Remouillage d'un grand fen continental après extraction de tourbe horticole : impacts sur les échanges de carbone et la végétation

Mémoire

Laurence Turmel-Courchesne

Maîtrise en biologie végétale - avec mémoire
Maître ès sciences (M. Sc.)

Québec, Canada

Remouillage d’un grand fen continental après extraction de tourbe horticole : impacts sur les échanges de carbone et la végétation

Mémoire

Laurence Turmel-Courchesne

Sous la direction de :

Line Rochefort, directrice de recherche
Maria Strack, codirectrice de recherche

Résumé

Les tourbières jouent un rôle important dans le cycle du carbone à l'échelle de la planète, principalement par la captation de dioxyde de carbone (CO_2) et l'accumulation de carbone dans la tourbe et par de considérables émissions de méthane (CH_4). Les activités d'extraction de tourbe horticole causent la dégradation des tourbières qui fournissent des services écologiques, dont la régulation du climat. Une méthode de restauration significative, robuste et efficace a été développée pour les tourbières acides dominées par les sphaignes. Il arrive toutefois que les conditions physico-chimiques de la tourbe résiduelle après extraction soient caractéristiques des tourbières minérotrophes (fens). Lorsqu'appliquée dans un contexte de restauration de fens, la méthode de restauration par transfert de la strate muscinale s'est avérée peu efficace pour le retour des espèces vasculaires et muscinales typiques des fens. Dans certains contextes, la technique de remouillage sans autre action de restauration pourrait s'avérer efficace pour restaurer les fens post-extraction. Le but de cette étude est d'évaluer l'efficacité du remouillage à rétablir la végétation caractéristique des fens, ainsi que leur fonction de séquestration du carbone, et cela une et dix saisons de croissance après remouillage. Le site à l'étude se trouve dans le sud-est du Manitoba, au Canada. Les données ont été récoltées durant les étés 2016 et 2017. Le remouillage peut rapidement mener à des échanges de CO_2 typiques des tourbières naturelles. Le remouillage a résulté en des écosystèmes dominés par des espèces vasculaires typiques des milieux humides et des tourbières minérotrophes et ombrotrophes. Dix saisons de croissance après remouillage, un tapis discontinu de mousses typiques des tourbières minérotrophes s'est rétabli. Le remouillage peut être utilisé de manière efficace pour la restauration de fens après extraction. La gestion des niveaux d'eau s'avère primordiale pour favoriser une structure de végétation semblable à celle retrouvée dans les fens naturels. De trop hauts niveaux d'eau sont à éviter pour empêcher de générer de très hautes émissions de CH_4 et maximiser la fonction de séquestration du carbone. Ce mémoire se divise en trois chapitres : une introduction générale au sujet, suivie d'un corps de mémoire sous forme d'article scientifique puis d'une courte conclusion.

Table des matières

Liste des tableaux

Liste des figures

Liste des abréviations et sigles

C	Carbone / Carbon
CH_4	Méthane / Methane
CO_2	Dioxyde de carbone / Carbon dioxide
EC	Corrected electro-conductivity
ER	Ecosystem respiration
GEP	Gross ecosystem productivity
GHG	Greenhouse gas
GRET	Groupe de recherche en écologie des tourbières
GWP	Global warming potential
MTTM / MLTT	Méthode de transfert du tapis muscinal / Moss Layer Transfer technique
NEE	Net ecosystem exchange
SD	Standard deviation
PAR	Photosynthetically active radiation
T_{air}	Air temperature
T_5	Soil temperature at a depth of 5 cm
WTL	Water table level

Secteurs expérimentaux

UNR	Unrewetted; conditions after peat extraction but without restoration actions
R1	Rewetted; Conditions after peat extraction and one growing season after rewetting
RP1	Rewetted; Conditions after peat extraction and one growing season after rewetting (*R*) and profiling (P)
R10	Rewetted; Conditions ten growing seasons after rewetting
REF	Reference ecosystem

Remerciements

Merci à ma directrice de recherche, Line Rochefort, pour m'avoir donné l'occasion de travailler sur ce beau sujet et pour toutes les ressources et incroyables opportunités mises à ma disposition au cours de mes études à la maîtrise. J'ai beaucoup appris en ta présence, tu es un exemple de détermination et une force de la nature! Merci à Maria Strack, ma codirectrice pour ses conseils et sa toujours grande précision et clarté dans ses réponses. Un grand merci à Marie-Claire LeBlanc pour tous les commentaires et réflexions qui m'ont permis de toujours aller plus loin dans ma compréhension. Merci à Sandrine Hogue-Hugron, Claire Boismenu et Brigitte Vimard pour leur appui au laboratoire et leur compagnie toujours appréciée. Je remercie Monique Poulin, Alison Munson et Marcel Darveau pour leur participation à mes séminaires de maîtrise. Vos commentaires et questions m'ont permis d'ouvrir mes horizons.

Merci également à tous mes collègues au sein GRET, Mélina Guêné-Nanchen, Sébastien Meilleur, Kathy Pouliot, Ariane Blier-Langdeau, Meike Lemmer et Sebastian Gutierrez Pacheco pour la camaraderie sans laquelle la persévérance est moins aisée. Merci à Lindsay Edwards, Melanie Hawes, Steven Patterson et Michelle Mico pour l'aide sur terrain.

Je suis reconnaissante envers Sun Gro Horticulture pour le soutien logistique et l'accès au très beau site de South Julius. Merci à Bruce et Bruce pour votre bonne humeur et vos multiples coups de pouce sur le terrain. Merci au Fonds de recherche Nature et technologies du gouvernement du Québec pour mon soutien financier personnel.

Le financement de cette recherche a été fourni par le Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), l'Association des producteurs de tourbe du Canada (CSPMA) et ses membres, de même que par le Gouvernement du Manitoba.

Finalement, merci à toute ma famille et à mon amoureux et complice, Marc-Antoine. Merci pour ton réconfort, tes encouragements et ton optimisme dans les moments plus ardus.

Avant-propos

L’article intégré dans ce mémoire n’a pas été soumis pour publication dans une revue scientifique. Moi, Laurence Turmel-Courchesne, suis l’auteure principale de ce mémoire et de l’article qui y est intégré. En vue de la préparation de l’article, j’ai amassé la plupart des données sur le terrain, veillé à leur analyse et à leur interprétation et effectué la rédaction en entier. Les coauteures de cet article sont Line Rochefort, Maria Strack et Marie-Claire LeBlanc qui m’ont conseillée sur le choix du dispositif expérimental final et aidée à l’interprétation critique des résultats.

Introduction

En Amérique du Nord, l'extraction industrielle de tourbe pour la production de tourbe horticole entraîne la dégradation des tourbières. Une méthode a été développée et appliquée avec succès pour la restauration des tourbières dont la tourbe résiduelle a des caractéristiques physico-chimiques typiques des tourbières à sphaignes. Lorsque les caractéristiques de la tourbe résiduelle sont similaires à celles retrouvées dans les tourbières minérotrophes (fens), cette méthode doit cependant être adaptée. Dans ce chapitre, la problématique entourant la restauration des fens après extraction de tourbe sera abordée.

1. Écologie des tourbières

Les tourbières sont des milieux humides où les taux de production de matière végétale excèdent les taux de décomposition de la matière végétale. Il en résulte l'accumulation d'un dépôt de matière organique appelée tourbe. On distingue généralement deux grands types de tourbières qui se distinguent par leur apport en eau : les tourbières acides dominées par les sphaignes et les tourbières plutôt dominées par les cypéracées et les mousses de la famille des *Amblystegiaceae* et des *Calliergonaceae* (Vitt, 2013). Les tourbières à sphaignes (ombrotrophes et fens pauvres) sont alimentées en eau et en nutriments uniquement par les précipitations ou faiblement par ruissellement. Les tourbières à cypéracées ou fens sont quant à elles connectées aux eaux de surface ou souterraines (minérotrophes), d'où un pH et un apport plus élevés en cations de base (Na^+, K^+, Ca^{2+}, Mg^{2+}) et en bicarbonate (HCO_3^-). En raison de leurs différentes conditions physico-chimiques, les deux types de tourbières supportent des cortèges de végétation différents (Wieder et al., 2006). En raison de la composition différente des débris végétaux formant la tourbe, les caractéristiques physico-chimiques de la tourbe produite et accumulée dans les tourbières à sphaignes diffèrent donc de celle des fens. Généralement, en Amérique du Nord, les tourbières à sphaignes passent par un stade initial minérotrophe (Glaser et Janssens, 1986). Au fil du temps, avec l'accumulation de matière organique, la surface de la tourbière se retrouvera privée des apports en eau obtenus à partir des eaux de surface et de l'eau souterraine. Elle ne pourra compter que sur les précipitations pour son alimentation en eau. La tourbière passera à un stade ombrotrophe. En résultante, la tourbe située dans le bas du profil de tourbe présente généralement des caractéristiques physico-chimiques plus semblables à celles retrouvées dans les fens. La couche de tourbe superficielle a quant à elle des propriétés typiques de celles retrouvées dans les tourbières à sphaignes. Certaines autres tourbières peuvent aussi ne jamais passer par le stade ombrotrophe pour plutôt demeurer minérotrophes.

Les conditions topographiques, géomorphologiques et climatiques dictent la distribution des tourbières au Canada (Payette et Rochefort, 2001). Dans l'hémisphère nord, les tourbières se sont développées durant l'Holocène sur des dépôts mal drainés d'origine glaciaire ou lacustre. Au Canada, la majorité des tourbières (95%) se retrouvent dans les régions subarctiques et boréales et principalement dans les régions des basses-terres de la Baie d'Hudson, dans la région de la vallée de la rivière Mackenzie et dans le nord de l'Alberta et du Manitoba (Tarnocai et al., 2011). Dans la province canadienne du Manitoba, les milieux humides couvrent 43% du territoire et 90% de ces milieux humides sont des tourbières (Halsey et al., 1997). Les conditions climatiques (précipitations, évapotranspiration et températures moyennes) ainsi que le substrat géologique (substrat granitique acide pour les tourbières à sphaignes et substrat calcaire pour les fens) régissent la répartition des tourbières dans la province (Halsey et al., 1997). Au sud du Manitoba, les tourbières fens sont le type de tourbières le plus rencontré, présentant fréquemment une structure comprenant des îlots ombrotrophes entourés de fens ouverts (Glaser, 1987; Halsey et al., 1997).

2. Extraction de la tourbe au Canada

Activités d'extraction au Canada

L'extraction de la tourbe en Amérique du Nord et au Canada vise principalement la production de substrat horticole. Au Canada, 29 750 ha de tourbières ont été utilisés ou sont présentement utilisés pour l'extraction de tourbe horticole (58% toujours sous extraction; 25% restaurées, 15% abandonnées; CSPMA, 2015). Les activités d'extraction se trouvent en majorité (plus de 75%) dans les provinces de l'Est du Canada, principalement au Québec et au Nouveau-Brunswick. L'extraction de tourbe dans les provinces de l'Ouest du Canada représente 22% de toute la tourbe extraite au Canada ; 11% de la tourbe extraite au Canada l'est au Manitoba (CSPMA, 2015).

Méthode d'extraction de la tourbe par aspiration

Au Canada, la majorité des activités d'extraction de tourbe se fait à l'aide de la méthode d'extraction par aspiration. Lors de l'ouverture d'un site, un canal de drainage principal (périphérique) est aménagé autour de la tourbière à extraire. Des canaux secondaires moins profonds (environ 1 m), qui se drainent dans le canal principal (jusqu'à 2,5 m), sont aussi aménagés parallèlement les uns aux autres (Landry, 2008). Une fois le niveau d'eau abaissé, la végétation de surface est retirée pour accéder au dépôt de tourbe. La surface de chaque champ ou « planche » de tourbe délimitée par les canaux secondaires est ensuite reprofilée pour lui donner une forme de dôme, ce qui facilite son drainage et l'assèchement de la tourbe. La tourbe est extraite par aspiration. À chaque passage des aspirateurs, une mince couche de tourbe est retirée. Le drainage se poursuit (activité de maintenance mécanique) durant tout le processus d'extraction. L'extraction de tourbe cesse lorsque le substrat minéral retrouvé sous la tourbière est atteint ou lorsqu'une couche de tourbe plus décomposée et moins intéressante au point de vue horticole est atteinte (Graf et al., 2012).

3. Impacts de l’extraction de la tourbe

Les activités d’extraction de tourbe induisent des changements majeurs dans l’hydrologie, la végétation de surface ainsi que dans le fonctionnement biogéochimique des tourbières. La prochaine section aborde les impacts causés par les activités d’extraction de tourbe sur les tourbières.

Impacts sur la végétation et l’hydrologie

Par le drainage de la tourbière, le retrait de sa végétation et les modifications de sa surface pour permettre l’aspiration et le passage répété de la machinerie, la tourbe est compactée et ses propriétés hydrauliques modifiées (Price et al., 2003). L’aération et la compaction du profil de tourbe entrainent une augmentation de sa densité apparente qui peut doubler comparativement à celle retrouvée dans une tourbière naturelle (Van Seters et Price, 2002). L’augmentation de la densité de la tourbe entraine une diminution de sa conductivité hydraulique et de sa capacité de stockage de l’eau. Les mouvements d’eau à l’intérieur du profil de tourbe s’en trouvent limités et la quantité d’eau disponible pour les plantes est réduite (Landry et Rochefort 2011). La réduction de la taille des pores de la tourbe, causée par sa compaction, entraine aussi une augmentation considérable des fluctuations du niveau de la nappe phréatique, comparativement à celles retrouvées en tourbière naturelle (Price et al., 2003). L’exposition de la tourbe, ayant une couleur foncée, peut entraîner des augmentations non négligeables de sa température de surface. Par ailleurs, l’abaissement de la nappe phréatique et l’oxygénation de la tourbe entraînent une décomposition accélérée de celle-ci. Cette décomposition accélérée constitue une contrainte au rétablissement spontané des végétaux, puisqu’elle entraîne l’exposition de leurs racines et nuit à leur croissance (Graf et al., 2012). Une contrainte supplémentaire à l’établissement spontané des végétaux peut se produire lorsque la tourbe est saturée d’eau au printemps et à l’automne lorsque des aiguilles de glace se forment à la surface de la tourbe entraînant des dommages physiques aux végétaux (Groeneveld et Rochefort, 2002). Les conditions après extraction par aspiration sont donc très hostiles à l’établissement et à la croissance de végétaux et tout particulièrement pour les espèces typiques des tourbières (Campbell et al., 2003). Finalement, en raison du retrait de la végétation de surface et d’une couche de tourbe il n’existe plus, après extraction, de banque de propagules dans la tourbe résiduelle (Graf et al., 2012). Voilà pourquoi, sans intervention, il est rare d’assister à un rétablissement spontané de la végétation et de l’hydrologie typiques des tourbières après extraction par aspiration (Campbell et al., 2003; Poulin et al., 2005; Price et al., 2003; Triisberg et al., 2013).

Perturbation du fonctionnement de l’écosystème

Par l’accumulation de tourbe, les tourbières constituent un puits de carbone (C) considérable à l’échelle planétaire : les tourbières ne représentent que 2,84% de la surface terrestre, mais constituent le plus grand réservoir de carbone terrestre (Joosten et al., 2016; Xu et al., 2018). Leur importance se manifeste aussi par leur effet refroidissant sur le climat. Par exemple, par la captation de dioxyde de carbone (CO_2) et la séquestration de carbone dans la tourbe, elles auraient eu un effet de refroidissement atmosphérique durant l'Holocène (Frolking et Roulet, 2007). En raison de leur saturation en eau, les tourbières sont aussi de grandes émettrices de méthane (CH_4), un gaz à effet de serre 28 fois plus puissant que le CO_2 sur un horizon de 100 ans (Myhre et al., 2013). De manière générale, les échanges de CO_2 priment sur les échanges de CH_4 et les tourbières représentent des puits de carbone. Bien que le carbone y circule sous d'autres formes, notamment dissoutes, le cycle du carbone en tourbière est dominé par les flux de CO_2 et de CH_4 (Fig. 1) (Limpens et al., 2008). En ce qui a trait aux fens, bien que la productivité primaire y soit plus élevée que celle des tourbières à sphaignes, les taux de décomposition y sont aussi généralement plus élevés, résultant en une capacité de séquestration du carbone semblable, voire inférieure à celle des tourbières à sphaignes (Lamers et al., 2015).

Le drainage et l'extraction de la tourbe entraînent des modifications marquées à la dynamique du carbone dans les tourbières (Fig. 1). La baisse du niveau de la nappe phréatique accroît la distance que doit parcourir le CH_4, dans le profil de tourbe, entre sa zone de production (zone saturée en eau) et l'atmosphère. Durant ce trajet dans la zone oxygénée du profil de tourbe, le CH_4 peut être entièrement oxydé par les bactéries méthanotrophes s'y retrouvant (Strack et Waddington, 2012). Les champs des tourbières post-extraction encore drainées peuvent ainsi présenter des émissions nulles de CH_4, voire représenter des puits de CH_4. Lorsque les émissions des canaux de drainage sont pris en compte, les tourbières post-extraction représentent de petites sources de CH_4 (Waddington et Day, 2007). D'autre part, l'aération et l'augmentation de la température de surface de la tourbe entraînent une augmentation notable de l'oxydation de la tourbe. Comme les tourbières post-extraction présentent peu ou pas de végétation pour capter le CO_2 atmosphérique, le bilan de CO_2 des tourbières s'inverse et elles passent de puits à sources de CO_2 (Rankin et al., 2018). D'autres pertes de C des tourbières dégradées comprennent également l'érosion des particules de C par le vent et l'eau, ainsi que l'écoulement de carbone organique et inorganique dissout (Joosten et al., 2016). Bref, les activités d'extraction de tourbe modifient drastiquement le fonctionnement biogéochimique des tourbières et les font passer de puits à substantielles sources de carbone (Waddington et al., 2002).

En résumé, les activités d'extraction de la tourbe causent des altérations de la végétation, de l'hydrologie et du cycle du carbone typique des tourbières naturelles. Leur fonction de séquestration du carbone est perdue. Pour retrouver les attributs et le fonctionnement typique des tourbières naturelles, des actions de restauration sont nécessaires.

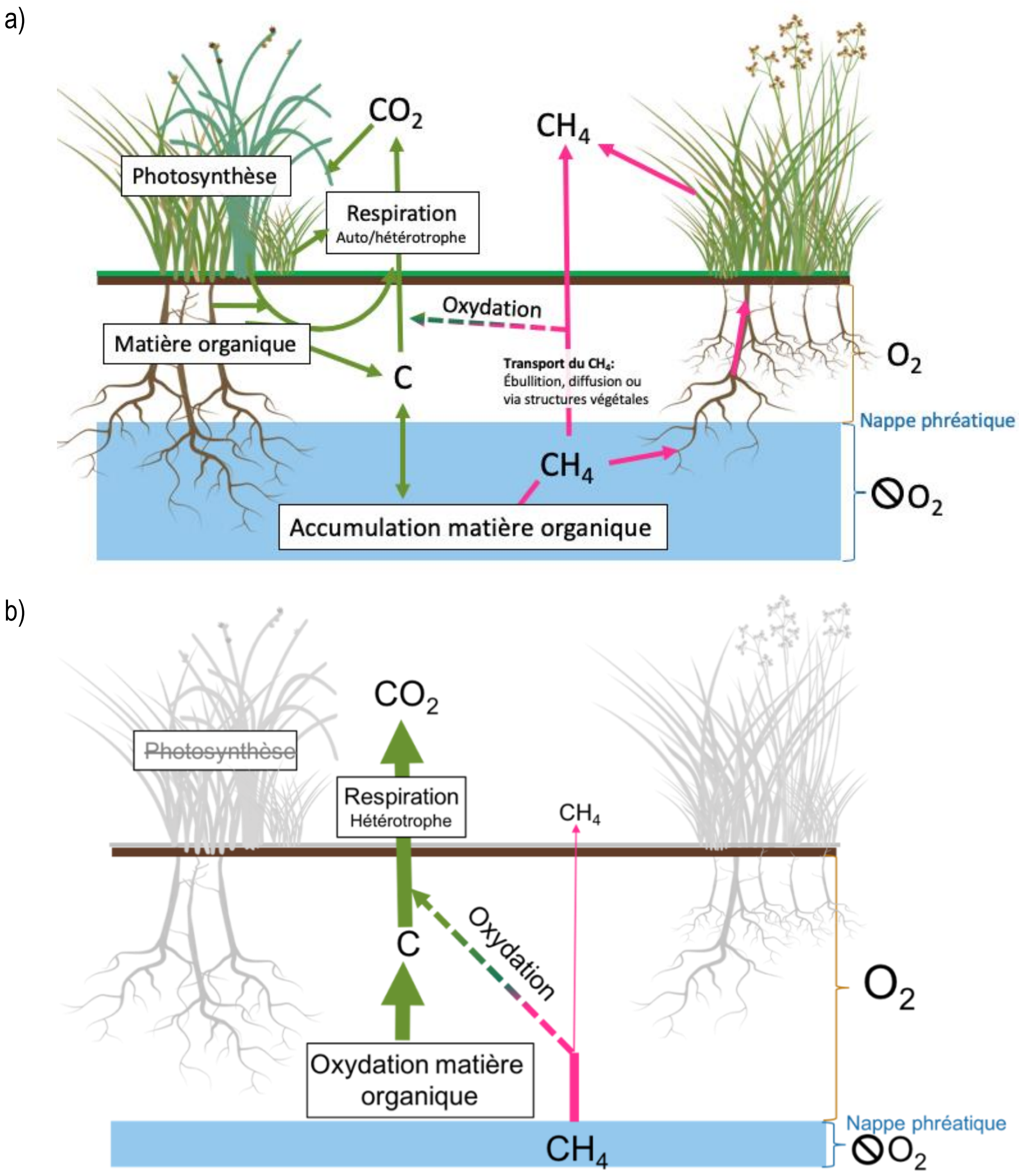


Figure 1 Schématisation du cycle du carbone a) en tourbière naturelle b) en tourbière post-extraction. Les lignes pointillées indiquent le processus d'oxydation par lequel le CH_4 peut être transformé en CO_2 dans la partie oxygénée du profil de tourbe. Lorsque la nappe d'eau est affleurante, des bulles de CH_4 peuvent se former pour rejoindre l'atmosphère (transport par ébullition) En b), la largeur des flèches indique le changement de magnitude (augmentation ou diminution) que subissent les émissions de CO_2 et de CH_4 à la suite des activités d'extraction.

