional bryophytes corresponded to species investing low effort into sexual reproduction and typically found in natural fens. Afterward, the individual cover of each species was added to calculate the total cover of the pioneer and late successional bryophytes. The covers obtained therefore accounted for the superposition of the species. Nomenclature follows Flora of North America (1993+) for bryophytes.

Table 2.1 Classification of the main bryophytes species based on their life strategy (adapted from During 1992).

Classification	Life-history strategies	Life span	Reproduction effort	Ecology	Main species
Late successional bryophytes	Late successional	> 10 years	Very low sexual reproduction effort	Habitats with stable conditions: peatlands, forest floor	
	a. Competitive			a. Characterized by their high growth rate	*Aulacomnium palustre* *Campylium stellatum* *Scorpidium cossonii* *Scorpidium scorpioides* *Hylocomium splendens*
	b. Stress tolerant			b. Characterized by high stress tolerance and morphological plasticity	*Drepanocladus aduncus* *Tomentypnum nitens* *Climacium dendroides*
Pioneer bryophytes	Colonist	< 5 years	High vegetative and sexual reproduction effort	Ephemeral and disturbed substrates	*Marchantia polymorpha* *Ptychostomum creberrinum* *Ptychostomum pallens* *Ptychostomum pseudotriquetrum* *Ceratodon purpureus*

Environmental conditions

Environmental conditions that could play a role in bryophyte regeneration were classified into four groups: meteorological conditions, fire variability, hydrological conditions, peat physicochemical conditions. Some environmental variables were measured at the plot level, others at the site level (Appendix 2.2).

Statistical analysis

Bryophyte regeneration

Descriptive analyzes were conducted to provide an overview of bryophyte regeneration in relation to the number of years since the fire and in the unburned reference sites. Considering all species, mean cover as well as diversity (species richness) were calculated for each type of site (burned and unburned reference) and for the late successional and pioneer bryophytes. Mean total cover and mean cover of the most abundant species of late successional and pioneer bryophytes were also presented according to the plot type (hummock and hollow).

Environmental conditions

Values of cover of all bryophyte species per plot were used to construct a response matrix (dimensions: 216 plots x 11 bryophyte species). Only 1 and 2 years post-fire sites from the Northwest Territories were included because we wanted to evaluate only the immediate post-fire succession. Also, 5 years post-fire sites from Alberta and Northwest Territories were excluded from this analysis to avoid collinearity between explanatory variables and time. Species with a mean cover lower than 0.5% were not included in the analysis. The bryophyte matrix was transformed using Hellinger transformation to avoid the double-zero problem (Legendre & Gallagher 2001).

To evaluate the role of each group of environmental conditions (fire variability, hydrological, peat physicochemistry and meteorological variables) on bryophyte cover, a redundancy analysis (RDA) was carried out on the bryophyte matrix. Because collinearity between environmental variables was expected, a forward selection was implemented before running the RDA. Environmental variables highly correlated with other environmental variables (Spearman coefficient > 0.7) were also removed. The significance of the RDA was tested with a permutation test using 9999 randomized runs (Legendre & Legendre 2012). In this analysis, the experimental unit considered is the plot and it might be considered as pseudoreplication due to repeated measurements within a burned site. To avoid underestimating the influence of environmental variables measured at the site level, a partial RDA approach using the site as a random factor was not used. By including a random site effect, variance linked to these environmental variables would have been lost.

All analyzes were conducted with R (version 3.3.1; R Core Team 2017) software, more precisely decostand, ordistep and rda from vegan (Oksanen et al. 2016).

Results

Bryophyte regeneration

Late successional bryophytes recovered slowly during the first two years following fire. A shift from pioneer bryophyte towards late successional bryophyte dominance was observed between the second and fifth year after fire, when the late successional bryophyte cover increased by nine times and the pioneer bryophyte cover slightly decreased (Figure 2.2a). Mean late successional bryophyte cover (27 ± 4% [mean ± $CI_{95\%}$]) 5 years after the fire was still lower than the unburned reference (49 ± 4% [mean ± $CI_{95\%}$]) (Figure 2.2a). Therefore, it takes more than 5 years to reach late successional bryophyte covers similar to what is found in natural fens. Mean pioneer bryophyte cover was still higher 5 years after the fire in comparison to unburned sites.

In the 1 year post-fire sites, late successional bryophyte regeneration was very low but slightly higher in hollows (Table 2.2). *Campylium stellatum*, *Scorpidium cossonii* and *Scorpidium scorpioides* were the only late successional moss present (Table 2.2). In the 5 years post-fire sites, *Aulacomnium palustre* regenerated better on hummocks and also showed the highest cover of all late successional bryophytes. Regardless of the species or the type of site, pioneer bryophytes regenerated better in hollows the first two years following fire. Mean water table level at the top of hummocks was -26 ± 2 cm and -13 ± 1 cm in hollows (mean ± $CI_{95\%}$). Water table levels were similar between all site types (based on the analysis of the confidence intervals [95%]).

Marchantia polymorpha, a liverwort and, *Ptychostomum pseudotriquetrum* and *Ceratodon purpureus*, two mosses, were the dominant bryophyte species in the 1 year post-fire sites (Table 2.2). *M. polymorpha* and *C. purpureus* cover decreased in 2 and 5 years post-fire sites and they were nearly absent in natural sites. In contrast, *P. pseudotriquetrum* cover increased with time and, was especially abundant in 2 years post-fire sites (11 ± 3% [mean ± $CI_{95\%}$]). This species was also present in natural sites but in lower abundance (3 ± 1%). The 5 years post-fire sites and unburned reference sites exhibited similar late successional bryophyte diversity (Figure 2.2b). The number of pioneer species remained higher in older burned fens, compared to unburned reference fens, even if a decrease was observed between the second and fifth year after the fire (Figure 2.2b). Bryophyte cover and species composition in the unburned reference fens were similar to the communities of natural rich fens of western Canada (Slack et al. 1980; Vitt and Chee 1990; Gignac et al. 1991) and eastern Canada (Bérubé 2017).

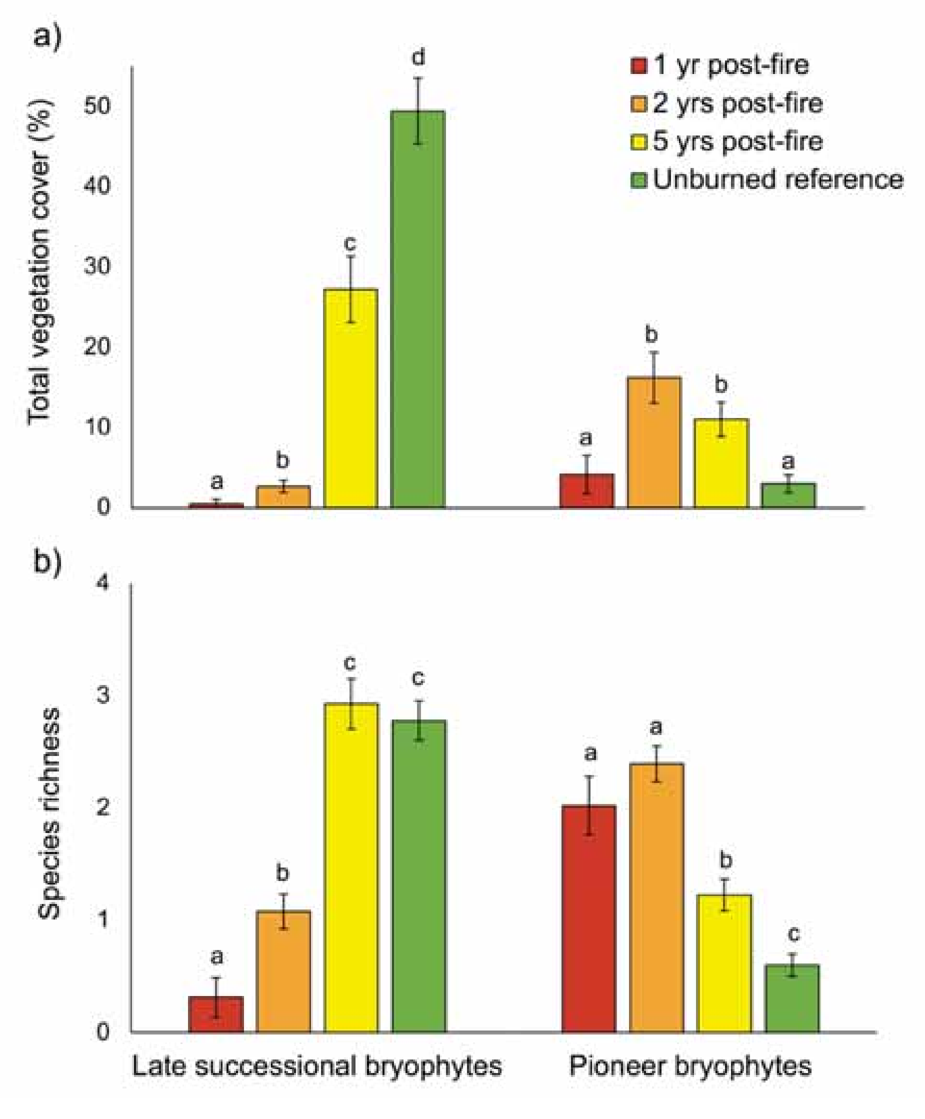

Figure 2.2 a) Total cover (%) and b) diversity (species richness) of the two bryophyte life strategies (late successional and pioneer) (mean ± $CI_{95\%}$) for each site type (1 year post-fire [n = 48 plots], 2 years post-fire [n = 168 plots], 5 years post-fire [n = 36 plots] and unburned reference [n = 120 plots]). Different letters indicate a significant difference between the site types within the two bryophyte life strategies (based on the analysis of the confidence intervals [95%]).

Table 2.2 Cover (%) of the most abundant bryophyte species (mean ± standard error [SE]) by strata and relative position of the water table (hummock and hollow) for each site type (1 year post-fire, 2 years post-fire, 5 years post-fire and unburned reference). A plus sign indicates a cover < 1 %.

	1 yr post-fire		**2 yrs post-fire**		**5 yrs post-fire**		**Unburned reference**	
	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow
Total late successional bryophytes	+	1 ± 1	2 ± 1	3 ± 1	30 ± 3	25 ± 3	56 ± 3	43 ± 3
Aulacomnium palustre	Absent	Absent	+	+	17 ± 3	4 ± 1	11 ± 2	1 ± 0.4
Campylium stellatum	+	+	+	1 ± 0.2	3 ± 1	4 ± 1	10 ± 2	15 ± 2
Drepanocladus aduncus	Absent	Absent	Absent	+	3 ± 1	8 ± 2	+	5 ± 2
Scorpidium cossonii	Absent	+	+	+	+	4 ± 2	5 ± 1	16 ± 2
Scorpidium scorpioides	Absent	+	+	2 ± 1	+	2 ± 1	+	+
Tomentypnum nitens	Absent	Absent	+	+	5 ± 2	+	28 ± 3	1 ± 1
Total pioneer bryophytes	2 ± 0.4	6 ± 2	10 ± 1	21 ± 3	11 ± 1	11 ± 2	2 ± 1	4 ± 1
Marchantia polymorpha	1 ± 0.3	2 ± 0.5	+	1 ± 0.4	+	+	+	+
Ptychostomum creberrinum	+	+	1 ± 0.4	3 ± 1	+	+	+	+
Ptychostomum pallens	Absent	+	+	2 ± 1	+	1 ± 0.4	+	+
Ptychostomum pseudotriquetrum	+	3 ± 1	7 ± 1	15 ± 2	8 ± 1	9 ± 2	2 ± 1	3 ± 1
Ceratodon purpureus	+	2 ± 0.9	+	+	2 ± 1	+	+	+
Plots (n)	24	24	78	90	60	60	90	90

Environmental conditions

The RDA model incorporating the preselected fire variability, hydrological, peat physicochemistry and meteorological variables explained 19% of the variability of the Hellinger transformed bryophyte matrix of the 1 and 2 years post-fire sites of the Northwest Territories (adjusted $r^2 = 0.186$, $F_{[12,\ 213]} = 5.09$, $p < 0.001$; Figure 2.3). The first two gradients of the RDA explained respectively 8 and 7% of the bryophyte cover variability (RDA1 and RDA2; Figure 2.3). All four environmental groups were significant in explaining bryophyte cover of the burned sites (1 and 2 years post-fire) and were (ranked in increasing order of importance): peat physicochemistry (13%), meteorological conditions (2%), fire variability (1%), hydrological conditions (1%) (Group contribution; Figure 2.3). Higher cover of bare substrate (Bare subs; Figure 2.3) and higher concentrations of most chemical elements and components (Ca, Mn, Na, P and NO_3^-; Figure 2.3) were observed for most of the recently burned sites (1 year post-fire) compared to 2 years post-fire sites. The first summer following fire for the 1 year post-fire sites was hotter compared for the one that followed fire for the 2 years post-fire sites (Tsum; Figure 2.3). Comparing the chemical characteristics of the burned and unburned sites, only Mg and NO_3^- concentrations were higher the first two years following fire, as the phosphorus, but its concentration only remained higher the first year after the fire (Table 2.3). The fire did not induce an increase or decrease in pH or EC in burned sites, compared to unburned sites (Table 2.3). Pioneer bryophytes (*M. polymorpha*, *C. purpureus, P. pseudotriquetrum, P. pallens* and *P. creberrimum*) were associated with higher values of the selected peat chemistry variables (except for K and NH_4^+) (Figure 2.3). Late successional bryophytes (*S. scorpioides, S. cossonii* and *C. stellatum*) were associated with higher peat moisture and negatively affected by higher concentrations of Ca, Mn, Na, P and NO_3^- (Figure 2.3).

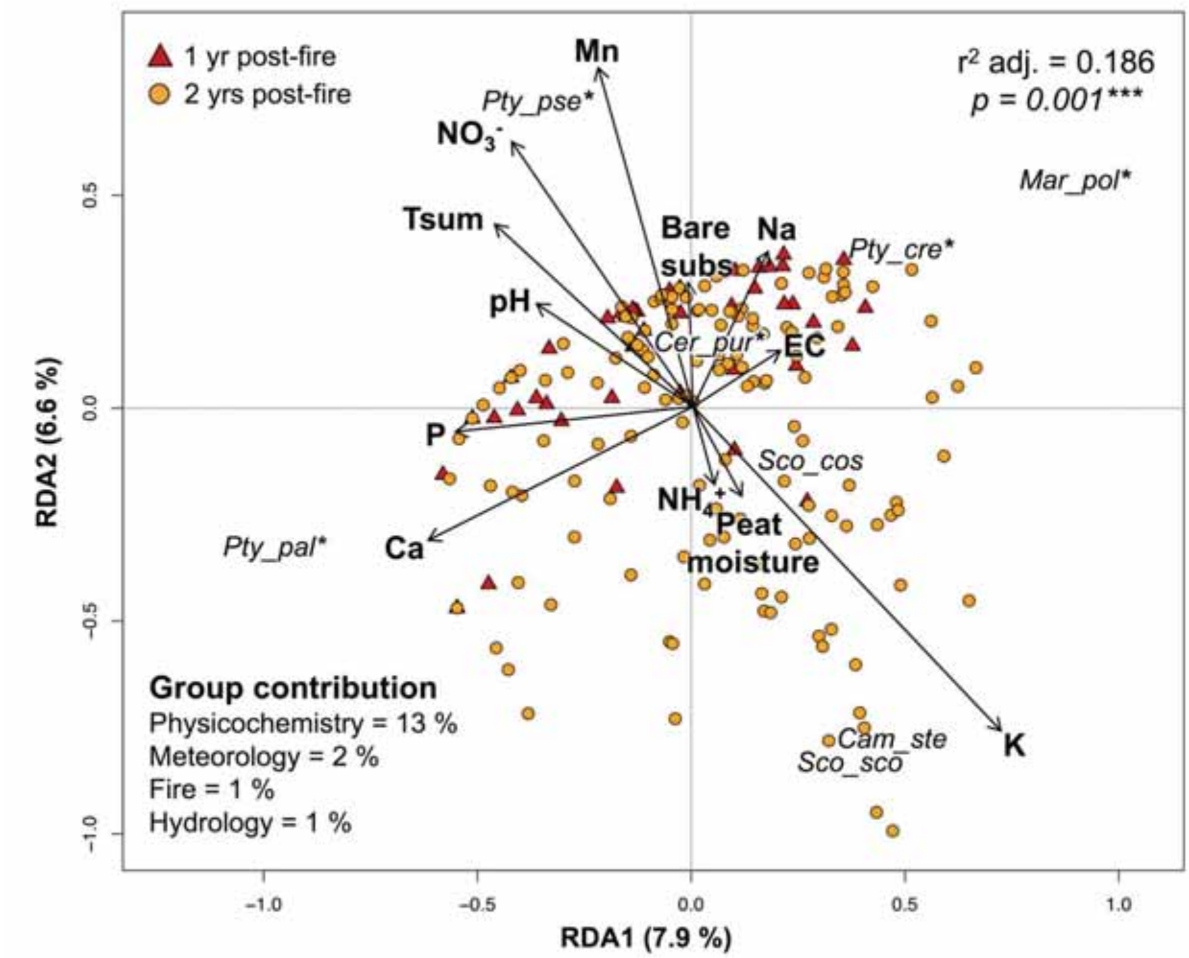

Figure 2.3 Redundancy analysis (RDA) triplot (scaling 1) with forward selected environmental variables constraining late successional and pioneer bryophyte cover (species name followed by an *) of the 1 and 2 years post-fire sites from the Northwest Territories burned sites (n = 216). The contribution of each group of variables was the adjusted R^2 of respective RDAs implemented for each group of variables and included independent and shared explained variance. The site scores are represented as weighted averages of the explanatory data.

Table 2.3 Mean peat pH, electrical conductivity (EC; µS/cm) and chemical elements and component concentrations (mg/g) (± confidence interval [95%]) of each site type (1 year post-fire [n = 4 sites], 2 years post-fire [n = 14 sites], 5 years post-fire [n = 10 sites] and unburned reference [n = 18 sites]) and from an ash sample collected on the field.

	1 yr post-fire	2 yrs post-fire	5 yrs post-fire	Unburned reference	Ash
pH	7.1 ± 0.2	7.1 ± 0.2	7.0 ± 0.3	7.2 ± 0.1	7.2
EC	740 ± 166	864 ± 182	760 ± 288	652 ± 122	1907
Ca	20.3 ± 4.4	20.4 ± 2.5	17.1 ± 3.9	18.2 ± 2.5	13.0
Mg	2.39 ± 0.25	3.31 ± 0.55	1.73 ± 0.41	1.65 ± 0.19	1.86
Fe	0.002 ± 0.002	0.002 ± 0.001	0.008 ± 0.007	0.005 ± 0.001	0
Mn	0.03 ± 0.01	0.02 ± 0.01	0.12 ± 0.08	0.25 ± 0.29	0.03
K	0.50 ± 0.08	0.91 ± 0.62	0.68 ± 0.18	0.93 ± 0.28	0.60
Na	0.64 ± 0.63	0.75 ± 0.43	0.93 ± 0.56	0.38 ± 0.09	0.56
P	0.27 ± 0.07	0.22 ± 0.12	0.25 ± 0.10	0.10 ± 0.03	0.69
NH_4^+	0.05 ± 0.01	0.05 ± 0.01	0.10 ± 0.03	0.09 ± 0.02	0.01
NO_3^-	0.09 ± 0.02	0.02 ± 0.007	0.01 ± 0.01	0.01 ± 0.001	0.003

Discussion

Bryophyte regeneration

Regeneration of bryophytes in burned minerotrophic peatlands is related to their life history strategies. Indeed, a pattern of secondary succession was found where pioneer bryophytes are replaced by late successional bryophytes between the second and the fifth years following fire. Pioneer species are colonists that are well adapted to colonize harsh environments, because of their high dispersal capacity and high tolerance (or need) of disturbed conditions, while late successional species have a low reproductive output but a longer life span and are more prevalent in stable habitats (During 1992). Nonetheless, the studied chronosequence was not sufficient to allow the return of typical composition of natural bryophyte communities, suggesting that secondary succession will, as expected, occur over a longer period as seen in other studies (González et al. 2013; Paquette et al. 2016). The recovery of the cover of late successional bryophytes in burned fens was similar to their establishment after introduction in a field mesocosm experiment (Borkenhagen & Cooper 2016). The authors observed a mean cover of 20% after three growing seasons (our study 27% after 5 years) where the water table level was at -20 cm, similar to our study. The fire decreased the diversity of late successional bryophytes only during the first two years following fire, meaning that all species were nearly able to regenerate from diaspores either dispersed (fragments, propagules or spores) or from the site that survived the fire (diaspore bank) in 5 years, as shown by Graf and Rochefort (2010). *Aulacomnium palustre* was one of the most promizing species in terms of regeneration performance. Gauthier et al. (2017) also found that this species regenerated to similar cover to its natural environment. Likewise, *A. palustre* showed the highest regeneration on bare peat among other bryophytes regardless of the nutrient levels in the study done by Li and Vitt (1994). Indeed, *A. palustre* has a wide ecological niche in the peatlands of western Canada (Gignac et al. 1991).

Regeneration of bryophytes also seemed to be related to their position relative to the water table. Late successional bryophytes regenerated better in their respective habitat niche. For example, hummock species *A. palustre* and *Tomentypnum nitens* regenerated better on hummocks after the fire. Likewise, Bokenhagen and Cooper (2016) found that introduced diaspores from *A. palustre* and *T. nitens* grew better when the hydrological conditions were more typical of hummocks (water table level = -30 cm). We hypothesized that late successional bryophytes regenerated mostly from remnant fragments left after the fire in their habitat niche. The regeneration ability of burned fragments from a remnant mosses carpet that was collected in a burned site was verified in the greenhouse (M. Guêné-Nanchen, unpublished data). New shoots were observed on the burned fragments after a few weeks. This supports the hypothesis that even if bryophyte carpets had burned in the surface, they were able to regenerate from physiological tissues protected in the more humid parts on the carpet.

Pioneer bryophytes regenerated better in hollows in burned fens, while they were equally abundant both in hummocks and hollows in natural peatlands. This suggests that their regeneration niche preference is either for wetter or richer habitats which could facilitate spore germination after disturbance. Even though it was not measured, it was assumed that in some sites, hollows presented a thinner acrotelm layer compared to the hummocks, which was even thinner after the peat fire and that could have exposed some of the underlying mineral soil. *Marchantia polymorpha*'s preferred niche was previously described as wetter habitats (Looman 1964). This species also quickly invades areas where the mineral soil has been exposed by fire (Zyryanova et al. 2010). *Marchantia polymorpha* and *Ceratodon purpureus* have been largely documented as pioneer bryophytes after fire in both peatlands and forests (Schimmel & Granstrom 1996; Ruokolainen & Salo 2009; Narita et al. 2015). *Ptychostomum pseudotriquetrum*, even though it has not been documented as a pioneer species in peatlands to the best of our knowledge, seems to proliferate in disturbed ecosystems and especially in wetter microhabitats (Borkenhagen & Cooper 2016; Rochefort et al. 2016; Cooper et al. 2017). The fire did increase the pioneer bryophyte diversity concordant with results found by other post-fire wetland studies (Ruokolainen & Salo 2009; Narita et al. 2015).

Environmental conditions

The effect of the environment on the recovery of bryophytes, both for late successional and pioneer bryophytes in burned fens is mainly controlled by the peat physicochemistry and indirectly by fire. The fire induced the liberation of some elements and components contributing to the soil nutrient composition as found by other post-fire studies (Smith et al. 2001; Dikici & Yilmaz 2006; Maynard et al. 2014). However, this “fertilizer effect” was ephemeral and limited to the first two years following fire.

Chemical elements and components seemed to have a differential effect depending on the bryophyte species. Most late successional bryophyte species, especially *Campylium stellatum*, *Scorpidium scorpioides* and *Scorpidium cossonii* seemed to be negatively affected by higher concentrations of chemical elements and components of the burned areas (except for K and NH_4^+). Even if some late successional bryophytes are able to establish on mineral sediments (Borkenhagen & Cooper 2016;

Gauthier et al. 2017) and saline deposits (up to 0.3 mg/g; Pouliot et al. 2013), concentrations of most elements and components in this study were higher compared to concentrations in other studies (Pouliot et al. 2013; Gauthier et al. 2017). Ca, Mg, Na, P and NO_3^- were reported in the literature to have a positive effect on the growth of some bryophyte species (Helsper et al. 1983; Li & Vitt 1997; Vagts & Kinder 1999). However, we think that the excess of some nutrients (especially of exchangeable cations) the first two years following fire caused the desiccation of some moss species by exosmosis (loss of water though the cell membranes due to nutrient deposits). Excess of nutrients has been observed to form a white crust on the tips of mosses when growing in rich and periodically dry habitats (Glime 2017). White crust on bryophyte tips were indeed often observed in 1 and 2 years post-fire sites (Appendix 2.4). Reduced and suppressed growth of some moss species has also been observed on burnt surfaces in Thomas et al. (1994).

All pioneer bryophytes (*Ptychostomum pallens, P. pseudotriquetrum, P. creberrimum, C. purpureus* and *M. polymorpha*) seemed to benefit from the chemical enrichment (except for K and NH_4^+) following fire. Pioneer species are the ones demonstrating a higher tolerance (or need) for higher pH and richer substrate (Norton & De Lange 2003). For instance, spore germination of *C. purpureus* is favored by high pH and high chemical concentrations (P-K fertilization; Huotari et al. 2007). The use of ash fertilizers has also improved the establishment of *C. purpureus* in a disturbed peatland (Huotari et al. 2007).

Warm temperatures during the first summer following fire probably impacted the recovery of late successional bryophytes. Fen mosses regenerate better with shading and when water table is close to the peat surface (Mälson & Rydin 2007; Graf & Rochefort 2010). Indeed, in Mälson and Rydin (2010), the regeneration of *S. cossonii*, *S. scorpioides* and *C. stellatum* was related to higher peat moisture. Fire in relatively open peatlands usually results in bare peat surfaces and the dark substrate is subjected to high temperatures and drought (Thomas et al. 1994). This harsh environment probably limited the desiccation tolerance of the late successional bryophytes. According to Thomas et al. (1994), evaporation can be 20 to 40 mm higher on burned peat surfaces compared to intact ones. Fire can also modify peat water availability by modifying peat physical properties (Lukenbach et al. 2016) that could impede late successional bryophyte capacity to extract water from the substrate. The depth of burn (DOB), that was used as an indicator for fire severity, was not selected as a significant explanatory variable because of its misevaluation. Indeed, it was difficult to evaluate the difference between the recently-formed and burned peat especially in older burned sites.

Insights for fen restoration

This study is the first of its kind and provides useful hints for the ecological restoration of fens. A more defined picture of what to expect in terms of regeneration trajectory of disturbed fens was described. The distribution and abundance of bryophytes in burned fens were controlled mainly by their differences in reproduction strategy (late successional or pioneer) as well as by the variable effect of the peat enrichment by the fire.