4. Restauration écologique des tourbières après extraction de tourbe

« La restauration écologique est une action intentionnelle qui initie ou accélère l'autoréparation d'un écosystème en respectant sa santé, son intégrité et sa gestion durable » (SER, 2004). Dans le cadre de la restauration des tourbières après extraction de tourbe en Amérique du Nord, le but de la restauration des tourbières est généralement le retour d'un écosystème accumulateur de tourbe par 1) la restauration du régime hydrique par l'élévation et la stabilisation du niveau de la nappe phréatique près de la surface et 2) le rétablissement d'un couvert végétal dominé par des espèces propres aux tourbières (Quinty et Rochefort, 2003).

En raison des propriétés de leur tourbe, plus intéressantes sur le plan horticole (notamment une meilleure capacité de rétention de l'eau et d'une décomposition moins rapide) les dépôts tourbeux dominés par les sphaignes sont les plus recherchés pour la fabrication de substrats de croissance (Caron et al., 2015). Comparativement aux fens, les tourbières ombrotrophes sont donc plus touchées par les activités d'extraction de tourbe au Canada. Depuis les années 1990, c'est ce type de tourbière qui a reçu la plus grande attention en matière de recherche en restauration, d'où le développement d'une méthode de restauration : la méthode de transfert du tapis muscinal (MTTM) (Graf et al., 2012). Cette méthode a été utilisée de manière probante pour restaurer l'hydrologie, et le couvert végétal des tourbières à sphaignes après extraction de tourbe (Boudreau et Rochefort, 2008; González et Rochefort, 2014; Poulin et al., 2013). Cette méthode a aussi un effet significatif sur le fonctionnement biogéochimique des tourbières en entraînant une diminution des émissions de CO_2 et une augmentation des émissions de CH_4 (Nugent et al., 2018; Strack et al., 2016). Cette méthode comporte une étape de rafraîchissement et de nivellement des surfaces (appelée reprofilage), la création d'andains et de digues pour retenir l'eau, l'épandage de matériel végétal en provenance d'un site donneur, un épandage de paillis, une fertilisation phosphatée pour favoriser des plantes compagnes favorables à l'établissement de la sphaine et un remouillage du site par le blocage des canaux de drainage. Pour consulter la méthode complète, voir Quinty et Rochefort (2003).

Restauration des fens en Amérique du Nord

Généralement, après les activités d'extraction, une couche de tourbe ombrotrophe demeure présente après extraction et la tourbe résiduelle présente des caractéristiques physico-chimiques similaires à celles retrouvées dans les tourbières à sphaignes naturelles. Cependant, en raison de l'utilisation de techniques d'extraction plus efficaces, de la diversification de l'utilisation des substrats de tourbe, du type de matériel récolté ou de la configuration particulière de certaines tourbières, la tourbe résiduelle laissée après extraction peut présenter des caractéristiques physico-chimiques caractéristiques de celles retrouvées dans les fens (GRET, 2016). Par exemple, dans certaines situations, l'extraction atteint la couche de tourbe de cypéracées sous-jacente à la couche de tourbe de sphaignes, la première s'étant formée plus tôt dans le développement de la tourbière.

L'abaissement de niveau du sol causé par l'extraction peut aussi provoquer une résurgence d'eau souterraine. Cette eau plus riche en éléments minéraux n'est pas propice au rétablissement d'espèces typiques des tourbières ombrotrophes et témoigne d'une hydrologie plus semblable à celle des tourbières minérotrophes (Rochefort et al., 2016). Le type d'écosystème visé par la restauration doit donc être ajusté en fonction des conditions actuelles du site à restaurer. Les actions de restauration viseront donc l'établissement d'un écosystème de tourbière minérotrophe plutôt qu'à celui d'une tourbière ombrotrophe (Graf, 2008; Lamers et al., 2015; Wind-Mulder et Vitt, 2000). Depuis les 25 dernières années, on assiste par ailleurs à un élargissement du domaine de la restauration des tourbières, qui s'était penché tout d'abord sur les tourbières à sphaigne et qui maintenant s'intéresse à tous les types de tourbières, incluant les fens (Chimner et al., 2016).

En Amérique du Nord, il existe peu d'études sur la restauration des fens après extraction de tourbe. Sur de petites surfaces, des essais de transplantation de cypéracées et d'autres espèces vasculaires typiques des tourbières minérotrophes ont été effectués avec succès (Cooper et MacDonald, 2000; Rochefort et al., 2015). En revanche, les coûts élevés liés à ce genre de technique de restauration rendent leur utilisation problématique pour la restauration de grandes surfaces. Des essais s'inspirant de la méthode de transfert du tapis muscinal initialement créée pour restaurer les tourbières à sphaignes ont également été effectués sur de petites surfaces en serre et sur le terrain (Cobbaert et al., 2004; Graf et Rochefort, 2008; Graf et Rochefort, 2010). Par exemple, Cobbaert et al. (2004) ont introduit avec succès, à partir de matériel végétal en provenance d'un site donneur, des espèces vasculaires typiques des fens sur des surfaces expérimentales de 5 x 5 m. Graf et al. (2008) ont introduit avec succès des mousses typiques des tourbières minérotrophes sur des surfaces expérimentales de 5 x 6 m. En Amérique du Nord, une seule étude a porté sur la restauration à grande échelle (site expérimental de 15 ha) d'une tourbière post-extraction dont la tourbe résiduelle présente des caractéristiques semblables à celles retrouvées dans les fens (Rochefort et al., 2016). Dans cette étude, l'épandage mécanisé de matériel végétal, tel que pratiqué dans la restauration des tourbières à sphaignes, n'a pas mené à l'établissement d'espèces muscinales typiques des fens. Cinq saisons de croissance après restauration, le recouvrement d'espèces vasculaires était quant à lui faible et hétérogène. Plus de recherche est nécessaire afin de mieux comprendre quelles sont les conditions pouvant assurer l'établissement des mousses de fen dans le cadre d'activités de restauration sur de grandes surfaces. Des défis supplémentaires, liés à l'hydrologie particulière des fens, qui reçoivent de leur eau non seulement des précipitations, mais aussi d'influx d'eau souterraine et/ou de surface, doivent aussi être résolus. Ces problématiques sont par exemple liées à l'érosion par l'écoulement d'eau de surface, la composition chimique de l'eau après restauration et la quantité d'eau entrant dans le site lors de la restauration (Chimner et al., 2016).

Restauration des fens en Europe

En Europe, plusieurs études portant sur la restauration des fens ont été réalisées (Lamers et al., 2015). Cependant, puisque les contextes et les buts de restauration diffèrent entre l'Europe et l'Amérique du Nord, les techniques développées en Europe sont peu transférables au contexte nord-américain (Graf et Rochefort, 2008). La plupart des études européennes portant sur la restauration des fens ont été réalisées sur des sites drainés à des fins agricoles ou de foresterie (Graf et Rochefort, 2008). En Amérique du Nord, les projets de restauration portent plutôt sur des sites dégradés par l'extraction de tourbe par aspiration. En plus des différences dans les conditions initiales des sites à restaurer, le enjeux de restauration rencontrés en Europe diffèrent de ceux rencontrés en Amérique du Nord. Par exemple, on retrouvera en Europe des problèmes d'eutrophisation et de compétition par les espèces végétales préexistantes ou présentes dans la banque de graines. En Amérique du Nord, l'extraction de tourbe ne laisse sur place aucune banque de graines et aucun résidu de fertilisation (Graf et Rochefort, 2008). Par ailleurs, en Europe, 52% de la surface originelle occupée par des tourbières a été perdue à la suite d'activités anthropiques et les fens figurent parmi les habitats les plus menacés (Joosten et Clarke, 2002; Priede, 2016). En Amérique du Nord, 90% de la surface occupée par les tourbières serait toujours intacte (Poulin et al., 2004). La restauration des fens en Europe visera donc davantage une amélioration de la biodiversité régionale et le maintien ou le retour d'espèces rares. En Amérique du Nord, on visera plutôt le retour des fonctions écologiques comme la séquestration du carbone. Bref, des techniques de restauration propres au contexte nord-américain doivent être développées (Graf et Rochefort, 2008).

5. Potentiel de la technique de remouillage pour la restauration des fens post-extraction

Une technique de restauration, le remouillage, présente un potentiel pour rétablir de manière efficiente un couvert de végétation typique des tourbières sur des sites post-extraction présentant une tourbe résiduelle minérotrophe. Le remouillage consiste à bloquer les canaux de drainage de sorte à permettre la remontée et à stabiliser le niveau d'eau près de la surface du sol. Dans certaines situations, une coupe d'arbres peut être réalisée afin de contribuer à cette remontée du niveau d'eau. Dans le premier projet de restauration à grande échelle d'un fen post-extraction en Amérique du Nord, Rochefort et al. (2016) ont souligné que la technique de remouillage présentait un fort potentiel pour appuyer l'expansion d'espèces de fens spontanément établies.

Le potentiel de cette technique repose notamment sur la plus grande propension des tourbières minérotrophes à être colonisées par des espèces de milieux humides ou de tourbières à la suite de la cessation des activités d'extraction de tourbe, comparativement aux tourbières ombrotrophes. Par exemple, Graf et al. (2008) ont effectué des relevés de végétation dans 28 fens post-extraction au Canada et au Minnesota (É.-U.). En moyenne, les sites présentaient un recouvrement d'espèces vasculaires de 25 à 60%. Les sites dont le système de drainage s'était effondré (non activement drainés), ce qui peut correspondre à un traitement de remouillage, présentaient un couvert de végétation nettement supérieur aux sites activement drainés, et ce, relativement rapidement après la fin des activités d'extraction (en moyenne 7 ans). Les sites non activement drainés présentaient un en effet couvert total de végétation de 50%, comparativement à 25 % pour les sites activement drainés. De plus, les sites non activement drainés présentaient un couvert de tourbe à nu de moins de 40% comparativement à 73% pour les sites activement drainés. Dans les tourbières à sphaignes post-extraction, les couverts de végétation spontanés se situent plutôt sous les 25% (Famous et al., 1991; Poulin et al., 2005). Gagnon (2016) s'est quant à lui penché sur la colonisation spontanée d'une tourbière minérotrophe post-extraction de 430 ha au Manitoba dont le système de drainage était hors d'usage. Ce site a été colonisé spontanément par différents assemblages de végétation typiques de milieux modérément riches ou de marais, selon le niveau d'eau et les caractéristiques physico-chimiques de la tourbe résiduelle. La position de la nappe phréatique, la présence à proximité d'un milieu pouvant fournir des propagules, ainsi que les conditions physico-chimiques de la tourbe résiduelle (p. ex. le pH) seraient les principaux facteurs influençant le rétablissement spontané d'une végétation typique des tourbières sur des sites post-extraction (Gagnon, 2016; Graf et al., 2008; Konvalinková et Prach, 2014; Priede et al., 2016). Il pourrait donc être possible de restaurer certains sites présentant des conditions propices (proximité d'une source de propagules et chimie adéquate) par la seule hausse des niveaux d'eau à l'aide d'une action de remouillage.

En résumé, l'un des seuls essais à grande échelle selon la méthode développée pour la restauration des tourbières à sphaignes (par transfert du tapis muscinal) n'a pas donné de résultats satisfaisants pour la restauration à grande échelle des fens post-extraction. Il faut donc trouver d'autres modes de restauration pour ces sites. Des méthodes de restauration adaptées au contexte nord-américain doivent aussi être développées. En réunissant certains facteurs, il serait possible d'encourager, par une simple hausse des niveaux d'eau, la colonisation des fens post-extraction par des espèces de tourbières. Il faut maintenant réunir ces conditions (soient une source de propagules à proximité et un niveau d'eau et des conditions physico-chimiques appropriées) et évaluer leur efficacité à rétablir les attributs et les fonctions typiques des fens naturels. De la même manière que pour les tourbières à sphaignes, une méthode de restauration appliquée aux fens devrait permettre le retour d'une végétation typique de ce type d'écosystème. Elle devrait aussi permettre le retour d'un écosystème fonctionnel accumulateur de tourbe.

6. Hypothèse générale et objectifs

L'objectif général de cette étude est d'évaluer, dans le contexte d'une restauration de fen post-extraction, l'effet de la technique de remouillage sur l'établissement de communautés végétales et d'échanges de carbone (CO_2 et CH_4) typiques des fens naturels. La première hypothèse est que les conditions induites par le remouillage permettront à une végétation typique des fens de s'établir, de prendre de l'expansion et de présenter, après quelques saisons de croissance, une structure et une composition similaires à celle d'un écosystème de référence local. La deuxième hypothèse émise est que le remouillage induira une diminution des émissions de CO_2 et une augmentation des émissions de CH_4 comparativement à une situation sans action de remouillage. Plus précisément, les objectifs spécifiques de cette étude sont les suivants :

1) Évaluer l'effet du remouillage sur le rétablissement de **flux de CO_2 et de CH_4 semblables** à ceux prévalant dans un écosystème de référence local.

2) Déterminer les **facteurs** environnementaux pouvant **expliquer les différences dans les flux** de CO_2 et de CH_4 entre les traitements de remouillage et l'écosystème de référence.

3) Réaliser le **bilan des échanges de CO_2 et de CH_4** des communautés végétales dominantes de chaque traitement pour une saison de croissance.

4) Déterminer l'effet du remouillage sur l'établissement de communautés végétales semblables à celles retrouvées dans un écosystème de référence local : **composition** et **structure** de la végétation.

Chapitre 1 Rewetting a minerotrophic peatland after peat extraction activities: Impact on carbon exchange and vegetation

1.1 Résumé

La méthode de restauration par transfert du tapis muscinal (MTTM) a été développée en Amérique du Nord pour restaurer la fonction de séquestration du carbone et la végétation des tourbières à sphaignes (ombrotrophes) post-extraction. Toutefois, lorsqu'utilisée sur des tourbières dont la couche de tourbe résiduelle présente des conditions similaires à celles retrouvées dans les tourbières minérotrophes (fens), la MTTM doit être adaptée. Lorsque certaines conditions sont réunies, un simple remouillage par le blocage des canaux de drainage pourrait être suffisant pour rétablir une végétation typique des fens et éventuellement la fonction de séquestration du carbone des fens post-extraction. Nous avons évalué l'effet du remouillage sur l'établissement de la végétation et sur les échanges de carbone (dioxyde de carbone : CO_2 et méthane : CH_4) une et dix saisons de croissance après remouillage sur une tourbière post-extraction du sud du Manitoba, au Canada. Après une saison de croissance, les échanges de CO_2 et de CH_4 étaient similaires à ceux observés dans l'écosystème de référence. Après dix saisons de croissance, les échanges de CO_2 étaient aussi similaires à ceux observés dans l'écosystème de référence. Toutefois, les émissions de CH_4 ont atteint une moyenne de 416 mg m^{-2} j^{-1} en juillet 2016, ce qui représente presque le quadruple des émissions observées à l'écosystème de référence pour ce même mois. Une et dix saisons de croissance après le remouillage, une dominance des espèces végétales typiques des tourbières était observée. Après dix saisons de croissance, un tapis discontinu d'espèces de mousses de tourbières ayant un recouvrement moyen de 18% était établi. Somme toute, le remouillage peut être une technique de restauration efficace lorsque les sites à restaurer se situent à proximité d'un fen pouvant fournir des propagules. La gestion des niveaux d'eau afin de conserver une nappe phréatique près de la surface du sol, est essentielle pour faciliter l'établissement et l'expansion des bryophytes. Les inondations devraient être évitées pour limiter les émissions de CH_4 et maximiser le potentiel de séquestration de carbone.

1.2 Abstract

In North America, a *Moss Layer Transfer Technique* (MLTT) has been developed to restore the carbon sequestration function and typical vegetation of *Sphagnum* dominated peatlands after peat extraction. However, when applied to peatlands with minerotrophic remnant peat conditions (fens), the MLTT does not appear to be as efficient. In certain contexts, the action of rewetting by blocking the drainage ditches could be sufficient to restore typical fen vegetation and eventually the carbon sequestration function of post-extraction fens. We evaluated, on a post-extraction peatland in Southeastern Manitoba (Canada), the effect of rewetting on the establishment of vegetation and carbon exchange (carbon dioxide: CO_2 and methane: CH_4) one and ten growing seasons after rewetting. One growing season after rewetting, CO_2 and CH_4 fluxes were similar to what is observed in the reference ecosystem. Ten growing seasons after rewetting, CO_2 fluxes were also similar to what is observed in the reference ecosystem. However, CH_4 emissions reached on average 416 mg m^{-2} d^{-1} in July 2016, almost four times the emissions at the reference ecosystem. One and ten growing seasons after restoration, peatland and wetland vascular plant species were dominant. Ten growing seasons after rewetting, a discontinuous mat of peatland mosses (mean cover of 18%) was established. Overall, rewetting can be an effective restoration strategy when the site to be restored is adjacent to a fen ecosystem that can provide propagules. However, water management to keep the water table level close to the ground surface is essential for bryophyte establishment and expansion. Inundation should also be avoided to limit CH_4 emissions and maximize the carbon sequestration potential.

1.3 Introduction

Through fluxes of carbon dioxide (CO_2), methane (CH_4) and dissolved forms of carbon, peatlands play a significant role in the global carbon (C) cycle and climate regulation (Baird, 2009; Joosten et al., 2016). Peatlands cover approximately 2.84% of the world land area (Xu et al., 2018), but represent the largest terrestrial C pool (Joosten, 2016). Waterlogged conditions prevailing in peatlands lead to an imbalance between uptake of CO_2, as gross ecosystem production (GEP), and CO_2 release, as ecosystem respiration (ER), resulting in accumulation of C into organic matter (Vasander and Kettunen, 2006). On a global scale, peatlands are also major CH_4 emitters (Baird, 2009), a greenhouse gas 28 times more potent than CO_2 on a 100-year time frame (Myhre et al., 2013). However, in the long term, CO_2 uptake by peatlands counterbalances C released, and radiative forcing, by CH_4 emission. For instance, their development during the Holocene likely resulted in a net cooling of the climate during that era (Frolking and Roulet, 2007). Conversely, degraded peatlands disproportionally contribute to the global anthropogenic CO_2 emissions with 3% of CO_2 emissions but covering only 0.4% of the land area *(*Joosten, 2009; Joosten et al., 2016; Quéré et al., 2015).

In North America, peat extraction for the production of horticultural substrate is a cause of disturbance to natural peatlands (Daigle and Gaudreau-Daigle, 2001). To allow the circulation of machinery and the extraction of peat, complete removal of the vegetation and lowering of the water level by the construction of drainage ditches must be achieved (Waddington and Price, 2000). Environmental conditions after the cessation of peat extraction activities are harsh for vegetation establishment: the peat is compacted and has modified hydraulic properties (Price et al., 2003); the lowering of the water table and consecutive aeration of the peat lead to its accelerated decomposition, exposing plant roots; the absence of vegetation and exposure of the dark colored peat can lead to high soil surface temperature (Graf et al., 2012); conversely, frost heaving, a form of substrate instability caused by the formation of ice needles in the peat can cause physical damage to vegetation (Groeneveld and Rochefort, 2002; Groeneveld and Rochefort, 2005). After extraction, peatlands can stay devoid of vegetation for decades or be colonized by vegetation assemblages not typical of natural peatlands (Lavoie et al., 2003; Poulin et al., 2005). Extraction also induces major changes in the biogeochemical functioning of peatlands. Absence of vegetation and aeration of the peat profile turns peatlands into large CO_2 sources (Rankin et al., 2018; Waddington et al., 2002). Methane emissions after peat extraction are considerably reduced due to the lowering of the water table (Waddington and Day, 2007)

Since the late 1990s, a restoration technique called the *Moss Layer Transfer Technique* (MLTT) (Rochefort et al., 2003), has been developed. This method aims at establishing, on post-extraction sites, vegetation communities that are representative of natural peatlands (Boudreau and Rochefort, 2008; González and Rochefort, 2014; Poulin et al., 2013). The MLTT includes the following steps: a surface preparation step called “profiling” which consist of removing spontaneously established vegetation, exposing fresh peat and levelling the peat surface; an introduction of plant material from a donor site located nearby the site to restore; the addition of straw mulch and phosphate fertilizer; and finally, a step called “rewetting”, consisting in the raising and stabilization the water table near the surface by blocking the drainage ditches (Rochefort et al., 2016). For more details on the technique, see González et Rochefort (2014). Considering the importance of peatlands within the global C cycle, the prime goal of peatland restoration after peat extraction in North America has been established as the return of the C sequestration function (Rochefort et al., 2003; Strack et al., 2016). To achieve this, restoration efforts aim to raise and stabilize the water table near the surface and to reestablish typical peatland plant communities (Quinty and Rochefort, 2003). The MLTT has proved to greatly alter CO_2 (decrease of emissions and return C sink) and CH_4 (increase of emissions) fluxes compared to unrestored sites (Nugent et al., 2018; Strack et al., 2016).

Poorly decomposed *Sphagnum* peat is the preferred type of peat for the production of horticultural substrate (Caron et al., 2015; Daigle and Gaudreau-Daigle, 2001). Poorly decomposed *Sphagnum* peat is essentially found in acidic *Sphagnum* dominated peatlands. Consequently, it is mainly *Sphagnum* peatlands that are targeted for peat extraction. After the cessation of extraction activities, the physicochemical characteristics of the residual peat are usually similar to those prevailing in natural *Sphagnum* peatlands. However, extraction activities sometimes reach deeper peat layers with physicochemical properties typical of minerotrophic peatlands (fens). Other situations like ground water discharge or hydrological connection to the watershed following extraction can also lead to residual peat conditions being more similar to fens than *Sphagnum* peatlands, *i.e.* richer and less acidic (Rochefort et al., 2016). In those cases, it is preferable to set the restoration goal to a fen ecosystem (Graf and Rochefort, 2008; Wind-Mulder and Vitt, 2000). However, restoration techniques adapted to those situations still need to be developed (Chimner et al., 2016).

There has been plenty of research on fen restoration in Europe (Lamers et al., 2015). However, little can be transferred to North America because of differences in past uses of sites to be restored and goals of restoration (Graf and Rochefort, 2008). For instance, most European restoration projects are realized on peatlands that had been drained for agriculture and forestry. Consequently, eutrophication (e.g. following fertilization) and the presence of a seed bank of unwanted species are often restoration issues to be addressed. Those issues do not apply to the North American context where peatland restoration activities follow peat extraction. Furthermore, fens are among the most endangered types of ecosystem in Europe. Consequently, biodiversity is often at the center of the restoration efforts. In North America, peatlands are less endangered and the restoration efforts are rather directed towards the return of the carbon sequestration function (Graf and Rochefort, 2008). Hence, fen restoration techniques adapted to North America must be developed.

In North America, the first trials where the MLTT was applied in post-extraction fen conditions in greenhouses and on small surfaces (≤ 30 m^2) in the field gave promising results in terms of bryophyte and vascular plant establishment (Cobbaert et al., 2004; Graf and Rochefort, 2008; Graf and Rochefort, 2010). However, when applied on a larger scale, the MLTT did not lead to bryophyte establishment and resulted in lower vascular plant covers compared to undisturbed fens and smaller scale experimental results (Rochefort et al., 2016). In the first ecosystem-scale post-extraction fen restoration project in North America, rewetting gave promising results in terms of vascular plant cover; where fen vegetation had spontaneously established, it has been suggested that this technique could be sufficient to promote expansion of vascular fen species (Rochefort et al., 2016). Furthermore, post-extraction fens with drainage systems that are no longer functional were observed to be recolonized quickly by peatland and wetland species (Gagnon, 2016; Graf et al., 2008). This likely indicates that the introduction of plant material might not be necessary to restore post-extraction fens when proper hydrological conditions are reestablished. Water table level, pH and the proximity of a source of propagules were identified as the main factors influencing the establishment of fen vegetation after cessation of peat extraction activities (Konvalinková and Prach, 2014; Priede, 2016). By ensuring that sites meet these conditions, it may be possible to restore post-extraction fens with rewetting alone.

The general aim of this study was to evaluate if rewetting could be sufficient to restore post-extraction peatlands with residual peat having physicochemical characteristics typical of those prevailing in fens. More specifically, the objectives were to compare a site, where different rewetting strategies were applied, to local reference ecosystems (natural fens) to 1) determine the effect of rewetting on the establishment of typical fen vegetation; 2) determine the effect of rewetting on CO_2 and CH_4 exchange. We also estimated the growing season greenhouse gas balance and investigated environmental factors explaining differences in CO_2 and CH_4 exchange between rewetted sectors and the reference ecosystem.

1.4 Methods

Study site

The study site is located in Southeastern Manitoba (49.931°N, 96.237°W), approximately 65 km east of Winnipeg, Canada, in the Boreal Shield ecozone (Smith et al., 1998). The mean annual precipitation, based on 1981-2000 measurements, at Pinawa meteorological station (28 km from the site) is 578.3 mm, 20% of which falls as snow. According to Environment Canada (2018), the annual mean temperature is 2.8°C (July: 19.8°C; January: -16.6°C;). The experimental site (excluding the reference ecosystem) is an area of 35 hectares located at the southeastern tip of a peat extraction site covering a total of 237 ha. It is located in a large peatland complex extending over several thousand hectares. Peatlands of the region are typically composed of graminoid fens and forested fens intermixed with *Sphagnum* peatland islands (Glaser, 1987). The reference ecosystem is composed of two natural fens located directly next to the experimental site. The first is located on the northeast side of the experimental site. It is a forested fen with *Larix laricina* and *Betula pumila* as main tree species (Fig. 2). The second is an open graminoid fen dominated by sedges (e.g. *Carex lasiocarpa*). It is located at the southwest and southeast sides of the experimental site (Fig. 2). Based on peat and water characteristics, and on floristic indicators (presence of *Scorpidium scorpioides* and abundance of *Scopirdium cossonii*), the natural fen surrounding the experimental area can be classified as extreme rich (Vitt, 2006; Walbridge and Navaratnam, 2006). The forested fen has a water pH of 7.3 ± 0.3 (mean ± SD, n=4) and a corrected electro-conductivity (EC; Sjörs (1950)) of 360 ± 63 (mean ± SD, n=4). The open graminoid fen has a water pH of 7.1 ± 0.5 (mean ± SD, n=4) and a corrected EC of 270 ± 42 (mean ± SD, n=4). See appendix A for complete information on water and peat chemistry.

Management history and site rewetting

The site was prepared for peat extraction between 2004 and 2014. Drainage ditches were dug to allow machinery circulation and peat extraction. A road was constructed, separating the site in half in a northwest-southeast axis. Two years after the digging of the drainage ditches, vegetation was removed from the entire surface of the experimental area. The peat substrate at the southeastern half of the experimental site had physicochemical characteristics typical of those prevailing in fens and therefore did not meet the quality requirements for the production of horticultural substrate. Consequently, peat was never extracted in that area. The unsuitable sector for commercial horticultural peat was rewetted by blocking the main drainage ditches with peat dikes immediately after the vegetation was cleared. Peat extraction, only occurred in the northwestern half of the site. In that area, 5 cm of peat were removed after which the fen peat layer was reached. The depth of the residual peat layer is greater than one meter over the whole experimental area.

In 2015, the site was surveyed to develop a restoration plan. An abundant cover of graminoid species (e.g. *Carex lasiocarpa*) had spontaneously established on the southeastern half of the site that had been cleared of vegetation and rewetted nine growing seasons earlier. No further restoration actions were planned for that area. The area where peat had been extracted was sparsely covered with grasses and ruderal species. Pore water showed pH values typical of poor fens: pH, 5.2 ± 0.4 (mean ± SD), n=7. Water samples collected in drainage ditches presented pH values of 6.6 to 7.1 and EC values of 201 to 330 $\mu S \cdot cm^{-1}$, characteristic of extreme rich fens (Vitt, 2006; Walbridge and Navaratnam, 2006). Because the residual peat layer consisted of fen peat and because of the location of the experimental area, embedded within an extreme rich fen, the restoration plan was developed to recreate a rich to extreme rich fen ecosystem.

Initially, about half of the extracted area was targeted for restoration actions inspired by the MLTT. However, as a result of the unusually abundant precipitation combined with blocking of the drainage ditches with peat dams and filling of the secondary ditches with peat, the area was flooded before the restoration actions were completed [1]. Before flooding, the surface of this area was profiled. Thus, this area will be considered as profiled and rewetted. The other half of the area that had been extracted was also rewetted by blocking the main ditches with peat dikes, but its surface was not profiled.

---

[1] Initially, four peat fields (5 ha) were targeted for restoration actions. In September 2015, the surface of the four peat fields targeted for restoration was profiled. Crescent-shaped bunds and dams were constructed to block the drainage ditches and to retain water on the site (rewetting action). During the winter 2016, plant material was collected from a donor site located in the forested area of the reference ecosystem. The plant material was piled near the restoration area. Spreading of the plant material and fertilization (rock phosphate (0-13-0), 150 kg/ha) were planned to be completed in spring 2016. However, the steps of fertilization and introduction of plant material were never completed because the area was flooded in spring 2016. Two additional peat fields were left as is to represent typical post-extraction conditions without restoration actions.

The final experimental design includes five experimental sectors (Fig. 2 and 3). The names of the sectors indicate the type of restoration action and the number of years/growing seasons elapsed since the restoration, at the moment of the study. The experimental sectors represent conditions 1) after peat extraction but without restoration actions (sector *unrestored*, named *UNR*); 2) after peat extraction and one growing season after rewetting (*R*) and profiling (*P*) (sector named *RP1*; this area is the one that was flooded after being partially restored); 3) after peat extraction and one growing season after rewetting (R; sector named *R1*); 4) ten growing seasons after rewetting (sector named *R10*) and 5) of the regional typical fen ecosystem, as a reference ecosystem (sector named *REF*). The reference ecosystem includes an open graminoid fen (located at the southwest and southeast sides of the sectors that had been rewetted) and a forested fen (located on the northeast side of the rewetted sectors).

At *RP1*, spring rainfall and snowmelt combined with rewetting operations resulted in flooding of the whole sector. In order to protect the active peat extraction area from flooding, an embankment made of peat was built on the northwest side of *RP1*. The presence of the embankment, combined with high precipitation persisting over the summer maintained inundation at *RP1* from May to September 2016.

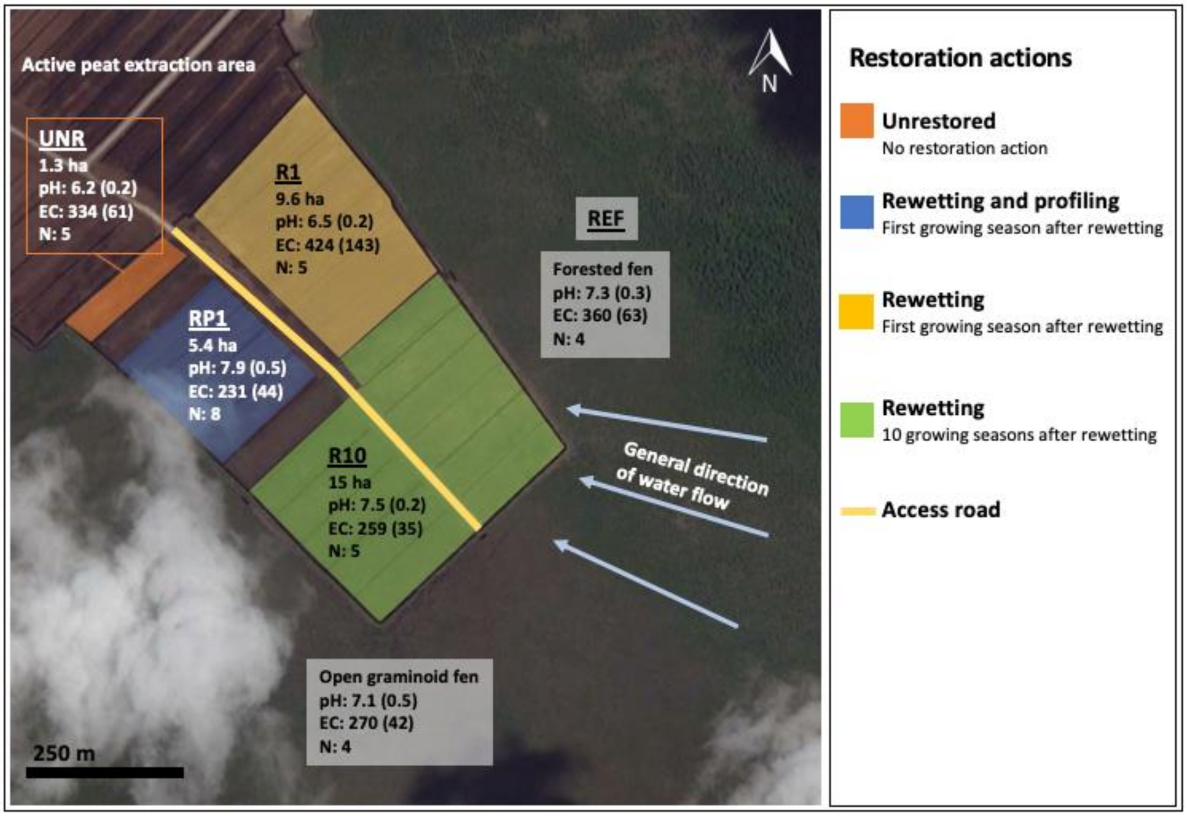
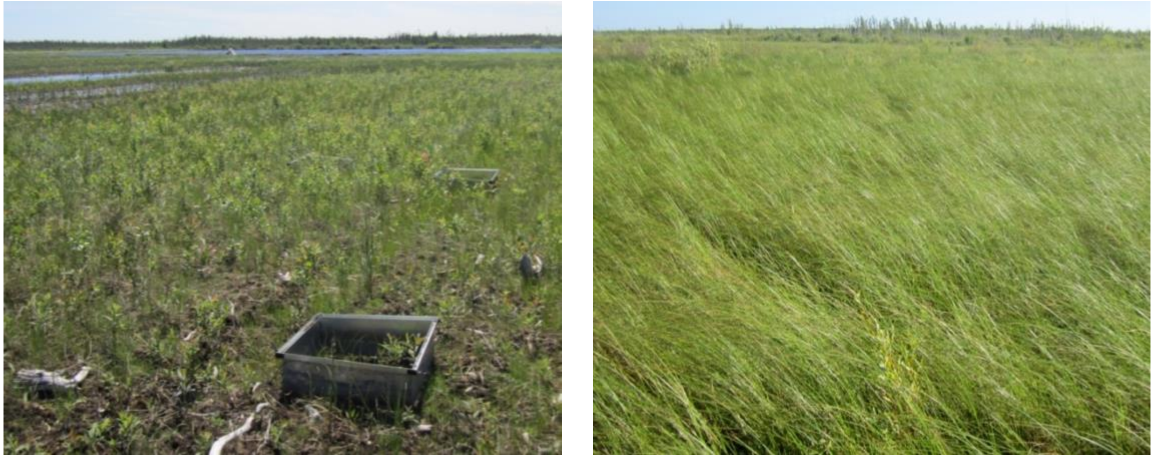


Figure 2 Experimental sectors of the study site in Southeastern Manitoba (49.931°N, 96.237°W), approximately 65 km east of Winnipeg, Canada. Colors indicate restoration actions. *UNR*: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem. The reference ecosystem (REF) is a rich fen located at the periphery of the experimental site. pH and corrected EC (µS cm^{-1}) values (SD) were measured in the field four times between May and August 2016 with portable meters (pH: Oakton pHTestr 10; EC: Oakton EC Testr 11+).

a) **UNR**: no restoration action

b) **RP1**: profiled, first growing season after rewetting



c) **R1**: first growing season after rewetting

d) **R10**: ten growing seasons after rewetting

e) **REF**: reference ecosystem (forested fen)

f) **REF**: reference ecosystem (graminoid fen)

Figure 3 Photographs and names of the experimental sectors of the study site in Southeastern Manitoba.

Carbon exchange measurement

Methane flux measurement

The closed chamber technique was used to measure CH_4 fluxes, as described in Strack et al. (2014)[2]. Opaque PVC chambers (60 x 60 x 30 cm) placed on steel collars (60 x 60 x 15 cm deep) were used to collect gas samples. Collars were installed at the beginning of May 2016 in each experimental sector (Fig. 4). Each chamber was equipped with a three-way valve, a battery-operated fan to mix the air inside the chamber and a thermocouple measuring temperature inside the chamber. Chambers were installed on collars for a period of 35 minutes. Samples were collected after 7, 15, 25, and 35 minutes and stored in pre-evacuated exetainers (Labco Ltd, UK). Samples were analyzed at the Wetland Soils and Greenhouse Gas Exchange Lab at the University of Waterloo. Methane concentration in each vial was measured with a Shimadzu GC-2014 (Shimadzu Corporation, Japan) gas chromatograph equipped with a flame ionization detector. Methane flux was calculated from the linear change in concentration over time corrected for air temperature inside the chamber and the volume of the chamber. Fluxes with a slope R^2 close to zero and concentration change within the precision of the gas chromatograph (0.5 ppm) were considered equal to zero. Inconsistent fluxes suggesting ebullition (slope $R^2 < 0.60$) were removed from the data set, inducing 7% data loss.

Carbon dioxide flux measurement

Carbon dioxide fluxes were measured using the closed chamber technique on the same plots used to measure CH_4 fluxes (Strack et al., 2014). A clear acrylic chamber (60 x 60 x 30 cm) equipped with a thermocouple, a battery-operated fan and connected to a portable infrared gas analyzer (EGM-4, PP Systems, Massachusetts, USA) was installed for 105 seconds on the sampling plots. Over that period, CO_2 concentration was recorded every 15 seconds. Net ecosystem exchange (NEE) was determined using the linear change in concentration of CO_2 in the chamber over the measurement period, corrected for temperature inside the chamber and the volume of the chamber. NEE fluxes were measured under different light levels created using a series of shades assessed with a photosynthetically active radiation (PAR) sensor installed on top of the chamber and connected to the IRGA. Completely dark conditions (PAR = 0) were used to determine ecosystem respiration (ER). Gross ecosystem productivity (GEP) was calculated as the difference between NEE and ER. Because of deep inundation throughout the summer at *R1*, we used air samples collected for CH_4 flux measurements to measure CO_2 fluxes. Consequently, only ER fluxes were obtained from *RP1* (fluxes under no light conditions). The concentration of CO_2 in the samples was determined in the laboratory with the gas chromatograph using a thermal conductivity detector. NEE fluxes with stable concentration (< 2 ppm) were assumed to be equal to zero.

---

[2] Both CH_4 and CO_2 fluxes were measured using the closed chamber technique. This technique allows the determination of local controls on fluxes and the effect of treatments that are conducted over small areas. Micrometeorological flux measurement techniques were excluded because of their lower spatial resolution.

Otherwise, non-linear fluxes (slope $r^2 \leq 0.75$) were deleted from data set resulting in 14% data loss for *RP1* and less than 1% for the other sectors.

Methane and CO_2 flux were measured every one to two weeks at each collar between May 12 and September 13, 2016. A flux with negative value is considered an uptake of carbon into the ecosystem; a positive value indicates a carbon loss from the ecosystem to the atmosphere. Location of the collars is presented in Fig. 4.

Environmental variables

Manual measurements

After each CO_2 and CH_4 flux measurement, water table level was measured inside a well. Wells were located less than 1 m from each collar. The soil temperature profile was also measured every 5 cm down to a depth of 20 cm with a thermocouple thermometer. A vegetation volume index was measured every two weeks at each collar following the methodology described by Davies et al. (2008). A stick painted in white and red bands was placed vertically in the collars. The proportion (%) of each band obscured by vegetation as well as the proportion (%) of vegetation cover in the collars (bryophyte and vascular species) were assessed. Five measurements inside individual collars were made each time and averaged. A computer program (*PObscured* available at www.firebeaters.org.uk) was used to transform obstruction values into a vegetation volume index. Additionally, vegetation surveys were completed in each collar at the end of the study period, in August 2016. In each collar, the proportion (%) of total vascular cover, bryophytes, graminoid species, shrub species and bare peat were assessed.

Continuous measurements

Soil temperature at a depth of 5 cm below the ground surface (T_5, °C; Onset HOBO Pro v2) was recorded at each sector, near the collars, every 30 minutes during the study period (May 24 to September 14, 2016). Water table level (*WTL*, cm; Solinst levelogger, corrected for barometric pressure with a barologger) was recorded at each sector every hour during the study period. A weather station located in the center of the experimental site (Fig. 4) measured PAR ($\mu mol\ m^{-2}\ s^{-1}$; quantum sensor LICOR, Lincoln, NE, USA) and air temperature (T_{air},°C; Campbell Scientific, Edmonton, Canada) every 20 minutes over the study period. Water pH and electrical conductivity were measured at each sector five times during the study period, and also before rewetting at *RP1*. Peat samples were collected at each sector in August 2016 (after rewetting). Chemistry analysis, measurements of electrical conductivity and pH were performed on peat samples at Université Laval (appendix A).