Species with high potential for regeneration in disturbed habitats should be part of the targeted species pool to reintroduce during fen restoration, particularly *Aulacomnium palustre* and *Ptychostomum pseudotriquetrum*. The first one because of its overall regeneration performance and wide niche habitat and the second because of its potential to be a nurse plant. But is the presence of pioneer species essential for late successional bryophyte establishment? Pioneer species have been described as the ones paving the way for future species establishment by modifying both biotic and abiotic environments (Connell & Slayter 1977). In this study, the effect of the most abundant pioneer bryophytes in burned fens (*Marchantia polymorpha, Ceratodon purpureus* and *Ptychostomum pseudotriquetrum*) on their environment was not verified and to the best of our knowledge, has never been documented. We can hypothesize that these species are good nurse plant candidates whose potential for “nursing” should be tested, especially for *P. pseudotriquetrum*. Unlike *M. polymorpha* and *C. purpureus*, *P. pseudotriquetrum* is usually present in natural fens but at a lower abundance than in burned sites. Therefore, this species would be present in the donor material used for fen restoration which is usually collected in natural fens. Also, contrary to the other two dominant pioneer species, *P. pseudotriquetrum* persisted five years after the fire and consequently, could act on a longer term as a nurse plant similarly to *Polytrichum strictum* in *Sphagnum*-dominated bogs. Also *P. pseudotriquetrum* possess some morphological attributes that could imply microclimate amelioration (such as soil stabilization with its rhizoid or water retention with its tomentum) and therefore, facilitation.

In conclusion, because of the difference of regeneration between species, we believe that no single ecological restoration method can be applied in rich fens, as methods should be adapted to the species’ ecological niche preference and to the conditions of the residual peat. Finally, since the plant communities observed in the study sites are relatively similar to the ones found in eastern Canada, our results could be relevant for restoration in northern regions but climatic differences should be considered when adapting to other contexts.

Implications for Practice

- *Aulacomnium palustre* and *Ptychostomum pseudotriquetrum* should be targeted species to reintroduce during fen restoration: the first because of its regeneration performance and wide niche preferences and the second because of its potential as a nurse plant – an approach that should be investigated experimentally.

- Fertilization could improve the establishment of pioneer bryophytes during fen restoration, as learned from the effect of the enrichment by burned biomass. Its effect on late successional bryophytes should be further examined.

- Techniques of reintroduction of late successional bryophytes in fens should consider species habitat niche. This suggests that there is no universal method for the restoration of moss carpets in rich fens, but that restoration methods need to be adapted to species and site conditions.

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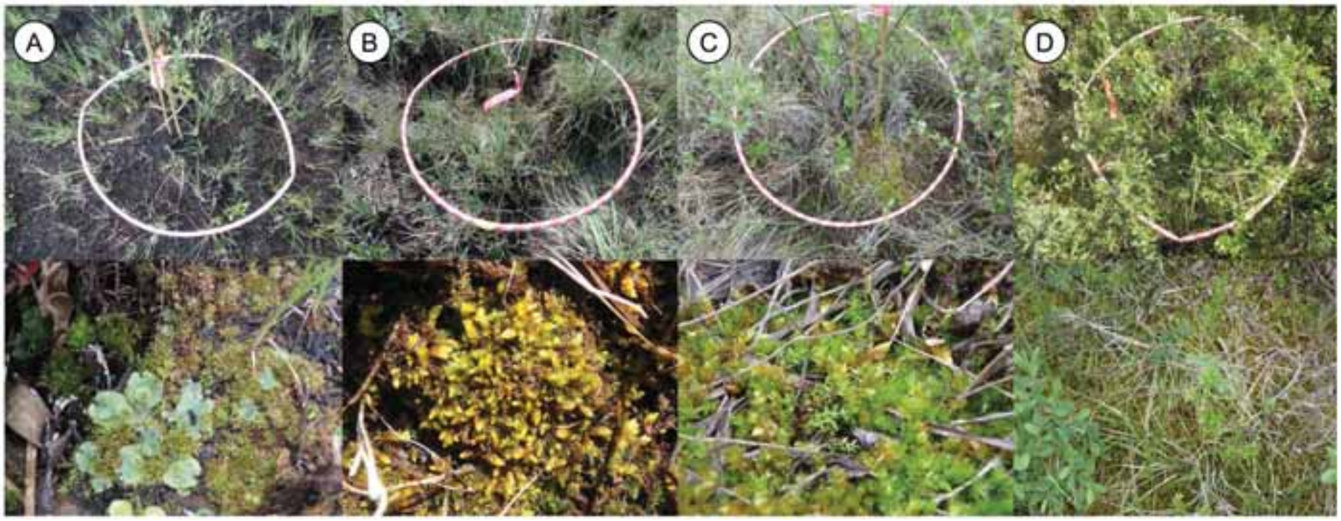
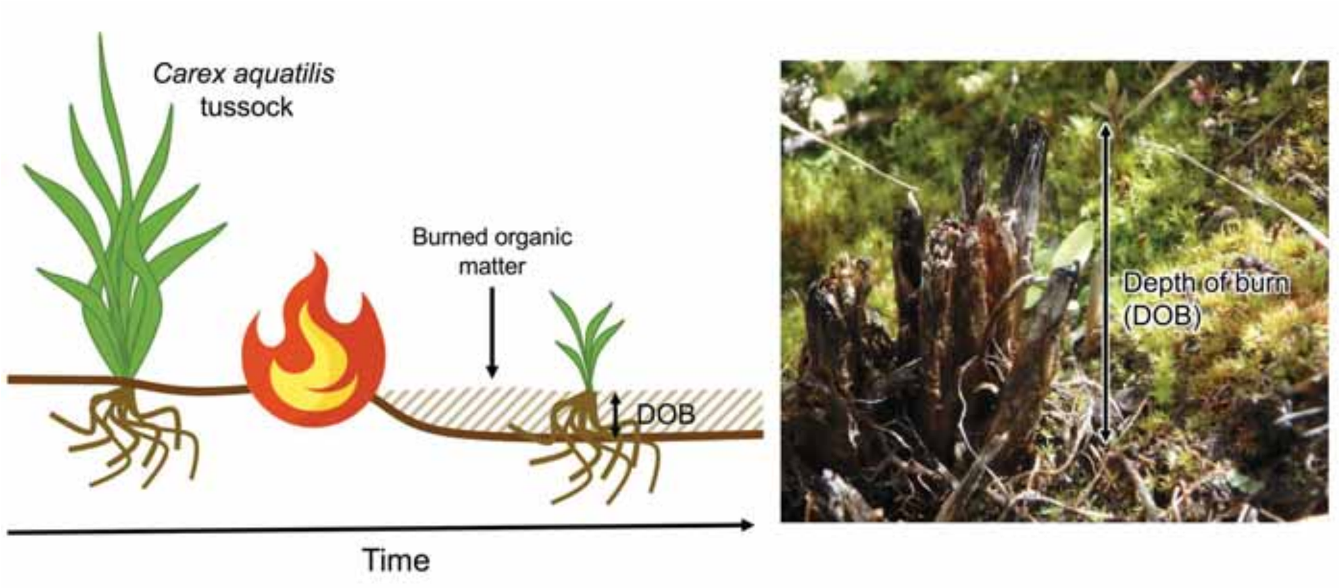
Appendixes



Appendix 2.1 Disposition of the 70-cm diameter subplot (top row) and bryophyte communities (bottom row) in A) 1 year post-fire sites, B) 2 years post-fire sites, C) 5 years post-fire sites and D) unburned reference sites.

Appendix 2.2 Description of the explanatory variables measured (fire variability, hydrological conditions, peat physicochemical and meteorological conditions).

Group	Name	Description
Meteorological conditions		Meteorological data for each site was retrieved from the closest meteorological station (from Hay River and Yellowknife stations in the Northwest Territories and from High Prairie and Fort McMurray stations in Alberta) (Environment Canada 2018). Only data from the first growing season post-fire were used. Chirino et al. (2006) showed that the weather during the first growing season affected *Sphagnum* regeneration more than in the subsequent years, and it was supposed that the same would apply for other bryophytes.
	Pspr, Psum, Pfall Tspr, Tsum, Tfall	Cumulative amount of precipitation (mm) and mean temperature (ºC) in spring (May, June), summer (July, August) and fall (September, October) were calculated.
	Per rain	Percentage of rainy days during the summer (%) was also calculated.
	AI	Aridity index which equals the annual precipitation falling as rain divided by the annual mean temperature plus 10 (Gignac & Vitt 1990) was used.
Fire variability	Bare subs	The proportion of the surface of the plot (%) covered by bare peat and charcoal was estimated during the vegetation survey.
	DOB	The depth of burn (cm) was measured at each subplot on a *Carex aquatilis* tussock as an indicator of fire severity (following the method in Mack et al. 2011). The roots of this graminoid species were expected to stay moist and resist burning and therefore provide a benchmark of the pre-fire thickness of the organic matter. Hence, the remnant structure of *C. aquatilis* roots after the fire served as a reference point to measure the depth of organic matter that had burned (Appendix 2.3).
	P prefire	The cumulative amount of precipitation before the fire (mm) was obtained from Environment Canada (2018). This included the thickness of the snow cover available at the beginning of the snowmelt and the amount of precipitation during the spring before the fire. Because a preceding winter with little snow accumulation and a drier spring could lead to more severe fire (Westerling et al. 2006, Holden et al. 2007), the cumulative amount of precipitation before the fire served as an indicator for fire severity.
Hydrological conditions	Water table	The water table level depth (cm) (distance to the peat surface) was measured once at each subplot. Water table depth was measured at all sites within one week in the Northwest Territories and another week in Alberta (during which no rainfall occurred) during the summer of 2016 (June 21 to July 15). Since the water table was usually very close to the surface, a small pit was dug by hand and the water table depth was measured after the water filled the pit (ca. 15 minutes). When the water table was deeper, the same procedure was performed but included a 24-hours waiting period to ensure the stabilization of the water level in the measuring pit.
	Peat moisture	Peat mean relative moisture (%) was obtained from three measurements systematically distributed in each subplot with a WET-2 Sensor (Delta-T Devices, Cambridge, United Kingdom). Peat moisture was measured once during the 2016 summer, at the same time as the measurement of the water level depth.
	Water class	The proportion of the surface of the plot (%) covered by water was noted during the vegetation surveys.
Peat physicochemical conditions		Peat physicochemistry was measured on composite peat samples collected at each site in July 2016 (at the peak of the growing season). Samples were collected wearing nitrile gloves and frozen (-4 ºC) until chemical analysis.
	pH EC	A sample saturated with deionized water (Soil Medium Extract method) was used to measure pH (AB150 pH meter, Fisher Scientific, Hampton, United States) and electrical conductivity (µS/cm) (A122 portable conductivity meter, Orion Star) which was corrected for temperature and pH with Sjörs (1950) formula.
	Ca, Mg, Fe, Mn, K, Na, P, NH_4^+, NO_3^-	Subsamples of approximately 100 g were sifted, dried at 40 ºC and analyzed to evaluate the concentration of Ca, Mg, Fe, Mn, K, Na, available P, NH_4^+ and NO_3^- (mg/g). The Ca, Mg, Fe, Mn, K and Na were extracted according to Amacher et al. (1990) and analyzed with an ICP spectrometer (Optima 4300 DV, Perkin-Elmer Instruments, Waltham, United States). Available P was extracted following the method from Bray and Kurtz (1945) and analyzed with the ICP. Finally, NO_3^- and NH_4^+ were extracted according to Keeney and Nelson (1982) and analyzed with a Quikchem 8500 series 2 FIA (Lachat Instruments, Loveland, United States).
	Peat depth	Peat depth (cm) was determined by measuring a metal rod inserted into the ground until the mineral soil was reached at each plot.



Appendix 2.3 Measurement method of the depth of burn (DOB).

Appendix 2.4 Nutrients posit on the tip of moss species (white crust) in a carpet of *Campylium stellatum* **and** *Scorpidium cossonii.*

Chapitre 3

Harvesting surface vegetation does not impede self-recovery of *Sphagnum* peatlands

Mélina Guêné-Nanchen, Sandrine Hogue-Hugron et Line Rochefort

Résumé

La restauration des écosystèmes implique fréquemment la réintroduction de matériel végétal dans les milieux perturbés. Lorsqu'il n'existe pas de plantules en pépinières ou de graines disponibles pour les espèces visées, le matériel végétal doit être récolté en nature dans des « écosystèmes donneurs ». Une évaluation complète de la régénération des écosystèmes donneurs est manquante, particulièrement pour les tourbières dominées par les sphaignes qui servent de sites donneurs où toute la végétation de surface est récoltée mécaniquement selon différentes pratiques de récolte. Ce projet vise à évaluer : 1) la régénération de la végétation, particulièrement des sphaignes, afin de déterminer quelles sont les pratiques de récolte optimales afin de maximiser la reprise des sites donneurs et 2) l'influence des conditions hydrologiques des sites donneurs et des variables météorologiques de la première saison de croissance complète suivant la récolte sur la régénération des mousses. Vingt-cinq sites donneurs couvrant une chronoséquence de 17 années (ayant été récoltés il y a 1 à 17 ans) ont été inventoriés, de même que 15 sites naturels de référence situés au Québec, au Nouveau-Brunswick et en Alberta (Canada). Tous les sites donneurs de plus de 10 ans sont dominés par la sphaigne, quoique la composition végétale entre les sites donneurs et leur référence naturelle associée diffère, notamment à cause des conditions plus humides dans les sites donneurs récoltés. Les pratiques de récolte ont fortement influencé la régénération des sites donneurs, démontrant qu'une bonne planification avant la récolte est un ingrédient essentiel au succès de la reprise. Les pratiques de récolte permettant de minimiser la perturbation des sites donneurs sont recommandées, comme le choix du site donneur approprié (localisation, conditions hydrologiques, végétation en place), le choix de méthodes de récolte les moins perturbatrices et la récolte sur sol gelé. Cette étude démontre que la récolte de la végétation de surface pour la restauration des tourbières n'est pas nuisible au rétablissement des écosystèmes de tourbières naturelles.

Abstract

Ecosystem restoration frequently involves the reintroduction of plant material in the degraded ecosystem. When there are no plant nurseries or seeds available on the market, the plant material has to be harvested in the wild, in a "donor ecosystem". A comprehensive assessment of donor ecosystem recovery is lacking, especially for *Sphagnum*-dominated donor peatlands, where all top vegetation is harvested mechanically using different practices. We aimed to evaluate 1) the regeneration of vegetation, especially of *Sphagnum* mosses, to determine which harvesting practices best enhance recovery and 2) to evaluate the influence of site hydrological conditions and meteorological variables of the first complete growing season post-harvest on peat moss regeneration. Twenty-five donor sites covering a 17-year chronosequence (harvested 1 to 17 years ago) were inventoried along with 15 associated natural reference sites located in Quebec, New Brunswick and Alberta, Canada. All donor sites aged 10 years or more were dominated by *Sphagnum* mosses. However, plant composition varied between donor and associated reference sites because of the wetter conditions at harvested donor sites. Harvesting practices strongly influenced donor site recovery, showing that the skills of the practitioner are an essential ingredient in successful regeneration. Harvesting practices minimizing donor site disturbances are recommended, such as the choice of the adequate donor site (localization, hydrologic conditions, vegetation), the use of less disruptive methods and harvesting when the soil is deeply frozen. This study demonstrated that harvesting surface plant material for peatland restoration is not detrimental towards the recovery of near-natural peatland ecosystems.

Introduction

Ecosystem restoration often involves reintroduction of plants in order to re-establish ecosystem biodiversity and functions. Vascular plants can be reintroduced from seedlings cultivated in nurseries, from seeds or by planting resprouting plants (e.g., willows) harvested in the wild or from nurseries. However, for non-vascular plants, like bryophytes, moss nurseries are rare. Therefore, reintroduction material still mostly comes from natural ecosystems. The recovery of these "donor ecosystems" after vegetation harvesting for ecosystem restoration has raised concerns among the restoration ecologists, and it has never been assessed for peatland ecosystems.

In North America, the Moss Layer Transfer Technique (MLTT; Quinty & Rochefort 2003 and Graf et al. 2012 for a detailed description of the method) has been applied by the Canadian horticultural peat industry for more than 100 restoration projects covering more than 1,100 ha across the country. This large-scale mechanized restoration technique is effective for re-establishing peatland vegetation (González & Rochefort 2014), hydrological attributes (Taylor et al. 2016) and restoring the carbon sink function (Strack & Zuback 2013). The MLTT restoration approach includes the active reintroduction of typical peatland plant fragments (Graf et al. 2012). The top 10 cm of plant material (including mostly *Sphagnum* mosses, but also aerial and underground parts of vascular plants, seeds and spores), are mechanically harvested in a nearby peatland. Harvesting plant material for restoration is done at a ratio of 1:10, meaning that the donor site is ten times smaller than the restored site (Quinty & Rochefort 2003; Graf et al. 2012).

Peatlands used as donor sites are preferably sectors within industrial peatland sites and are reserved for this purpose in the peatland management plan of the peat industries. Donor sites can be sectors that are to be opened for peat extraction or peatlands in a near-natural state that are machinery-accessible within industrial peatland sites. Harvesting of plant fragments and other diaspores ideally occurs when the conditions are not too wet. Harvesting methods generally consist of shredding the surface vegetation, more commonly with a rototiller, but a rotary harrow or a forest mulcher has been used. After the fragments are collected with an excavator or bulldozer.

Donor site regeneration raises concerns amongst environmental communities, governments and certification agencies. There is a need to evaluate the impact of restoration, in other words, is it worth it to restore a peatland if the donor site (a natural peatland ecosystem) is destroyed? This is especially important in areas where pristine peatlands are scarce and often legally preserved, and where finding peatland plant material for reintroduction becomes a challenge. If donor site regeneration is not assured, should we find other sources of plant material (culture in greenhouses or in outdoor farming settings) and forget the approach of harvesting in natural peatlands? Are the conservation of natural peatlands and peatland restoration activities complementary or opposed?

At a global scale, an increasing number of policies from environmental and climate agencies are requiring more responsible and sustainable management practices for peatlands affected by human activities (e.g., United Nations Framework Convention on Climate Change, Reducing Emissions from Deforestation and Forest Degradation, EU Habitats Directive; Stoneman et al. 2016). Another example, the Veriflora certification, prevalent in the North American horticultural and floral industries, encourages that all peat fields where peat extraction activities recently ceased should be restored with the MLTT and that donor sites should be set aside during the peatland development plan (SCS Global Services 2012). Outside North America, there is also an increasing demand for *Sphagnum* propagules as plant reintroduction material within the MLTT (e.g., in Estonia - Karofeld et al. 2016; Lithuania - Sendzikaite et al. 2017; United Kingdom - Peacock et al. 2013; Australia - Whinam et al. 2010; Chile - Domínguez 2014) or for the implantation of *Sphagnum* farms (in Canada - Pouliot et al. 2015; Germany - Gaudig et al. 2017; Japan - Hoshi 2017). The demand for little-decomposed *Sphagnum* mosses (*Sphagnum* fibers) for orchid propagation or plant packaging market is also increasing (Zegers et al. 2006) for which top surface *Sphagnum* fibers are harvested in natural peatlands (New Zealand - Whinam & Buxton 1996; Finland - Silvan et al. 2017; Chile - Díaz & Silva 2012). Demand for little-decomposed *Sphagnum* fibers translates into pressure and environmental impacts on natural peatlands, and their recovery after harvesting needs to be investigated as well as the influence of harvesting practices and environmental factors.

Hydrology has been found to be the main environmental factor controlling *Sphagnum* regeneration in natural hand-harvested peatlands, in Chile (Díaz & Silva 2012) and New Zealand (Whinam & Buxton 1996). According to Whinam and Buxton (1996), peatlands selected for harvesting should have a stable water table level, but they do not refer to a specific level. The same authors recommended that the microtopography at the surface of the donor site after plant harvesting should ideally be even to optimize water distribution and drainage. Also, according to them, the use of machinery should be minimized or avoided because it causes ruts, irregular water distribution and exposes more humified peat resulting in slowed or absent *Sphagnum* regeneration. Lastly, the presence of leftover *Sphagnum* fragments (~ 30 % of cover) fostered recovery in natural hand-harvested peatlands (Whinam & Buxton 1996). The landscape context of machinery-harvested plant material for reintroduction in North America provides post-harvested peatland conditions that differ from hand-harvested peatlands and requires a comprehensive evaluation of their recovery potential and trajectory.

This study is the first to evaluate the regeneration of donor sites at a broad geographical scale, including 25 donor sites across Canada. We aimed to (1) evaluate the regeneration of vegetation (*Sphagnum* mosses, other cryptogams (mosses and lichens), and vascular plants) in terms of abundance and composition, (2) determine the impact of different harvesting practices (e.g., donor site localization, harvesting methods and season) on the regeneration of vegetation and (3) evaluate the influence of site hydrology and meteorology of the first-year post plant material harvesting on the regeneration of *Sphagnum* mosses. We hypothesized that vegetation in donor sites should follow a similar pattern of regeneration than restored peatland sites, but their regeneration should be faster. The impact of harvesting practices should have an equal importance as hydrologic conditions on the regeneration of donor sites.

Methods

Study area

This study was conducted on 25 peatlands that were used as donor sites for *Sphagnum*-dominated peatland restoration with the Moss Layer Transfer Technique. The donor sites were located in the province of Quebec, New Brunswick (eastern Canada) and Alberta (western Canada) and were monitored for 1 to 17 years post-harvesting (Appendix 3.1; Figure 3.1). Sites are located in four major Canadian climatic regions: the Northeastern Forest Region (Quebec), the Great Lakes and St. Lawrence Lowlands Region (Quebec), the Atlantic Region (New Brunswick) and the Northwestern Forest Region (Alberta) (Appendix 3.1) (Environment and Climate Change Canada 2016). These peatlands are mainly rain-fed open bogs (National Wetlands Working Group, 1997) dominated by *Sphagnum* mosses and ericaceous shrubs.

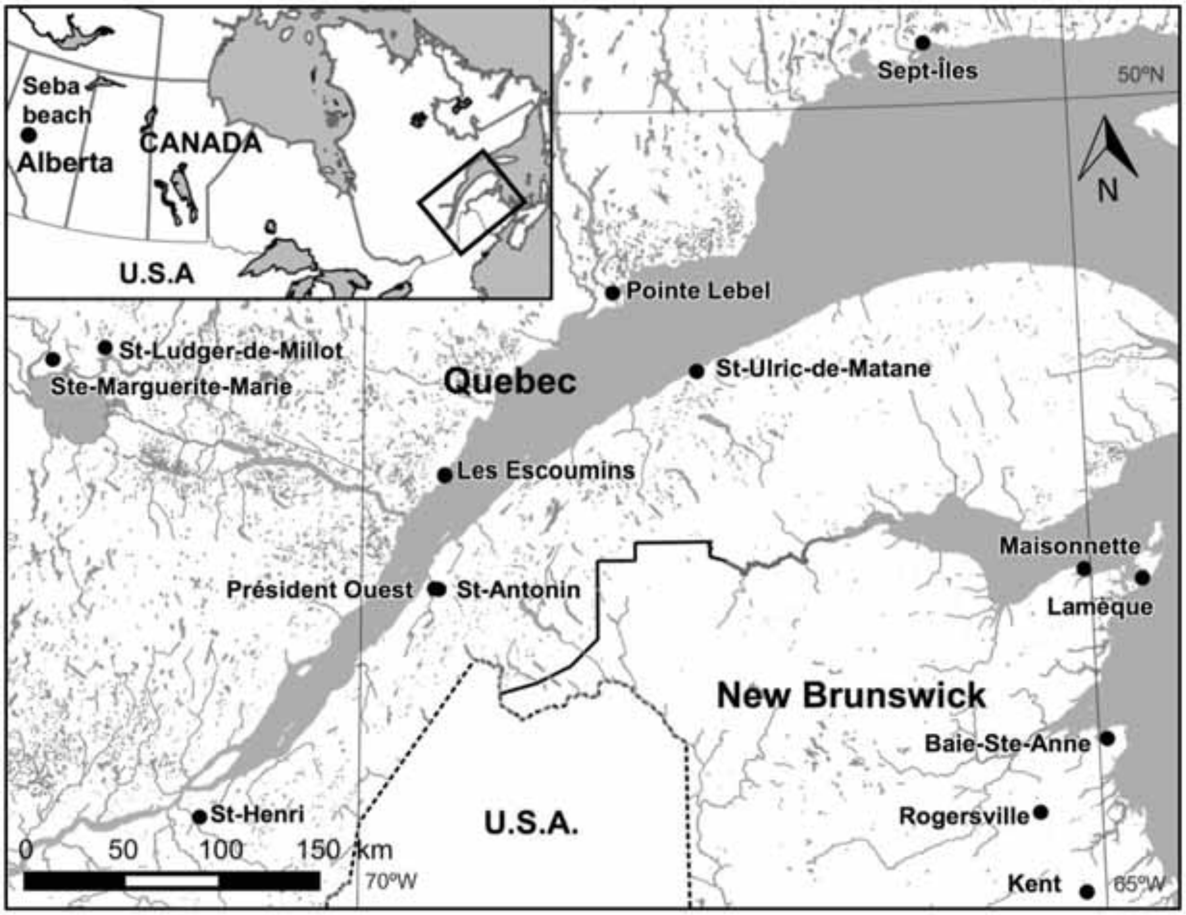


Figure 3.1 Location of the 15 peatlands with donor sites in the provinces of Quebec, New Brunswick and Alberta (Canada).

Donor sites were selected by peatland managers and supposed to contain at least 50 % ground cover of *Sphagnum* mosses from the *Acutifolia* subgenus (mainly *Sphagnum fuscum*, *Sphagnum rubellum*) and *Polytrichum strictum* (Quinty & Rochefort 2003; Graf et al. 2012). Donor sites are usually chosen among suitable ones to minimize the distance to the restoration sites to reduce transportation costs. Therefore, donor sites are often surrounded by or adjacent to drained peat fields. Because different sectors of an extracted peatland can be restored in different years, there were 25 surveyed donor sites located in 15 peatland sites / industrial entities (Appendix 3.1).

Site description

A major constraint to donor site selection for this ecological assessment was that some sites no longer existed at the time of this study because they have been opened for peat extraction. Therefore, the assessment does not represent an age continuum and is not replicated. To avoid misinterpretation based on low effective sample size per age, the donor sites were classified into three categories: 5 years or less (*n* = 12), between 5 and 10 years (*n* = 6) and 10 years or more since harvesting (*n* = 7).

Natural reference sites represent the potential vegetation composition of the donor sites before collection of the diaspores and act as a standard comparison for donor site recovery. One reference site per peatland site was selected, so a given reference site could be the reference for several donor sites. Sometimes, when all of the open parts of the *Sphagnum* peatland were harvested, there was no adjacent natural *Sphagnum* peatland to serve as a reference. In these few cases (*n* = 5), the reference site was just aside the donor site but corresponded more to a treed *Sphagnum* peatland (Appendix 3.2).