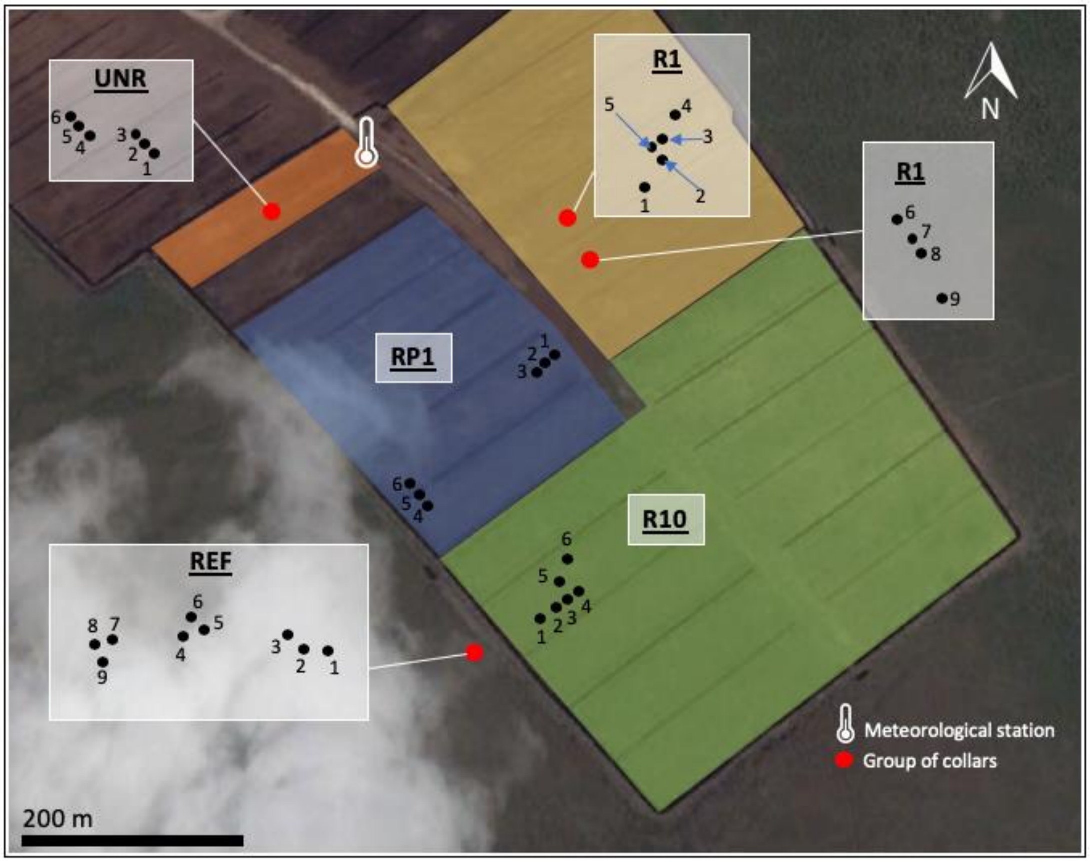


Figure 4 Approximate location of collars for carbon exchange measurements at each sector of the study site in Southeastern Manitoba in 2016. Three collars per predominant vegetation communities were placed in each sector. Dominant vegetation types at each collar are the following: 1) **UNR** collars 1-2-3: herbaceous vegetation; collars 4-5-6: bare peat 2) **R1** collars 1-2-3: shrubs; collars 5-6-7: herbaceous vegetation; 4-8-9: bare peat 3) **RP1** collars 1 to 6: standing water 4) **R10** collars 1-2-3: herbaceous vegetation; collars 4-5-6: shrubs 5) **REF** collars 1-2-6-7: herbaceous vegetation; collars 3-4-5-8-9: shrubs. *UNR*: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Data analysis

Differences in CO_2 and CH_4 fluxes between sectors

Mixed models with the plot name as a random factor (*lme* command from *nlme* package in R; (Pinheiro et al., 2018)) were used to compare fluxes between sectors. Only GEP and NEE fluxes with PAR > 1000 µmol $m^{-2}s^{-1}$ were compared between sectors. As fixed effects, mixed models included the rewetting strategy (i.e. the sectors), the period of the summer in which the flux was measured (early :May-June, mid: July or late-summer: August-September) and their interaction. The partitioning of the growing season into three periods was established based on vegetation development on site. The rewetting strategy was used as a grouping factor inside the models (*varIdent* function of *nlme* package) to account for heterogeneity of the variance between sectors. A random factor was included to account for repeated measurements on individual plots over the growing season. Models were visually inspected for normality and homogeneity of the residuals and possible leverage effect. When a factor significantly explained variation in the data, Tukey pairwise comparisons were executed in order to evaluate differences in CO_2 and log (CH_4+10) fluxes between sectors (*lsmeans* package; Lenth et Love (2018)). A significance level of $\alpha = 0.05$ was used for all tests.

Environmental controls on CO_2 and CH_4 fluxes

To investigate the controls on CO_2 and CH_4 fluxes, mixed models were built using, as fixed factors, air temperature, vegetation volume index, water table position, as well as an interaction between each of these and the restoration state. One model was built for each carbon flux component (ER, GEP, NEE, log(CH_4+10)). A random factor was included to account for repeated measurements on individual plots over the study period. The state of restoration was used as a grouping factor inside the models (*varIdent* function of *nlme* package) to account for heterogeneity of the variance between sectors. In all cases, NEE and GEP used in this investigation included only values in which PAR photon flux density was greater than 1000 µmol m^{-2} s^{-1}, representing rates when PAR is saturating (Bubier et al., 2003). Because of inundation and absence of vegetation at *RP1*, specific linear mixed effect models were built to investigate controls over CO_2 and CH_4 fluxes for that sector. For *RP1*, water table position and soil temperature or air temperature were used in mixed models as fixed factors.

Greenhouse gas balance and carbon balance

For each sample plot, ER and GEP empirical models were built to estimate total growing season CO_2 exchange. Depending on the available data and the best fit, models were estimated for two or three distinct periods of the summer 2016 (generally as follows: early summer (May-June); midsummer (July) and late summer (August-September)). As described by Strack et al. (2014), GEP models were based on the relation between GEP and PAR using a rectangular hyperbola:

1. $$GEP = \frac{PAR \times Q \times GP_{max}}{(PAR \times Q + GP_{max})}$$

ER models were based on the relation between ER and soil or air temperature (*T*; depending on the best fit) and water table level (*WTL*) using multiple linear regressions:

2. $$ER = aT + bWTL + c$$

For each model, parameters *a*, *b* and *c* were fitted with least square regressions. Once the models were determined, data from the weather station (PAR and air temperature) and/or data recorded at each sector (water table level and soil temperature) were then used to estimate ER and GEP for each hour of the study period. Hourly values were finally summed to estimate the total balance at each plot. Estimations of GEP and ER balances were based on a 113-day study period (May 24 to September 14, 2016).

Total CH_4 exchange for each sample plot was estimated by linear interpolation between measurements using:

3. $$F_{g,1-2} = \frac{1}{2}\left(f_{g,1} + f_{g,2}\right)(t_2 - t_1)$$

where $F_{g,1-2}$ is the integrated CH_4 flux between a pair of instantaneous fluxes or measurements (f_g) at Time 1 and Time 2 (t_1, t_2) (Green and Baird, 2017). The F_g values were added together to give the total value of CH_4 exchange at each sample plot. As for the CO_2 balance estimations, CH_4 linear interpolations were based on a 113-day study period.

For each plot, the total GHG balance (based on CH_4 and CO_2) was calculated using the *Global Warming Potential Method* (GWP). Total CH_4 exchange values obtained by interpolation were multiplied by 28 (GWP of CH_4 for a time horizon of 100 years; Myhre et al., 2013) to be transformed into CO_2 equivalents (g CO_2-e m^{-2}) and added to the total CO_2 exchange values. The carbon budget was also calculated for each individual plot by adding the modelled NEE values multiplied by 0.27 (representing only the C component of CO_2 molecules) to the total net emissions of CH_4 multiplied by 0.75 (representing only the C component of CH_4 molecules).

Effect of rewetting on vegetation

Vegetation monitoring

In the rewetting sectors, vegetation surveys were conducted in August 2016 and 2017 along 50 m transects parallel to the drainage ditches (Fig. 5). The starting position of each transect was randomly selected along the length of the peat fields. The reference ecosystem was characterized by surveying a total of three areas within the open graminoid and forested fen (Fig. 5). Within each of those areas, vegetation surveys were conducted along three transects. In each sector, the number of transects was proportional to their surface area.

Along each transect, vegetation was evaluated in five equally distant plots. One plot corresponds to one 1 x 1 m quadrat and ten 30 x 30 cm quadrats placed inside (8) and outside (2) each 1 m x 1 m quadrat. Inside each 1 x 1 m quadrat, the proportion (%) of the surface covered by each vascular plant species was assessed by vertical projection (for detailed information about the method, see González and Rochefort, 2014). The proportion (%) of the surface covered by vegetation strata was also assessed according to the following categories: *Peat and litter*; *Bryophytes*; *Ericaceous species*; *Herbs* excluding *Carex*; *Carex* and *Trees and shrubs*.

Inside each 30 x 30 cm quadrat, the proportion (%) of the surface covered by each moss species was evaluated by vertical projection. Because of inundation and absence of vegetation, no vegetation surveys were completed at *R1P*.

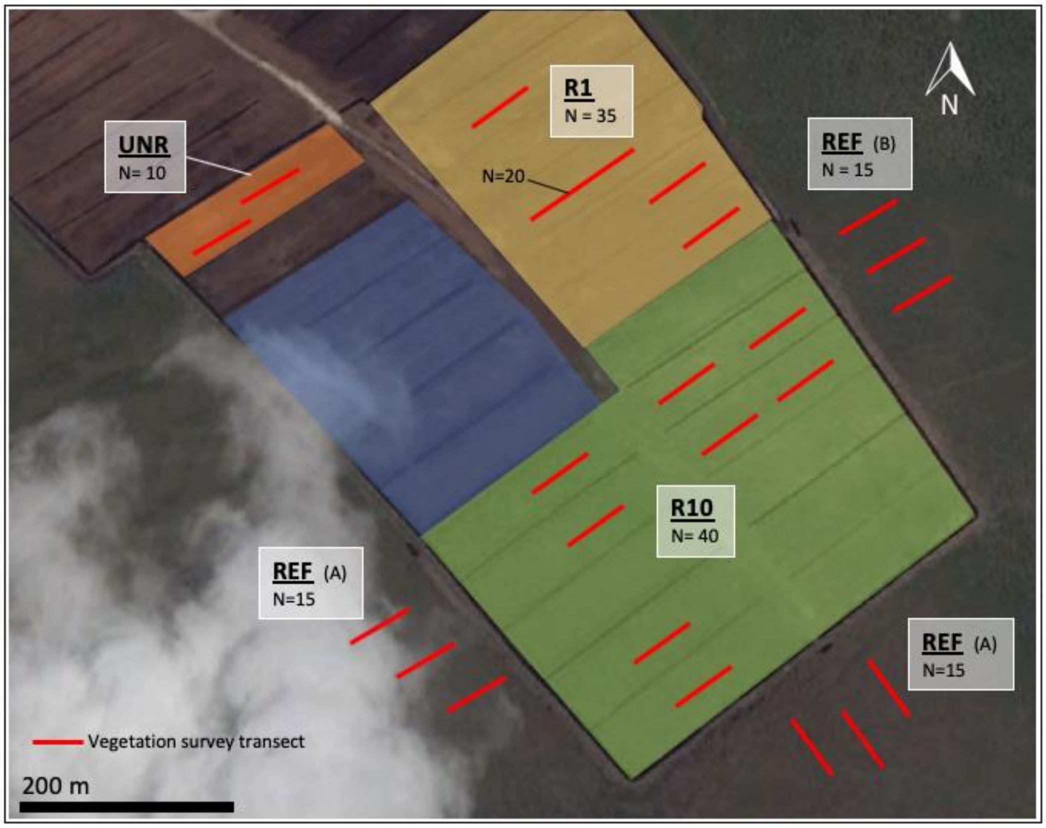


Figure 5 Approximate location of vegetation survey transects. In the reference ecosystem, vegetation was surveyed in the open graminoid (A) and forested (B) fens. At each sector N is the number of vegetation survey plots. A plot corresponds to one 1 x 1 m quadrat, for the assessment of vascular plant species and ten 30 x 30 cm quadrats for the assessment of moss species. *UNR*: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Species classification

After the completion of the surveys, bryophytes and vascular plant species were classified in four preferential habitat categories (*Peatland* species; *Wetland* species, Wetland *facultative* species and *Other* species) following a methodology adapted from Poulin et al. (2013). *Peatland* species are preferentially found in peatlands (*Sphagnum* peatlands or fens). *Wetland* species can be found in peatlands (but not preferentially), as well as other types of wetlands (e.g. marshes). Wetland *facultative* species can be found in wetlands, but not preferentially. *Other* species are not usually found in wetlands, but in other types of ecosystems like uplands. Vascular plant species were classified following Payette et Rochefort (2001); Jeglum (1991); USDA (2018; Wetland indicator status from the *Great plains* and *Midwest* regions of North America); Gignac et al. (2004) (*Cyperaceae* family). Moss species were classified following classifications by Payette et Rochefort (2001); Vitt (2014); Faubert (2012; 2014) and FNA (1993+).

Results

Environmental conditions

The 2016 growing season was particularly rainy. Precipitation was 28% higher than the 1981-2010 normal (May to September; Pinawa weather station; Environment Canada, 2018). Consequently, water levels measured in the rewetted sectors and reference ecosystem were probably higher than those of a typical growing season. Water levels at *RP1*, *R10* and *REF* were above the ground surface during the whole study period. Water levels were the highest at the end of June and in July (Fig. 6). Water table position varied greatly between sectors (Fig. 6). Monthly mean air temperatures were close to the normal and average soil temperatures were generally similar between sectors (Table 1). Because of high water levels, there was no vegetation at *RP1*. In other sectors, vegetation cover was the greatest at *REF* and *R10* and the lowest at *UNR* (vegetation in collars: Table 2; vegetation over entire sectors see section 2.4.3.). Vegetation typically found in peatlands and wetlands were dominant in the collars: at *R10*, *REF* and *R1*. Species not preferentially found in peatlands or wetlands predominated at *UNR*.

Table 1 Soil temperature at 5 cm below the ground surface (± SD) for each period of the study period in 2016.

Sector	Soil temperature (° C)			
	Early summer	Mid summer	Late summer	Study period average
UNR	16.1 (2.4)	20.0 (1.2)	18.0 (2.4)	17.9 (2.6)
RP1	21.3 (1.5)	22.5 (1.1)	18.9 (2.2)	20.4 (2.5)
R1	18.2 (3.4)	21.7 (1.0)	19.4 (2.1)	19.6 (2.8)
R10	16.0 (1.7)	19.4 (0.9)	17.7 (1.7)	17.6 (2.0)
REF	16.5 (2.0)	19.4 (1.)	21.2 (1.3)	19.2 (2.6)

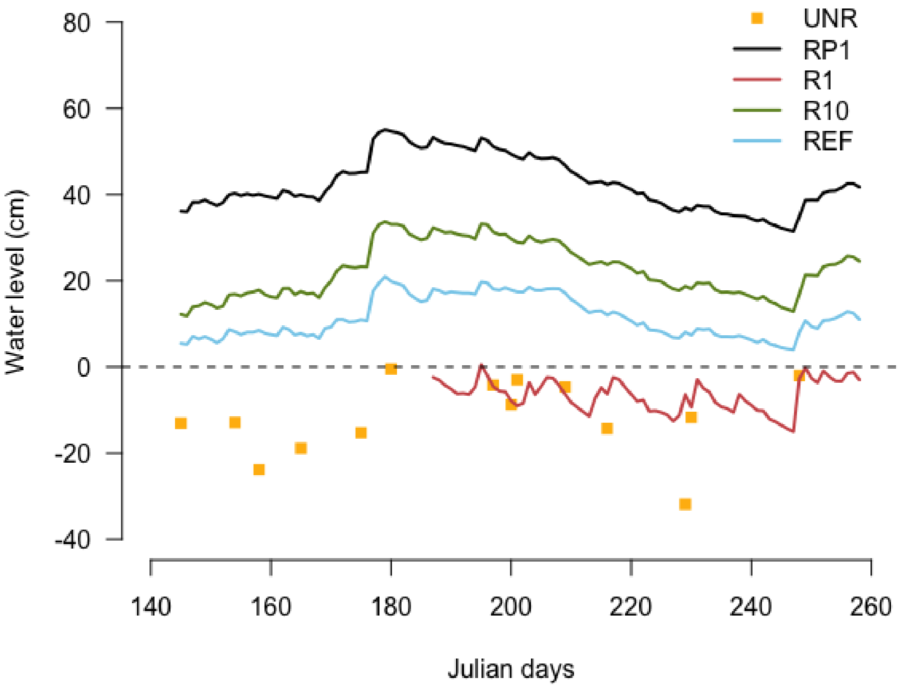


Figure 6 Water table levels recorded in experimental sectors, 0 cm corresponding to the ground level. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem. At UNR, dots represent manual measurements. At R1, the levelogger was installed on July 5, 2016 (Julian day 187).

Table 2 Number of collars per sector; vegetation type, vegetation strata cover and vegetation volume inside the collars.

Sector	Type of cover [a]	# Collars	% Cover (± SD)				Vegetation volume index [b]
			Vascular	Shrubs	Graminoid	Bryophytes	
UNR	Bare	3	16 (7)	0	7 (7)	0	0
	Herbaceous	3	40 (10)	0	40 (13)	4 (4)	12.2 (7.6)
RP1	Open water	6	-	-	-	-	-
R1[b]	Bare	3	20 (10)	4 (7)	14 (9)	1 (1)	6.5 (4.9)
	Herbaceous	3	47 (20)	5 (6)	43 (19)	2 (3)	19.6 (4.5)
	Shrubs	3	67 (10)	37 (3)	47 (21)	4 (4)	25.2 (4.5)
R10	Herbaceous	3	57 (8)	2 (3)	57 (8)	-	14.1 (4.9)
	Shrubs	3	77 (8)	23 (6)	75 (5)	-	28.1 (6.6)
REF	Shrubs	4	53 (14)	19 (16)	31 (9)	53 (19)	18.1 (6.6)
	Herbaceous	5	58 (15)	5 (5)	52 (19)	44 (18)	3.4 (6.6)

[b] *Herbaceous* and *Bare* collars were located at both predominantly dry microsites, (were the water table under the peat surface) and at predominantly moist microsites (were the water table at or above the peat surface). The number of collars at dry microsites is Bare: 1 collar, Herbaceous: 1 collar. The number of collars at moist microsites is *Bare*: 2 collars, *Herbaceous*: 2 collars. Collars with shrubby vegetation (*Shrubs*) were located at predominantly dry microsites.

[a] Vegetation volume is from a calculated index (see *Methods*). Mean vegetation volume calculated over the entire growing season is presented.

- : No data.

UNR: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Effect of rewetting on carbon exchange

Carbon dioxide fluxes

There was no seasonal trend for ER, GEP or NEE under full light condition (PAR >1000 µmol m^{-2} s^{-1}) for any sector. Mean study period values of ER, GEP and NEE for all sectors are presented in Table 3. Mean ER was generally similar between sectors, except for *RP1* with significantly lower ER rates (Fig. 7 and Table 3). *R1* and *R10* had significantly higher GEP rates than *UNR*. As a result, CO_2 sequestration (NEE) at *R1* and *R10* was significantly higher than at *UNR* and similar to *REF*.

Variations in GEP were significantly related to interactions between the factors rewetting strategy (i.e., the experimental sectors), water table level, vegetation volume and air temperature (Table 4; Fig. 8). For all sectors, a greater volume of vegetation was related to a greater productivity, although the slope of the relation was different between them. Higher water tables were associated with enhanced productivity at *UNR* but were associated with lower productivity rates at *R1* and *REF*. In general, variations in NEE followed the same patterns as GEP. Higher vegetation volumes led to higher CO_2 sequestration rates except at *R10* where none of the tested variables explained variation in NEE. There was a significant relation between NEE and water table level at *R1* where higher water table levels were associated with lower CO_2 sequestration rates (F=15.8, P=0.0002; appendix B). Across all sectors, higher water table levels were related to lower respiration rates (Fig. 8 and appendix B) although that relation was only statistically significant at *R1* (almost significant at *REF*; F=3.9, P=0.0534). For all sectors, higher vegetation volumes were associated with higher respiration rates (Table 4 and Appendix B), although the regression slopes varied between sectors (Fig. 8). Ecosystem respiration increased with temperature at a faster rate at *UNR* and *R1* than at *REF*. At *R10*, vegetation volume was the only factor explaining variations in ER and GEP, where higher vegetation volumes led to higher ER and GEP rates. At *RP1*, ER was only significantly related to water table level with higher water levels leading to lower respiration rates (Table 4).

Table 3 Mean gross CO_2 fluxes and CH_4 emissions for the study period [95% confidence interval]. GEP: gross ecosystem productivity, ER: ecosystem respiration, NEE: net ecosystem exchange. GEP and NEE are measured at photon flux density of photosynthetically active radiation greater than 1000 µmol m^{-2} s^{-1}. Negative values represent uptake by the ecosystem.

Sector	CO_2 (g CO_2 m^{-2} d^{-1})			CH_4 (mg CH_4 m^{-2} d^{-1})		
	ER	GEP	NEE	Early summer	Midsummer	Late summer
UNR	10.5 [7.4, 13.6]	-12.7 [-20.9, -4.5]	-2.1 [-7.5, 3.3]	2.2 [-3.2, 10.1]	3.5 [-2.8, 12.9]	3.0 [-3.1, 12.1]
RP1	1.16 [0, 4.0]	-	-	21.4 [5.7, 49.0]	1.8 [-4.4, 11.5]	82.2 [43.6, 146.0]
R1	14.2 [11.5, 16.9]	-32 [-38.9, -25.1]	-17.7 [-22.2, -13.1]	15.4 [4.7, 32.0]	69.3 [43.0, 107.5]	64.9 [39.6, 101.8]
R10	10.8 [7.6, 13.9]	-31.3 [-62.6, -22.4]	-20.5 [-26.5, -14.6]	93.5 [57.0, 148.6]	416.5 [257.4, 668.8]	164.0 [98.4, 267.4]
REF	7.9 [5.7, 10.0]	-20.9 [-27.0, -14.7]	-13.0 [-17.3, -8.8]	8.7 [1.0, 20.2]	107.9 [69.4, 163.8]	31.1 [16.2, 53.2]

UNR: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

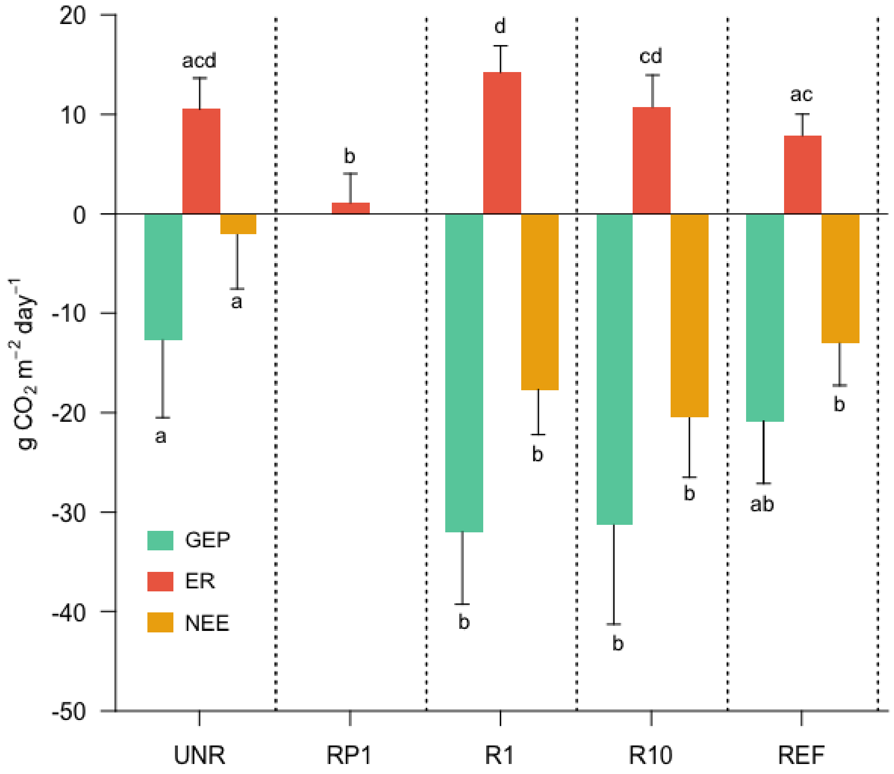


Figure 7 Mean gross ecosystem productivity (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) (g CO_2 m^{-2} d^{-1}) where GEP and NEE are measured at photon flux density of photosynthetically active radiation greater than 1000 µmol m^{-2} s^{-1}. Negative values represent uptake by the ecosystem. Bars sharing a letter are not significantly different (Tukey pairwise comparisons, α=0.05). Letters should be compared only within one flux component. Error bars represent the 95% confidence intervals of the means. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Table 4 Controls over CO_2 and CH_4 fluxes from linear mixed effect models.

Flux component	Fixed effects [a]	$F_{num, den}$	P	R^2GLMM [b]
Ecosystem respiration (ER)				
RP1 [c]	WTL	$F_{1, 25} = 7.16$	0.0129	0.19
	Intercept	$F_{1, 25} = 12.71$	0.0015	
Others [d]	WTL	$F_{1, 181} = 51.2$	<0.0001	0.42
	Vol_veg	$F_{1, 22} = 72.65$	<0.0001	
	T_{air}	$F_{1, 181} = 68.75$	<0.0001	
	Rewetting_str	$F_{3, 22} = 8.62$	0.0006	
	Rewetting_str *WTL	$F_{3, 181} = 2.1$	0.102	
	Rewetting_str *Vol_veg	$F_{3, 22} = 2.93$	0.0056	
	Rewetting_str *T_{air}	$F_{3,181} = 6.93$	0.0002	
	Intercept	$F_{1, 81} = 778.24$	<0.0001	
Gross ecosystem productivity (GEP)				
	WTL	$F_{1, 181} = 33.36$	<0.0001	0.51
	Vol_veg	$F_{1, 22} = 155.78$	<0.0001	
	T_{air}	$F_{1, 181} = 2.32$	0.13	
	Rewetting_str	$F_{1, 22} = 39.85$	<0.0001	
	Rewetting_str *WTL	$F_{3, 181} = 7.42$	0.0001	
	Rewetting_str *Vol_veg	$F_{3, 22} = 7.85$	0.001	
	Rewetting_str *T_{air}	$F_{3, 181} = 4.99$	0.0024	
	Intercept	$F_{1, 181} = 965.3$	<0.0001	
Net ecosystem exchange (NEE)				
	WTL	$F_{1, 177} = 32.5$	<0.0001	0.27
	Volume_veg	$F_{1, 22} = 407.6$	<0.0001	
	T_{air}	$F_{1, 177} = 15.3$	0.0001	
	Rewetting_str	$F_{1, 22} = 12.5$	0.0001	
	Rewetting_str *WTL	$F_{3,177} = 15.0$	<0.0001	
	Rewetting_str *Vol_veg	$F_{3, 22} = 11.3$	0.0001	
	Rewetting_str *T_{air}	$F_{3,177} = 4.2$	0.007	
	Intercept	$F_{1, 177} =651.4$	<0.0001	
Net CH_4 emissions				
RP1	WTL	$F_{1, 31} = 45.5$	<0.0001	0.54
	Intercept	$F_{1, 31} = 301.7$	<0.0001	
Others	WTL	$F_{1, 211} = 9.9$	<.0001	0.49
	Volume_veg	$F_{1, 211} = 1.3$	0.25	
	T_5	$F_{1, 211} = 34.9$	<0.0001	
	Rewetting_str	$F_{3, 26} = 28.4$	<0.0001	
	Rewetting_str *WTL	$F_{3, 211} = 23.2$	<0.0001	
	Rewetting_str *Vol_veg	$F_{3, 211} = 2.03$	0.11	
	Rewetting_str *T_5	$F_{3, 211} = 18.1$	<0.0001	
	Intercept	$F_{1, 211} =2109.5$	<0.0001	

[a] Fixed effects are the following *WTL*: Water table level (cm); *Volume_veg*: vegetation volume index; *T_{air}*: Air temperature (° C); *Rewetting_str*: Rewetting strategy (the experimental sectors). [b] R^2 GLMM accounts for variance explained by fixed factors only.
[c] Sector RP1 was analyzed separately because it was flooded and devoid of vegetation. At RP1, only ER and CH_4 fluxes were measured. [d] Other sectors include: UNR, R1, R10 and REF. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

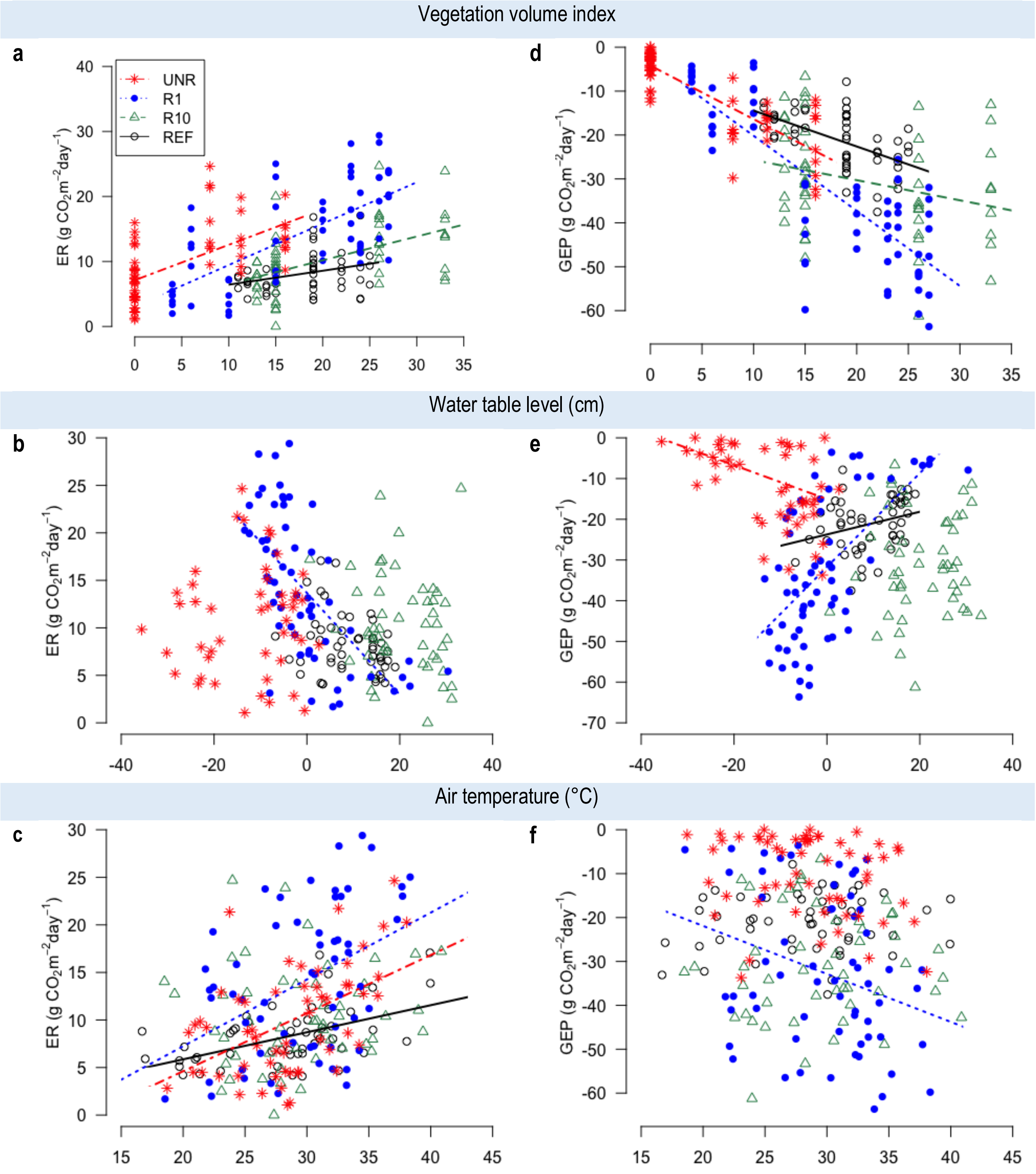


Figure 8 Ecosystem respiration (ER g CO_2 m^{-2} d^{-1}) and gross ecosystem productivity (GEP g CO_2 m^{-2} d^{-1}) under full light conditions (PAR >1000 µmol m^{-2} s^{-1}) against a) and d) vegetation volume (based on a vegetation volume index); b) and e) water table level (cm) c) and f) air temperature (°C). Only statistically significant regression lines are displayed. Regression equations are given in appendix B. Negative fluxes represent carbon uptake into the ecosystem. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Methane fluxes

For all sectors, there was a significant evolution of CH_4 fluxes over the three periods of the growing season (significant interaction between the fixed factors *Periods* and *Rewetting strategy*). Therefore, mean CH_4 fluxes are presented separately for each period of the summer. Methane emissions at *UNR* stayed close to zero the entire the study period (Fig. 9). Throughout the study period, *R10* was characterized by consistently higher CH_4 fluxes than any other sector, though the difference was not statistically significant in August and September between *R10* and the other rewetted sectors. There was a peak in CH_4 emissions in July for *R10* and *REF*. Values were especially high at *R10* with a mean emission of 416.6 mg CH_4 m^{-2} d^{-1}. Methane fluxes at *R1* were similar to *REF* throughout the study period (Fig. 9).

Variations in CH_4 fluxes were explained by variations in water table level and soil temperature, both interacting with the factor rewetting strategy (i.e. the experimental sectors). Methane fluxes were significantly related to water table level at *R10* and *R1* with higher water levels leading to higher CH_4 emissions (Fig. 10). There was no effect of the water table level on CH_4 emissions at *UNR* or at *REF*. At *R10* and *REF*, higher soil temperatures resulted in higher CH_4 emissions (Fig. 10). There was no significant effect of variation of soil temperature on CH_4 emissions at *UNR* and *R1*. CH_4 emissions at *RP1* were significantly related to water table levels (Fig. 10).

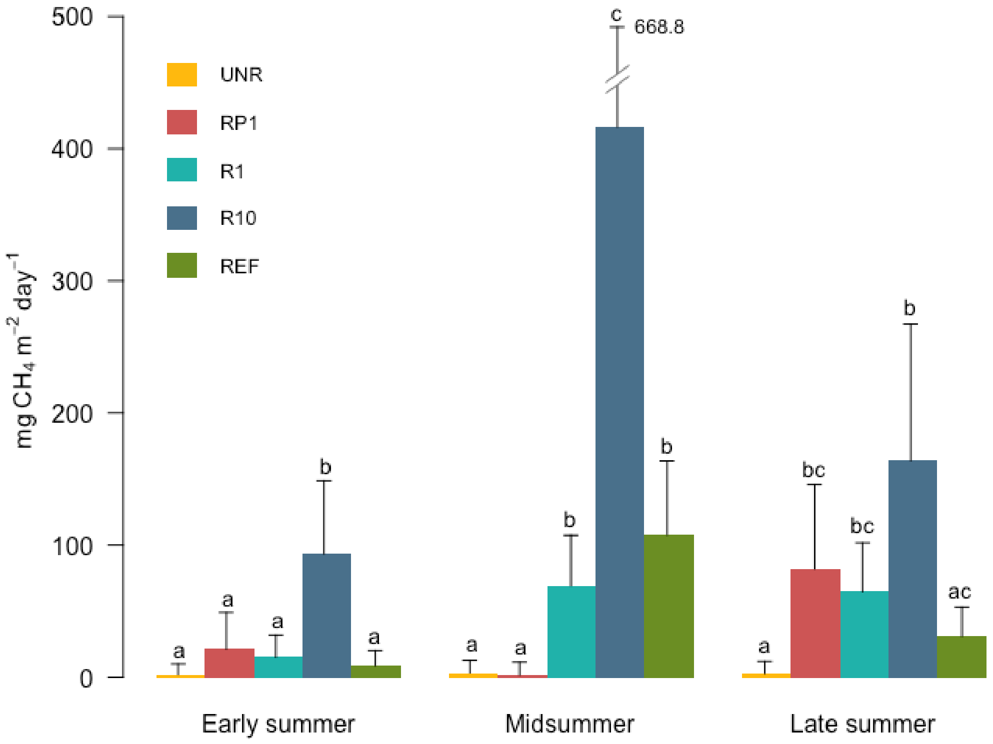
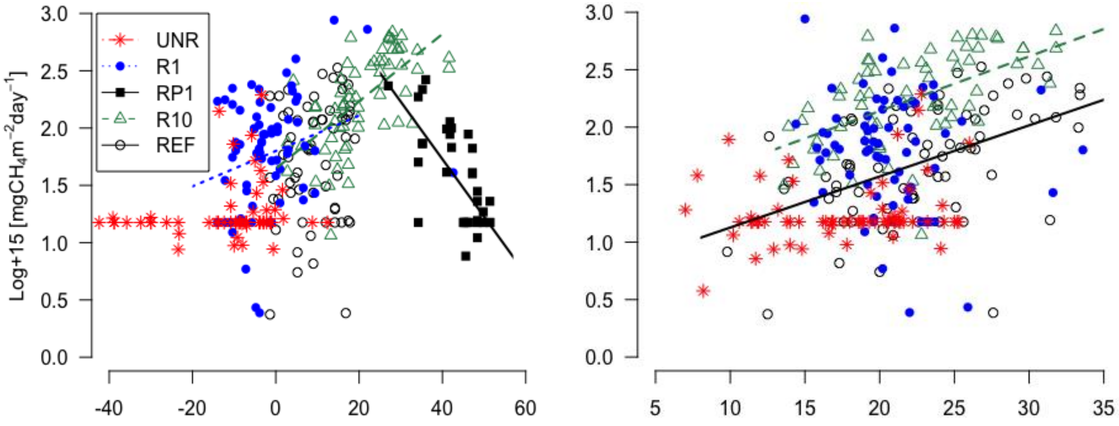


Figure 9 Mean CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) for each sector for each period of the study period. Results are displayed according to three periods of the summer because of a significant interaction between the fixed effects *rewetting strategy* and *period of the summer*. Within one period, values sharing a letter are not significantly different (Tukey pairwise comparisons, α=0.05). Error bars represent the 95% confidence intervals of the means. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.



a) Water table level (cm)

b) Soil temperature (-5 cm)

Figure 10 a) Net methane emission (log[CH_4+15]; mg CH_4 $m^{-2}d^{-1}$) in relation to water table level (WTL) and b) net methane emission (log[CH_4+15]; mg CH_4 $m^{-2}d^{-1}$) in relation to soil temperature (T_5; -5 cm below the ground surface). Only significant regression lines are displayed. Regression equations are A) R1: log[CH_4+15] = 0.01544(*WTL*) + 1.8; R10: log[CH_4+15] = 0.02936(*WTL*)+1.65 B) R10: log[CH_4+15] = 0.04756(T_5) + 1.19; *REF*: log[CH_4+15] = 0.04447(T_5) + 0.68. *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

CO_2 and CH_4 balance and global warming potential

Over the study period, vegetated collars at *UNR* acted as CO_2 sinks (-104 to -220 g CO_2 m^{-2}) while bare peat collars acted as CO_2 sources (91 to 217 g CO_2 m^{-2}). On average, plots at *UNR* were small CO_2 sinks (Table 5). Plots at *R1* acted on average as CO_2 sinks although there was much variation between the plots with, study period NEE values ranging from -1343 to 136 g CO_2 m^{-2}. All plots at *R10* and *REF* acted as CO_2 sinks (*R1* : -649 to -832 g CO_2 m^{-2} ; *REF* : -1100 to -42 g CO_2 m^{-2}) and all plots at *RP1* acted as CO_2 sources (30 to 320 g CO_2 m^{-2}). Net CH_4 emissions at *RP1*, *R1* and *REF* were similar. Methane emissions at *R10* were more than three times greater than *REF* (Table 5).

After summing net study period CO_2 and CH_4 exchange values, global warming potential values were -210 to 231, -1214 to 40, -845 to -127, -954 to 166 and 68 to 840 g CO_2–e m^{-2} at *UNR*, *R1*, *R10*, *REF* and *RP1* respectively (Table 5). High CH_4 emissions considerably reduced the greenhouse gas sequestration potential at R10, with mean decrease of 68%. In comparison, the decrease of greenhouse gas sequestration potential due to CH_4 emissions was 33% and 36% at *R1* and *REF*, respectively.

Table 5 Mean [a] (± SD) net ecosystem exchange (NEE), net methane exchange (CH_4), carbon balance (C) and global warming potential (GWP) calculated over the study period for each experimental sector. Negative values represent uptake by the ecosystem.

	UNR	RP1	R1	R10	REF
NEE (g CO_2 m^{-2})	-5.4 (201.5)	138.4 (107.8)	-779.3 (551.5)	-1244.8 (355.7)	-577.8 (408.2)
CH_4 (g CH_4 m^{-2})	1.1 (1.4)	8.7 (8.7)	9.2 (7.3)	30.0 (8.4)	7.5 (4.6)
Total C (g C m^{-2})	-0.67 (54.4)	44.3 (30.1)	-212.5 (150.4)	-316.9 (92.7)	-152.0 (109.3)
GWP (g CO_2-e m^{-2})	24.8 (180.1)	300.3 (292.0)	-521.0 (583.7)	-403.9 (255.3)	-368.6 (350.8)

[a] Values displayed are means calculated over all plots for each sector.

UNR: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Effect of rewetting on vegetation

Because of the absence of vegetation at *RP1* caused by flooding, this sector is excluded from this section. At the rewetted sectors (*R1* and *R10*), total vegetation cover was higher than the unrewetted sector (*UNR*), but lower than at the reference ecosystem because of greater bryophytes cover in this last sector (Fig. 11). Furthermore, the cover of vascular plants at the rewetted sectors was only about 10 % lower than what was observed at the reference ecosystem (Table 6). The composition of vegetation communities differed between the rewetted and unrewetted sectors (Fig. 12; Table 6). The unrewetted sector was mostly dominated by species not preferentially found in wetlands or peatlands, mainly *Hordeum jubatum* and *Agrostis scabra,* which are known ruderal species (e.g. *Agrostis scabra*, *Cirsium arvense* and *Hordeum jubatum;* Manitoba (2017), MAPAQ and MFFPQ (2018)). The cover of species preferentially found in peatlands (mainly of the genus *Carex*) and wetlands was larger at *R1* compared to the unrewetted sector. Peatland species, mainly *Carex lasiocarpa*, were predominating at *R10*.

Mean moss cover of 18% at *R10* was much greater than at *UNR* (<1%). The low bryophyte cover at *R1* (<1%) was similar to *UNR* (Fig. 11 and 12). *R10* and *REF* were dominated by the same two moss species: *Campylium stellatum* and *Scorpidium cossonii*. However, there was greater bryophyte diversity at *R1* with five moss species typically found in peatlands (*Aulacomnium palustre*, *Bryum pseudotriquetrum*, *C. stellatum*, *Polytrichum strictum* and *S. cossonii*) compared to one at *UNR* (*B. pseudotriquetrum*) (Table 6). Five *Sphagnum* species were recorded in the shrubby area of *REF* (*S. angustifolium*, *fuscum*, *papillosum*, *russowii* and *warnstorfii*) with a mean cover of 6 ± 15% whereas only *S. fallax* was recorded (<1% cover) at *R10*.