Assessment approach

Vegetation inventories

The post-harvesting surveys were performed in 40 sites (25 donor sites and 15 reference sites) and documented the plant communities in 141 plots (5 x 5 m) (Appendix 3.1). Two to four plots were surveyed per donor site or reference site depending on the size of the site and heterogeneity of regeneration. Plots were located randomly and distributed within each site to represent the site heterogeneity. In each donor site or reference site, vegetation was surveyed either during the summer of 2015 or 2016. Donor site location was sometimes difficult to determine, especially for older sites. A set of GPS points provided by the peatland managers was used to find the general location of the site and the specific perimeter of the harvest was determined using physical parameters of the vegetation (such as a uniform lower height of the ericaceous shrubs stratum).

The total cover for all vegetation, peat and litter and disturbed substrate were estimated by their vertical projections on the ground in the 5 x 5–m plots. Total vascular plant cover and cover by vascular species were evaluated within four quadrats (1 x 1 m) nested within the 5 x 5–m plots, while total bryophyte cover, total *Sphagnum* cover and bryophyte cover by species were recorded in 12 quadrats (25 x 25 cm) that were systematically distributed within the plot. In addition, the total cover of trees and shrubs, ericaceous shrubs, graminoid plants, forbs, mosses other than *Sphagnum*, lichens, and liverworts per plot were calculated by adding the mean cover of each species corresponding to these strata, and therefore, included species superposition.

Nomenclature follows VASCAN, the Database of Vascular Plants of Canada (Brouillet et al. 2010+), Flora of North America Editorial Committee (1993+) for bryophytes and Lichens of North America (Brodo et al. 2001) for lichens.

Harvesting and environmental conditions

Explanatory variables that could influence donor site regeneration were classified into three groups, harvesting, hydrological proxies and selected meteorological variables or indices known to be particularly meaningful to the regeneration of mosses (González & Rochefort 2014; Table 3.1). Some explanatory variables were measured at the plot level, others at the donor site level.

Table 3.1 Description and units of the explanatory variables measured (harvesting, hydrology, meteorology).

Group	Name	Description	Notes
Harvesting	Time	Time since harvesting (year)	The number of complete growing seasons since the harvesting was provided by the peatland managers.
	Shape	The shape of the area harvested (2 classes: rectangle or square)	Long and narrow (rectangle) donor sites are supposed to facilitate the work with the machinery and minimize sinking (Quinty & Rochefort 2003).
	Method	Harvesting method (4 classes: rotary harrow, mulcher, rototiller, excavator with a large bucket with comb teeth)	The rotary harrow, mulcher and rototiller were pulled by a tractor within the donor site, while the excavator with a large bucket with comb teeth were operated from outside the donor site.
	Season	Harvesting season (4 classes: spring, summer, fall, winter)	The season was not used to represent a phenological variable but rather a reflection of the different levels of site disturbance caused by the machinery during harvesting. For example, there is a greater likelihood for the machinery to cause ruts in the summer because there is no ice underneath the peat to support the machinery.
	Natural Extracted Restored Unrestored Anthropic	Relative use of the 500-m buffer zone around the donor site (%)	Using satellite images from Google Earth, a buffer zone of 500 m around the donor sites was determined in which the relative areas (%) of the following uses was calculated: natural (mainly forest, water bodies and peatlands), current peat extraction, previously extracted and restored peatland, previously extracted and not restored peatland and anthropic land uses other than peat extraction (mainly agriculture). Satellite images from the first or second year following the harvesting were used.
Hydrological	Dist ditch	Distance to the closest drainage ditch (2 classes: < 15 m, > 15 m)	Hydrology at each plot was evaluated using two hydrological proxies. Proxies were used because donor sites were not monitored at the same period of the summer nor at the same year. Implementing a hydrology monitoring program with water table depth measures during the growing season was too expensive and intensive to put in place, due to site remoteness and the number of sites. By photo interpretation of satellite images (Google Earth) from the first or second year following the harvesting and validation on the field, the approximate distance to the closest drainage ditch and its status was determined for each plot.
	Ditch type	Type of drainage ditch (2 classes: open active, blocked)	
Meteorological	Pspr Psum Pfall	Cumulative precipitations (mm)	Weather data for each site was retrieved from the closest meteorological station (Environment Canada). Only data from the first complete growing season was used because weather during subsequent years had a minor effect on *Sphagnum* establishment (Chirino et al. 2006). Cumulative precipitation and mean temperature for spring (May, June), summer (July, August) and fall (September, October) were calculated.
	Tspr Tsum Tfall	Mean temperature (ºC)	
	Per rain	Percentage of rainy days (%)	Total percentage of rainy days and the maximum number of consecutive days without precipitation (0 mm) during the summer were calculated.
	Max noP	Maximum number of days without rain	
	A.I	Aridity index	Aridity index equals the annual precipitation falling as rain divided by the annual mean temperature plus 10 (Gignac & Vitt 1990).

Statistical analysis

Regeneration of the vegetation

Firstly, a linear regression was run to evaluate the effect of the number of years post-harvesting on the total cover of *Sphagnum* mosses in the donor sites. Quadrat means per plot of total *Sphagnum* cover were used (donor sites: n = 90, natural reference: n = 51).

Secondly, absolute cover values for each vegetation layer (vascular plants, trees and shrubs, ericaceous shrubs, graminoid plants, forbs, bryophytes, *Sphagnum* mosses, other mosses than *Sphagnum*, lichens, liverworts, peat and litter, disturbed substrate) were averaged per quadrat and per plot per site to generate a vegetation stratum matrix with one row per site (donor and reference) and one column per stratum (dimensions: 40 x 12). Stratum cover data were transformed using the Hellinger transformation method prior to analysis to avoid the double-zero problem (Legendre & Gallagher 2001). The Hellinger-transformed vegetation stratum matrix was subjected to a k-means partitioning. This analysis allowed us to group the observations into k groups that could be interpreted in terms of vegetation regeneration. SSI (Simple Structure Index) criterion was used to determine the appropriate number of clusters. This criterion was used instead of the Calinski-Harabasz criterion recommended by Milligan (1996) because it suggested a more interpretable number of clusters. Then, the distribution of each type of site (< 5 years, 5–10 years, > 10 years and reference) was calculated in each k groups. The k-means partitioning results were visualized using a principal component analysis (PCA) biplot using the same vegetation matrix where a circle of equilibrium contribution was drawn to determine which strata contributes significantly to the PCA (Legendre & Legendre 2012).

Thirdly, cover values for each species (vascular plants and cryptogams) were averaged per plot to generate a species matrix with one row per plot per site (donor and reference) and one column per species (dimensions: 40 x 52). This species matrix was also transformed using the Hellinger transformation. Only species of a frequency and/or a mean abundance of more than 5 % were included to minimize the bias induced by rare species. An indicator species analysis (IndVal; Dufrêne & Legendre 1997) was run on the Hellinger transformed species matrix to identify indicator species in each previously determined k-means group. This analysis calculates measures of specificity and fidelity for each species to each group. Afterward, it calculates an IndVal value for each species that ranges from 0 to 1; when a value is close to 1, this species is considered to be an indicator and specific to a certain group. The signification of the indicator value of each species was evaluated with a randomization procedure with 9999 permutations (Legendre & Legendre 2012).

Finally, to give a general portrait, descriptive analyzes of the vegetation data of the previously determined k-means groups were done.

Influence of harvesting and environmental conditions on vegetation

Using only donor sites, cover values for previously selected vegetation layer by the circle of equilibrium contribution per plot were used to generate a vegetation stratum matrix with one row per plot and one column per stratum (dimensions: 90 x 5). Stratum cover data were transformed using Hellinger transformation method prior to analysis to avoid the double-zero problem (Legendre & Gallagher 2001).

To evaluate the role of each explanatory group (harvesting, hydrology and meteorology) on vegetation regeneration, a redundancy analysis (RDA) was carried out on the vegetation stratum matrix per plot. Because collinearity between explanatory variables was expected, a forward selection was implemented before running the RDA. Explanatory variables that were highly correlated (Spearman coefficient > 0.7) were also removed. The RDA was run with the selected significant explanatory variables. The significance of the RDA was tested with a permutation test using 9999 randomized runs (Legendre & Legendre 2012). In this analysis, the experimental unit considered is the plot, therefore this might be considered as pseudoreplication (repeated measurements within a donor site). A partial RDA approach using site as a random factor was not used, because that way, the influence of explanatory variables on the stratum matrix will be underestimated. Indeed, many explanatory variables (from harvesting and meteorology) were measured at the donor site level, not at the plot level. By including a random site effect, variance linked to these explanatory variables would have been lost. Finally, to distinguish the effect of time from the other harvesting variables and the relative contribution of all previously selected explanatory variables, a variation partitioning analysis was carried out on the vegetation stratum matrix.

All analyzes were conducted with R (R Core Team 2016, version 3.3.1) software, more precisely decostand, cascadeKM, ordistep, rda, RsquareAdj and varpart from vegan package (Oksanen et al. 2016), ordiequilibriumcircle from BiodiversityR (Kindt & Coe 2005) and indval from labdsv (Roberts 2016).

Results

Regeneration of the vegetation

Sphagnum cover in donor sites linearly increased with the number of years since harvesting (Figure 3.2; Adjusted $r^2 = 0.66$, $F_{[1,13]} = 15.33$, $p < 0.001$). According to the regression equation (Figure 3.2), a *Sphagnum* cover of 70 %, which is the mean value in reference sites, could be obtained in ~ 11 years.

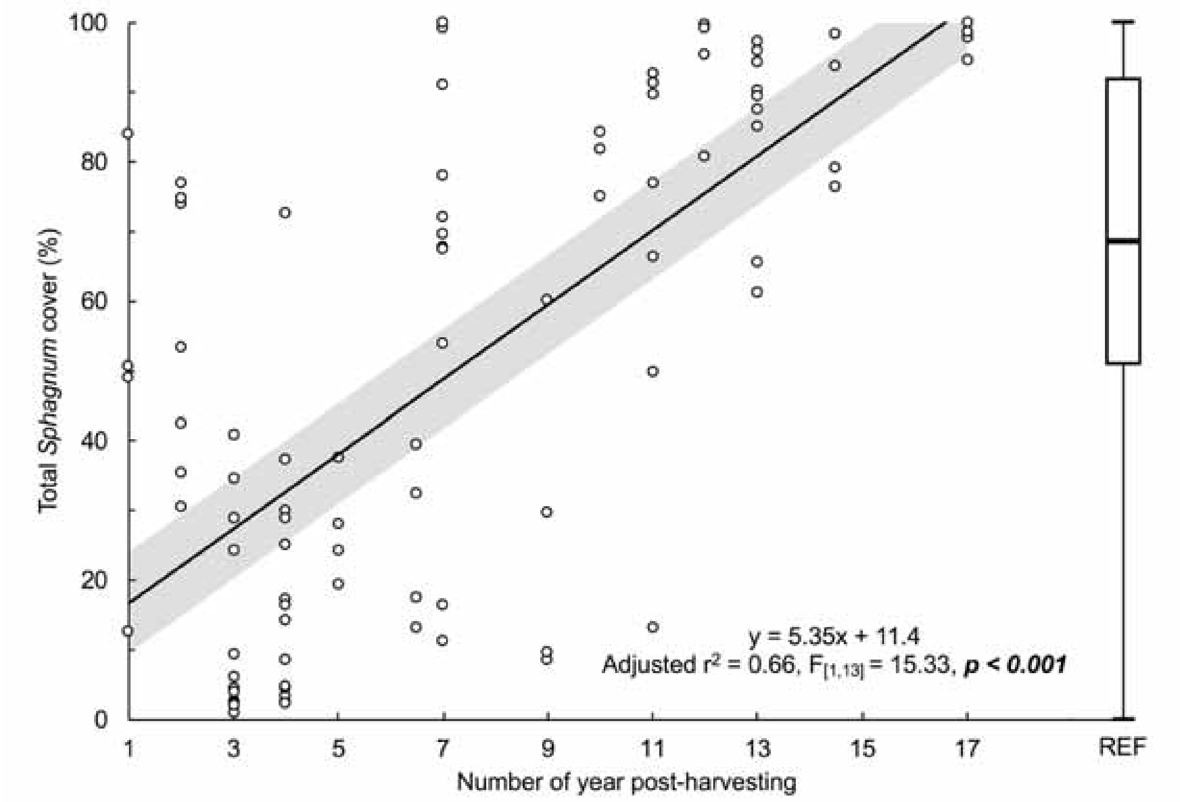
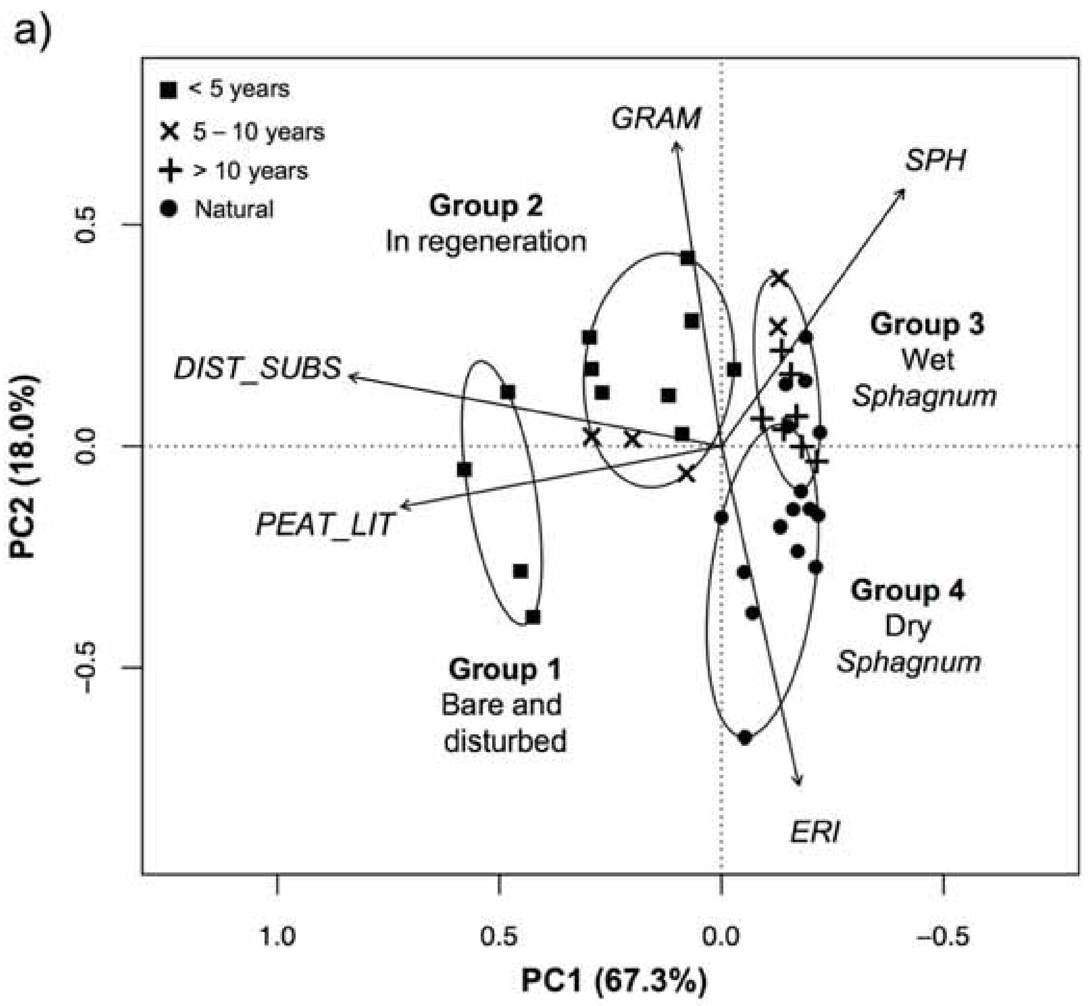


Figure 3.2 Relation between the total *Sphagnum* cover (%) (mean ± $CI_{95\,\%}$ [gray area]) per plot (*n* = 90 plots) according to the number of years post-harvesting in donor sites. Total *Sphagnum* cover values found in natural reference sites (REF) are represented in a boxplot (*n* = 51 plots).

Donor sites and reference sites were grouped in the ordination diagram (Figure 3.3) into four groups that were defined in terms of vegetation regeneration: bare and disturbed, in regeneration, wet *Sphagnum* and dry *Sphagnum* (Figure 3.3a & Appendix 3.3). Only the cover of peat and litter, disturbed substrate, graminoid plants, *Sphagnum* mosses and ericaceous shrubs contributed significantly to the pattern of the ordination (circle of equilibrium radius = 0.41).



b)

Group	< 5 years	5 – 10 years	> 10 years	Reference
1 – Bare and disturbed	33	0	0	0
2 – In regeneration	67	60	0	0
3 – Wet *Sphagnum*	0	40	100	25
4 – Dry *Sphagnum*	0	0	0	75

Figure 3.3a) Principal component analysis (PCA) biplot (scaling 1) of the total cover of the following strata: PEAT_LIT = peat and litter, DIST_SUBS = disturbed substrate, GRAM = graminoid plants, SPH = ***Sphagnum*** **mosses and ERI = ericaceous species. The significant strata were selected with the equilibrium circle procedure (not shown). The groups obtained by k-means partitioning are represented by ellipses (bare and disturbed, in regeneration, wet** ***Sphagnum*** **and dry** ***Sphagnum*****). b) Distribution (%) of each type of site (< 5 years, 5–10 years, > 10 years and natural reference) in each of the groups of the k-means partitioning done on the vegetation stratum matrix (bare and disturbed, in regeneration, wet** ***Sphagnum*** **and dry** ***Sphagnum*****).**

The bare and disturbed group ($n = 4$) was characterized with a low cover of living vegetation (~ 15 %), a high cover of bare peat and litter (~ 85 %) with still visible disturbed substrate (~ 75 %) (Table 3.2) and comprised exclusively sites of less than 5 years old (Figure 3.3b). *Eriophorum vaginatum* and *Betula* spp. were indicators for this group (Table 3.3; IndVal = 0.54, $p = 0.02$ and IndVal = 0.27, $p = 0.03$ respectively). The in regeneration group ($n = 12$) showed an intermediate cover of *Sphagnum* mosses (~ 30 %) and the highest cover of graminoid plants of all four groups (~ 15 %), of which *E. vaginatum* was the dominant species (Table 3.2).

Table 3.2 Percentage of cover (%) of the most abundant strata and species (mean ± standard error [SE]) in each of the groups of the k-means partitioning (bare and disturbed, in regeneration, wet *Sphagnum* and dry *Sphagnum*). An asterisk indicates a cover lower than 1 %.

	1- Bare and disturbed	2- In regeneration	3 - Wet *Sphagnum*	4 -Dry *Sphagnum*
Total vegetation	17 ± 2	56 ± 3	94 ± 2	89 ± 2
Peat and litter	85 ± 4	49 ± 4	9 ± 1	13 ± 3
Disturbed substrate	76 ± 8	31 ± 5	2 ± 0.5	2 ± 2
Trees and shrubs	*	*	2 ± 0.4	5 ± 1
Betula papyrifera	*	*	*	*
Larix laricina	*	*	1 ± 0.4	*
Picea mariana	*	*	*	3 ± 0.9
Ilex mucronatus	*	0	0	*
Ericaceous shrubs	12 ± 3	16 ± 2	25 ± 2	57 ± 3
Chamaedaphne calyculata	4 ± 0.6	7 ± 0.9	9 ± 0.9	10 ± 2
Kalmia angustifolia	5 ± 2	4 ± 1	6 ± 1	25 ± 4
Rhododendron groenlandicum	1 ± 0.3	2 ± 0.4	5 ± 1	11 ± 2
Herbaceous species	3 ± 0.9	16 ± 2	7 ± 1	4 ± 0.7
Eriophorum vaginatum	1 ± 0.6	11 ± 2	4 ± 1	*
Sphagnum **mosses**	6 ± 2	33 ± 4	85 ± 3	60 ± 5
Sphagnum angustifolium	*	3 ± 1	5 ± 2	4 ± 2
Sphagnum fuscum	2 ± 0.5	3 ± 1	10 ± 4	23 ± 5
Sphagnum magellanicum	*	6 ± 2	10 ± 2	3 ± 1
Sphagnum rubellum	5 ± 1	15 ± 3	51 ± 5	21 ± 4
Other cryptogams	4 ± 0.6	12 ± 2	8 ± 1	19 ± 3
Polytrichum strictum	3 ± 0.5	6 ± 1	5 ± 1	4 ± 1
Cladonia spp.	*	1 ± 0.4	*	10 ± 3

Most of the sites aged of 5 years and less and sites between 5 and 10 years old were in the in regeneration group (Figure 3.3b). Unidentified *Sphagnum* mosses in regeneration were strong indicators of the group (Table 3.3; IndVal = 0.70, *p* = 0.01). The wet *Sphagnum* group (*n* = 12) was described by the highest cover of *Sphagnum* mosses (~ 85 %) characterized with a high proportion of wetter microhabitat species (*S. angustifolium, S. rubellum, S. magellanicum*) compared to the next group that had a higher proportion of hummock species (Table 3.2). *Chamaedaphne calyculata* was the only ericaceous species reaching similar cover than in the next group (Table 3.2). All donor sites aged of more than 10 years old were classified in this group (Figure 3.3b). No indicator species were found for this group, meaning that no species were exclusively present in this group nor present in all of the sites of the group. The dry *Sphagnum* group (*n* = 12) also exhibited a high *Sphagnum* species cover (~ 60 %) characterized this time by a higher presence of hummock species (*S. fuscum*) associated with a higher presence of ericaceous shrubs particularly dominated by *Kalmia angustifolia*, evidence of drier conditions (Table 3.2). Most of the reference sites were grouped in this group (Figure 3.3b). *Kalmia angustifolia*, *Rhododendron groenlandicum* and *Picea mariana* were indicator species of the dry *Sphagnum* group (Table 3.3) and their cover was at least two times higher than in any other group. Lichens, mainly *Cladonia* spp. had the highest cover in this group and was only present (< 1 %) in other groups (Table 3.2).

Table 3.3 Indicator species, IndVal, *P* and frequency (number of occurrences) in each of the groups of the k-means partitioning done on the vegetation stratum matrix (bare and disturbed, in regeneration, wet *Sphagnum* and dry *Sphagnum*). There was no indicator species for the wet *Sphagnum* group.

Group	Species	IndVal	*p*	Frequency
1 - Bare and disturbed	*Eriophorum vaginatum*	0.54	0.02	8
	Betula spp.	0.27	0.03	6
2 - In regeneration	Unidentified *Sphagnum*	0.70	0.01	3
4 - Dry *Sphagnum*	*Picea mariana*	0.63	0.007	13
	Rhododendron groenlandicum	0.60	0.006	14
	Kalmia angustifolia	0.58	0.001	31

Influence of harvesting and environmental conditions on vegetation

The selected harvesting, hydrological and meteorological variables (see Appendix 3.4 for all selected explanatory variables) explained 77 % of the variability of the vegetation surveyed in the 25 donor sites (Figure 3.4) and all groups of explanatory variables had a significant influence. The harvesting group explained most of the variability (21 %), followed by the time since harvesting (17 %), the meteorology of the growing season following harvesting (9 %) and the hydrology (3 %) (independent variance without any interactions with the other groups; Figure 3.5). The first gradient of the RDA separated the plots along a gradient of *Sphagnum* moss cover (RDA1; Figure 3.4).

Bare and disturbed donor sites were more rectangle shaped, harvested with a rototiller, during the summer, adjacent to peat fields currently extracted and/or natural areas, and experienced a warm and dry first summer (Tsum and Max noP; Figure 3.4). Wet *Sphagnum* donor sites were more common when there were more precipitations during the first summer after the harvesting (Psum and Per rain; Figure 3.4). Wet *Sphagnum* donor sites were mostly harvested with a rotary harrow during spring and were adjacent to unrestored peat fields and anthropic land (mainly agriculture). They were generally far (> 15 m; Figure 3.4) from open active drainage ditches. In regeneration donor sites were distributed between the two previous groups. The dry *Sphagnum* group is not displayed on Figure 3.4, because this group includes only reference sites (Figure 3.3b).

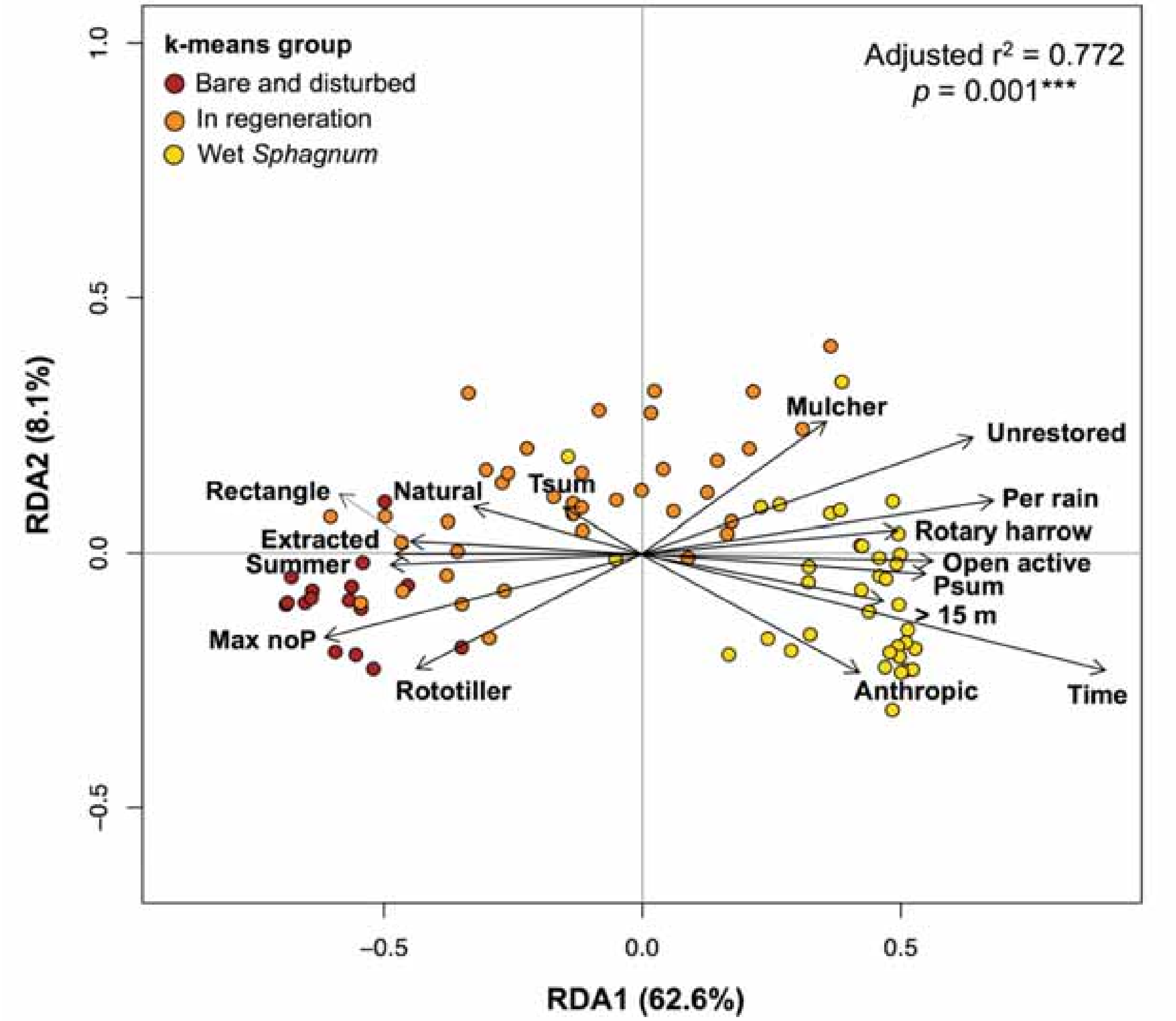


Figure 3.4 Redundancy analysis (RDA) triplot (scaling 1) with forward selected explanatory variables constraining the total cover of the dominant strata (peat and litter, disturbed substrate, graminoid plants, *Sphagnum* mosses, ericaceous species [not displayed]). To improve the visual clarity, only the most important explanatory variables were represented (Spring, Restored, Tspr and A.I were selected but not represented on the RDA). The first axis of the RDA corresponds to a gradient of *Sphagnum* cover from low (left) to high (right). The site scores are represented as weighted averages of the explanatory data. Appendix 3.5 presents correlation between all explanatory variables.

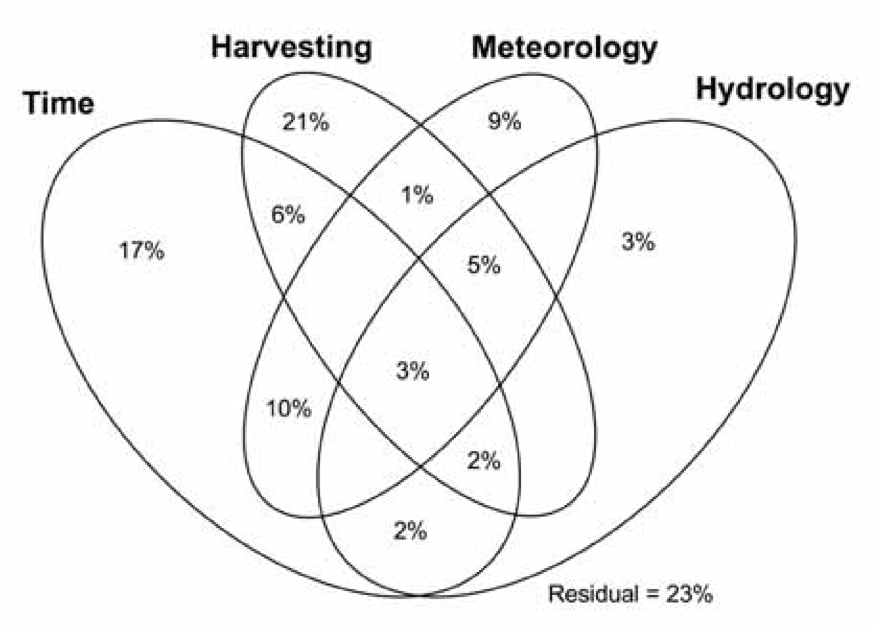


Figure 3.5 Venn diagram of the variation partitioning of the selected explanatory variables from each group (variable of time since harvesting, harvesting group (excluding time), meteorology group, hydrology group) carried out on the vegetation stratum matrix (see Appendix 3.4 for selected explanatory variables). Independent variances represent the variance explained by one group while the effects of other groups are controlled. Relative contributions of less of 1 % were not represented.

Discussion

Regeneration of the vegetation: species abundance and composition

This study demonstrated that harvesting *Sphagnum* diaspores for peatland restoration in North America was possible without impeding the natural ability of self-regeneration of peatland ecosystems. Even if the *Sphagnum* layer is expected to regenerate within a 10-year timespan, our results show that a change in plant community structure and composition should also be expected.

For instance, trees and shrubs regenerated slowly in donor sites (Murray et al. 2017). Their regeneration, germination, survival and growth are affected by substrate water saturation (Chimner & Hart 1996; Hörnberg et al. 1997). Harvesting in donor sites lowers and flattens the surface, thus harvested donor sites become wetter (Murray et al. 2017) and do not exhibit the microtopographic variation required for tree and shrub germination. *C. calyculata* was the only ericaceous shrub that regenerated more quickly; this species grows well in hollow habitats (González et al. 2013). In contrast, *Kalmia angustifolia*, *Rhododendron groenlandicum* (Pouliot et al. 2012) and *Picea mariana* (Ohlson & Zackrisson 1992) were associated with natural peatlands and preferred hummock habitats. These species might also have been over-represented in reference sites. As previously described, often all open parts of the peatland were harvested for donor material and the remaining adjacent non-harvested area left for natural reference inventory corresponded more to a treed *Sphagnum* peatland (Appendix 3.2). This explained the higher cover of *K. angustifolium*, *R. groenlandicum* and *P. mariana* in the dry *Sphagnum* group that are prevalent in drier forested *Sphagnum* peatlands (Rydin & Jeglum 2013).

Eriophorum vaginatum has often been designated as a pioneer species (Buttler et al. 1996; Hughes & Dumayne-Peaty 2002) or invasive species (Tomassen et al. 2004; Lavoie et al. 2005) in disturbed peatlands. Because of its high wind-dispersal potential and relatively high fecundity, it is the most common herbaceous species in unrestored and restored extracted peatlands (Salonen 1987; Campbell et al. 2003) and in donor sites (Murray et al. 2017). In a previously extracted and unrestored peatland, Lavoie et al. (2005) found that *E. vaginatum* extent increases drastically with the rise of water level and started to decrease nine years later. In successfully restored peatlands, *E. vaginatum* cover reached almost 40 %, five to six years after the restoration and decreased afterward (Rochefort et al. 2013).

As found by Poulin et al. (2013), González et al. (2013) and Karofeld et al. (2016), *S. rubellum* was more abundant in regenerating peatlands than in natural peatlands. This species has a wide ecological amplitude (Gignac 1992) and is competitive when environmental conditions are variable (Pouliot 2011). The presence or absence of the other cryptogam species (bryophytes and lichens) in donor sites is reflected by their habitat preference. For example, *Cladonia* species preferred drier habitat (Jasieniuk & Johnson 1982). Also, donor sites are usually selected to contain few lichens, and therefore, *Cladonia* spp. could be over-represented in natural sites.

Indeed, species that prefer wetter habitats (e.g., *C. calyculata*), that are pioneers (e.g., *Eriophorum vaginatum*) or are competitive species (e.g., *S. rubellum*) were more abundant in regenerating donor sites, while species with a slow growth rate (trees, shrubs and lichens) were more abundant in reference sites. This highlights that plant species regeneration is related to their life-history strategy (pioneer vs late successional species) and habitat niche preference (opportunist vs specialist species).

Influence of harvesting: time versus harvesting conditions

Sphagnum regeneration in donor sites was linearly related to the number of years post-harvesting. Indeed, all donor sites aged 10 years or more had a similar *Sphagnum* cover as the reference sites.

Faster regeneration was observed (2 to ~ 5 years) in the oldest restoration projects (Rochefort et al. 1997; Rochefort & Campeau 2002). In these studies, the harvesting of the plant fragments and other diaspores was carried out during spring with a bulldozer scraping the surface of peat mosses just above the ice. This method created little disturbance and harvested only the top 10 cm of the *Sphagnum* layer but requires specific operations similar to the creation of northern Canadian winter roads over peatlands (i.e., the snow is compacted in early winter to allow better penetration of the frost into the soil). However, this harvesting method is not used anymore because it requires the preparation described previously, which is time-consuming. Contrasting these earlier studies with our results, it suggests that a winter harvest above frozen peat could induce low levels of soil disturbance and can speed up *Sphagnum* regeneration. This suggests that harvesting practices might be more important than time since harvesting.

Indeed, harvesting variables were the most influential factors on the recovery of the *Sphagnum* carpet in our study rather than time since harvesting. In the case of donor sites, this result means that choosing appropriate harvesting practices could accelerate *Sphagnum* regeneration. For example, the use of a rototiller and/or harvesting during the summer could create more ruts and reduce the overall wetness of the donor sites by preventing even water distribution (Price et al. 1998). The use of less disruptive methods such as a rotary harrow or a forest mulcher and/or harvesting when the soil deeper layers are frozen are thus recommended. However, it is important to note that the season of harvesting does not always ensure that the soil is frozen and the presence of a thick layer of frozen peat should be validated before harvesting. Contrary to what is recommended by Quinty & Rochefort 2003, harvesting in a long and narrow strip seemed to have a negative influence on *Sphagnum* regeneration. Though, this factor might have been misevaluated, because of the difficulty of determining the shape of the donor area a long time after harvesting. Overall, disturbances to donor sites should be kept to a minimum by reducing the exposure of bare peat and creation of ruts by sinking the machinery. To do so, the choice of adequate donor sites might be the solution, as the choice of other harvesting practices. Indeed, donor sites that are too wet should be avoided or only harvested when the soil is frozen. However, choosing drier donor sites to avoid machinery sinking might reduce *Sphagnum* regeneration after harvesting and the quality of the restoration material. This latter recommendation applies if the drier donor sites are dominated by trees, shrubs (e.g., *K. angustifolia*), forest mosses (e.g., *Pleurozium scheberi* and *Dicranum* spp.), lichens and present a low *Sphagnum* content.

In terms of *Sphagnum* regeneration, selecting a donor site close to currently extracted peat fields was not optimal because of surface drainage in extracted peat fields (Landry & Rochefort 2012) and probably also, of aerial peat deposition by wind on regenerating *Sphagnum* mosses (Faubert & Rochefort 2002). However, in terms of logistical and practical constraints, these donor sites adjacent to extracted fields should not be overlooked because they represent cheap and easily accessible propagules for restoration. The proximity of natural areas surprisingly decreased *Sphagnum* regeneration. Even if it can provide a source of diaspores for recolonization, natural areas were mainly composed of forests, which lowered water table levels by evapotranspiration (Ahti & Hökkä 2006). Even if donor sites were surrounded by intact peatlands, *Sphagnum* mosses have a low potential of recolonization by spores (Campbell et al. 2003). The presence of unrestored peatland fields had a positive influence on *Sphagnum* regrowth, because they often imply inactive ditches that filled up over time. Also, wind erosion of peat is reduced in unrestored peatland fields with the formation of a surface crust (Campbell et al. 2002).

Influence of the environment conditions

Meteorological factors also had a significant contribution in explaining *Sphagnum* moss recovery. As found by Chirino et al. (2006), warm temperatures and prolonged drought during the first summer negatively affected the recolonization by mosses. Reduced air humidity decreased the desiccation resilience potential of *Sphagnum* mosses (Sagot & Rochefort 1996). On the other hand, high precipitation well-distributed during the first summer positively influenced *Sphagnum* regeneration, agreeing with Chirino et al. (2006) and Backéus (1988).

Hydrology had a less important influence than expected, probably because of collinearity which masked its importance. Also, the proxies chosen were not appropriate or misestimated, especially for the evaluation of the type of drainage ditch using satellite images. The use of the adjacent area might be a better proxy for the evaluation of hydrology. Also, unlike restored peatlands, donor sites still have an acrotelm that increases soil wetness and reduces water tension (Price et al. 2003). Because of the presence of an acrotelm and the peat properties (e.g., low hydraulic conductivity), the influence of drainage on donor sites might have been minor.

In conclusion, this study is the first to our knowledge to demonstrate that harvesting of *Sphagnum* propagules in a natural peatland for ecosystem restoration is not damaging to peatland ecosystems. (1) We showed that the *Sphagnum* layer could regenerate back to covers similar to natural peatlands within an approximately 10 years period which is relatively rapid compared to Silvan et al. (2017) (30 years) and Elling & Knighton (1984) (20 years). Species abundance and composition varied between donor sites and natural peatlands. Pioneer, competitive and species preferring wet microhabitats were more abundant in donor sites. (2) Furthermore, in order to improve the regeneration of donor sites, the skills of the practitioner are an essential ingredient, because harvesting practices are the most influencing variables for vegetation regeneration. (3) Prolonged drought during the first summer following harvesting impeded donor site recovery and the importance of hydrologic conditions on vegetation regeneration may have been underestimated due to the wrong choice of proxies. Finally, donor sites could even be used as "nurseries" – i.e. to use them multiple times for subsequent restoration projects – but more research will be needed on the impact of cyclical harvesting on *Sphagnum* regeneration potential.

Implications for practice

- The use of adequate harvesting practices and donor sites can speed up *Sphagnum* regeneration in the donor sites.

- Drier donor sites with a high cover of trees and ericaceous shrubs, forest mosses and lichens should be avoided as a source of diaspores for peatland restoration. They provide vegetation material of poor quality for restoration (low *Sphagnum* content) and the recovery of these sites might be impeded by their drier nature.

- The disturbance of donor sites should be minimal (exposition of bare peat, machinery sinking, ruts). Best practices for harvesting would be avoiding very wet donor sites and harvesting in the midsummer should be avoided when mosses are at their lowest regeneration potential and when the risk of machinery sinking is high.

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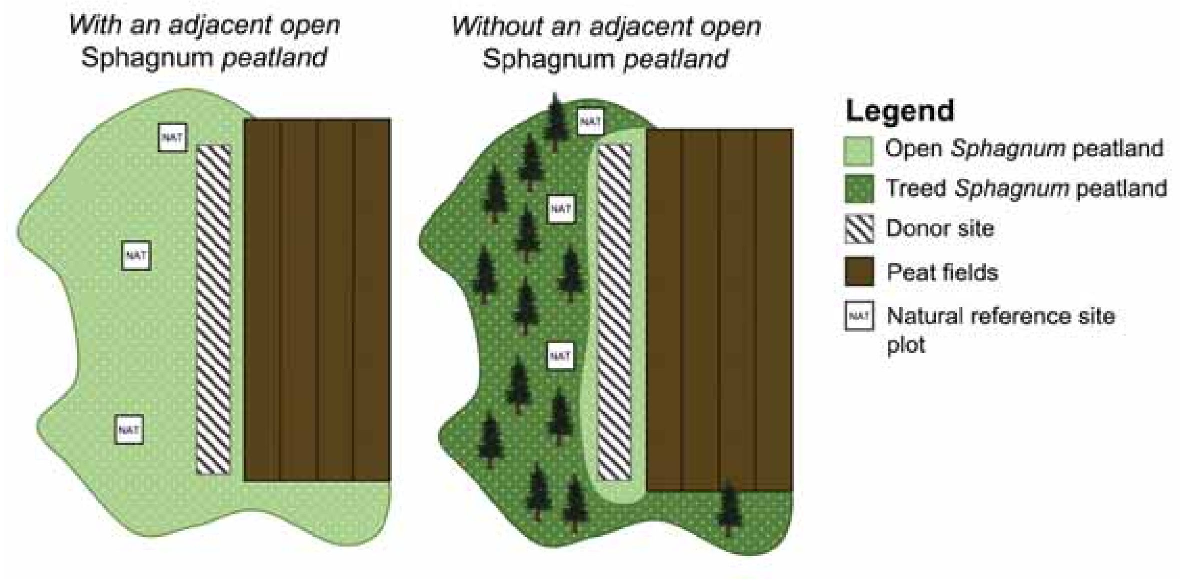
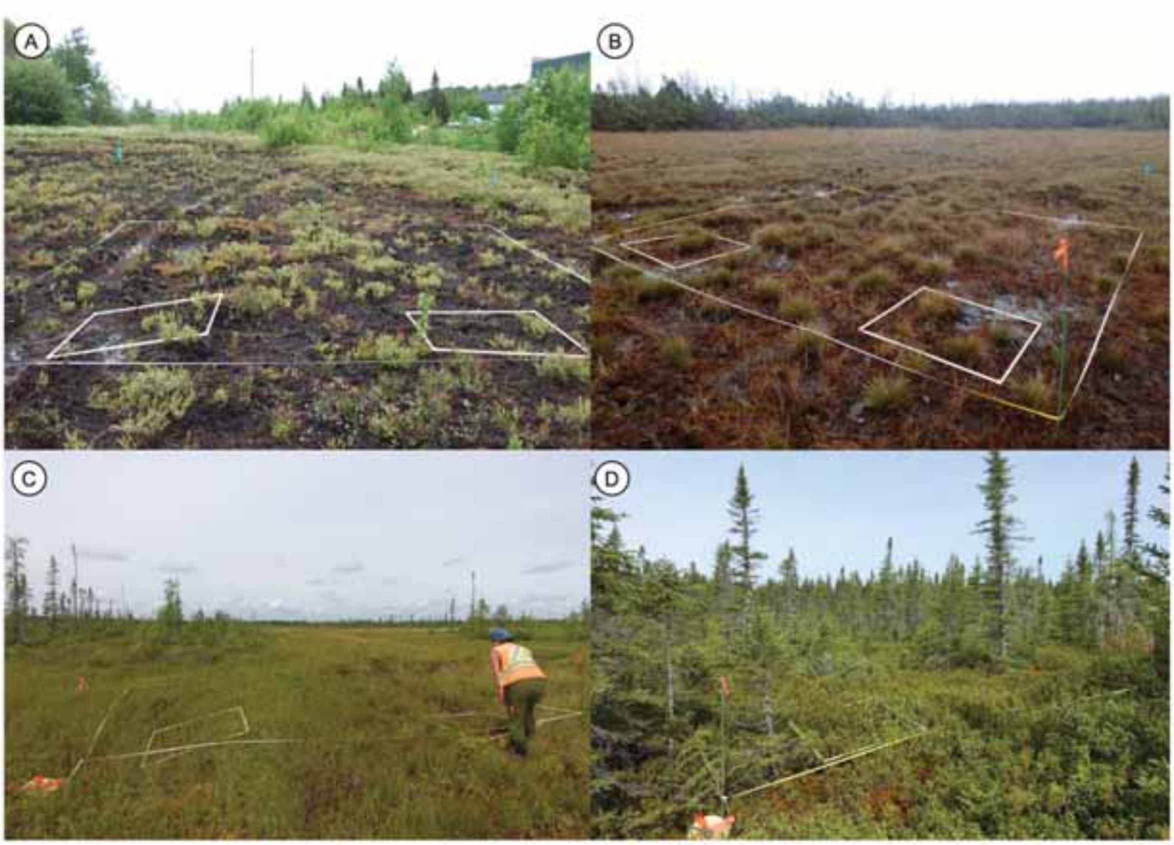
Appendixes

Appendix 3.1 Characteristics of the 25 donor sites.

Industrial peatland site	Number of year post-harvest	Latitude	Longitude	Harvest	
				Method	Season
Northeastern Forest Region (province of Quebec)					
Les Escoumins	5	48º 18' 55" N	69º 26' 6" W	Rototiller	Fall
Pointe Lebel	6.5	49º 9' 34" N	68º 15' 38" W	Rototiller	Fall
Sept-Iles	3	50º 17' 16" N	66º 0' 19" W	Rototiller	Fall
St-Ludger-de-Millot	4	48º 52' 6" N	71º 47' 49" W	Rototiller	Summer
St-Ulric-de-Matane	4	48º 47' 20" N	67º 40' 38" W	Rototiller	Fall
Ste-Marguerite-Marie	14.5, 17	48º 47' 59" N	72º 11' 13" W	Rototiller	Spring
Great Lakes and St. Lawrence Lowlands Region (province of Quebec)					
Président Ouest	3, 4	47º 47' 18" N	69º 30' 3" W	Rototiller	Fall
St-Antonin	3, 11, 12, 13	47º 47' 8" N	69º 28' 23" W	Rototiller	Fall
St-Henri	2	46º 42' 28" N	71º 4' 5" O	Rototiller	Fall
Atlantic Region (province of New Brunswick)					
Baie-Ste-Anne	2, 2	47º 2' 1" N	64º 56' 24" W	Bucket with comb teeth	Fall
Kent	7, 7, 13	46º 18' 33" N	65º 8' 19" W	Rotary harrow	Fall
Lamèque	3	47º 49' 7" N	64º 33' 20" W	Rototiller	Spring
Maisonnette	9, 16	47º 48' 53" N	65º 3' 3" W	Rototiller	Fall
Rogersville	1	46º 41' 34" N	65º 25' 12" W	Bucket with comb teeth	Fall
Northwestern Forest Region (province of Alberta)					
Seba beach	4, 7	53º 28' 31" N	114º 52' 38" W	Mulcher	Winter



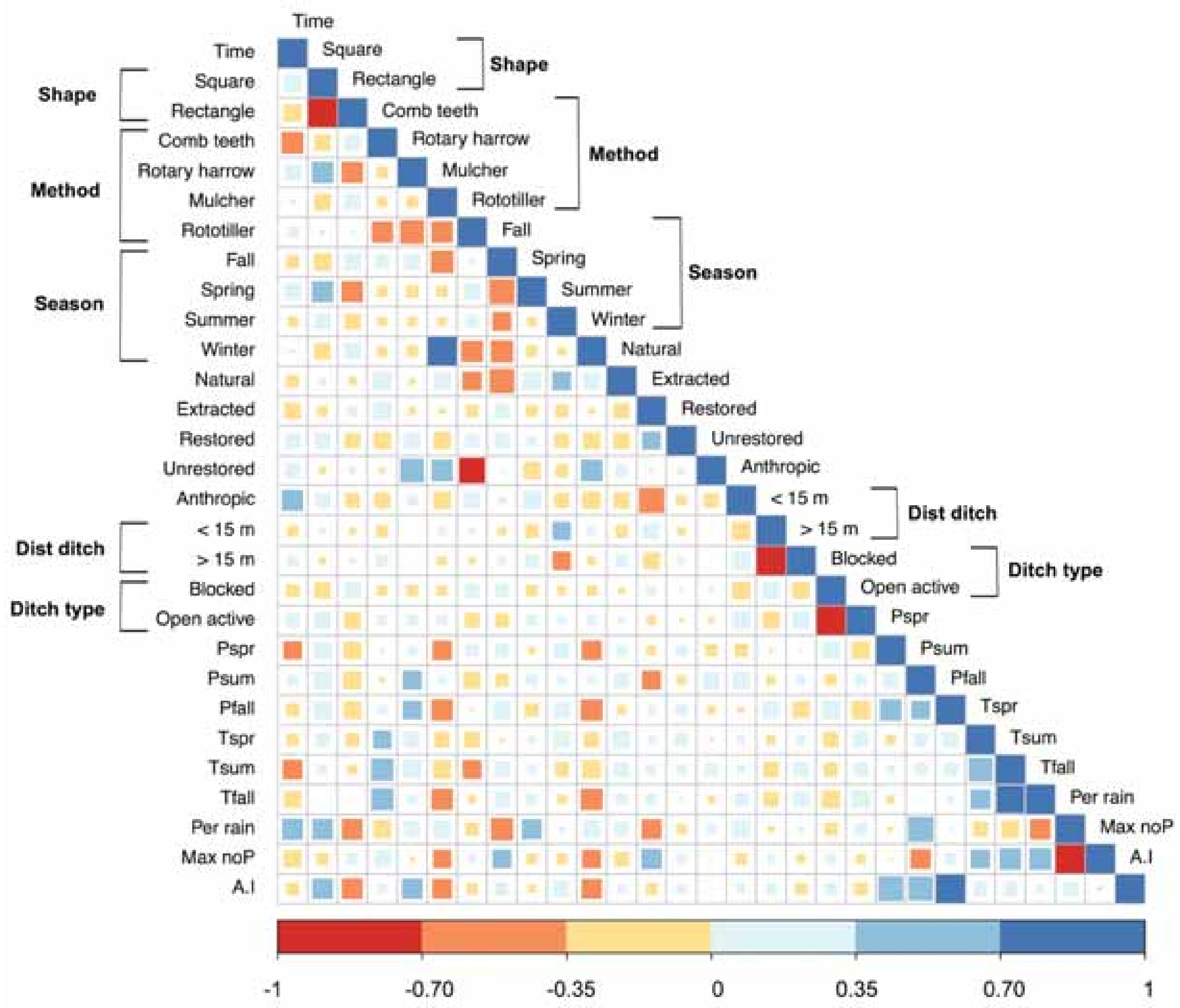
Appendix 3.2 Disposition of natural reference site plot in the case of the presence and absence of an adjacent open *Sphagnum* peatland.



Appendix 3.3 Pictures of the vegetation plot in the a) bare and disturbed b) in regeneration c) wet *Sphagnum* d) dry *Sphagnum* sites.

Appendix 3.4 Explanatory variables selected during the forward selection procedure for the RDA done on the vegetation stratum matrix for all the donor sites. An asterisk indicates variable that are not shown on the RDA triplot to improve the visual clarity (Figure 3.4). Appendix 3.5 presents correlation between all explanatory variables.

Group	Variables	df	AIC	F	*p*
Management	Time	1	168.77	54.06	0.005
	Unrestored	1	138.51	13.50	0.005
	Anthropic	1	150.26	14.37	0.005
	Season (spring*, summer)	1	161.06	5.74	0.005
	Extracted	1	166.11	6.76	0.005
	Restored*	1	170.09	5.63	0.005
	Method (rototiller, rotary harrow, mulcher)	1	179.12	6.23	0.005
	Shape (rectangle)	1	183.30	5.61	0.01
	Natural	1	194.69	3.96	0.01
Hydrology	Ditch type (*open active*)	1	203.18	7.21	0.005
	Dist ditch (> *15 m*)	1	181.33	4.29	0.01
Meteorology	Tsum	1	186.95	5.06	0.02
	Tspr*	1	189.09	3.62	0.02
	Max noP	1	192.06	4.32	0.01
	Per rain	1	197.71	4.24	0.005
	A.I*	1	219.00	10.43	0.005
	Psum	1	201.33	2.97	0.04



Appendix 3.5 Triangular correlation matrix between explanatory variables based on Spearman correlation. Categorical variables (shape of donor site, method and season of harvesting, the distance to the closest drainage ditch and its type) were presented as dummy variables. Therefore, classes within categorical variables composed of only 2 classes were strongly correlated with each other.

Chapitre 4

Is the presence of graminoid plants beneficial to moss carpet development in a restored fen?