The structure of the vegetation communities (assessed by the surveys of the vegetation strata) of the rewetted sectors was more similar to the reference ecosystem than the unrestored sector (Fig. 11). All vegetation strata at the reference ecosystem were also present at *R10*, which was not the case for *R1*, the ericaceous species and mosses being virtually absent. Species composing the *Trees and shrubs* stratum differed between both the rewetted sectors and the reference ecosystem. Three and four species of *Salix* have been inventoried at respectively *R1* and *R10*, while only one *Salix* species was inventoried at the reference ecosystem (Table 6). At the latter, *Betula pumila*, *Dasiphora fruticosa, Larix laricina* and *Thuja occidentalis* were the dominant trees and shrubs species (Table 6). Since peat and litter were surveyed as a single category, differences in the proportion of each across sectors are not shown. Nevertheless, it was clear on site that the unrewetted sector was dominated by bare peat whereas *R10* was rather dominated by sedge litter with very few patches of bare peat. *R1* was unevenly covered by surfaces occupied by vegetation, bare peat and litter.

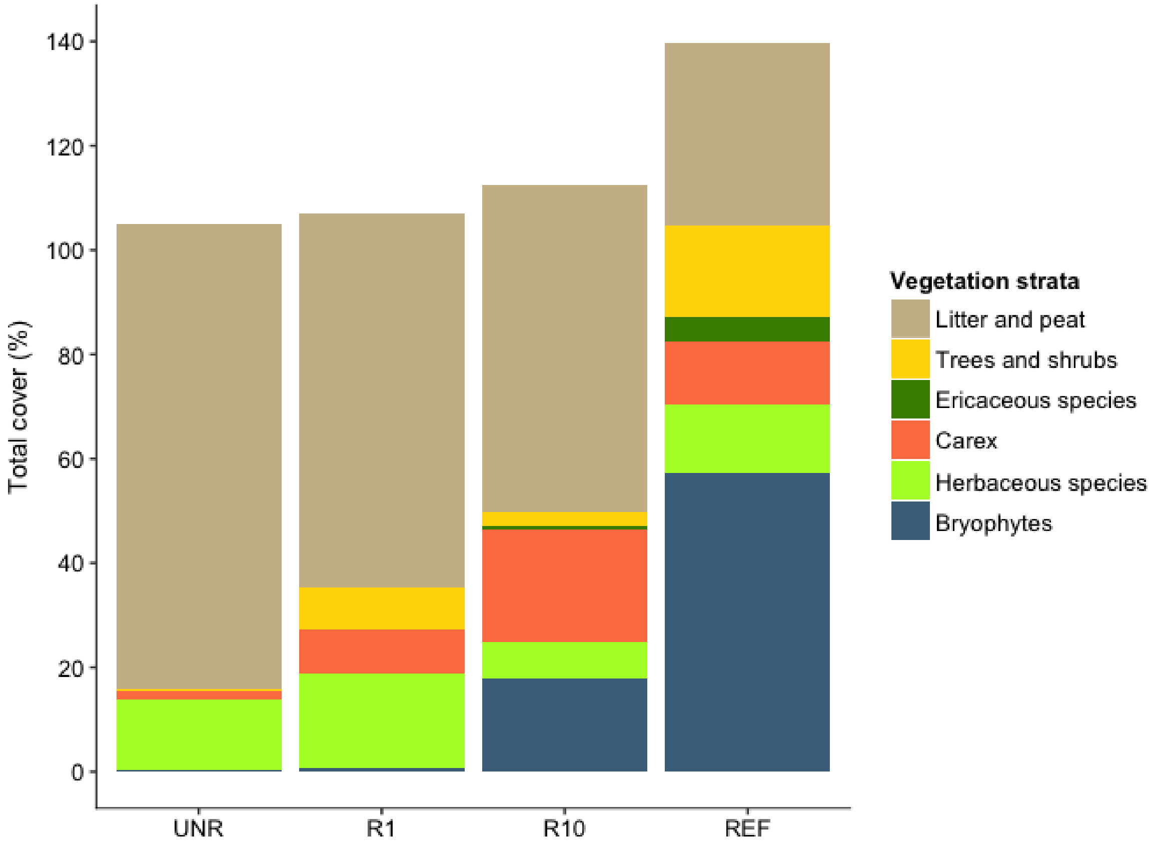


Figure 11 Mean cover (%) of vegetation strata for each experimental sector. *UNR*: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

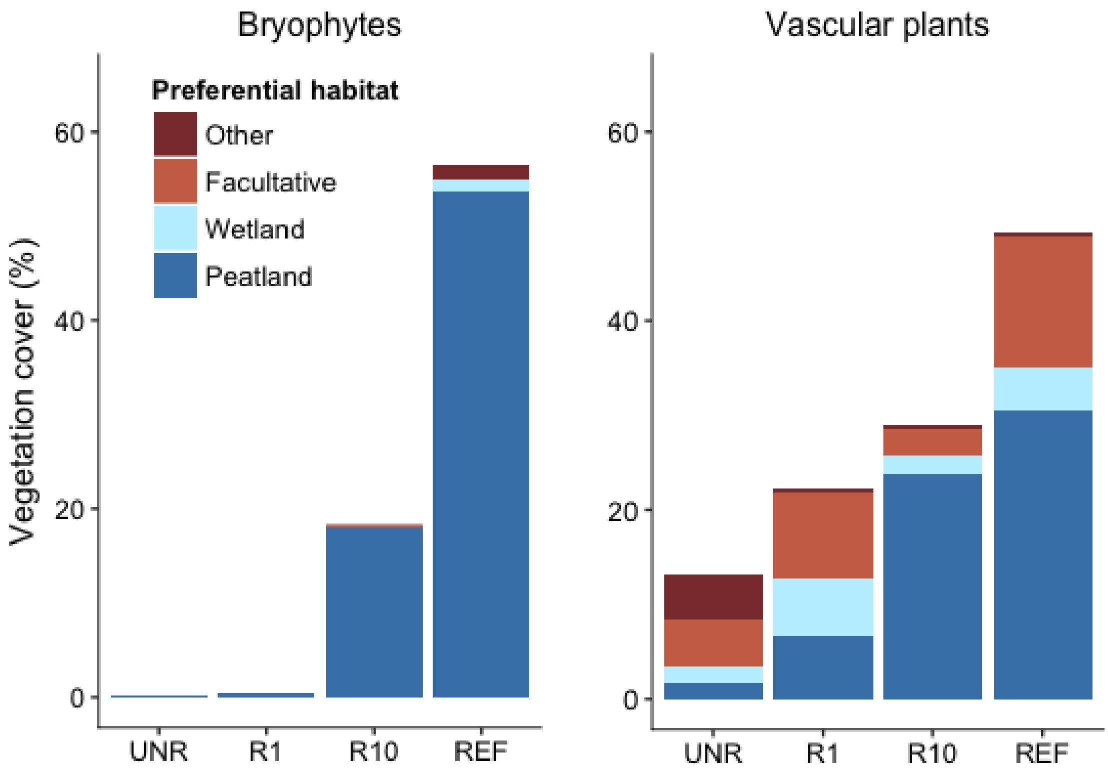


Figure 12 Mean cover (%) of bryophytes and vascular species for each experimental sector. Species are classified according to their preferential habitat. *Peatland*: species preferentially found in peatlands (*Sphagnum* peatlands of fens), *Wetland*: species preferentially found in wetlands, *Facultative*: species that can occur in wetlands, but not preferentially, *Other*: species preferentially found in other types of ecosystem (e.g. upland ecosystem). See *Methods* for details on species categorization. *UNR*: unrewetted; *R1*: first growing season after rewetting; *RP1*: profiled, first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Table 6 Cover (% ± (SD)) of each vegetation strata and vascular and bryophyte species [a]. Species are classified according to their preferential habitat.

		Sector [b]			
		UNR	R1	R10	REF
Sampling effort	Number of vascular sampling units (1 m^2)	10	35	40	45
	Number of bryophyte sampling units (900 cm^2)	100	350	400	450
Total vegetation cover		13 (7)	26 (11)	39 (28)	73 (18)
Total vascular plant cover		13 (7)	26 (11)	28 (8)	40 (12)
Total bryophyte cover		<1	1 (1)	18 (18)	57 (19)
Vegetation strata	Pref. habitat [c]				
Trees and shrubs		<1	8 (7)	3 (4)	18 (13)
Betula pumila Linnaeus	Peatland		<1	1 (3)	7 (8)
Dasiphora fruticosa (Linnaeus) Rydberg	Facultative		<1	<1	5 (8)
Larix laricina (Du Roi) K. Koch	Facultative		<1		6 (11)
Populus balsamifera Linnaeus	Facultative		1 (1)		
Salix bebbiana Sargent	Facultative		1 (1)	<1	
Salix discolor Muhlenberg	Facultative		1 (2)	1 (1)	
Salix pedicellaris Pursh	Peatland			<1	1 (2)
Salix serissima (L.H. Bailey) Fernald	Wetland		2 (3)	<1	
Thuja occidentalis Linnaeus	Facultative				2 (6)
Ericaceae				1 (1)	5 (7)
Andromeda polifolia Linnaeus	Peatland		<1	1 (1)	1 (2)
Rhododendron groenlandicum (Oeder) Kron & Judd	Wetland			<1	2 (6)
Vaccinium oxycoccos Linnaeus	Peatland		<1	<1	2 (4)
Carex		2 (2)	8 (6)	22 (11)	12 (6)
Carex aquatilis Wahlenberg	Peatland	<1	<1	2 (3)	3 (5)
Carex chordorrhiza Linnaeus	Peatland			1 (2)	<1
Carex interior L.H. Bailey	Peatland	<1	3 (4)	<1	
Carex lasiocarpa Ehrhart	Peatland	1 (2)	1 (1)	17 (10)	9 (7)
Carex tenuiflora Wahlenberg	Peatland		1 (2)	<1	<1
Carex trisperma Dewey	Peatland	<1	1 (4)		
Herbaceous species		14 (5)	18 (12)	7 (6)	13 (10)
Agrostis scabra Willdenow	Facultative	4 (5)	2 (2)		
Bidens cernua Linnaeus	Wetland	1 (2)	<1		
Calamagrostis stricta (Timm) Koeler	Facultative		<1	1 (1)	<1
Cirsium arvense (Linnaeus) Scopoli	Other	1 (1)	<1		
Comarum palustre Linnaeus	Peatland			<1	1 (2)
Eleocharis acicularis (Linnaeus) Roemer & Schultes	Wetland		1 (4)		
Epilobium ciliatum Rafinesque	Facultative	1 (1)	<1	<1	
Equisetum fluviatile Linnaeus	Wetland	<1	<1	1 (1)	<1
Hordeum jubatum Linnaeus	Other	4 (4)	<1		
Juncus brevicaudatus (Engelmann) Fernald	Wetland		1 (3)		

Maianthemum trifolium (Linnaeus) Sloboda	Wetland			<1	1(3)
Menyanthes trifoliata Linnaeus	Peatland			2 (3)	5 (8)
Persicaria pensylvanica (Linnaeus) M. Gómez de la Maza	Facultative				1 (3)
Rubus arcticus Linnaeus	Peatland			<1	1 (2)
Sarracenia purpurea Linnaeus	Peatland				1 (2)
Scirpus cyperinus (Linnaeus) Kunth	Wetland		1 (3)		
Bryophytes		<1	<1	18 (18)	57 (19)
Aulacomnium palustre (Hedw.) Schwägr	Peatland		<1	<1	2 (4)
Brachythecium acutum (Mitt.) Sull	Peatland				4 (12)
Bryum pseudotriquetrum (Hedw.) G. Gaertn., B. Mey. & Scherb	Peatland	<1	<1	1 (2)	
Calliergon giganteum (Schimp.) Kindb	Wetland				1 (4)
Straminergon stramineum (Dicks. ex Brid.) Hedenäs	Peatland				<1
Campylium stellatum (Hedw.) C.E.O. Jensen	Peatland		<1	12 (12)	18 (13)
Climacium dendroides (Hedw.) F. Weber & D. Mohr	Other				<1
Dicranum undulatum Schrad. ex Brid	Peatland				1 (3)
Pleurozium schreberi (Willd. ex Brid.) Mitt	Other				1 (5)
Scorpidium cossonii (Schimp.) Hedenäs	Wetland		<1	4 (6)	22 (15)
Scorpidium scorpioides (Hedw.) Limpr	Peatland			<1	1 (4)
Sphagnum angustifolium (Warnst.) C.E.O. Jensen	Peatland				1 (5)
Sphagnum fuscum (Schimp.) H. Klinggr	Peatland				3 (13)
Sphagnum russowii Warnst	Peatland				1 (6)
Sphagnum warnstorfii Russow	Peatland				1 (4)

[a] Only species with a cover higher than 1% are listed in this table. For the list of all inventoried species, see appendix C.

[b] *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

[c] *Peatland*: species preferentially found in peatlands (*Sphagnum* peatlands or fens), *Wetland*: species preferentially found in wetlands, *Facultative*: species that can occur in wetlands, but not preferentially, *Other*: species preferentially found in other types of ecosystem (e.g. upland habitats).

Note: Vascular plant species classified following classifications by Payette and Rochefort (2001), Jeglum (1991), USDA (2018), Gignac et al. (2004). Moss species classified following classifications by Payette and Rochefort (2001), Vitt (2014), Faubert (2012; 2014) and FNA (1993+). See section *Methods* for details on categorization of species. Vascular plant nomenclature according to Brouillet et al. (2010+); bryophyte nomenclature according to Faubert (2012; 2014).

Discussion

Our study took place in a growing season where precipitation was more abundant than the 1981-2010 normal. Seasonal and interannual variations in environmental conditions greatly influence carbon exchange in peatlands (Bubier et al., 2003; Lafleur et al., 2003; Noyce et al., 2014). In a boreal landscape near Thompson (MB, Canada), CH_4 emissions were 60% larger during a wet year compared to a dry year (Bubier et al., 2005). Methane emissions were mainly driven by wetlands, and especially sedge dominated wetlands. At the same station, differences in temperature and wetness between years also converted a fen ecosystem from a sink to a source of CO_2 (Joiner et al., 1999). In the present study, the very wet growing season and resulting high water tables at all sectors likely impacted CH_4 and CO_2 fluxes compared to a normal drier year.

Effect of rewetting on carbon dioxide fluxes

Except for *RP1*, which acted as a net CO_2 source over the growing season 2016, all experimental sectors acted as CO_2 sinks during the same time period. There is considerable variability in CO_2 exchange values reported in the literature for natural and restored peatlands. For instance, Saarnio et al. (2007) report values of -370 to 370 g CO_2 m^{-2} y^{-1} for natural boreal peatlands in Europe and North America. Ten years after restoration in a post-extraction peatland in Québec, Canada, Strack and Zuback (2013) reported positive seasonal net CO_2 exchange during the growing season (source of 83 ± 72 g CO_2 m^{-2}). At the same site, 14 years after restoration, Nugent et al. (2018) reported mean growing season NEE of -587 ± 55 g CO_2 m^{-2} (fluxes measured over three growing seasons). Soini et al. (2010) reported net CO_2 sink of 500 ± 410 g CO_2 m^{-2} in a fen in central Finland that had been restored 10 years prior to their measurements. Values from *R1* and the reference ecosystem in the present study are similar to those reported by Soini et al. (2010) and Nugent et al. (2018), and are among the highest from the range of reported values. Consequently, with a seasonal CO_2 balance of -1245 ± 355 g CO_2 m^{-2}, *R10* represented a considerable CO_2 sink. High CO_2 uptake at the rewetted sectors was likely caused by elevated water table leading to lower heterotrophic respiration rates, and by vegetation establishment following rewetting. Newly restored peatland ecosystems can represent considerable CO_2 sinks because of an increase in microbial and plant biomass (Wilson et al., 2013). Over time, CO_2 sequestration rate is likely to decline. In the long run, high water tables at *R10* could further result in a decline of productivity caused by a lack of CO_2 and O_2 to the submerged parts of the plants (Joosten, 2016). It is also important to keep in mind that this study only covered four months of the growing season 2016. Losses of CO_2 through decomposition during the rest of the growing season and cold months are likely to be high given the labile nature of the sedge litter (Bridgham et al., 2013). Carbon loss during the rest of the year will result in a considerably lower net C sequestration in the restored sectors (Nugent et al., 2018).

Rewetting was successful at promoting vegetation establishment at the rewetted sectors. As a result, productivity rates and net CO_2 uptake were significantly greater at *R1* and *R10* than at *UNR.* This is consistent with previous studies showing that restoration and subsequent plant establishment may transform extracted peatlands to growing season CO_2 sinks a few years after restoration (e.g. Tuittila et al., 1999; Waddington et al., 2010). Ecosystem respiration rates at *R1* and *R10* were similar to *UNR*. Because of enhanced plant respiration, restoration can lead to similar respiration rated in unrestored plots where peat oxidation is the main component of ER (Strack et al., 2016; Strack et al., 2014; Strack and Zuback, 2013). Although mean CO_2 fluxes were similar among the three rewetted sectors and the reference ecosystem, controls over fluxes differed. At *R1*, all environmental variables tested (air temperature, vegetation volume and water table level) were significant controls of both GEP and ER, which was not the case at *REF* were ER was controlled by vegetation volume and air temperature and GEP by vegetation volume and water table level. The response of CO_2 fluxes to changes in environmental conditions was also more pronounced at *R1* than at *REF* as indicated by steeper regression slopes (Fig. 8). That response was representative of the variability of micro-habitats and type of vegetation at *R1* compared to *REF*. The surface of *R1* was not levelled before rewetting leaving a variety of microforms, resulting in different water table position and colonization by different and diverse vegetation communities. Vegetation at dry microsites was often composed of large sedge cover and willows, whereas wet microsites generally presented low sedge covers. That resulted in higher ER and GEP in dry areas and lower GEP and ER at wetter locations. That kind of contrast was not observed at *REF* where environmental conditions and vegetation communities were less diverse. Similarly, at *R10*, water table position and soil temperature did not act as controls over CO_2 fluxes due to their relatively low variation during the study period linked to the flat surface and relatively homogeneous conditions across the site. Vegetation volume was the only significant control over GEP and ER at *R10*.

Effect of rewetting on methane fluxes

Methane fluxes in natural peatlands are highly variable usually ranging from 5 to 80 mg CH_4 m^{-2} d^{-1} (Blodau, 2002), up to 200 mg CH_4 $m^{-2}d^{-1}$ (Moore et al., 1990), and even more than 1000 mg CH_4 m^{-2} d^{-1} (Klinger et al., 1994). In North America, mean growing season CH_4 fluxes in restored peatlands are also variable, from a slight uptake to 23.4 mg CH_4 m^{-2} d^{-1} (Strack et al., 2016; Strack et al., 2017; Strack and Zuback, 2013; Waddington and Day, 2007). Methane emissions from European restored fens can reach 400 mg CH_4 m^{-2} d^{-1} (Hendriks et al., 2007; Jordan et al., 2016; Vanselow-Algan et al., 2015). In the present study, mean CH_4 fluxes in the rewetted sectors R1 and R10 (respectively 69.3 and 416.5 mg CH_4 m^{-2} d^{-1} in July) and *REF (*107.9 mg CH_4 m^{-2} d^{-1} in July) were in the highest range of reported values. High water table levels combined with productive vegetation likely resulted in high CH_4 emissions. This was especially true at *R10* where CH_4 emissions were at least four times larger than those prevailing at *REF*. Because they act on CH_4 production and oxidation rates, soil temperature, water table position and vegetation type and cover are major drivers of CH_4 fluxes in peatlands (Lai, 2009;

Vasander and Kettunen, 2006). Due to small differences in soil temperatures between *REF* and *R10* (Table 1), this factor was not likely the cause of differences in CH_4 emissions between these two sites. The inundation that persisted over the entire growing season partly explains the very high emissions at *R10*. At *REF,* not all plots were permanently inundated, allowing for CH_4 oxidation in the peat profile. In addition to higher water table levels, differences in plant communities also played a key role in the high CH_4 emissions at *R10*. The large cover of *Carex lasiocarpa* at *R10* provided a direct means of transportation for CH_4 from the production zone to the atmosphere, bypassing the oxidation zone in the water column (Bubier, 1995; Couwenberg and Fritz, 2012) . Vascular vegetation produces fresh litter and root exudates, two sources of labile carbon for methanogens (Saarnio et al., 2004; Shannon et al., 1996; Waddington and Day, 2007). Exudation from roots is also positively related to plant productivity (Ström et al., 2005). In the present study, by providing good quality substrate for methanogens, very productive *Carex lasiocarpa* and considerable cover of submerged litter (also from *Carex lasiocarpa*) were presumably the main causes of very high CH_4 emissions at *R10*. In comparison, vegetation at *REF* was more diverse with a considerable cover of bryophytes. Compared to vascular plants, bryophyte litter is generally more resistant to decomposition, and thus provides less labile carbon for methanogens (Bérubé and Rochefort, 2018; Turetsky, 2003). Symbiosis between fen mosses and methanotrophic bacteria could also have reduced CH_4 emissions at *REF*, compared to *R10* (Liebner et al., 2011). Altogether, availability of good quality substrate for CH_4 production and a higher water table at *R10* led to very high CH_4 emissions at *R10*.

Mean CH_4 exchange at *R1* was similar to *REF*. However, the controls over CH_4 fluxes differed between *R1* and *REF*, indicating that the biogeochemical function was not similar to *REF*. Methane fluxes at *R1* were mainly driven by variations in water table position whereas in *REF*, they were driven by variations in soil temperature. The more variable moisture conditions at *R1* compared to *REF* likely explain the importance of water table position as a control over CH_4 fluxes at the former.