Mélina Guêné-Nanchen et Line Rochefort

Résumé

Des plantes graminoïdes peuvent croître avec des sphaignes dans les tourbières restaurées et elles pourraient avoir un impact sur la structuration des tapis muscinaux en minimisant les variations du microclimat ou en servant d'échafaudage. Cette étude vise à évaluer l'effet d'une plante graminoïde sur le développement annuel des tapis de *Sphagnum warnstorfii* dans une tourbière minérotrophe restaurée. Le développement annuel du couvert, de l'épaisseur, de la densité et de la biomasse de *S. warnstorfii* a été mesuré sur des transects où le couvert, la densité et la biomasse de *Carex aquatili*s et de litière ont été évalués. Le microclimat (température, humidité, luminosité) sous différentes densités de *C. aquatilis* et de litière a été décrit. Les régressions ont révélé que l'effet du *C. aquatilis* sur le développement annuel du tapis de *S. warnstorfii* était principalement contrôlé par sa litière plutôt que par la structure de la plante graminoïde vivante. La litière de *C. aquatilis* avait un effet négatif sur le développement annuel de *S. warnstorfii*, en réduisant l'accessibilité à la lumière, et ce même si des seuils de couvert et de biomasse de litière ont été observés en dessous desquels *S. warnstorfii* pouvait tolérer la présence de litière. Ainsi, dans un contexte de restauration, la présence d'une communauté dense d'une plante graminoïde accumulant beaucoup de litière n'est pas idéale pour développer des tapis de *S. warnstorfii* productifs. Cependant, les seuils spécifiques de couvert et de biomasse de litière présentés dans cette étude doivent être considérés avec prudence en raison de certaines erreurs méthodologiques potentielles.

Abstract

Graminoid plants are often growing with *Sphagnum* mosses in restored peatlands and could have an impact on moss carpet structure by minimizing microclimate variations or serving as scaffolding. This study aims to evaluate the effect of a graminoid plant on annual *Sphagnum warnstorfii* carpet development in a restored minerotrophic peatland. *Sphagnum* annual carpet development (cover, thickness, density and biomass) was measured on transects where the cover, density and biomass of the sedge, *Carex aquatilis* and litter were evaluated. Microclimate (temperature, humidity, light) in relation to different densities of *C. aquatilis* and litter was characterized. The regressions revealed that the effect of *C. aquatilis* on *S. warnstorfii* annual development was controlled by the litter rather than by the structure of the living plant. Litter had a negative impact on *S. warnstorfii* annual development, by reducing light accessibility, even though thresholds of litter cover and biomass were observed, below which *S. warnstorfii* could tolerate the presence of litter. Therefore, in the context of restoration, the presence of dense graminoid plant communities that accumulate a lot of litter is not ideal to develop productive *S. warnstorfii* carpets. Though, the specific threshold of litter cover and biomass presented in this study should be considered with caution because of potential methodological errors.

Introduction

During peatland restoration, reintroduction of plants from a natural peatland favors the establishment of the target species (generally mosses) but also of other plants transferred along with the target plant material. Graminoid plants that are pioneers in restored peatlands establish especially rapidly and sometimes densely. Their influence on the development of moss carpets has been discussed in the literature in different contexts (Malmer et al. 1994, Malmer et al. 2003, Pouliot et al. 2011), except in the context of restored peatlands.

Appropriate peatland restoration practices are essential to re-establish typical plant composition and structure of peatland vegetation and their ecological functions (e.g., carbon sink, biodiversity refuge). The restoration method developed by the Peatland Ecology Research Group (PERG), the Moss Layer Transfer Technique (MLTT; Quinty and Rochefort 2003), achieves these goals (Rochefort et al. 2013, Strack and Zuback 2013). This restoration method has been applied to more than 50 *Sphagnum*-dominated bogs (González and Rochefort 2014), one moderately rich fen (Rochefort et al. 2016), one well pad (Gauthier et al. 2017) and three *Sphagnum* farming stations in Canada (Pouliot et al. 2015, Brown et al. 2017), with additional applications of the MLTT currently underway in Europe (Karofeld 2015).

Even if the peatland restoration methods aim to improve certain environmental conditions, the restored peatland can remain hostile for the first few years up to well-developed *Sphagnum* carpet (Chimner et al. 2016). Facilitative relations between plants are known to predominate in environments with harsh conditions (Callaway 1995, Callaway and Walker 1997), therefore, we could expect graminoid plants to have a facilitative effect on *Sphagnum* in restored peatlands.

Graminoid plants have a beneficial effect for *Sphagnum* carpet development by serving as a scaffolding matrix for growth. A dense cover of graminoid plants increased *Sphagnum* fiber length but decreased the overall biomass production (Pouliot et al. 2011, Guêné-Nanchen et al. 2017, Chapter 5 of this thesis). Graminoid plants can also facilitate *Sphagnum* moss establishment and development by improving microclimate conditions. For instance, intermediate levels of vascular plant biomass favor bryophyte growth because radiation and moisture conditions are optimal (Tuittila et al. 2000, Bergamini et al. 2001, Peach and Zedler 2006). Indeed, shading by vascular plants can benefit bryophytes if at the same time, it reduces water loss by evaporation, and photoinhibition. Under intense light conditions, photoinhibition controls photosynthesis and *Sphagnum* productivity (Harley et al. 1989, Murray et al. 1993, Nelson et al. 1998, Zona et al. 2011). Relative humidity and air temperature also have an important role in desiccation resilience of *Sphagnum* (Sagot and Rochefort 1996). *Sphagnum* carpet could also benefit from graminoid litter during the growing season because litter can act as a protective mulch (Tuittila et al. 2000).

However, depending on graminoid plant growth form and litter accumulation potential, they can also compete with *Sphagnum* for resources. For example, the sedge, *Eriophorum vaginatum* L. grows in tussocks that can compete with *Sphagnum* for space. Under a complete (100 %) cover of *E. vaginatum*, Pouliot et al. (2011) observed that *Sphagnum* frequency was 42 % lower if the dominant species was *E. vaginatum* rather than *E. angustifolium* Honck. (grows in unique stems). Malmer et al. (1994) also proposed that litter could inhibit *Sphagnum* growth in the fall when hydrologic conditions are ideal because of decreased light accessibility (Malmer et al. 1994). In fact, these authors suggested that the effect of shading by the graminoid plants on *Sphagnum* carpets was rather controlled by the accumulation of above-ground litter than by the plant direct shading. The accumulation of litter has been considered as an important phenomenon controlling vegetation structure (Facelli and Picket 1991, Xiong and Nilsson 1999). Establishment of plant species was pointed out as one of the most sensitive processes to the presence of litter (Grubb 1977). A meta-analysis evaluating the effects of plant litter on the vegetation reported an overall negative effect of litter (Xiong and Nilsson 1999). However, this effect varied according to multiple factors, such as the litter abundance and type, the ecosystem types and the target species.

The different conditions of restored peatlands, such as their residual peat chemical conditions and the diaspores source used for plant reintroduction, could influenced the colonization by different graminoid plant species. In Canada, different graminoid plants were observed in restored sites, mainly *Eriophorum* spp. and *Trichophorum* spp. in *Sphagnum*-dominated bogs (González et al. 2013), and *Scirpus* spp., *Carex* spp. and *Calamagrostis* spp. in fens (Rochefort et al. 2016). The goal of this study is to evaluate the effect of one common graminoid plant species, *Carex aquatilis* Wahlenb., specifically the effect of living part of the graminoid plant and its litter on *Sphagnum* in a restored minerotrophic peatland where this graminoid plant and *Sphagnum warnstorfii* Russow had been reintroduced. We hypothesized that the effect of *Carex aquatilis* on *Sphagnum warnstorfii* carpet, should be mainly controlled by its litter. Low cover of litter (< 50 %; Pouliot et al. 2011) should have the positive effect of a natural mulch by increasing relative humidity and minimizing temperature fluctuations but at higher cover (> 75 %; Malmer et al. 1994), its effects should be negative by limiting the light accessibility.

Materials and methods

Study area

The study site is a minerotrophic peatland (*i.e.* a fen) in the Lower-St-Laurence region (48º 19' N 68º 50' W) in Quebec, Eastern Canada. Mean annual temperature is 4.4 ºC and cumulative annual precipitation reach 959 mm of which 72 % falls as rain (Government of Canada 2017). Originally, the peatland was a shallow lake, where organic matter accumulation started 5000 years ago to form a rich fen and then an ombrotrophic peatland around 2000 years ago. This peatland was extracted from 1946 to 2000. The residual sedge peat layer was characterized as poor to moderately rich minerotrophic conditions (Bérubé et al. 2017): pH = 6.0 ± 0.4 (mean ± SD), corrected electrical conductivity = 229 ± 141 µS cm^{-1}. Von Post degree of decomposition ranged between H3 and H6 and the peat layer was from a few centimeters to 1–2 m thick depending on the location.

Context of the experimental design

In 2009, the peatland was restored using an adapted version of the MLTT (Rochefort et al. 2016). At the same time, in a sector that was only rewetted, fen plants (e.g., *Carex aquatilis*, *Myrica gale* L., *Sphagnum warnstorfii, Tomentypnum nitens* (Hedw.) Loeske) were reintroduced manually in an area covering around 850 m^2. By 2014, the *C. aquatilis* planted had grown densely across the whole area, from an original density of 26 stems m^{-2} to a maximum of 500 stems m^{-2} (Figure 4.1).

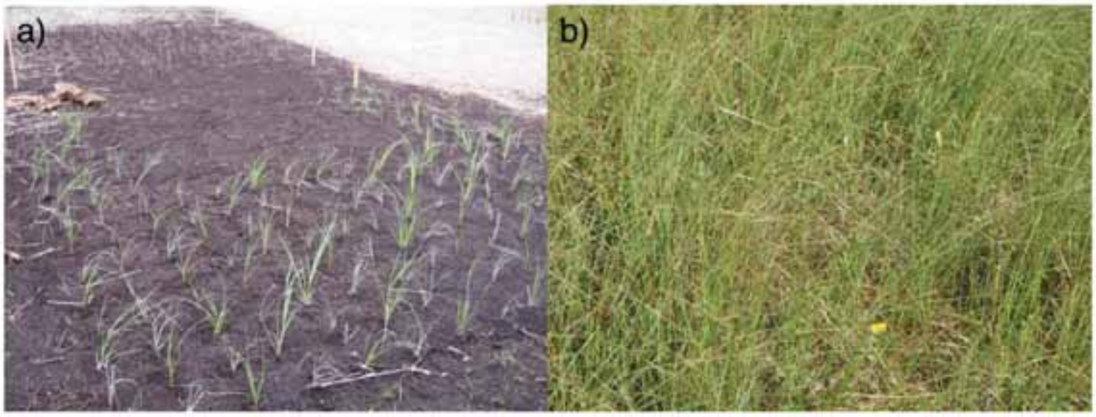


Figure 4.1a) Original density of plants of *Carex aquatilis* seedlings in 2009 and b) density of *Carex aquatilis* in 2014.

In 2014, 35 transects 3 m long were disposed randomly in the whole area. They had to be in areas characterized by variable cover of *C. aquatilis* (10 to 40 %) and its litter (30 to 90 %), presence of *S. warnstorfii*, low cover of other plants (< 1 %) and a water table depth of ca. -10 cm at the time of transect assignment. *Sphagnum warnstorfii* carpets were considered to be well established (ca. 10 cm thick) on all transects. In 2014, nine quadrats (15 cm x 15 cm) were disposed on one side of each transect for a total of 315 quadrats (Figure 4.2). Small quadrats were used to minimize our impact on the vegetation. However, analysis of the 2014 data was inconclusive, probably because the small size of the quadrat made it difficult to correctly estimate vegetation variables and, induced a lot of unwanted variability and experimental error. Therefore, inventories were repeated in 2015 with 3 larger quadrats (30 cm x 60 cm) that were disposed on each transect but on the other side (Figure 4.2).

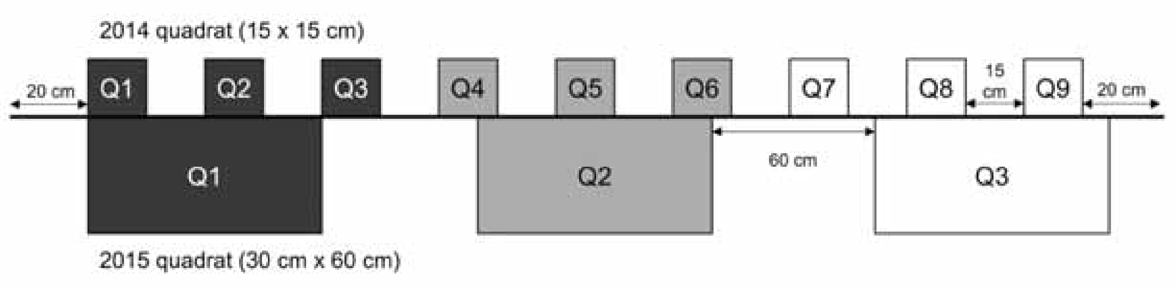


Figure 4.2. Disposition of the quadrats inventoried in 2014 (15 cm x 15 cm) and 2015 (30 cm x 60 cm). 2014 quadrats of the same color indicate quadrats whose sum was used to match with the 2015 quadrat of the same color.

Experimental approach

Vegetation inventories

In early June of 2014 and 2015, *S. warnstorfii*, *C. aquatilis* and its litter percent cover were visually estimated in each quadrat. *C. aquatilis* density (number of stems) was also evaluated in each quadrat. *Sphagnum warnstorfii* carpet thickness to the surface of residual peat was measured in five points systematically placed in the 2014 quadrats and in nine points in the 2015 quadrats. *Sphagnum warnstorfii* density (number of capitula) was evaluated in one subsample of 42 cm² in the 2014 quadrats and in three subsamples of 42 cm² in the 2015 quadrats. Then, all of the aerial biomass above the residual peat in the quadrat was harvested at the end of July (general peak of biomass production for this geographical location) and brought back to the laboratory. Biomass was sorted according to

S. warnstorfii, *C. aquatilis*, and its litter, dried and weighed. Biomass of the subsamples was added to the total biomass after capitulum counting.

Microclimate

Microclimate (temperature, humidity, light) was measured during 2015 growing season. Air temperature and relative humidity were measured at 30 minutes intervals from JD 165 to 229 with a HOBO U23 Pro V2 data logger RH/T (Onset, Bourne, MA, USA) in five *C. aquatilis* densities (ca. 0, 25, 50, 75, 100 %). The HOBO probe was installed 3 cm just above the *S. warnstorfii* carpet under a reflecting metallic cover to minimize the incidence of light and rain (Figure 4.3). *Carex aquatilis* and litter cover around the HOBO probe were evaluated three times in 50 cm x 50 cm quadrats during the measurement period. *Carex aquatilis* and litter cover were visually estimated within the following classes: < 1 %, 1–10 %, 11–25 %, 26–50 %, 51–75 % and 76–100 %.

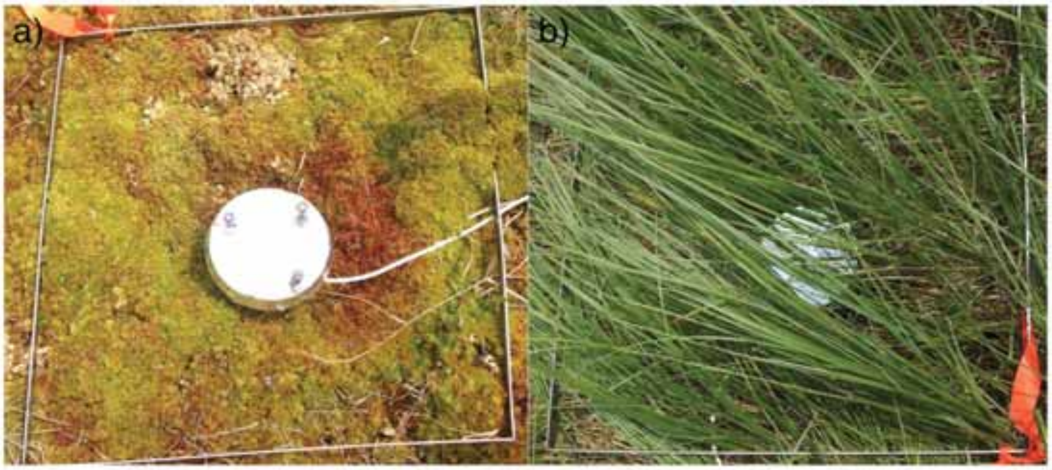


Figure 4.3. Examples of the HOBO probe disposition in a) <1 % and b) 76–100 % class densities of *Carex aquatilis* and litter under a metallic protective cover. *Carex aquatilis* and litter cover were estimated in the 50 cm x 50 cm quadrat around the probe.

Photosynthetically active radiation (PAR) was measured with a Sunscan Canopy Analysis System (Delta T-Devices, Cambridge, UK) in five *C. aquatilis* and litter densities, once, at the end of the summer just above the *S. warnstorfii* carpet. For the five densities, *C. aquatilis* and its litter covered approximately 0, 25, 50, 75 and 100 % of the probe. 50 light measures were recorded at each density. Measurements were taken during the JD 230 between 11:00 and 14:00 when the sky was completely clear.

Statistical analysis

In order to evaluate the effect of *C. aquatilis* on the annual development of the *S. warnstorfii* carpet, each *S. warnstorfii* parameter (cover, moss layer thickness, capitulum density and biomass) from the 2014 quadrats was subtracted from the same parameter from the 2015 quadrats. To do so, values obtained for the first three 2014 quadrats on the transect were averaged to match with the first 2015 quadrat on the transect and the same was done for the following trios of quadrats (Figure 4.2). Therefore, experimental units (EU) are each annual difference calculated from the 2014 and 2015 quadrat (n = 105). Annual differences could be positive or negative meaning either an increased or a decreased development respectively. Regressions were run to quantify the relationship between the annual difference of the *S. warnstorfii* parameters (cover, moss layer thickness, capitulum density and biomass) and the *C. aquatilis* parameters measured in 2015 (living plant: cover, density, biomass; litter: cover, biomass). The regressions were tested for linear, polynomial and logarithmic relationships. Because data comprise multiple measures on each transect, analyzes were completed using mixed effects (LME) models with transect as a random factor. All models were visually inspected for normality and homogeneity of residuals. A more severe alpha ($\alpha = 0.01$) was chosen to minimize the type 1 error rate because multiple mathematical operations were operated before running the regressions.

Because microclimate fluctuations were expected to be greater around the zenith, only data from 10:00 to 15:00 were kept. Daily maximum air temperature and minimum relative air humidity were interpreted with cumulative curves according to *C. aquatilis* and litter cover classes for the period of measurements. PAR was analyzed according to a polynomial regression with *C. aquatilis* and litter cover as an explanatory variable (0, 25, 50, 75 and 100 %). R software (R Development Core Team 2016) was used to perform all analyzes.

Results

Effect of *Carex aquatilis*

Only the litter of *Carex aquatilis* had a significant negative effect on the annual development on the *Sphagnum warnstorfii* carpet. *Sphagnum warnstorfii* was only significantly impacted in terms of cover and accumulation of biomass (Appendix 4.1). According to the Figure 4.4, increased abundance of litter caused a reduction of the annual *S. warnstorfii* cover only over a threshold of 50 % of litter cover and of 170 g m^{-2} of litter biomass, demonstrating that the presence of litter could be tolerated by *S. warnstorfii*. Decreased annual development of *S. warnstorfii* biomass was also observed over a threshold of 70 % of litter cover and 368 g m^{-2} of litter biomass. Of both litter parameters, the litter cover explained most, the variability of the annual development on the *S. warnstorfii* carpet (Appendix 4.1).

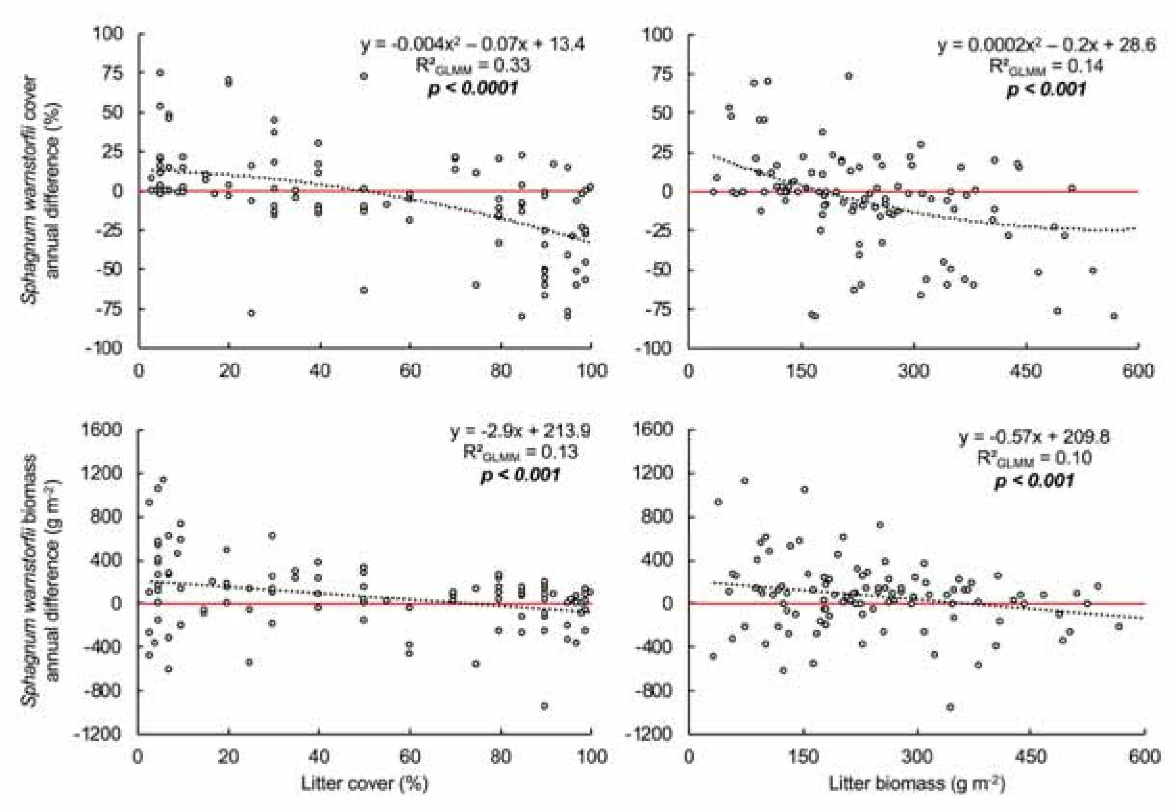


Figure 4.4. Significant regressions (α = 0.01) between the annual difference of *Sphagnum warnstorfii* parameters (cover and biomass) and *Carex aquatilis* litter parameters (cover and biomass). (%). Each point represents a value from a single experimental unit (n = 105). R^2_{GLMM} accounted for the variance explained by the fixed factor only.

Microclimate

Daily maximum air temperature and minimum relative air humidity did vary under different covers of *C. aquatilis* and litter, but no clear trend was observed. Between 10:00 and 15:00, the daily maximum temperature was equal or higher than 28 to 32 ºC for all vegetation classes 50 % of the time. During the same period, the daily minimum relative humidity was equal or lower than 48 to 60 % for all vegetation classes 50 % of the time (Table 4.1). A significant negative polynomial effect of *C. aquatilis* and litter cover was observed on the PAR ($R^2 = 0.99$, $p < 0.0001$; Figure 4.5).

Table 4.1. Maximum daily air temperature (ºC) and minimum daily relative air temperature found 50 % of the time between 10:00 and 15:00 from JD 165 to 229 in the different cover classes (< 1 %, 1–10 %, 11–25 %, 26–50 %, 51–75 % and 76–100 %) of *Carex aquatilis* and litter.

	Cover class	Maximum daily air temperature (ºC)	Minimum daily relative air humidity (%)
Carex aquatilis	< 1 %	29	53
	1–10%	31	48
	11–25%	32	60
	26–50%	31	57
	51–75%	30	54
Litter	< 1 %	29	53
	1–10%	28	48
	11–25%	32	59
	26–50%	31	57
	51–75%	29	60
	76–100%	31	48

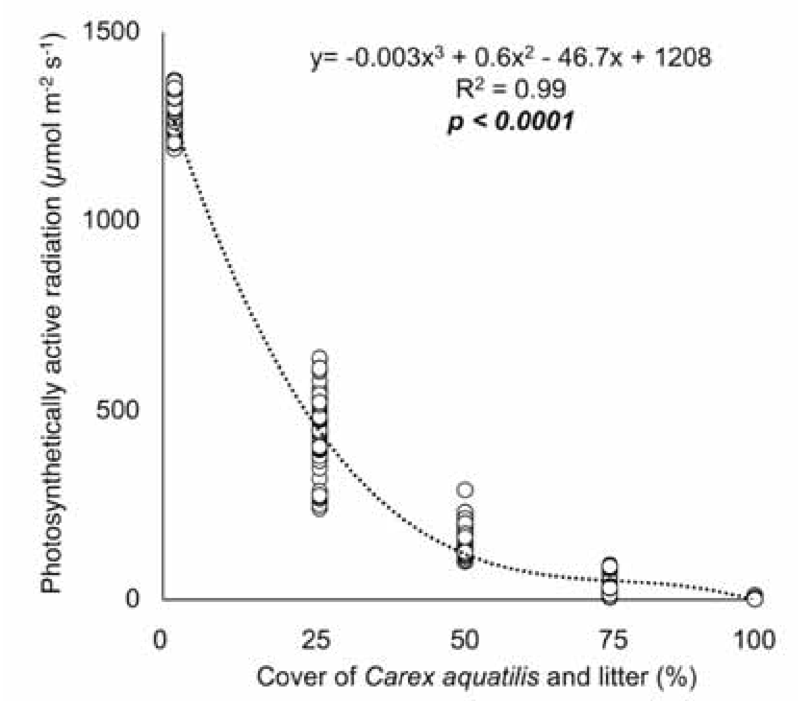


Figure 4.5. Photosynthetically active radiation (PAR) (µmol m^{-2} s^{-1}) varied with *Carex aquatilis* and litter cover (estimated together) analyzed with a polynomial regression model (α = 0.05) (n = 250).

Discussion

Effect of *Carex aquatilis*

This experiment showed that the effect of *C. aquatilis* on the *S. warnstorfii* carpet annual development was mainly controlled by the litter rather than by the plant itself. An increase in litter abundance induced a decrease in the annual development of the *S. warnstorfii* carpet in terms of cover and biomass. However, in this experiment, it is important to note that the methodology did not allow us to completely separate the effect of the litter from the effect of the plant itself. Malmer et al. (1994) also found that the decrease of *Sphagnum* production observed with the presence of graminoid plants was the result of the aboveground litter accumulation on the moss carpet rather than the effect of shading caused by the vascular plant itself. But, Malmer et al. (1994) did not fully discriminate the effect of shading by the litter compared to the one produced by the plant alone. Considering the structure of *C. aquatilis* plant, it can be supposed that its litter should affect more the underlying vegetation rather than its unique standing stems.

According to Bartsch and Moore (1985), *C. aquatilis* plant have a high aboveground production (164 ± 97 g m^{-2} per year) and therefore, this species was expected to produce high quantity of litter. The impact of litter is related to its decomposition rate (Meentemeyer 1978, Berg et al. 1993). Among other graminoid plants, *Carex* leaves decompose slowly. Losses by decomposition were evaluated to vary from 12 to 18 % over a year (Bartsch and Moore 1985), to be of 37 and 46 % over two years (respectively Arp et al. 1999 and Thormann et al. 2001). In this experiment, *C. aquatilis* accumulated substantial amount of biomass over a 6-year period (maximum value of dry litter biomass recorded = 600 g m^{-2}). Nonetheless, litter biomass was not the most important variable affecting *S. warnstorfii*. A considerable amount of litter biomass was incorporated in the *Sphagnum* matrix and therefore did not directly impact light accessibility for *S. warnstorfii*, compared to the litter cover.

Microclimate variations

This study did not find a clear effect of *C. aquatilis* or its litter on the microclimate variables of air temperature and relative humidity. The maximum daily air temperature was expected to be greater and minimum daily relative air humidity lower in lowest cover classes of *C. aquatilis* and litter. The protective covers installed above the HOBO probe may have been too protective to allow detection of variations of microclimate differences under different *C. aquatilis* and litter cover. Consequently, the variations between the different individual plants and litter cover could have been related to microvariations in local conditions (e.g., water table depth, vegetation composition) occurring at very small spatial scales. However, graminoid plant and litter cover did show a major impact on incident light radiation. Vascular plants and their litter are known to have a direct impact on the light reaching the underlying stratum (Facelli and Pickett 1991, Xiong and Nilsson 1999, Weltzin et al. 2005). *Sphagnum warnstorfii* is known to be adapted to shady environments and its compensation point around 60 μmol m^{-2} s^{-1} (Harley et al. 1989). An annual increase of *S. warnstorfii* cover and biomass was possible under moderate-high cover of litter (50–70 %) and biomass litter (170 g m^{-2}). However, above these thresholds, there is probably not enough light to maintain the *Sphagnum* mats.

Potential methodological errors

Looking back at our choice of the methodological approach, we think there were a few experimental errors that might have compromised our results. First of all, when using only the data collected in 2014 to regress the *S. warnstorfii* parameters along the *C. aquatilis* parameters, all regressions were not significant and they explained very low percentage of *S. warnstorfii* parameters variation (R^2 < 1 %). Our inability to detect the effect of *C. aquatilis* on *S. warnstorfii* was probably caused by the small size of the vegetation quadrat used (15 cm x 15 cm). Indeed, such small quadrats made it very difficult to collect the biomass of *S. warnstorfii* and litter while respecting the edges of the quadrat, and induced a boundary bias (Elzinga et al. 1998).

In 2015, we adjusted the vegetation quadrat size (30 cm x 60 cm). Using a bigger quadrat minimized the boundary bias caused by a high ratio perimeter: area which was of 0.26 for the 15 cm x 15 cm quadrat and of 0.1 for the 30 cm x 60 cm. When using values obtained in 2015 to implement the same regressions as in 2014, we obtained significant regressions. Therefore, this meant that an effect of *C. aquatilis* on *S. warnstorfii* existed when measured the appropriate way.

Even, if we were able to make up in 2015 by adjusting the quadrat size, using only the 2015 data caused another problem. We knew that *S. warnstorfii* was reintroduced everywhere in the study area in 2009, however, we did not have data on the evolution of the *C. aquatilis* community, which was planted in some areas in 2009 but had invaded the whole study area by 2014. Therefore, we decided to evaluate the effect of the current *C. aquatilis* community (2015 data) on the *Sphagnum* annual development between 2014 and 2015, assuming that the *C. aquatilis* community was similar between 2014 and 2015. To do that, the values of the *Sphagnum* parameters measured in 2014 were subtracted from the ones of 2015. However, we believe that the boundary bias caused by the quadrat size in 2014 was translated in the calculation of the *Sphagnum* annual development and induced an error. Assuming that *Sphagnum* carpets were uniform in the study area might have caused some errors. Indeed, if *Sphagnum* carpets, in terms of cover, carpet thickness, biomass and density, were slightly different between the two sides of the transect, this might explain the important values of annual differences. Also, the fact that the 2014 and 2015 quadrats were not randomly chosen to be on one side of the transect induced another bias.

Conclusion

Interactions between graminoid plants and *Sphagnum* carpets are complex, but it is now clearer that litter accumulation has an important impact on the *Sphagnum* layer, sometimes more than the standing plant itself for species accumulating large amounts of litter. By reducing light accessibility, litter negatively impacted the annual development of the *S. warnstorfii* carpet in terms of cover and biomass. In the context of restoration aiming to develop a productive moss carpet, the presence of *C. aquatilis* and especially of its litter is not recommended if it is present in high densities (> 50–70 % of cover, 170–368 g m^{-2} of biomass) similar to our experiment. However, no recommendation on a specific threshold of *C. aquatilis* litter could be withdrawn from this study considering the bias induced by dubious methodology. However, the general recommendation to consider the effect of litter more than the effect of the standing plant itself when in presence of *C. aquatilis* is applicable.

Acknowledgments

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Appendix

Appendix 4.1 Results of the regressions between *Sphagnum warnstorfii* annual difference of the growth parameters (cover, thickness, biomass and density), *Carex aquatilis* plant (cover, density, biomass) and litter (cover and biomass) (NS = not significant, α = 0.01; n = 105). R^2_{GLMM} accounted for the variance explained by the fixed factor only.

		Carex aquatilis				
		Living plant			**Litter**	
	Variables	Cover (%)	Density (no. of stem m^{-2})	Biomass (g m^{-2})	Cover (%)	Biomass (g m^{-2})
Sphagnum warnstorfii **annual difference**	Cover (%)	NS	NS	NS	Poly 2nd negative $R^2_{GLMM} = 0.33$ $p < 0.0001$	Poly 2nd negative $R^2_{GLMM} = 0.14$ $p < 0.001$
	Thickness (cm)	NS	NS	NS	NS	NS
	Biomass (g m^{-2})	NS	NS	NS	Linear negative $R^2_{GLMM} = 0.13$ $p < 0.001$	Linear negative $R^2_{GLMM} = 0.10$ $p < 0.001$
	Density (no. of capitula m^{-2})	NS	NS	NS	NS	NS

Chapitre 5

Effect of repeated mowing to reduce graminoid plant cover on the moss carpet at a *Sphagnum* farm in North America

Mélina Guêné-Nanchen, Rémy Pouliot, Sandrine Hogue-Hugron et Line Rochefort

Résumé

La culture de sphaignes se définit comme la production durable de biomasse de sphaignes sur une base cyclique et renouvelable. Dans cet article, l'influence et la nécessité de contrôler les plantes graminoïdes afin d'optimiser la croissance des sphaignes dans les bassins de culture de sphaignes ont été examinées. La coupe répétée a été appliquée pour réduire le couvert des plantes graminoïdes dans deux cycles de production (tapis de sphaignes âgés d'un an et de sept ans au début de l'expérience) à une station expérimentale de culture de sphaignes dans l'est du Canada. La croissance des sphaignes (recouvrement, biomasse, épaisseur du tapis) a été mesurée après trois ans de coupe. De plus, une expérience en serre a été effectuée afin de déterminer s'il existe un seuil du couvert de plantes graminoïdes au-delà duquel la coupe devient nécessaire. Le recouvrement et l'accumulation de biomasse de sphaignes n'étaient pas affectés par la coupe répétée, même si la coupe a réduit le couvert de plantes graminoïdes. Il semble donc que la coupe n'est pas nécessaire si la plante vasculaire dominante est une plante graminoïde qui, comme *Eriophorum angustifolium*, accumule peu de litière. De plus, des couverts élevés d'*Eriophorum angustifolium* (jusqu'à 85 %) n'ont pas affecté le recouvrement de sphaignes dans l'expérience en serre. Lorsque le but spécifique de la culture de sphaignes est la production de biomasse de sphaignes, la décision de contrôler les plantes graminoïdes devrait être prise en considérant le couvert, la forme de croissance et le potentiel d'accumulation de litière de l'espèce graminoïde dominante.

Abstract

Sphagnum farming is defined as the sustainable production of non-decomposed *Sphagnum* biomass on a cyclical and renewable basis. In this article, the influence and necessity of mowing graminoid plants to optimize *Sphagnum* growth in *Sphagnum* farming basins are examined. Repeated mowing was applied to reduce graminoid plant cover at two different stages of the production cycle (one-year-old and seven-year-old *Sphagnum* moss carpet at the beginning of the experiment) at an experimental *Sphagnum* farm in eastern Canada. *Sphagnum* growth (cover, biomass, moss layer thickness) was measured after three years of mowing. In addition, a greenhouse experiment was carried out to determine whether there is a threshold for graminoid plant cover beyond which mowing becomes necessary. *Sphagnum* cover and biomass were not affected by repeated mowing, even if mowing reduced the cover of graminoid plants. Thus, it appears that mowing is unnecessary if the dominant vascular species is a graminoid plant such as *Eriophorum angustifolium*, which accumulates minimal amounts of litter. Furthermore, high cover of *Eriophorum angustifolium* (up to 85 %) did not affect *Sphagnum* cover in a density-controlled greenhouse experiment. When the specific goal is *Sphagnum* fiber production, decisions about control of graminoid plants should be made after considering the cover, life form and litter accumulation potentials of the dominant graminoid species involved.

Introduction

Sphagnum farming is the sustainable production of non-decomposed *Sphagnum* fibers on a cyclical and renewable basis, i.e. it can be produced over repeated production cycles and it can replenish itself over time. As the market for *Sphagnum* fiber expands (Zegers et al. 2006), the sustainable production of *Sphagnum* biomass will become increasingly important to reduce human pressure on the natural bogs where *Sphagnum* fiber is usually harvested (Díaz & Silva2012). *Sphagnum* fiber can be substituted for industrially extracted peat, perlite or vermiculite in peat-based horticultural substrates without impeding plant growth and even increasing it in some cases (e.g. Emmel 2008, Reinikainen et al. 2012, Jobin et al. 2014, Aubé et al. 2015), thus minimizing the carbon footprint of peat-based growing media. *Sphagnum* farming ensures more responsible management of peatlands and more sustainable horticulture (Joosten & Clarke 2002, Caron & Rochefort 2013).

Despite these numerous benefits and the growing interest of the peat industry in cultivating *Sphagnum* mosses, research on *Sphagnum* farming is less than two decades old (Gaudig et al. 2014). A previous study by Pouliot et al. (2015) demonstrated that optimizing the water supply to *Sphagnum* mosses is critical for maximizing yields in large-scale *Sphagnum* farms. Other factors that can influence *Sphagnum* biomass accumulation are the interactions between *Sphagnum* and other plants (other *Sphagnum* species, other mosses, and vascular plants). When *Sphagnum* farming sites are established, graminoid plants and ericaceous species can be introduced (as seeds, rhizomes etc.) along with the *Sphagnum* diaspores or recruited naturally via seed rain or animal movements. Therefore, the presence of vascular plants is inevitable in large-scale outdoor farms.

Significant cover of *Juncus effusus* L. has been observed in *Sphagnum* farming basins in Germany (Gaudig & Krebs 2016, Gaudig et al. 2017) and is regularly mown to keep graminoid plant cover below 20–30 %, but this is done as a precautionary measure without formal evaluation of any effects. Temmink et al. (2017) also mowed vascular plants to prevent competition with *Sphagnum* mosses but did not evaluate the effects of mowing. In Canada, vascular plants are present at all of the *Sphagnum* farming stations, but their cover does not generally exceed 25 % (L. Rochefort personal observation). Vascular plant cover in the first years following initiation of *Sphagnum* farms is dominated by fast-growing graminoids (e.g. *Eriophorum* spp., *Carex* spp., *Scirpus* spp.) while the cover of ericaceous shrubs remains low. Therefore, we focus here on the effect of controlling graminoid plant density on *Sphagnum* biomass accumulation.

The presence of graminoid plants could benefit *Sphagnum* farming by improving microclimate (e.g. by reducing daily range of air humidity, increasing relative air humidity, moderating the light environment; Tuittila et al. 2000, Bergamini et al. 2001, Pouliot et al. 2011). Graminoid plants can also increase the upward growth of *Sphagnum* moss when its density is moderate (around 50 %), by serving as ‘scaffolding’ (Malmer et al. 1994, Pouliot et al. 2011). However, Pouliot et al. (2011) also found that a very dense cover of vascular plants tends to reduce biomass accumulation because the *Sphagnum* mosses become more etiolated and ‘fluffy’, and grow in less dense communities. In addition, various experiments have demonstrated that the interception of light by vascular plants reduces *Sphagnum* growth when the photosynthetically active radiation (PAR) is reduced by at least 50 % (Clymo & Hayward 1982, Hayward & Clymo 1983). On the other hand, it is known that bryophytes generally have low compensation points (between 40 and 70 µmol m^{-2} s^{-1}), which allows them to tolerate low light conditions (Collins 1976). However, depending on the graminoid species present (especially their density and/or litter deposition), graminoid plants could have a negative effect on *Sphagnum* biomass accumulation overall by competing with *Sphagnum* growth and by lowering the substrate quality (Facelli & Pickettt 1991, PERG unpublished data). In the context of *Sphagnum* farming, whatever final use is intended for the *Sphagnum* fibers, the issue of whether graminoid plants increase *Sphagnum* biomass accumulation or impede its growth needs to be addressed. In other words, is it necessary to control graminoid density?

The general goals for this study were to evaluate the effect of reducing graminoid plant cover by repeated mowing and to determine if there is a threshold above which graminoid plants should be controlled in a *Sphagnum* farming system. More specifically, we examined the effect of graminoid plant cover and density on *Sphagnum* cover, moss layer thickness and biomass accumulation in: 1) a *Sphagnum* farming station where repeated mowing reduced graminoid plant cover; and 2) a greenhouse experiment where a *Sphagnum* carpet was established under different densities of graminoid plants. We hypothesized that, even if mowing reduced graminoid plant cover, it would not be necessary at the *Sphagnum* farm because graminoid cover was already relatively low, but a threshold should be observed in the greenhouse.

Methods

Mowing at a *Sphagnum* farming station

Study site

This study was conducted at an experimental *Sphagnum* farm on a cutover bog in eastern Canada (47° 40' N, 64° 43' W). Mean annual temperature is 4.8 °C and mean annual precipitation is 1077 mm, of which 70 % falls as rain (seasonal distribution of rainfall = 27 % in spring, 34 % in summer, 29 % in autumn, 10 % in winter) (Environment Canada 2015). Peat extraction was carried out from 1941 to 1971, using the block-cut method, and the resulting topography of baulks and trenches is still present. A complete description of the site is available in Pouliot et al. (2015).

From the different *Sphagnum* farming production cycles, moss carpets that were installed in two different years (2006 and 2012) were chosen to allow comparison of two contrasting developmental stages: 1) a seven-year-old (7 yr old) pre-established moss carpet; and 2) a one-year-old (1 yr old) moss carpet still in its establishment phase. The two developmental stages were located in adjacent *Sphagnum* basins within the same trench (see Figure 5.1a). In both production cycles, *Sphagnum* mosses (mainly *Sphagnum fuscum* (Schimp.) H. Klinggr., *S. rubellum* Wilson, *S. flavicomans* (Cardot) Warnst. and *S. magellanicum* Brid.) were re-introduced using an adaptation of the Moss Layer Transfer Technique (Graf et al. 2012). *Sphagnum* fragments (diaspores) were obtained from a natural peatland by shredding the uppermost 10 cm of vegetation, then spread onto bare peat at the *Sphagnum* farming site. Ditches were cleaned to a depth of approximately 30 cm. A wooden dam was installed to retain water in the basins over summer and allow discharge of surplus water from snowmelt in spring. Over time, with the establishment of *Sphagnum* mosses, the ditches slowly re-filled and became inactive (Figure 5.1).

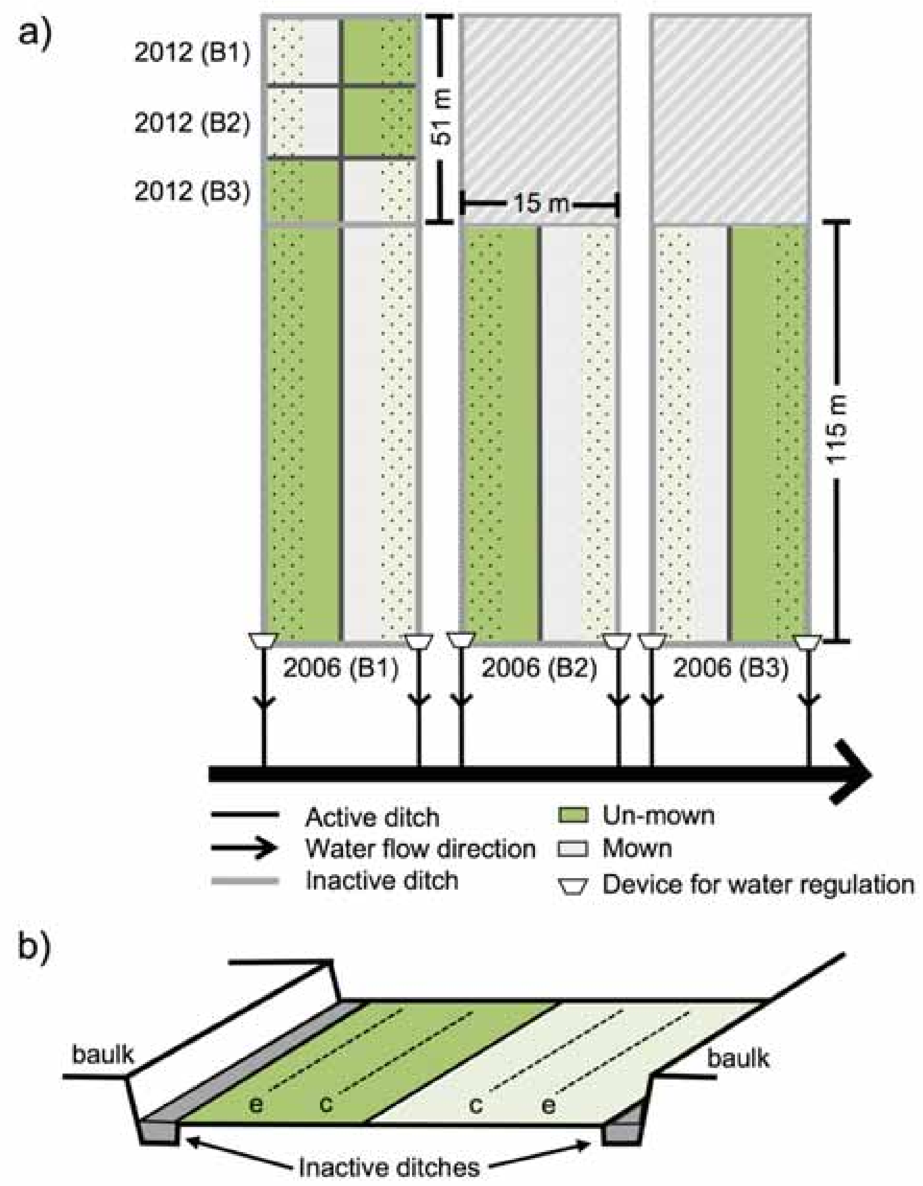

Figure 5.1a) Production cycle, block disposition (B1, B2, B3 = block [replica]) and treatment disposition (stippled = edge, unshaded = center) in the *Sphagnum* farming basins (hatched area is not part of the experiment) (2012 = 1 yr old production cycle and 2006 = 7 yr old production cycle). b) Example of the treatment disposition for one block with the mowing treatments (un-mown or mown) and the sub-treatments (e = edge, c = center). Dashed lines indicate the disposition of vegetation transects. The particular topography of trenches and baulks created by the block-cut peat extraction method is represented here. Inactive ditches were the old ditches used by the block-cut extraction that were re-dug to a depth of 30 cm during *Sphagnum* farming site installation. Over time, they re-filled with *Sphagnum* and peat. Devices for water regulation were wooden dams placed during site installation. This figure is not to scale.

Mean water table levels were -4.6 cm for the 7 yr old moss carpet and -15.5 cm for the 1 yr old moss carpet (calculated from Table 2 in Pouliot et al. 2015). *Sphagnum* cover at the beginning of the experiment was ~ 90 % in the 7 yr old moss carpet and ~ 60 % in the 1 yr old moss carpet, the majority of it being *S. rubellum* (Pouliot et al. 2012). At the same time, many graminoid plants (~ 40 % cover) were observed in the 7 yr old vegetation and few (~ 1 % cover) in the 1 yr old *Sphagnum* carpet. The 7 yr old graminoid plant cover was dominated by *Eriophorum angustifolium* Honck. with 1 % of *Eriophorum vaginatum* L. and 3 % of ericaceous species. The same species were observed in the 1 yr old moss carpet, but all with cover < 1 % (PERG unpublished data). Because it was considered highly likely that graminoid plants would disperse from one of the 7 yr old basins into the 1 yr old production cycle, precautionary mowing of the 1 yr old basin was included in its management regime. This provided an opportunity to test whether a control method should be applied directly after site installation or as a corrective measure.

Experimental design

The effect on moss carpet development of mowing (main plot) and proximity to the edge of the culture basin (sub-plot) was investigated using a split-block design replicated 3 times. The different 1 yr old and 7 yr old production basins were divided into three blocks. The 7 yr old block size was 115 m × 15 m and the 1 yr old block size was 17 m × 15 m. Each of the blocks was divided lengthwise and one side was randomly chosen to be mown three times each growing season during three consecutive years (2013, 2014 and 2015) while the other side was not mown (Figure 5.1a). Mowing was carried out with a weed trimmer because this is a simple and efficient control method that does not disturb the physical integrity of the *Sphagnum* carpet. Weed trimmer operatives wore snowshoes to minimize the impact of trampling. Mowing was done in June (just after graminoid plant investment for flower production), in July, and in late August (at the end of the growing season for graminoid plants in this climatic region).

Vegetation survey

After three years of mowing treatments, vegetation surveys were performed on one transect disposed lengthwise per sub-plot. The transects were 95 and 14 meters long for 7 yr old and 1 yr old cycles respectively, and positioned in the centers of the sub-plots. Transect position (basin edge or center) was used as two sub-treatments to verify whether an edge effect (Figure 5.1b) was caused by the presence of the ~ 1.5 m wide baulks and various plants colonizing them (which were cut in the third year of treatments). *Sphagnum* cover, biomass and moss layer thickness were measured. To assess the efficiency of the mowing method, cover values for graminoid plants, litter and ericaceous species were also determined (Table 5.1).

Table 5.1 Number of samples (n) for each variable measured per experimental unit (UE) in the *Sphagnum* farm experiment for each production cycle and a description of the methodology.

Variables measured		n 7 yrs	 1 yr	Methodology
Cover (%)	*Sphagnum* Graminoid plants Graminoid litter Ericaceous species	9	2	Estimated visually in rectangular 1 m x 5 m quadrats placed systematically along each transect
Thickness (cm)	*Sphagnum*	46	6	Measured every 2 m on each transect
Biomass ($g\ m^{-2}$)	*Sphagnum*	5	2	Measured in 25 cm x 25 cm quadrats placed systematically along each transect where all vegetation above peat surface was collected. *Sphagnum* fibers were separated from other plant material, dried at 70 ºC and weighed.

After three years, graminoid plant cover differed significantly between the un-mown (22–34 %) and mown (4–14 %) treatments ($CI_{95\ \%}$) (see Table 5.2 for all t and p values) and graminoid litter cover was reduced from 6–7 % to 3–4 % ($CI_{95\ \%}$) in the 7 yr old cycle. For the 1 yr old cycle, only graminoid plant cover exhibited a significant decrease with mowing, from 5–11 % to 2–3 %. Ericaceous species cover was ~ 1 % lower on the mown side for both production cycles.

Table 5.2 Mean graminoid plant, its litter and ericaceous species cover ± CI (95 %) after three years of mowing for un-mown and mown treatments. Significant differences are bolded (p-value < 0.05) (Paired t-test, α = 0.05). Paired T-tests (where the mown edge (or center) of one basin is compared with the un-mown edge (or center) of the same basins) were performed to evaluate the effect of mowing on graminoid plants, its litter and ericaceous species. Paired T-tests were realized with R software (version 3.3.1).

	Treatments	Un-mown	Mown	df	t	*p*
7 yrs	Graminoid plant cover (%)	28 ± 6	9 ± 5	5	4.34	**0.007**
	Graminoid litter cover (%)	6 ± 0.5	3 ± 0.5	5	13.84	**> 0.001**
	Ericaceous species cover (%)	2 ± 0.5	1 ± 0.5	5	2.81	**0.009**
1 yr	Graminoid plant cover (%)	8 ± 3	2 ± 0.5	5	4.25	**0.008**
	Graminoid litter cover (%)	2 ± 3	Presence	5	1.43	0.09
	Ericaceous species cover (%)	2 ± 1	1 ± 0.2	5	2.32	**0.021**

Greenhouse experiment

Experimental design

This experiment was conducted in the greenhouse complex at Université Laval using mesocosms. The greenhouse conditions were set at 22 °C / 50 % RH during the day and 18 °C / 85 % RH during the night. The mesocosms were plastic containers measuring 61 × 41 × 42 cm (length × width × height) which were filled with rewetted horticultural peat (mean peat pH = 3.77 ± 0.03 SE). Each mesocosm accommodated two experimental units (EUs) with different treatments.

The experiment was implemented as a completely randomized design where five densities of *E. angustifolium* (0, 2, 4, 6 or 8 stems) were planted in each EU, and each EU was repeated 12 times. Individual stems of *E. angustifolium* were harvested on a post-extracted *Sphagnum*-dominated bog near Rivière-du-Loup, Québec (47° 50' N, 69° 27' W) and planted in the mesocosms in the following days. *Sphagnum* moss (*S. rubellum*) was collected from a natural peatland near Québec City (46° 39' N, 71° 19' W) and stored at 4 °C for one week before introduction to the mesocosms. *S. rubellum* was chosen because it was dominant in the field experiment and is often used in *Sphagnum* farms. The *Sphagnum* was spread immediately after the *E. angustifolium* was planted, as fragments ~ 5 cm long with capitula, on the peat surface in the mesocosms at a ratio of 1:5 (meaning that moss collected from 1 m^2 of natural mire was spread over 5 m^2 of mesocosm surface). The *Sphagnum* fragments formed a carpet about 1 cm thick covering all of the peat surface. The water level in each mesocosm was maintained independently, between 20 and 25 cm below the peat surface, by a system of perforated pipes and drains. Twice a week, the mesocosms were watered with rainwater until water escaped by the drainage holes. Between watering they were lightly misted to keep the moss carpet humid.

Measurements

After six months of growth, cover values for *Sphagnum* mosses and *E. angustifolium* were visually estimated by vertical projection in each EU. By visually estimating the *E. angustifolium* cover, its impact on the adjacent EU was considered because, if a leaf covered part of the inventory quadrat, it was included in the estimation no matter where it was rooted. *Sphagnum* moss carpet thickness (distance from the moss surface to the peat surface) was measured at ten points placed systematically within each EU, and *Sphagnum* capitula were counted in two 30 cm^2 circular samples placed systematically within each EU. Finally, *Sphagnum* biomass accumulated during the experiment was harvested for each EU, dried at 70 ºC and weighed (including the material used for the capitulum count). The amount of *Sphagnum* moss initially spread was the same in all treatments (weighed before spreading). The initial *Sphagnum* cover, biomass, *Sphagnum* moss layer thickness and number of capitula were all assumed to be zero. As new capitula grow on *Sphagnum* stem fragments, the initial number of capitula was negligible and the final *Sphagnum* cover and thickness arose from new capitula. As part of the initial material would have decomposed during the experiment, the initial weight of *Sphagnum* moss was not deducted from the final *Sphagnum* biomass. Thus, final *Sphagnum* biomass may have been slightly overestimated, but the effect was similar for all EUs.