Methane emissions following peatland restoration can considerably reduce C sequestration potential of peatlands or even turn them into C sources (Joosten et al., 2016). Three years after rewetting a cutaway peatland in Finland, the loss of carbon as CH_4 in terms of CO_2 equivalent represented 15% of the seasonal CO_2 sequestration by vegetation (Tuittila et al., 1999; Tuittila et al., 2000). On the wettest area of a restored boreal *Sphagnum* peatland in western Canada, CH_4 emissions represented an average 125% of the seasonal greenhouse gas uptake as CO_2 sequestration by newly established vegetation (Strack et al., 2014). In the present study, at *R10*, CH_4 emissions represented 68% of radiative forcing by CO_2 sequestration and thus considerably reduced the carbon and greenhouse gas sequestration potential of the sector. In comparison, CH_4 emissions at *R1* and *REF* represented, respectively, 33% and 36% of greenhouse gas uptake through CO_2 sequestration. Sites with water levels above -20 cm are generally larger CH_4 emitters than sites with a deeper water table because of their shallower oxic layer of peat, in which CH_4 can be oxidised before reaching the atmosphere (Couwenberg and Fritz, 2012). However, it has also been suggested that water tables above the peat surface could also lead to large rates of CH_4 oxidation in the water column, because of the presence of oxygen in the latter (Bubier, 1995). This phenomenon could explain the decline in CH_4 emissions at RP1 with elevation of the water table, as shown in Figure 10a. In the present study, high cover of *Carex lasiocarpa* and waterlogged conditions at *R10* were optimal for very high CH_4 emissions. Management of the water table position in order to avoid inundation will thus be critical in future fen restoration projects, especially when graminoid vegetation is dominant, when the prime goal of restoration is maximizing the greenhouse gas sequestration function.

The effect of inundation on carbon exchange

Water bodies such as drainage ditches, ponds and lakes are significant contributors to peatland carbon balance, often representing hot-spots of CH_4 emissions (Waddington and Day, 2007; Wilson et al., 2009). On the other hand, the initial creation of lakes after peat extraction has also been pointed out as a possible way to quickly decrease GHG emissions by limiting heterotrophic respiration and pave the way to vegetation establishment (Jordan et al*.,* 2016). In the present study, mean exchange of CO_2 (1.16 g CO_2 m^{-2} d^{-1}; 138.4 g CO_2 m^{-2} over the study period) and CH_4 (1.8 to 82.2 mg CH_4 m^{-2} d^{-1}; 8.7 g CH_4 m^{-2} over the study period) at *RP1* were in the range of reported values for ditches and ponds in natural and restored peatlands (Schrier-Uijl et al., 2011; Strack and Zuback, 2013; Waddington and Day, 2007). Absence of vegetation and of an aerated layer in the peat profile resulted in low mean ecosystem respiration, nine times lower than at *UNR*. Nevertheless, absence of CO_2 uptake by vegetation led *RP1* to represent a rather large CO_2 source over the study period. *RP1* was also a substantial source of methane (8.7 g CH_4 m^{-2}), larger than the reference ecosystem (7.5 g CH_4 m^{-2}). Carbon dioxide and CH_4 fluxes were negatively related to water table position. The low CH_4 emissions in the middle of the summer can be explained by higher CH_4 oxidation rates in the water column due to a longer time of transportation to the atmosphere (Bubier, 1995; Schrier-Uijl et al., 2011). Though not measured in this study, variation in CO_2 and CH_4 emissions at *RP1* could also have been caused by variations in quality and concentration of dissolved organic carbon (DOC) (Strack et al., 2015). DOC can contribute to both reduce CH_4 emissions and increase CO_2 emissions in freshwater environments and peatlands (Franke et al., 2013; Heitmann et al., 2007). After restoration, production and export rates of DOC may increase or decrease compared to drained systems, and may also evolve over time (e.g. Armstrong et al., 2010; Strack and Zuback 2013; Wickland et al., 2007; 2008; Wilson et al., 2011). There is uncertainty about future water table levels and vegetation establishment at *RP1* and future rates of CO_2 and CH_4 emissions at *RP1* will evolve with the environmental conditions.

Effect of rewetting on vegetation

Graf et al. (2008) studied spontaneous establishment of vegetation in 28 peat extracted sites with residual fen peat and compared it to vegetation in 11 undisturbed peatlands across Canada and in Minnesota (USA). Post-extraction fens with collapsed drainage systems (i.e. hydrological conditions similar to a site where rewetting operations were conducted) were quickly revegetated by wetland species but typical fen species (e.g. *Carex* and *Sphagnum* species) did not establish in covers similar to undisturbed fens. They attributed this low establishment to the lack of fen species in the immediate surroundings of the sites (Graf et al., 2008). However, they suggested that environmental conditions (e.g. hydrology, peat and water chemistry, bulk density) in post-extracted fens with collapsed drainage system could be suitable for the establishment fen bryophytes and vascular species. Therefore, rewetted post-extraction fens closely located to undisturbed fens could regenerate with fen vegetation without further intervention (e.g. introduction of plant material). Conversely, in post-extraction *Sphagnum* peatlands, poor spontaneous vegetation establishment was attributed to harsh conditions during the establishment phase and not a lack of immigrant propagules (Campbell et al., 2003). In the present study, both conditions were met to favour the spontaneous establishment of fen species in the sectors that had been rewetted (*R1* and *R10*): 1) the experimental site was surrounded by a natural fen, which is a large source of propagules and 2) the rise of the water table following blocking of the drainage ditches seemingly provided suitable conditions for the propagules to establish and expand. The location of the experimental site within a large water track at the landscape level could also have played a role in maintaining stable and suitable hydrological conditions at the rewetted sectors. Furthermore, periodical flooding of the site with water in contact with the natural fen, a large source of propagules, probably supported migration of propagules to the site (Pfadenhauer and Grootjans, 1999). Only one growing season after rewetting, wetland and peatland species, both vascular and moss species, already had established. Ten growing seasons after rewetting, fen species were dominant in the ecosystem. *Carex lasiocarpa*, well established at *R10*, is typical of natural fens in the region of the study site (Glaser, 1987). This species frequently forms large colonies and contributes to the evolution of regional fen ecosystems (Glaser, 1987). The high cover of *C. lasiocarpa* and other typical peatland species at *R10* is likely an indication that this ecosystem is evolving towards the typical natural fen structure. In future years, fen vegetation will likely continue to expand and become more similar to the surrounding natural fen.

Bryophytes are important components of natural fen vegetation communities (Rydin et al., 2013). As major peat formers in peatlands, they play a major role in their carbon sequestration function (Bérubé and Rochefort, 2018; Vitt et al., 2009). Promoting bryophyte establishment and expansion is thus a major goal of peatland restoration in North America (Rochefort, 2000). The first attempt at rewetting a post-extraction fen at large scale in North America without a re-introduction of propagules gave poor results in terms of bryophyte establishment (Rochefort et al., 2016). Five growing seasons after rewetting, the average bryophyte cover was lower than ten percent. Our results show, however, that peatland mosses can establish as soon as one growing season after rewetting.

Fast bryophytes establishment was also observed after two and three growing seasons in a constructed fen in Alberta, indicating that diaspore re-introduction is not always mandatory when proper hydrological and environmental conditions are met (Vitt and House, 2015; Vitt et al., 2016). In the present study, ten growing seasons after rewetting, the cover of typical fen mosses, mainly *C. stellatum* and *S. cossonii,* was close to 20%, in a dense cover of herbaceous species, supporting the idea that rewetting alone can be used as an effective restoration strategy for fen bryophytes establishment. However, ten years after rewetting the moss cover is still more than three times lower than the reference ecosystem. Some factors seemingly impeded or slowed bryophyte expansion following their establishment. Episodes of flooding following blockage of the drainage ditches at *R10* could have been one of these factors. Ecological niches of fen mosses are largely constrained by the position of the water table relative to the soil surface (Gignac et al., 1991). As carpet and lawn species, C. *stellatum* and S*. cossonii* are preferentially found where the water table is near or at the level of the soil surface (Rochefort et al., 2012). Also, after restoration, inundated or temporarily inundated areas are likely to be devoid of bryophytes (Vitt and House, 2015; Vitt et al., 2016). However, response of mosses to flooding is poorly documented and their response does not always coincide with their ecological niches relatively to the water table position, making it difficult to predict the response of particular species to flooding (Borkenhagen and Cooper, 2018). High cover of *C. lasiocarpa* at *R10* could also be an indication that water table levels were above the surface of the ground for at least a certain period of time each year since rewetting. *C. lasiocarpa* reaches its highest abundance when water table is shallow or above the ground surface (Gignac et al., 2004; Wheeler et al., 1983). In very wet conditions, *C. lasiocarpa* can become the dominant species, occurring with a limited number of other vascular plant species (Wheeler et al., 1983). By providing shade, large cover of live *Carex* and litter could have limited bryophyte expansion at *R10* (Emsens et al., 2018).

Compared to other studies, the vascular plant cover of 26% and 28% one and ten growing seasons after rewetting, respectively, may seem low. For instance, seven years after the end of peat extraction activities, at sites with collapsed drainage ditches in Canada and Minnesota (USA), mean vegetation cover of 50% were reported (Graf et al., 2008). In another study, Rochefort et al. (2016) reported a mean vascular plant cover of 65 % at a restored fen in Québec, five growing seasons after rewetting. However, the lower vascular plant covers in the present study are not the result of a poor establishment of vegetation after rewetting (see Figure 3), but can be explained by the similarity between live graminoid plants and graminoid litter. This was especially the case at *R10* where sedges were dominant. The vascular plant cover reported for the reference ecosystem in the present study is also lower than in other studies by Graf et al. (2008) and Rochefort et al. (2016). Actually, the difference in vascular plant cover between the reference ecosystem and the rewetted sectors is lower in the present study compared to studies by Graf et al. (2008) and Rochefort et al. (2016). Therefore, the relatively low cover of vascular plants reported in this study is likely due to a bias caused by the type of vegetation surveyed, and does not represent a poor vegetation establishment following rewetting. The presence of five species of peatland bryophytes one growing season after rewetting and the bryophyte cover of 18%, 10 growing seasons after rewetting also supports that the rewetting was effective at promoting fen vegetation establishment. In studies by Graf et al. (2008) and Rochefort et al. (2016), bryophytes were virtually absent from the sites. Our results suggest that rewetting can be used to rapidly initiate a successional trajectory towards an ecosystem similar to a local reference ecosystem. The rapid shift in vegetation composition following rewetting is also noticeable at *R1* where the cover of species not typically found in wetlands or peatlands, some of which are considered as ruderals or "unwanted" species (e.g. *Agrostis scabra*, *Cirsium arvense* and *Hordeum jubatum;* Manitoba (2017), MAPAQ and MFFPQ (2018)) was ten times lower than at *UNR* and similar to what was observed at *R10* and *REF*. The cover occupied by peatland and wetland species in the rewetted sectors was also more than two times higher than *UNR*.

Conclusion

Rewetting can be an appropriate restoration option for post-extraction fens, inducing a rapid shift in vegetation communities towards composition and structure similar to what is observed in natural fens. Rewetting and subsequent colonization of former peat extraction sites by vegetation can also lead to the fast return of the growing season C sequestration function. However, before deciding to rely only on rewetting to restore a site with residual fen peat, site managers should ensure that certain conditions are met: 1) a source of propagules should be located in the surroundings of the site and 2) water levels should be monitored and managed with great care. For instance, systems that can manage water levels with precision could be used to provide restored sites with water during dry years and avoid flooding during wet years by pumping water out of the system. Gradual blocking of the drainage ditches over several years could also be a way to reach the desired water table level and avoid flooding during the first years post-restoration. In order to promote bryophyte establishment and avoid high CH_4 emissions to maximize the C sequestration potential, a water level close to the surface should be targeted and flooding should be avoided. For the sites where the adjacent pool of species is not composed of species fen species (*Sphagnum* dominated peatlands ecosystems are often the dominant ecosystem surrounding the post-extraction areas), active re-introduction of targeted species should be considered.

Discussion générale et conclusions

Pour cette étude, nous nous étions fixés les objectifs suivants :

1) Évaluer l'effet du remouillage sur le rétablissement de flux de CO_2 et de CH_4 semblables à ceux prévalant dans un écosystème de référence local.
2) Déterminer les facteurs environnementaux pouvant expliquer les différences dans les flux de CO_2 et de CH_4 entre les traitements de remouillage et l'écosystème de référence.
3) Réaliser le bilan des échanges de CO_2 et de CH_4 des communautés végétales dominantes de chaque traitement pour une saison de croissance.
4) Déterminer l'effet du remouillage sur l'établissement de communautés végétales semblables à celles retrouvées dans un écosystème de référence local : composition et structure de la végétation.

Les résultats de cette étude montrent que :

1) Le remouillage peut avoir un effet marqué sur les échanges de CO_2 et de CH_4. Une et dix saisons de croissance après remouillage, les échanges de CO_2 étaient similaires à ceux observés dans l'écosystème de référence. Le secteur ayant été remouillé depuis une saison de croissance présentait des émissions de CH_4 similaires à celles de l'écosystème de référence. Les émissions de CH_4 du secteur ayant été remouillé depuis dix saisons de croissance présentait quant à lui de fortes émissions de CH_4 comparativement à l'écosystème de référence.
2) Le niveau de l'eau est un facteur clé dans le contrôle des échanges de carbone et notamment dans les émissions de CH_4. Selon les niveaux d'eau et les espèces végétales en place, de hautes émissions de CH_4 peuvent être générées. Dans le cas présent, l'inondation du secteur remouillé depuis dix saisons de croissance et couvert par des espèces graminoïdes (surtout le *Carex lasiocarpa*) a généré, durant le pic de juillet, des émissions de CH_4 quatre fois plus élevées que celles mesurées dans l'écosystème de référence.
3) Le remouillage peut induire un retour rapide de la fonction de séquestration du carbone durant la saison de croissance, selon le type de végétation qui s'y établi. Les secteurs remouillés il y a une et dix saisons de croissance et étant recouverts de végétation ont présenté un bilan de carbone négatif pour la saison de croissance et ont donc séquestré du carbone.
4) Le remouillage peut avoir un effet considérable sur l'établissement de la végétation. Aussi rapidement qu'une saison de croissance après remouillage, des différences quant à la composition et à la structure de la végétation tant muscinale que vasculaire peuvent être observées comparativement à un milieu non remouillé. Après dix saisons de croissance, l'écosystème résultant était dominé par des espèces de fens et un tapis discontinu de mousses de fens s'y était établi.

Certaines actions peuvent être prises pour appuyer l'action de remouillage. Par exemple, éviter le nivellement de la surface pour conserver des espèces spontanément établies entre l'arrêt de l'extraction et la restauration d'un site peut être une option intéressante pour s'assurer de non seulement réduire les émissions de CO_2 après remouillage, mais aussi favoriser sa captation par la végétation.

À la lumière des résultats obtenus, le remouillage peut être considéré comme une méthode de restauration pouvant faire partie de l'arsenal du restaurateur de tourbières. L'efficience de cette stratégie est aussi avantageuse lors de la restauration de grandes surfaces. Cependant, plusieurs questions restent encore à être étudiées avant d'émettre des recommandations et lignes directrices précises en matière de restauration des fens post-extraction. Par exemple, quels sont les niveaux d'eau optimaux à viser pour favoriser le retour des bryophytes et de la végétation vasculaire sans toutefois générer des émissions trop élevées de CH_4 et comment obtenir les niveaux d'eau désirés et éviter les inondations? À ce sujet, différentes solutions devraient être explorées : éviter de bloquer tous les canaux de drainage simultanément et plutôt remouiller par étapes, sur plusieurs années. Étudier l'implantation de systèmes de gestion des niveaux d'eau pour atteindre et maintenir des niveaux d'eau appropriés, par l'apport ou le retrait d'eau du système. Par ailleurs, le contexte hydrologique de chaque site à restaurer devrait être pris en compte au moment de la conception d'un plan de restauration. La restauration des sites se situant dans des vastes complexes de tourbières et de milieux humides tels que rencontrés dans les provinces de l'Ouest du Canada différera de celle des sites ayant davantage une hydrologie de fen de bassin, rencontrés dans l'Est du Canada. Par ailleurs, dans la présente étude, un élément clé du succès de la restauration aura été la proximité avec un fen naturel pouvant fournir des propagules aux secteurs remouillés. Dans une situation où un site n'est pas à proximité immédiate d'une tourbière, d'autres stratégies devraient être combinées au remouillage pour s'assurer de l'introduction et de l'établissement d'espèces de tourbières. Pour conclure, tel que souligné par Lamers et al. (2015), les approches de restauration des écosystèmes de milieux humides, dont celles portant sur les fens, ont longtemps été fondées sur une approche par essais et erreurs. Afin de transformer une pratique basée sur l'essai-erreur à une pratique basée sur les données probantes, une meilleure compréhension des processus biogéochimiques et écologiques régissant ces écosystèmes reste toujours à être développée (Lamers et al., 2015). À terme, les trajectoires de restauration seraient plus facilement prédites et les actions de restauration seraient sélectionnées en conséquence.

Bibliographie

(CSPMA) Canadian Sphagnum Peat Moss Association. 2015. 2015 Statistics about peatland areas managed for horticultural peat harvesting in Canada. [En ligne] Récupéré de http://tourbehorticole.com/la-tourbe-en-chiffres/ [accédé le 31 août 2018].

(GRET) Groupe de recherche en écologie des tourbières. 2016. Restauration des tourbières minérotrophes: État des connaissances 2015. Université Laval. Québec. 22 p.

(MAPAQ et MFFPQ) Ministère de l'Agriculture des Pêcheries et de l'Alimentation et ministère des Forêts de la Faune et des Parcs du Québec. 2018. Herbier du Québec. [En ligne] Récupéré de http://herbierduquebec.gouv.qc.ca/ [accédé le 24 juillet 2018].

(SER) Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER International Primer on Ecological Restoration. Society for Ecological Restoration International. Tuscon, Arizona. 15 p. http://www.ser.org/.

Armstrong, A., Holden, J., Kay, P., Francis, B., Foulger, M., Gledhill, S., McDonald, A. T., Walker, A. 2010. The impact of peatland drain-blocking on dissolved organic carbon loss and discolouration of water; results from a national survey. *J. Hydrol.,* **381**(1), 112-120.

Baird, A. J. 2009. Carbon cycling in northern peatlands. Washington D.C.: American Geophysical Union.

Bérubé, V., Rochefort, L. 2018. Production and decomposition rates of different fen species as targets for restoration. *Ecol. Indic.,* **91**, 105-115.

Blodau, C. 2002. Carbon cycling in peatlands a review of processes and controls. *Environ. Rev.,* **10**(2), 111-134.

Borkenhagen, A., Cooper, D. J. 2018. Tolerance of fen mosses to submergence, and the influence on moss community composition and ecosystem resilience. *J. Veg. Sci.,* **29**(2), 127-135.

Boudreau, S., Rochefort, L. 2008, 8-13 juin. Plant establishment in restored peatlands: 10 years monitoring of sites restored from 1995 to 2003. Présenté à la conférence: Proceedings of the 13th International Peat Congress: After Wise Use – The Future of Peatlands, Tullamore, Ireland.

Bridgham, S. D., Cadillo-Quiroz, H., Keller, J. K., Zhuang, Q. 2013. Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Glob. Change Biol.,* **19**(5), 1325-1346.

Brouillet, L., Coursol, F., Meades, S. J., Favreau, M., Anions, M., Belisle, P., Desmet, P. 2010+. VASCAN, Base de données des plantes vasculaires du Canada. [En ligne] Récupéré de http://data.canadensys.net/vascan/ [accédé le 30 Juillet 2018].

Bubier, J., Crill, P., Mosedale, A., Frolking, S., Linder, E. 2003. Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochem. Cy.,* **17**(2).

Bubier, J., Moore, T., Savage, K., Crill, P. 2005. A comparison of methane flux in a boreal landscape between a dry and a wet year. *Global Biogeochem. Cy.,* **19**(1).

Bubier, J. L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J. Ecol.,* **83**(3), 403-420.

Campbell, D. R., Rochefort, L., Lavoie, C. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. *J. Appl. Ecol.,* **40**(1), 78-91.

Caron, J., Price, J., Rochefort, L. 2015. Physical Properties of Organic Soil: Adapting Mineral Soil Concepts to Horticultural Growing Media and Histosol Characterization. *Vadose Zone J.,* **14**(6).

Chimner, R. A., Cooper, D. J., Wurster, F. C., Rochefort, L. 2016. An overview of peatland restoration in North America: where are we after 25 years? *Restor. Ecol.*

Cobbaert, D., Rochefort, L., Price, J. S. 2004. Experimental restoration of a fen plant community after peat mining. *Appl. Veg. Sci.,* **7**(2), 209-220.

Cooper, D. J., MacDonald, L. H. 2000. Restoring the vegetation of mined peatlands in the Southern Rocky Mountains of Colorado, U.S.A. *Restor. Ecol.,* **8**(2), 103-111.

Couwenberg, J., Fritz, C. 2012. Towards developing IPCC methane 'emission factors' for peatlands (organic soils). *Mires peat,* **10**.

Daigle, J.-Y., Gaudreau-Daigle, H. 2001. Canadian peat harvesting and the environment. Second edition. North American Wetlands Conservation Council. Ottawa, Ontario. 41 p.

Davies, G. M., Hamilton, A., Smith, A., Legg, C. J. 2008. Using visual obstruction to estimate heathland fuel load and structure. *Int. J. Wildland Fire,* **17**(3), 380-389.