Statistical analysis

For the *Sphagnum* farm experiment, two-way ANOVAs were performed to evaluate the effect of mowing (main plot) and transect position (sub-plot) on development of the *Sphagnum* carpet. Error terms were adjusted to take into consideration that randomization is not complete in sub-plots (split-block design). The variables analyzed were: mean *Sphagnum* moss cover, thickness and biomass. Following the ANOVAs, protected Fisher's LSDs were run. Analyzes were performed separately for the 7 yr old cycle and the 1 yr old cycle. The MIXED procedure of the SAS software was used (SAS Statistical System Software, v. 9.2, SAS Institute Inc., Cary, NC, USA). If needed, the GROUP statement of the function REPEATED was used to model variance and ensure homogeneity and normality of variances. Degrees of freedom were adjusted accordingly and the best model was selected by using the Akaike Information Criterion (AIC). Confidence intervals of 95 % are used to illustrate significant differences between treatments in Figure 5.2.

For the greenhouse experiment, linear regressions were run to quantify the relationships between *Sphagnum* moss metrics (cover, moss layer thickness, capitulum density and biomass) and *E. angustifolium* cover values. Means per EU were used for moss layer thickness and capitulum density. Because of fungal infections, 14 EU (of 60) were not considered in the analyzes, meaning that 46 EU were kept for the regressions. R software (R Development Core Team 2016) was used to perform the analyzes.

Results

Mowing at a *Sphagnum* farming station

After three years of mowing, *Sphagnum* cover and biomass in the pre-established moss carpet (7 yr old cycle) were not significantly different between mowing treatments (UM = un-mown, M = mown), regardless of position within the basin (c = center, e = edge) (Figure 5.2; no significant interaction between factors; see Appendix 5.1 for F and p-values). Cover and biomass accumulation hardly differed between the mowing treatments (for *Sphagnum* cover, $CI_{95\,\%} =$ 92–99 % [UM], 95–100 % [M]; for biomass accumulation, $CI_{95\,\%} =$ 991–1462 g m^{-2} [UM], 995–1477 g m^{-2} [M]). However, *Sphagnum* carpet thickness was significantly greater in the un-mown treatment ($CI_{95\,\%} =$ 26.9–29.9 cm [UM], 22.8–25.5 cm [M]). There were only small differences between center and edge of the basin for all of these factors (for *Sphagnum* cover, $CI_{95\,\%} =$ 91–99 % [c], 96–100 % [e]; for biomass accumulation, $CI_{95\,\%} =$ 967–1463 g m^{-2} [c], 1024–1472 g m^{-2} [e]; and for *Sphagnum* carpet thickness, $CI_{95\,\%} =$ 24.4–27.4 cm [c], 25.2–28.0 cm [e]).

In the establishing *Sphagnum* carpet (1 yr old cycle), *Sphagnum* cover and moss layer thickness were significantly higher in the ‘edge’ sub-plots (for *Sphagnum* cover, $CI_{95\,\%} =$ 64–82 % [c], 90–96 % [e]; for *Sphagnum* carpet thickness, $CI_{95\,\%} =$ 1.8–2.7 cm [c], 3.1–4.3 cm [e]). According to the confidence intervals, there also seemed to be a tendency towards higher biomass accumulation at the basin edge ($CI_{95\,\%} =$ 200–568 g m^{-2} [c], 462–825 g m^{-2} [e]), but the p-value was high ($p = 0.246$). Mowing did not significantly affect *Sphagnum* cover or biomass (for *Sphagnum* cover, $CI_{95\,\%} =$ 72–88 % [UM], 76– 96 % [M]; for biomass accumulation, $CI_{95\,\%} =$ 287– 686 g m^{-2} [UM], 339–743 g m^{-2} [M]. Even though a tendency towards thicker moss layer on the un-mown sides of the plots was observed, no significant difference was found for *Sphagnum* carpet thickness ($CI_{95\,\%} =$ 2.9–4.1 cm [UM], 1.9–3.0 cm [M]).

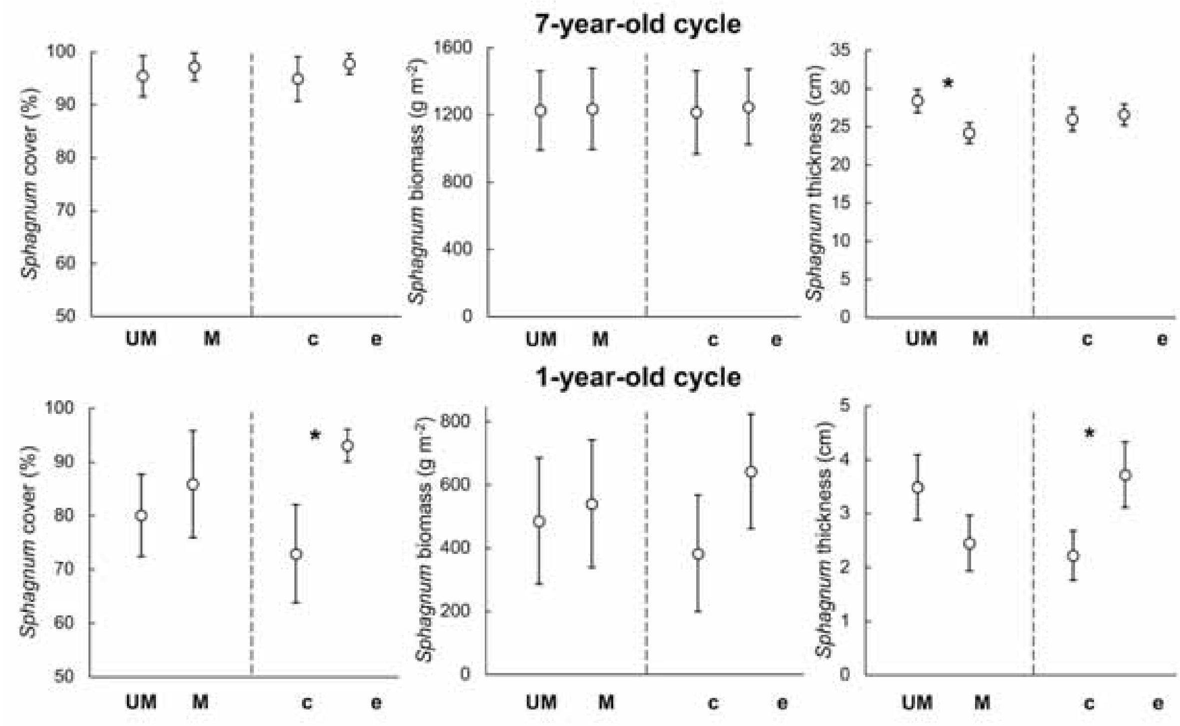

Figure 5.2 Means ± CI (95 %) for *Sphagnum* moss cover, moss layer thickness and biomass according to mowing treatment (UM = un-mown or M = mown) and transect position (c = center or e = edge) for both production cycles (simple effects). An asterisk (*) indicates a significant difference between treatments (p-value < 0.05) (LSD protected, α = 0.05). There was no significant interaction between factors (mowing and transect position). Production cycles were analyzed separately.

Greenhouse experiment

After six months of growth in a greenhouse, the different planting densities of *E. angustifolium* resulted in cover values ranging from 0 to 85 %. Except for *Sphagnum* carpet thickness, negative linear relations were found between *Sphagnum* growth variables and *E. angustifolium* cover (Figure 5.3). The regressions explained 18–45 % of the variance (adjusted R^2; Figure 5.3). The highest cover of *E. angustifolium* (85 %) induced reductions in *Sphagnum* cover, density and biomass of 14, 37 and 18 %, respectively, relative to the values when *E. angustifolium* was absent (equations; Figure 5.3).

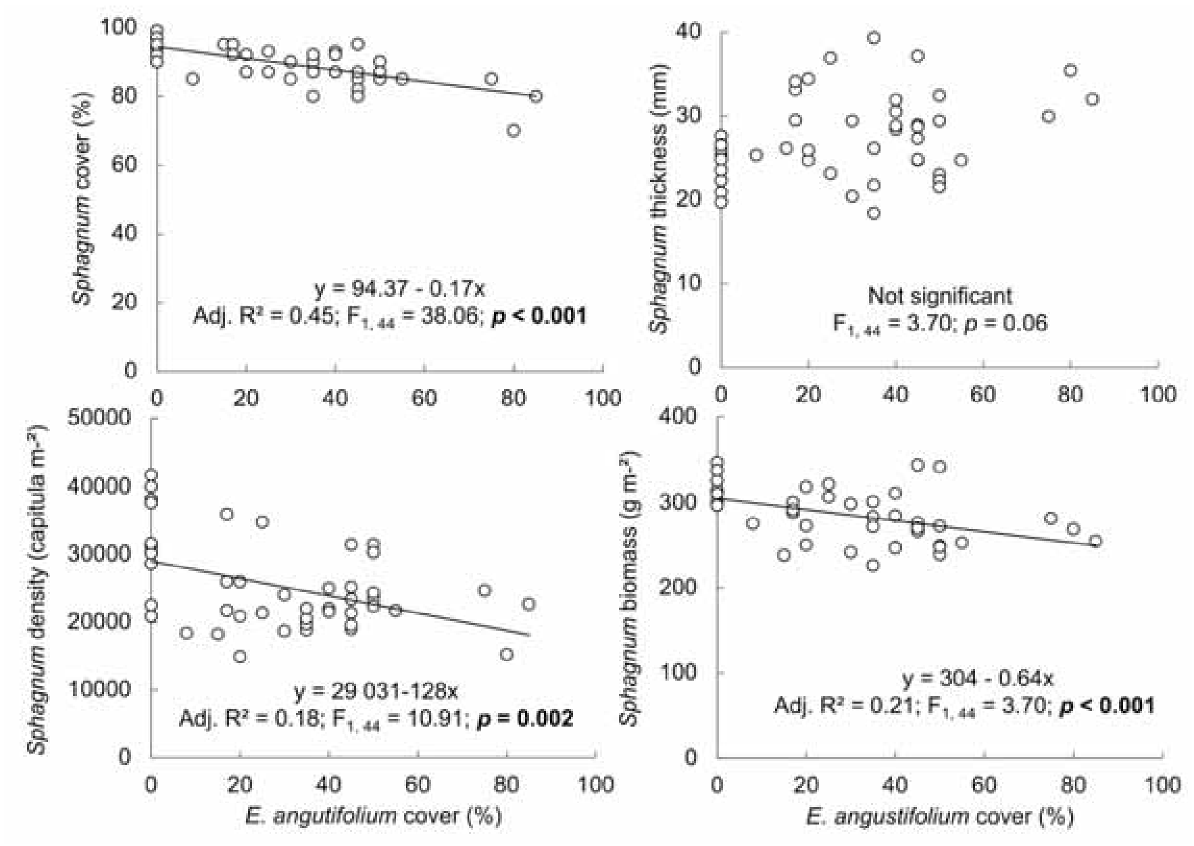

Figure 5.3. Relations between *Sphagnum* moss growth metrics (cover, carpet thickness, capitulum density and biomass) and *Eriophorum angustifolium* cover for the greenhouse experiment. Each point represents a value for an individual experimental unit (n = 46).

Discussion

Effect of mowing

In the *Sphagnum* farming basins studied, the effect of reducing graminoid plant cover by repeated mowing was not detectable in our measurements of *Sphagnum* moss production (cover and biomass accumulation), whether the *Sphagnum* carpet was pre-established (7 yr old cycle) or still establishing (1 yr old cycle). However, it was possible to observe the ‘scaffolding effect’, where the increase of graminoid plant cover promotes the elongation of *Sphagnum* fibers (Malmer et al. 1994, Pouliot et al. 2011), (only) when the *Sphagnum* carpets were pre-established (7 yr old cycle). Indeed, *Sphagnum* moss carpets were thicker in the un-mown treatments for the 7 yr old cycle. However, the increased fiber length in the 7 yr old cycle did not translate into an increase in biomass accumulation, indicating that the *Sphagnum* stems are probably etiolated and fluffy. The shade caused by graminoid plant cover reduced the accessibility of light for *Sphagnum* mosses and could have caused fiber etiolation

(Heijmans et al. 2002, Pouliot et al. 2011). Another hypothesis is that fibers on the un-mown side were not etiolated, but it was rather the repeated trampling with snowshoes during mowing (three times per year for three years) that compressed the *Sphagnum* moss carpet on the mown side. The greenhouse experiment supports the latter hypothesis since no relation was found between *Sphagnum* moss elongation (moss layer thickness) and increasing *E. angustifolium* cover. But the reduction of the thickness on the mown side is probably not entirely an artefact of trampling by snowshoes, because it was not found in the 1 yr old cycle. Our inability to detect the effect of graminoid plants on *Sphagnum* carpet thickness in the 1 yr old cycle is probably due to low number of samples or high variations because the *Sphagnum* carpet was still establishing.

Edge effect

In relation to the basin edge effect, the field experiment showed that the presence of wetter conditions on the edges of the basins positively affected the *Sphagnum* moss cover and thickness in the 1 yr old cycle. Wet conditions were probably caused by collapsed drainage ditches blocking drainage, as well as the shade created by the baulks (Figure 5.1b). Well rewetted conditions were found to be a driver for better *Sphagnum* establishment and biomass accumulation at the basin scale (one basin compared to another one) within this same experimental *Sphagnum* farm (Pouliot et al. 2015). In this study, the same tendency could also be observed at a smaller scale, within the basin itself, for the basins with *Sphagnum* mosses in the process of establishment. However, this tendency seems to decrease over time as *Sphagnum* mosses establish, because there was no effect of basin edge for the pre-established 7-year-old *Sphagnum* carpet.

Need for mowing

Overall, the difference in *Sphagnum* accumulation between mown and un-mown treatments was negligible. Even if mowing tended to increase *Sphagnum* cover and biomass in the 1 yr old cycle, the range of increase was very low (7 % for cover and 10 % for biomass). For practical and economic considerations, mowing is probably not necessary. This recommendation is, however, specific to sites dominated by *E. angustifolium*. Indeed, in our study, *E. angustifolium* cover as high as 34 % had no detectable effect on the production of *Sphagnum* mosses in the field experiment. The greenhouse experiment showed that increasing *E. angustifolium* cover to higher levels could impede development of the *Sphagnum* moss carpet, but the magnitude of the decrease was small (14 % for cover and 18 % for biomass). Pouliot et al. (2011) demonstrated that *E. angustifolium* cover around 50 % did not significantly impact the *Sphagnum* moss carpet, and 100 % cover induced only a 21 % loss in frequency and a 35 % loss in biomass if compared to a carpet without *E. angustifolium*. Heijmans et al. (2002) speculated that at least 60 % cover of *E. angustifolium* was needed to impede *Sphagnum* moss growth, but this threshold was not empirically tested by the researchers. Consequently, we believe that any investment in controlling *E. angustifolium* at a *Sphagnum* farm would probably not be justifiable in terms of gains in biomass, but a cost-benefit analysis studying this aspect would be necessary.

Importance of site-specific conditions

Nevertheless, mowing may be necessary when the dominant graminoid species present is not *E. angustifolium*. Some sedges are not rhizomatous and tend to grow in tussocks, a life form that can compete with *Sphagnum* moss for space. It is the case for *Eriophorum vaginatum*, which is regarded as an invasive species in unrestored peatlands (Lavoie et al. 2003, 2005). Under a complete (100 %) cover of that graminoid plant, Pouliot et al. (2011) observed that *Sphagnum* frequency was 42 % lower if the dominant species was *E. vaginatum* rather than *E. angustifolium*, but no significant decrease in biomass was observed. However, tussock cover of at least 50 % is generally needed to significantly affect development of the *Sphagnum* moss carpet (Hogg et al. 1995 for Molinia spp., Pouliot et al. 2011 for *E. vaginatum*). Apart from life form, other factors should be taken into account when one considers controlling the density of vascular plants in a *Sphagnum* farm. For instance, according to Malmer et al. (1994), the decrease of *Sphagnum* moss production observed with the presence of graminoid plants is the result of above-ground litter accumulation on the moss carpet rather than the effect of shading caused by the vascular plant itself. For example, a low cover of *Carex aquatilis* Wahlenb. negatively affected *Sphagnum* moss production, probably because this plant produces substantial amounts of litter (~ 50 % litter cover with 25 % cover of *C. aquatilis*; M. Guêné-Nanchen, unpublished data; Chapter 4 of this thesis). Compared to *C. aquatilis*, *E. angustifolium* (another rhizomatous plant) is known to produce low amounts of annual litter (Phillips 1954, Heijmans et al. 2002). Indeed, litter cover generally did not exceed 7 % in the studied *Sphagnum* farming basins, even if plant cover reached 34 %. Also, site-specific factors such as water table level should be considered; for example, in this *Sphagnum* farm, drier conditions promote *E. vaginatum* whereas wetter conditions promote *E. angustifolium*. *Sphagnum* farming stations established on richer peat could be colonized by *Carex* and *Scirpus* species. Therefore, recommendations for graminoid plant control in *Sphagnum* farms should be made according to the dominant graminoid plant present: its cover, its life form, its litter production, its invasive potential and the conditions on the site.

Practical considerations

Depending on the *Sphagnum* farming site, mowing might not be needed to maximize biomass accumulation, but it may be considered for other reasons. For example, vascular plants can impede mechanical *Sphagnum* fiber harvesting by blocking the machinery mechanisms and a control method may be necessary to facilitate harvesting. The end use of the fibers may also influence the decision to control vascular plants. If *Sphagnum* fibers are destined to be used as fibers for specialized horticultural substrates such as orchid propagation, vascular plants might need to be eradicated to minimize the risks of contamination by seeds. However, if cultivated *Sphagnum* mosses are intended to be used as diaspores for ecological restoration projects, the presence of vascular plants is not a concern and could even allow for the return of typical peatland vascular plants. Different studies have shown that graminoid plant cover generally declines spontaneously after 6–8 years in post-regenerating block-cut peatlands (field observations in Salonen 1990, Robert et al. 1999) and restored peatlands (from 80 % to 50 %) (D'Astous et al. 2013, Rochefort et al. 2013). This phenomenon was observed in the oldest cycle at the *Sphagnum* farm studied here, where graminoid plant cover naturally decreased between the beginning and the end of the experiment (from 7 to 10 years) from around 40 % to 28 % in the un-mown side (PERG unpublished data). If *Sphagnum* mosses grow fast enough to allow harvesting within a five-year cycle, control methods maybe needed. However, if production cycles are longer, it would be possible to wait for the decrease of graminoid plants through spontaneous succession and the self-engineering of *Sphagnum* behaviour (Van Breemen 1995). Moreover, graminoid plant cover in the studied *Sphagnum* farming station remained low after seven growing seasons and were lower than in restored peatlands (Rochefort et al. 2013, Pouliot et al. 2015), adding yet another argument for site-specific decision-making for vascular plant control. Thus, ultimately, the need for control of vascular plants in *Sphagnum* farming basins is determined by the life forms of the vascular species in combination with logistical constraints linked to harvesting and the specific use of the *Sphagnum* fibers.

Conclusion

The improvement of growth conditions will continue to be a major concern in *Sphagnum* farming research. This study is the first of its kind to make recommendations for graminoid plant control and to study its effect on the structure of the *Sphagnum* carpets. For this particular *Sphagnum* farming site, located in the maritime provinces of Canada, control of graminoid plants is not deemed necessary to improve *Sphagnum* productivity regardless of the age of the *Sphagnum* carpet. However, this recommendation cannot be applied to all *Sphagnum* farming sites and is limited to graminoid plants with similar growth habits to *E. angustifolium* (individual stems, spreading by rhizomes and producing minimal amounts of litter). The decision to control the density of vascular plants will be specific to each *Sphagnum* farming station and recommendations must be made in light of the dominant graminoid plant species present in culture basins. The graminoid species cover, life form, litter accumulation and potential for invasion are factors that should be considered when deciding whether or not to cut graminoid plants. Moreover, this decision should be made according to the intended final use of the *Sphagnum* fibers. Therefore, we suggest that further studies should be conducted with other graminoid plants or dominant vascular plants, and in *Sphagnum* farming stations in different climates. Moreover, the effect of mowing on increasing vegetative reproduction by rhizomes in graminoid plants should also be evaluated.

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Appendixes

Appendix 5.1 ANOVA in a split-block design was used to evaluate the effect of mowing (main treatment) and transect position (sub-treatment) on mean *Sphagnum* moss cover (9 measures for the 7 yr old basin and 2 measures for the 1 yr old basin), thickness (46 measures per transect for 7 yr old basin and 6 measures for 1 yr old basin) and biomass (5 samples per transect for 7 yr old basin and 2 samples for 1 yr old basin) for both production cycles. Significant differences are bolded (LSD protected, α = 0.05).

Sphagnum **moss cover**

Production cycle		**7 yrs**			**1 yr**	
Variation sources	df	F	p	df	F	p
Block	2			2		
Mowing	1	0.82	0.417	1	0.87	0.377
Error main treatment	2			2		
Transect	1	2.09	0.222	1	10.44	0.012
Error sub-treatment	2			2		
Mowing x Transect	1	0.46	0.536	1	NA[1]	NA[1]
Error interaction	2			2		
Total	11			11		

Sphagnum **moss thickness**

Production cycle		**7 yrs**			**1 yr**	
Variation sources	df	F	p	df	F	p
Block	2			2		
Mowing	1	9.16	0.023	1	1.86	0.245
Error main treatment	2			2		
Transect	1	0.00	0.958	1	53.66	0.002
Error sub-treatment	2			2		
Mowing x Transect	1	0.28	0.619	1	0.12	0.746
Error interaction	2			2		
Total	11			11		

Sphagnum **moss biomass**

Production cycle		**7 yrs**			**1 yr**	
Variation sources	df	F	p	df	F	p
Block	2			2		
Mowing	1	0.75	0.455	1	0.02	0.9057
Error main treatment	2			2		
Transect	1	1.91	0.257	1	1.91	0.246
Error sub-treatment	2			2		
Mowing x Transect	1	12.08	0.0601	1	0.50	0.523
Error interaction	2			2		
Total	11			11		

Chapitre 6

Conclusions générales

Conclusions, contributions et limites

Nous pensons, comme plusieurs chercheurs (Mitsch et Wilson 1996; Hilderbrand et coll. 2005) que les approches de développement ou d'adaptation des méthodes de restauration doivent se baser sur l'étude de la régénération naturelle des écosystèmes. Cette démarche visant à étudier et imiter le caractère et les processus de régénération des systèmes naturels devrait permettre de trouver des solutions ayant plus de succès dans la restauration des écosystèmes. En utilisant cette approche, l'objectif principal de la présente thèse était d'évaluer la régénération des bryophytes dans les tourbières perturbées ainsi que l'influence des contraintes environnementales, de dispersion et des interactions interspécifiques. Cette thèse permet premièrement d'améliorer nos connaissances fondamentales sur la régénération naturelle des tourbières et, deuxièmement, d'améliorer les pratiques de gestion et de restauration de ces tourbières. Les conclusions générales de cette étude sont résumées dans la Figure 6.1.

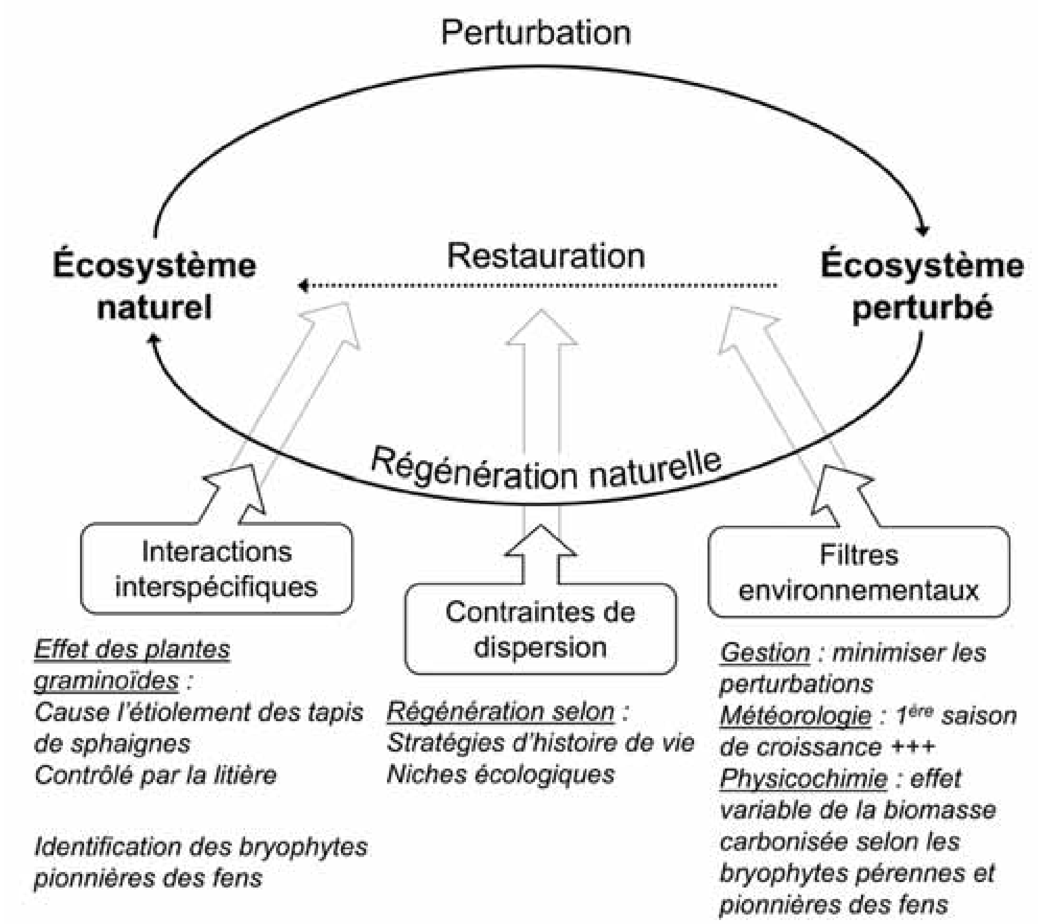

Figure 6.1 Résumé des principales conclusions de la thèse. Une description complète du cadre conceptuel est disponible à la Figure 1.1. Les connaissances acquises dans cette thèse montrent que les processus de régénération naturelle des tourbières sont affectés par de nombreux facteurs, tant à une échelle locale que régionale. Les filtres environnementaux affectent les espèces qui se régénèrent au niveau local par le biais des perturbations. Notamment plus il est possible de minimiser les perturbations par une gestion responsable, plus la régénération sera accélérée. Également, la perturbation par le feu, par l'apport de biomasse carbonisée semble avoir un effet mitigé selon les espèces de mousses de fen riche. Celle-ci pourrait simuler l'effet de la fertilisation lors de la restauration, mais son effet doit être davantage examiné. Les conditions météorologiques à l'échelle régionale ont un effet sur la régénération qui ne doit pas négliger. La dispersion des espèces dans les tourbières perturbées est contrôlée par leur stratégie d'histoire de vie et par la disponibilité de leur niche écologique, notion qui devrait être intégrée lors de la restauration. Il a été démontré que les plantes graminoïdes causent l'étiolement des tapis de sphaignes et que leur effet est principalement contrôlé par leur litière plutôt que par la structure de la plante elle-même, indiquant que le potentiel d'accumulation de litière dans les tourbières en restauration devrait être considéré. Puis, les bryophytes pionnières des fens riches ont été identifiées, de celles-ci certaines sont ciblées comme potentielles plantes compagnes qui pourraient être utilisées dans la restauration des fens.

Tourbières minérotrophes brûlées

À notre connaissance, les études sur la régénération naturelle des tourbières minérotrophes après perturbation sont quasi-inexistantes dans la littérature; elles sont en fait plus rares que les études sur leur restauration (Klimkowska et coll. 2010; Rochefort et coll. 2016; Cooper et coll. 2017). Toutefois, comme préalablement mentionné, nous pensons que le développement de méthodes de restauration adéquates et fonctionnelles pour les tourbières minérotrophes doit d'abord passer par l'étude de leur régénération naturelle. L'étude de la régénération des tourbières minérotrophes ayant brûlé s'avérait donc une occasion unique et constituait un premier pas dans cette direction.

Suite à mon étude, nous avons maintenant une image plus claire de la trajectoire de régénération dans les tourbières minérotrophes riches ayant été perturbées. Une initiation de succession secondaire a été observée durant les cinq premières années suivant le feu, où un changement de dominance entre les bryophytes pionnières et les bryophytes de succession tardive a été observée entre la deuxième et cinquième année. Deuxièmement, la diversité des mousses de fens s'est rétablie cinq ans après le feu suggérant que la majorité des mousses de fens ont été en mesure de se régénérer à partir de fragments, mais la régénération entre les espèces était variable et reliée à leur niche écologique. C'est sans doute pourquoi *Aulacomnium palustre* a été désignée comme la mousse de fens ayant le meilleur potentiel de régénération, sa niche écologique étant de large dimension dans l'Ouest canadien (Gignac et coll. 1991). Il semble donc que pour les mousses de fens, l'intégration de la notion de niche écologique soit primordiale lors de la restauration. Pour une première fois, les bryophytes pionnières des tourbières minérotrophes ont été identifiées. De celles-ci, *Ptychostomum pseudotriquetrum*, qui est également présente en moindre abondance dans les tourbières non perturbées, semble présenter un bon potentiel de plante compagne, et ce dernier devrait être plus largement étudié. L'apport de nutriments par la biomasse carbonisée semble avoir eu un effet bénéfique fertilisant pour les bryophytes pionnières. Alors que l'augmentation de la concentration de certains éléments et composés chimiques (Ca, Mg, Na, P et NO_3^-) semble plutôt être nuisible pour les mousses de fens de succession tardive, du moins durant les deux premières années suivant le feu. C'est pourquoi nous recommandons que l'effet de la fertilisation sur les mousses de fens soit davantage examiné. Notamment, le contenu nutritionnel des bryophytes pourrait être étudié. Les conclusions générales de ce chapitre sont résumées dans la Figure 6.2.

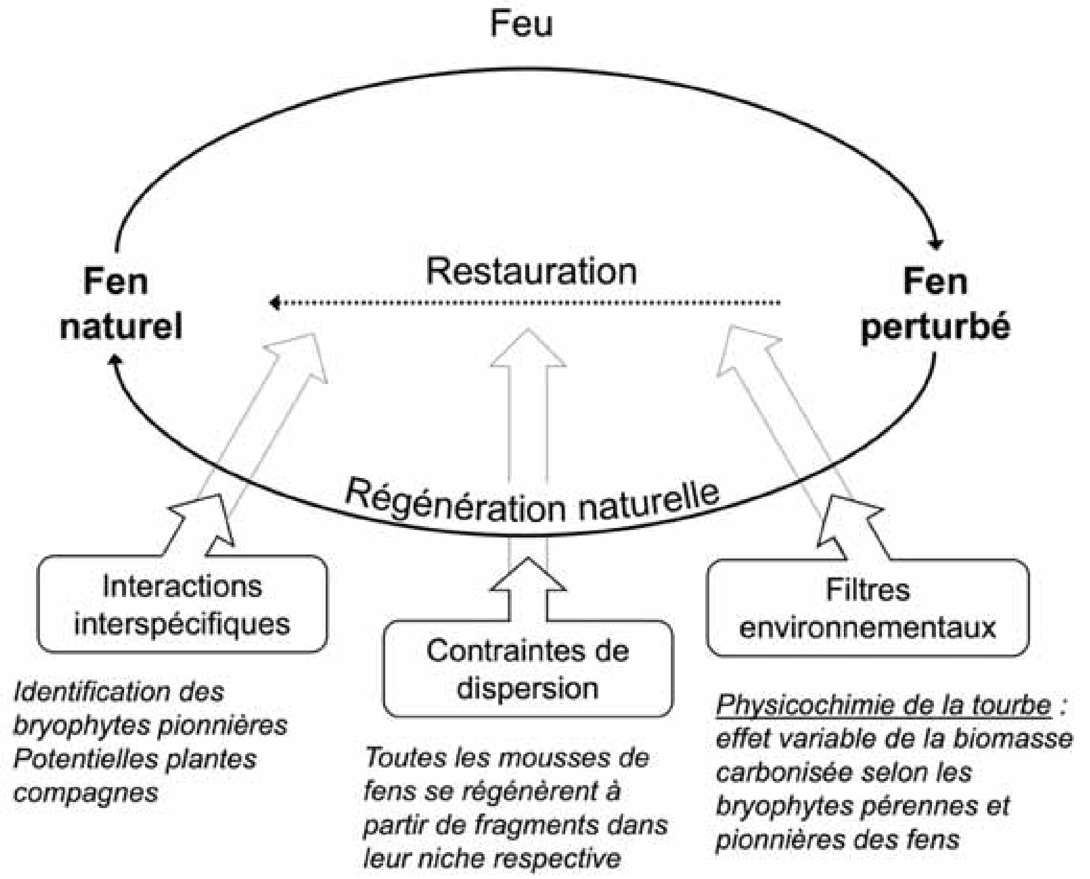

Figure 6.2 Résumé des principales conclusions du chapitre 2 sur la régénération des bryophytes dans les tourbières minérotrophes riches (fens) brûlées. Une description complète du cadre conceptuel est disponible à la Figure 1.1. Les connaissances acquises dans ce chapitre montrent qu'au niveau des filtres environnementaux, l'apport d'éléments et de composés chimiques par la biomasse carbonisée semble avoir un effet variable selon la stratégie d'histoire de vie des bryophytes. Toutes les espèces de mousses de fens sont en mesure de se régénérer à partir de fragments et l'intégration de la notion de la niche écologique des espèces semble être critique pour leur régénération. Différentes bryophytes pionnières des fens ont été identifiées et le potentiel de celles-ci d'agir comme des plantes compagnes lors de la restauration des fens devrait être davantage examiné.

Malgré, les premiers pas effectués ici, cette étude présente certaines lacunes. Notamment, les tourbières n'ont pas été étudiées individuellement dans le temps. L'utilisation de différentes tourbières perturbées à différents moments a permis une substitution *space-for-time* comme chronoséquence pour servir de solution de rechange à un suivi temporel. Toutefois, il y a donc eu comme supposition de base que les communautés végétales avant le feu étaient semblables entre les tourbières, ce qui aura pu induire certaines erreurs dans l'étude de la variation de la composition et l'abondance végétale dans le temps suivant le feu. L'effet des conditions hydrologiques sur la régénération des bryophytes est bien connu (Mälson et Rydin 2007; Graf et Rochefort 2010), toutefois, cet effet n'a pas été relevé comme critique dans la présente étude. Le manque de variabilité de conditions hydrologiques entre les sites brûlés durant la période d'échantillonnage pourrait expliquer la sous-estimation de l'effet hydrologique sur la régénération des bryophytes. L'instrumentation de mesures hydrologiques sur une base annuelle ou saisonnière pour évaluer les conditions des sites aurait été favorable, mais complexe à mettre en place, étant donné que la campagne de terrain s'est déroulée sur 2 mois à l'été 2016. Nous sommes également critiques quant à l'utilisation de la mesure de profondeur de brûlage (*depth of burn*) comme indicateur de sévérité du feu. Cette mesure habituellement évaluée sur des racines d'arbres (Kasischke et coll. 2008) a ici adaptée pour être évaluée sur des touradons d'*Eriophorum vaginatum* par Mack et coll. 2011. Dans notre étude, l'approche de Mack et coll. (2011) a été adaptée pour mesurer la profondeur de brûlage sur des touradons de *Carex aquatilis*; toutefois nous doutons de la véracité de ces valeurs, particulièrement pour les sites brûlés les plus âgés, où la différence entre la tourbe néoformée et la tourbe brûlée était difficile à reconnaitre. La variation en termes de régénération entre les différentes années de feu a probablement été sous-estimée étant donné que les tourbières brûlées dans leur région respective (Territoires du Nord-Ouest et nord de l'Alberta) ont été soumises à des conditions météorologiques similaires. Finalement, cette étude fournit des éléments de pistes intéressantes quant à la restauration des tourbières minérotrophes riches dominées par les bryophytes. Comme les cortèges d'espèces végétales étaient relativement semblables à celles des tourbières de l'est du Canada, les résultats pourraient y être appliqués; toutefois, les différences régionales climatiques devront être tenues en compte lors de l'adaptation à d'autres contextes.

Tourbières perturbées par la récolte de la végétation

Si les efforts de restauration des tourbières boréales persistent, on peut s'attendre à observer une augmentation de la pression sur les sites donneurs tant que des solutions à la récolte en tourbières naturelles n'existent pas. Le chapitre 3 de cette thèse visait à déterminer si les sites donneurs se régénéraient facilement spontanément et à détailler leur reprise en termes de composition et d'abondance des espèces, et finalement à déterminer s'il était possible d'accélérer leur régénération.

Dans un premier temps, il a été démontré que les sites donneurs se régénèrent en moyenne en dix ans en terme de recouvrement de sphaignes, et ce, peu importe les méthodes de gestion employées et les conditions environnementales présentes la première année suivant la perturbation. Toutefois, des différences au niveau de la composition et l'abondance des espèces sont toujours observables entre les sites donneurs dix ans après la récolte et les tourbières naturelles. Notamment, les espèces à croissance lente, comme *Picea mariana*, *Kalmia angustifolia* et *Cladonia* spp., sont nettement moins abondantes dans les sites donneurs. Au contraire, les espèces préférant les dépressions et les platières, comme *Chamaedaphne calyculata*, ou les espèces compétitives, comme *Sphagnum rubellum*, sont plus abondantes dans les sites donneurs. Ceci confirme l'hypothèse selon laquelle la régénération des espèces dépend de leur caractère intrinsèque, soit de leurs stratégies d'histoire de vie et de leurs niches écologiques. Dans un deuxième temps, il a été démontré qu'il était possible d'accélérer la reprise dans les sites donneurs en sélectionnant les pratiques de récolte appropriées. En fait, d'après nos résultats et ceux de l'étude de Rochefort et Campeau (2002), les pratiques de gestion pour la récolte influencent davantage la régénération de la végétation que les pratiques de gestion post-récolte (ajout de propagules de sphaignes et de paille).

L'étude de la régénération de 25 sites donneurs dans ce chapitre corrobore les recommandations présentées dans Quinty et Rochefort (2003) qui n'étaient alors basées que sur quelques cas de figure. Nos résultats renforcent donc leurs recommandations, mais qui ne sont toujours pas nécessairement toujours appliquées sur le terrain selon nos observations. Par exemple, le choix du site donneur ainsi que le moment de la récolte sont primordiaux pour assurer une reprise rapide. Il est recommandé d'éviter les sites trop secs avec un faible couvert de sphaignes et de minimiser les perturbations lors de la récolte. Pour ce faire, la récolte devrait s'effectuer lorsque le sol est gelé. Nous pensons même que toutes les mesures devraient être mises en place pour s'assurer que le sol du site donneur soit gelé avant la récolte. Des résultats de reprise rapide (3-4 ans) ont été obtenus dans une étude préalable à cette thèse lorsque des efforts supplémentaires étaient appliqués pour s'assurer de la pénétration du gel (Rochefort et Campeau 2002). Également, les sites donneurs trop humides, où le risque d'enlisement est élevé et où les communautés de sphaignes ne sont pas adéquates selon le but de la restauration en Amérique du Nord (p. ex., sous-genre Cuspidata; Chirino et coll. 2006), devraient être évités. Finalement, bien qu'elles soient non contrôlables par les gestionnaires de tourbières, les conditions météorologiques de la première saison de croissance suivant la récolte ont une importance non négligeable sur la reprise de la végétation. Les conclusions générales de ce chapitre sont résumées dans la Figure 6.3.

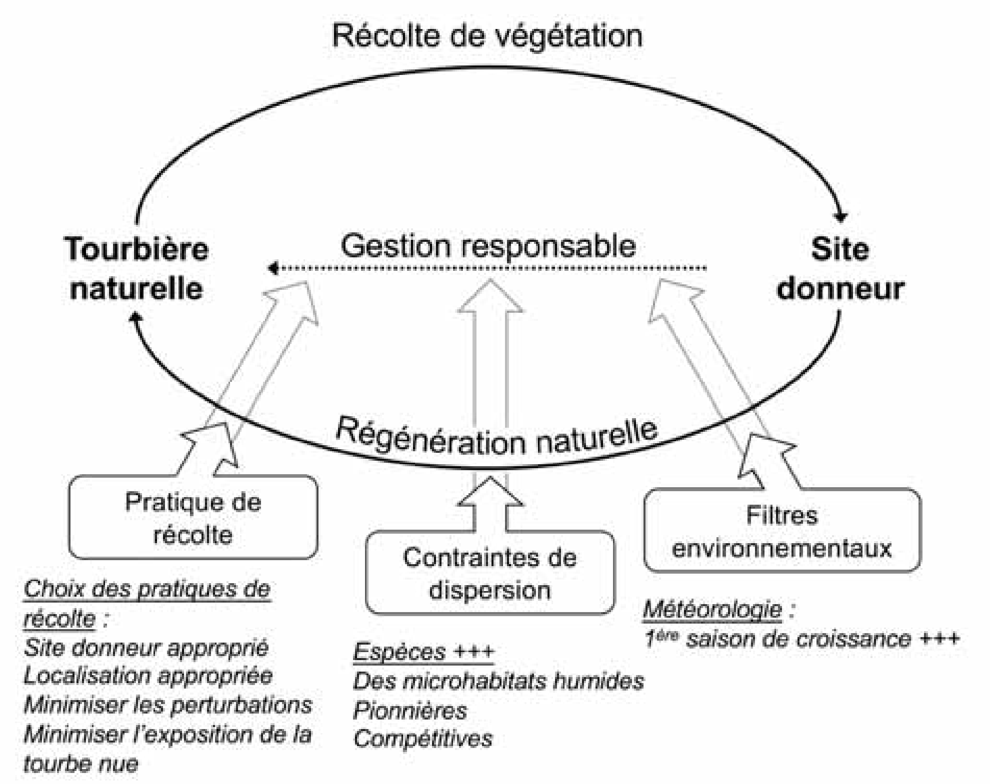

Figure 6.3 Résumé des principales conclusions du chapitre 3 sur la régénération des sphaignes dans les tourbières perturbées par la récolte de végétation (sites donneurs). Une description complète du cadre conceptuel est disponible à la Figure 1.1. Les connaissances acquises dans ce chapitre montrent que les conditions météorologiques de la première saison croissance suivant la récolte de végétation jouent un rôle important sur la régénération des sites donneurs. L'analyse de la régénération des 25 sites donneurs a démontré que les sphaignes se régénéraient bien en deçà 10 ans. Cependant, les communautés végétales variaient en termes de composition et d'abondance entre les sites donneurs et les tourbières naturelles adjacentes, notamment que les espèces préférant les microhabitats humides, les espèces pionnières et compétitives étaient davantage abondante dans les sites donneurs. Il est possible d'adopter des pratiques de gestion responsables afin d'accélérer la reprise des sphaignes dans les sites donneurs. Il est, entre autres, recommandé de choisir le site d'emprunt de nature (tourbière dominée par les sphaignes du sous-genre Acutifolia) et de localisation appropriée, de minimiser les perturbations lors de la récolte et l'exposition de la tourbe nue.

Cette étude est unique et constitue une primeur dans le domaine, puisqu'elle est la première à documenter la régénération de 25 sites donneurs. Malgré le fait que le dispositif expérimental n'ait pas été élaboré selon les règles de l'art, un grand nombre de sites ont été évalués, et ce sur une échelle temporelle allant de 1 à 17 ans, constituant une excellente source d'information permettant de faire le point sur la gestion des sites donneurs.

Mais, en effet, le dispositif expérimental n'était pas parfait, en particulier en ce qui concerne la répartition des différentes méthodes de récolte à travers les sites donneurs. En effet, des 25 sites donneurs, 17 ont été récoltés avec un rotoculteur, trois avec une herse rotative, trois avec une pelle avec des dents larges et deux avec un broyeur forestier. Même si les variables catégoriques n'ont pas besoin d'être parfaitement balancées dans des analyses multivariées (Legendre et Legendre 2012), ceci nous empêche de tirer des conclusions solides quant aux méthodes à utiliser pour la récolte, puisque celles-ci n'ont été utilisées que sur trois sites ou moins, sauf pour le rotoculteur. De plus, même si nous voulions tirer des conclusions quant à la méthode à utiliser, de nombreuses informations sur l'implémentation même de la récolte sont demeurées manquantes (p. ex., création d'ornières ou enlisement lors de la récolte, profondeur de récolte). Par ailleurs, l'utilisation de la saison de récolte n'est pas un indicateur très précis pour déterminer si le sol était gelé ou non. D'autre part, tout comme González et Rochefort (2014), les variables choisies pour évaluer l'influence des conditions hydrologiques sur la régénération des sphaignes n'ont pas permis de conclure que celles-ci avaient eu une influence sur la régénération des sphaignes; cette influence est néanmoins bien connue (Price et Whitehead 2001). Il est possible que les variables choisies (distance du canal de drainage le plus proche et son type : ouvert ou bloqué) soient peu pertinentes dans un site de tourbière industrielle où les sites donneurs sont entourés de canaux drainage. Il est également possible que les sites donneurs soient moins affectés par les conditions hydrologiques que les sites restaurés, puisqu'une partie de l'acrotelme est conservée. Finalement, comme toutes les récoltes avaient déjà été effectuées au moment de l'étude, il n'était plus possible d'évaluer la végétation présente avant la récolte. Nous avons par conséquent utilisé la végétation de la zone adjacente à titre comparatif, en supposant que la végétation du site donneur y était semblable avant la récolte. D'après nous, c'était le cas pour la majorité des sites étudiés, car la composition végétale des tourbières ombrotrophes dans le sud du Canada est relativement uniforme (Payette 2001). Pour les quelques sites faisant exception, la zone adjacente était davantage forestière.

Effet des plantes graminoïdes pionnières

Quoique les études sur les relations entre les plantes vasculaires et les sphaignes dans les tourbières sont relativement nombreuses (Malmer et coll. 1994, 2003; Bergamini et coll. 2001), le cas spécifique des plantes graminoïdes a été peu examiné dans le contexte de réintroduction de tapis de mousses en tourbière par une méthode de restauration. Ici, le but était de déterminer si leur présence est bénéfique en restauration ou si une méthode de contrôle devrait être appliquée, en évaluant l'effet de l'abondance des plantes graminoïdes sur les tapis de sphaignes.

Une première sous-expérience conduite dans un fen modérément riche restauré colonisé par le *Carex aquatilis* a permis de montrer que la litière de cette plante avait plus souvent un effet négatif sur le développement annuel des sphaignes que la plante elle-même en réduisant l'accessibilité à la lumière. Dans un contexte de restauration, la présence d'une communauté dense d'une plante graminoïde accumulant beaucoup de litière comme *Carex aquatilis* ne semble pas être bénéfique pour développer des tapis de sphaignes productifs. Les conclusions générales de ce chapitre sont résumées dans la Figure 6.4.

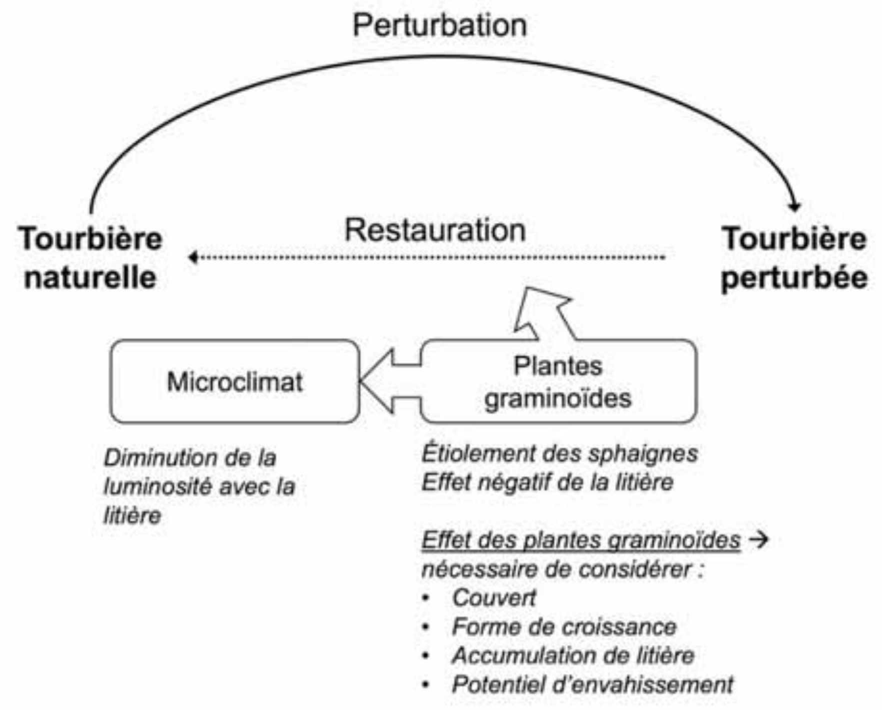

Figure 6.4 Résumé des principales conclusions des chapitres 4 et 5 sur l'influence des plantes graminoïdes sur le développement des tapis de sphaignes dans des tourbières restaurées. Une description complète du cadre conceptuel est disponible à la Figure 1.1. Les connaissances acquises dans ce chapitre montrent que les plantes graminoïdes entrainent l'étiolement, soit l'élongation des fibres de sphaignes, étant donné la diminution de l'accessibilité à la lumière, sans toutefois augmenter l'accumulation de biomasse. L'effet négatif des plantes graminoïdes sur le développement des tapis de sphaignes est principalement contrôlé par leur litière. Afin d'évaluer l'effet d'une plante graminoïde sur le développement des tapis de sphaignes, il est important de considérer son couvert, sa forme de croissance (touradon, tige unique), son potentiel d'accumulation de litière et d'envahissement.

Toutefois, les conclusions doivent être utilisées avec prudence, en raison des erreurs méthodologiques liées au choix de la taille de quadrats utilisés en 2014 (15 cm x 15 cm). Les valeurs obtenues dans ces quadrats ont permis d'obtenir les valeurs de différences annuelles du tapis de *S. warnstorfii* entre 2014 et 2015 présentées dans le Chapitre 4. Cependant, les quadrats utilisés en 2014 possédaient un ratio bordure : aire élevé (0,26), il devenait donc plus difficile d'évaluer correctement ce qui se trouvait à l'intérieur ou à l'extérieur du quadrat. Il est généralement considéré que dans ces situations les expérimentateurs ont tendance à surestimer les valeurs mesurées lorsque le ratio bordure : aire est élevé (Elzinga et coll. 1998). En effet, il était très ardu par exemple, de respecter les bordures du quadrat, lorsque la biomasse de sphaignes était récoltée en 2014 en présence de grandes plantes graminoïdes. Donc, des valeurs surestimées en 2014 auraient engendré des valeurs faussées de différences annuelles, comme les valeurs de 2014 ont été soustraites à celle de 2015. Finalement, un effet positif de la plante graminoïde sur le microclimat n'a pas été relevé. Les sondes utilisées pour mesurer l'humidité relative et la température étaient placées sous un couvert protecteur artificiel et ce couvert protecteur rendait difficile la détection de différences de microclimat sous les différents couverts de *Carex aquatilis* et de litière et au contraire, devait homogénéiser les conditions microclimatiques.

Une seconde sous-expérience conduite dans une tourbière à sphaignes où des tapis de sphaignes ont été réintroduits dans le but de produire des fibres de sphaignes (culture de sphaignes) et qui a été colonisée par l'*Eriophorum angustifolium* a permis de montrer que le contrôle par coupe répétée n'est pas nécessaire si le but est d'accroitre l'accumulation de biomasse de sphaignes. En effet, même si les tapis de sphaignes où la densité de graminoïdes a été contrôlée étaient plus épais, ceux-ci ont accumulé autant de biomasse que les tapis sans contrôle; ils étaient donc étiolés. Cette conclusion est applicable pour cette plante graminoïde. En effet, l'*E. angustifolium* présentait un recouvrement moyen de 30 % et produisait peu de litière qui se décomposait rapidement. Toutefois, la recommandation de ne pas contrôler ne peut être appliquée à tous les contextes. Nous pensons qu'il est essentiel de considérer, bien sûr, le couvert de la plante, mais aussi sa forme de croissance (tige unique vs touradons), de même que son potentiel d'accumulation de litière et d'envahissement. Les conclusions générales de ce chapitre sont résumées dans la Figure 6.4.

Pour cette sous-expérience, il est important de mentionner que l'effet de la coupe des plantes graminoïdes sur l'épaisseur des tapis de sphaignes (tapis moins épais lorsque la densité était contrôlée) a pu être confondu avec un certain piétinement. En effet, les coupes ont été effectuées par un expérimentateur portant des raquettes. Bien que le port de raquettes eût pour but de minimiser la perturbation du tapis de sphaignes, il est fort possible qu'une compression ait été exercée par le piétinement de l'expérimentateur trois fois durant l'été pendant trois étés.

En conclusion, cette thèse ne visait pas uniquement à répondre à des problématiques spécifiques. Elle a permis d'apporter une compréhension améliorée des processus de régénération des écosystèmes naturels de tourbières et des facteurs qui l'influencent. Elle a également approfondi nos connaissances sur les réponses des plantes et des communautés aux changements environnementaux. Ces nouvelles notions pourront être intégrées dans le développement d'outils pour la restauration des tourbières. Les tourbières sont des écosystèmes uniques, et même si leur valeur a été prouvée maintes fois, elles continuent d'être dégradées. Cette thèse est un pas de plus dans la direction d'une gestion améliorée et responsable des tourbières.

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