Emsens, W.-J., Aggenbach, C. J. S., Rydin, H., Smolders, A. J. P., van Diggelen, R. 2018. Competition for light as a bottleneck for endangered fen species: An introduction experiment. *Biol. Conserv.,* **220**, 76-83.

Famous, N. C., Spencer, M., Nilsson, H. 1991. Revegetation patterns in harvested peatlands in central and eastern North America. Présenté à la conférence: Peat and Peatlands: The Resource and its Utilization. Proceedings of the International Peat Symposium, Duluth.

Faubert, J. 2012; 2014. Flore des bryophytes du Québec-Labrador (Vol. 2 : Mousses, première partie. xiv + 402 p., illus; Vol. 3 : Mousses, seconde partie, viii + 456 p., illus.). Saint-Valérien, Québec: Société québécoise de bryologie.

Franke, D., Bonnell, E. J., Ziegler, S. E. 2013. Mineralisation of dissolved organic matter by heterotrophic stream biofilm communities in a large boreal catchment. *Freshwater Biol.,* **58**(10), 2007-2026.

Frolking, S., Roulet, N. T. 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Glob. Change Biol.,* **13**(5), 1079-1088.

Gagnon, F. 2016. La régénération spontannée d'une tourbière manitobaine après extraction de la tourbe : diversité des assemblages végétaux et propositions d'aménagement. Mémoire de maîtrise., Université Laval, Québec. 54 p.

Gignac, L., Vitt, D., Zoltai, S. C., Bayley, S. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedwigia,* **53**(1-2), 27-71.

Gignac, L. D., Gauthier, R., Rochefort, L., Bubier, J. 2004. Distribution and habitat niches of 37 peatland *Cyperaceae* species across a broad geographic range in Canada. *Can. J. Botany,* **82**(9), 1292-1313.

Glaser, P. H. 1987. The Development of Streamlined Bog Islands in the Continental Interior of North America. *Arctic Alpine Res.,* **19**(4), 402-413.

Glaser, P. H., Janssens, J. A. 1986. Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. *Can. J. Botany,* **64**(2), 395-415.

González, E., Rochefort, L. 2014. Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. *Ecol. Eng.,* **68**, 279-290.

Graf, M., Rochefort, L., Poulin, M. 2008. Spontaneous revegetation of cutaway peatlands of North America. *Wetlands,* **28**(1), 28-39.

Graf, M. D. 2008. Restoring fen plant communities on cutaway peatlands of North America. Thèse de doctorat, Université Laval, Québec. 166 p.

Graf, M. D., Bérubé, V., Rochefort, L. 2012. Restoration of peatlands after peat extraction: Impacts, restoration goals, and techniques. *Dans* Restoration and Reclamation of Boreal Ecosystems (p. 259-280). D. H. Vitt et J. S. Bhatti (Éditeurs), Cambridge University Press. Cambridge, United Kingdom.

Graf, M. D., Rochefort, L. 2008. Techniques for restoring fen vegetation on cut-away peatlands in North America. *Appl. Veg. Sci.,* **11**(4), 521-528.

Graf, M. D., Rochefort, L. 2010. Moss regeneration for fen restoration: Field and greenhouse experiments. *Restor. Ecol.,* **18**(1), 121-130.

Green, S., Baird, A. 2017. Using 'snapshot' measurements of CH_4 fluxes from an ombrotrophic peatland to estimate annual budgets: interpolation versus modelling. *Mires peat,* **19**.

Groeneveld, E. V., Rochefort, L. 2002. Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems. *Suo,* **53**(3-4), 73-85.

Groeneveld, E. V. G., Rochefort, L. 2005. *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. *Restor. Ecol.,* **13**(1), 74-82.

Halsey, L., Vitt, D., Zoltai, S. 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. *Wetlands,* **17**(2), 243-262.

Heitmann, T., Goldhammer, T., Beer, J., Blodau, C. 2007. Electron transfer of dissolved organic matter and its potential significance for anaerobic respiration in a northern bog. *Glob. Change Biol.,* **13**(8), 1771-1785.

Hendriks, D., van Huissteden, J., Dolman, A., van Der Molen, M. 2007. The full greenhouse gas balance of an abandoned peat meadow. *Biogeosciences,* **4**(3), 411-424.

Jeglum, J. K. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicator. *Annales Botanici Fennici,* **28**(3), 175-192.

Joiner, D. W., Lafleur, P. M., McCaughey, J. H., Bartlett, P. A. 1999. Interannual variability in carbon dioxide exchanges at a boreal wetland in the BOREAS northern study area. *J. Geophys. Res-Atmos.,* **104**(D22), 27663-27672.

Joosten, H. 2009. The Global Peatland CO_2 Picture: peatland status and drainage related emissions in all countries of the world. Wageningen, Netherlands: Wetlands International.

Joosten, H. 2016. Peatlands across the globe. *Dans* Peatland Restoration and Ecosystem Services: Science, Policy and Practice (p. 19-43). A. Bonn, H. Joosten, M. Evans, R. Stoneman, et T. Allott (Éditeurs), Cambridge University Press. Cambridge.

Joosten, H., Clarke, D. 2002. Wise use of mires and peatlands: International Mire Conservation Group and International Peat Society.

Joosten, H., Sirin, A., Couwenberg, J., Laine, J., Smith, P. 2016. The role of peatlands in climate regulation. *Dans* Peatland Restoration and Ecosystem Services: Science, Policy and Practice (p. 63-76). A. Bonn, T. Allott, M. Evans, H. Joosten, et R. Stoneman (Éditeurs), Cambridge University Press. Cambridge.

Jordan, S., Stromgren, M., Fiedler, J., Lundin, L., Lode, E., Nilsson, T. 2016. Ecosystem respiration, methane and nitrous oxide fluxes from ecotopes in a rewetted extracted peatland in Sweden. *Mires Peat,* **17**(7).

Klinger, L., Zimmerman, P., Greenberg, J., Heidt, L., Guenther, A. 1994. Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. *J. Geophys. Res-Atmos.,* **99**(D1), 1469-1494.

Konvalinková, P., Prach, K. 2014. Environmental factors determining spontaneous recovery of industrially mined peat bogs: A multi-site analysis. *Ecological Engineering,* **69**, 38-45.

Lafleur, P. M., Roulet, N. T., Bubier, J. L., Frolking, S., Moore, T. R. 2003. Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochem. Cy.,* **17**(2).

Lai, D. Y. F. 2009. Methane Dynamics in Northern Peatlands: A Review. *Pedosphere,* **19**(4), 409-421.

Lamers, L. P. M., Vile, M. A., Grootjans, A. P., Acreman, M. C., van Diggelen, R., Evans, M. G., Richardson, C. J., Rochefort, L., Kooijman, A. M., Roelofs, J. G. M., Smolders, A. J. P. 2015. Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. *Biol. Rev.,* **90**(1), 182-203.

Landry, J. 2008. Impacts environnementaux d'une nouvelle technique de récolte de la tourbe. Mémoire de maîtrise, Université Laval, Québec, Québec. 71 p.

Landry, J., Rochefort, L. 2011. Le drainage des tourbières: impacts et techniques de remouillage. Groupe de recherche en écologie des tourbières. Université Laval, Québec. 53 p.

Lavoie, C., Grosvernier, P., Girard, M., Marcoux, K. 2003. Spontaneous revegetation of mined peatlands: An useful restoration tool? *Wetl. Ecol. Manag.,* **11**(1), 97-107.

Lenth, R., Love, J. 2018. Least-Squares Means. R package version 2.27-62,. Récupéré de https://cran.r-project.org/web/packages/lsmeans.

Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E.-M., Knoblauch, C. 2011. Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. *J. Ecol.,* **99**(4), 914-922.

Limpens, J., Berendse, F., Blodau, C., Canadell, J., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G. 2008. Peatlands and the carbon cycle: from local processes to global implications - a synthesis. *Biogeosciences,* **5**(5), 1475-1491.

Manitoba. 2017. The Noxious Weeds Act, C.C.S.M. c. N110.

Moore, T., Roulet, N., Knowles, R. 1990. Spatial and temporal variations of methane flux from subarctic/northern boreal fens. *Global Biogeochem. Cy.,* **4**(1), 29-46.

Myhre, G., D. Shindell, F.-M. Bréon, W. Collins, J. Fuglestvedt, J. Huang, D. Koch, J.-F. Lamarque, D. Lee, B. Mendoza, T. Nakajima, A. Robock, G. Stephens, Takemura, T., Zhang, H. 2013. Anthropogenic and Natural Radiative Forcing. *Dans* Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. D. Q. [T.F. Stocker, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and

P.M. Midgley] (Éditeur), Cambridge University Press. Cambridge, Royaume-Uni et New York, États-Unis.

Noyce, G. L., Varner, R. K., Bubier, J. L., Frolking, S. 2014. Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions. *J. Geophys. Res-Biogeo.,* **119**(1), 24-34.

Nugent, K. A., Strachan, I. B., Strack, M., Roulet, N. T., Rochefort, L. 2018. Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. *Glob. Change Biol.,* **24**(12), 5751-5768.

Payette, S., Rochefort, L. 2001. Écologie des tourbières du Québec-Labrador. [Sainte-Foy, Québec]: Les Presses de l'Université Laval.

Pfadenhauer, J., Grootjans, A. 1999. Wetland restoration in Central Europe: aims and methods. *Appl. Veg. Sci.,* **2**(1), 95-106.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., R-Core Team. 2018. Linear and Nonlinear Mixed Effects Models. R package version 3.1-137. Récupéré de http://cran.r-project.org/package=nlme.

Poulin, M., Andersen, R., Rochefort, L. 2013. A new approach for tracking vegetation change after restoration: A case study with peatlands. *Restor. Ecol.,* **21**(3), 363-371.

Poulin, M., Rochefort, L., Pellerin, S., Thibault, J. 2004. Threats and protection for peatlands in Eastern Canada. *Géocarrefour,* **79**(4), 331-344.

Poulin, M., Rochefort, L., Quinty, F., Lavoie, C. 2005. Spontaneous revegetation of mined peatlands in eastern Canada. *Can. J. Botany,* **83**(5), 539-557.

Price, J. S., Heathwaite, A. L., Baird, A. J. 2003. Hydrological processes in abandoned and restored peatlands: An overview of management approaches. *Wetl. Ecol. Manag.,* **11**(1), 65-83.

Priede, A. 2016. Spontaneous revegetation of cutaway fens: can it result in valuable habitats? : International Mire Conservation Group, International Peat Society.

Priede, A., Mezaka, A., Dobkevica, L., Grinberga, L. 2016. Spontaneous revegetation of cutaway fens: can it result in valuable habitats? *Mires peat,* **18**(6).

Quéré, C. L., Moriarty, R., Andrew, R., Peters, G., Ciais, P., Friedlingstein, P., Jones, S., Sitch, S., Tans, P., Arneth, A. 2015. Global carbon budget 2014. *Earth Syst. Sci. Data,* **7**(1), 47-85.

Quinty, F., Rochefort, L. 2003. Guide de restauration des tourbières (2e éd.). Québec, Québec: Association canadienne de mousse de sphaigne et Ministère des Ressources naturelles du Nouveau-Brunswick.

Rankin, T., Strachan, I. B., Strack, M. 2018. Carbon dioxide and methane exchange at a post-extraction, unrestored peatland. *Ecol. Eng.,* **122**, 241-251.

Rochefort, L. 2000. Sphagnum: A Keystone Genus in Habitat Restoration. *Bryologist,* **103**(3), 503-508.

Rochefort, L., LeBlanc, M., Hogue-Hugron, S., Pouliot, R., D'Amour, N., Boismenu, C. 2015. Restauration écologique des tourbières de Bic-Saint-Fabien et de Saint-Fabien-sur-Mer dans le bas Saint-Laurent (Projet R719.1). Groupe de recherche en écologie des tourbières, Université Laval, Québec. 76 p.

Rochefort, L., LeBlanc, M.-C., Bérubé, V., Hugron, S., Boudreau, S., Pouliot, R. 2016. Reintroduction of fen plant communities on a degraded minerotrophic peatland. *Botany,* **94**(11), 1041-1051.

Rochefort, L., Quinty, F., Campeau, S., Johnson, K., Malterer, T. 2003. North American approach to the restoration of Sphagnum dominated peatlands. *Wetl. Ecol. Manag.,* **11**(1), 3-20.

Rochefort, L., Strack, M., Poulin, M., Price, J. S., Graf, M., Desrochers, A., Lavoie, C. 2012. Wetland habitats of North America: ecology and conservation concerns. *Dans* Northern peatlands (p. 119-134). D. R. B. A. H. Baldwin (Éditeur), University of California Press. Los Angeles.

Rydin, H., Jeglum, J. K., Bennett, K. D. 2013. The biology of peatlands (2e éd.). Oxford: Oxford University Press.

Saarnio, S., Morero, M., Shurpali, N., Tuittila, E., Makila, M., Alm, J. 2007. Annual CO_2 and CH_4 fluxes of pristine boreal mires as a background for the lifecycle analyses of peat energy. *Boreal Environ Res.,* **12**(2), 101-113.

Saarnio, S., Wittenmayer, L., Merbach, W. 2004. Rhizospheric exudation of *Eriophorum vaginatum* L. Potential link to methanogenesis. *Plant Soil,* **267**(1), 343-355.

Schrier-Uijl, A., Veraart, A., Leffelaar, P., Berendse, F., Veenendaal, E. 2011. Release of CO_2 and CH_4 from lakes and drainage ditches in temperate wetlands. *Biogeochemistry,* **102**(1), 265-279.

Shannon, R. D., White, J. R., Lawson, J. E., Gilmour, B. S. 1996. Methane efflux from emergent vegetation in peatlands. *J. Ecol.,* **84**(2), 239-246.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north swedish mire waters. *Oikos,* **2**(2), 241-258.

Smith, R. E., Veldhuis, H., Mills, G. F., Eilers, R. G., Fraser, W. R., Lelyk, G. W. 1998. Terrestrial ecozones, ecoregions, and ecodistricts, an ecological stratification of Manitoba's landscapes. Techninal Bulletin 98-9E. Land Resource Unit, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada. Winnipeg, Manitoba. 324 p.

Soini, P., Riutta, T., Yli-Petäys, M., Vasander, H. 2010. Comparison of vegetation and CO_2 dynamics between a restored cut-away peatland and a pristine fen: evaluation of the restoration success. *Restor. Ecol.,* **18**(6), 894-903.

Strack, M., Cagampan, J., Hassanpour Fard, G., Keith, A. M., Nugent, K., Rankin, T., Robinson, C., Strachan, I. B., Waddington, J. M., Xu, B. 2016. Controls on plot-scale growing season CO_2 and CH_4 fluxes in restored peatlands: Do they differ from unrestored and natural sites? *Mires peat,* **17**(5), 1-18.

Strack, M., Keith, A. M., Xu, B. 2014. Growing season carbon dioxide and methane exchange at a restored peatland on the Western Boreal Plain. *Ecol. Eng.,* **64**, 231-239.

Strack, M., Mwakanyamale, K., Hassanpour Fard, G., Bird, M., Bérubé, V., Rochefort, L. 2017. Effect of plant functional type on methane dynamics in a restored minerotrophic peatland. *Plant Soil,* **410**(1), 231-246.

Strack, M., Waddington, J. M. 2012. Effects of peat extraction and restoration on greenhouse gas exchange from Canadian peatlands. *Dans* Restoration and reclamation of boreal ecosystems : attaining sustainable development (p. 386-403). D. H. Vitt et J. S. Bhatti (Éditeurs), Cambridge University Press. Cambridge.

Strack, M., Zuback, Y., McCarter, C., Price, J. 2015. Changes in dissolved organic carbon quality in soils and discharge 10 years after peatland restoration. *J. Hydrol.,* **527**, 345-354.

Strack, M., Zuback, Y. C. A. 2013. Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences,* **10**(5), 2885-2896.

Ström, L., Mastepanov, M., Christensen, T. 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry,* **75**(1), 65-82.

Tarnocai, C., Kettles, I. M., Lacelle, B. 2011. Peatlands of Canada ; Geological Survey of Canada, Open File 6561; map, scale 1: 6 500 000). Natural Resources of Canada / Ressources naturelles Canada.

Triisberg, T., Karofeld, E., Paal, J. 2013. Factors affecting the re-vegetation of abandoned extracted peatlands in Estonia: a synthesis from field and greenhouse studies. *Est. J. Ecol.,* **62**(3), 192.

Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Laine, J. 1999. Restored cut-away peatland as a sink for atmospheric CO_2. *Oecologia,* **120**(4), 563-574.

Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Nykänen, H., Martikainen, P. J., Laine, J. 2000. Methane dynamics of a restored cut-away peatland. *Glob. Change Biol.,* **6**(5), 569-581.

Turetsky, M. R. 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist,* **106**(3), 395-409.

USDA - NRCS. 2018. The PLANTS database (http://plants.usda.gov/). Greensboro, NC 27401-4901 USA.

Vanselow-Algan, M., Schmidt, Sr., Greven, M., Fiencke, C., Kutzbach, L., Pfeiffer, E. 2015. High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. *Biogeosciences,* **12**(14), 4361-4371.

Van Seters, T. E., Price, J.S. 2002. Towards a conceptual model of hydrological change on an abandoned cutover bog, Quebec. Hydrol. Process., **16**, 1965-1981.

Vasander, H., Kettunen, A. 2006. Carbon in boreal peatlands. *Dans* Boreal Peatland Ecosystems (p. 165-194). R. K. Wieder et D. H. Vitt (Éditeurs), Springer Berlin Heidelberg. Berlin, Heidelberg.

Vitt, D. H. 2006. Functional Characteristics and Indicators of Boreal Peatlands. *Dans* Boreal Peatland Ecosystems (p. 9-24). R. K. Wieder et D. H. Vitt (Éditeurs), Springer Berlin Heidelberg. Berlin, Heidelberg.

Vitt, D. H. 2013. Peatlands. *Dans* Reference Module in Earth Systems and Environmental Sciences. Elsevier

Vitt, D. H. 2014. A key and review of bryophytes common in North American peatlands. *Evansia,* **31**(4), 121-158.

Vitt, D. H., House, M. 2015. Establishment of bryophytes from indigenous sources after disturbance from oil sands mining. *Bryologist,* **118**(2), 123-129.

Vitt, D. H., House, M., Hartsock, J. A. 2016. Sandhill Fen, an initial trial for wetland species assembly on in-pit substrates: lessons after three years. *Botany,* **94**(11), 1015-1025.

Vitt, D. H., Wieder, R. K., Scott, K. D., Faller, S. 2009. Decomposition and peat accumulation in rich fens of boreal Alberta, Canada. *Ecosystems,* **12**(3), 360-373.

Waddington, J., Day, S. 2007. Methane emissions from a peatland following restoration. *J. Geophys. Res-Biogeo.,* **112**(G3).

Waddington, J., Strack, M., Greenwood, M. 2010. Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO_2 exchange to ecosystem-scale restoration. *J. Geophys. Res-Biogeo.,* **115**(G1).

Waddington, J., Warner, K., Kennedy, G. 2002. Cutover peatlands: A persistent source of atmospheric CO_2. *Global Biogeochem. Cy.,* **16**(1), 1-7.

Waddington, J. M., Price, J. S. 2000. Effect of peatland drainage, harvesting, and restoration on atmospheric water and carbon exchange. *Phys. Geogr.,* **21**(5), 433-451.

Walbridge, M. R., Navaratnam, J. A. 2006. Phosphorous in Boreal Peatlands. *Dans* Boreal Peatland Ecosystems (p. 231-258). R. K. Wieder et D. H. Vitt (Éditeurs), Springer Berlin Heidelberg. Berlin, Heidelberg.

Wheeler, G. A., Glaser, P. H., Gorham, E., Wetmore, C. M., Bowers, F. D., Janssens, J. A. 1983. Contributions to the flora of the Red Lake peatland, northern Minnesota, with special attention to Carex. *Am. Midl. Nat.,* **110**(1), 62-96.

Wickland, K., Neff, J., Aiken, G. 2007. Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. *Ecosystems,* **10**(8), 1323-1340.

Wieder, R. K., Vitt, D. H., Benscoter, B. W. 2006. Peatlands and the boreal forest. *Dans* Boreal Peatland Ecosystems (p. 1-8). R. K. Wieder et D. H. Vitt (Éditeurs), Springer Berlin Heidelberg. Berlin, Heidelberg.

Wilson, D., Alm, J., Laine, J., Byrne, K. A., Farrell, E. P., Tuittila, E.-S. 2009. Rewetting of cutaway peatlands: are we re-creating hot spots of methane emissions? *Restor. Ecol.,* **17**(6), 796-806.

Wilson, D., Farrell, C., Mueller, C., Hepp, S., Renou-Wilson, F. 2013. Rewetted industrial cutaway peatlands in western Ireland: a prime location for climate change mitigation. *Mires peat,* **11**(1), 1-22.

Wilson, L., Wilson, J., Holden, J., Johnstone, I., Armstrong, A., Morris, M. 2011. Ditch blocking, water chemistry and organic carbon flux: Evidence that blanket bog restoration reduces erosion and fluvial carbon loss. *Sci. Total. Environ.,* **409**(11), 2010-2018.

Wind-Mulder, H. L., Vitt, D. H. 2000. Comparisons of water and peat chemistries of a post-harvested and undisturbed peatland with relevance to restoration. *Wetlands,* **20**(4), 616-628.

Xu, J., Morris, P. J., Liu, J., Holden, J. 2018. PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena,* **160**, 134-140.

Annexe A Water and peat chemistry data for each sector of the study site

Means ± (SD) of water chemistry data for each sector of the experimental site.

	Sector [a]	# samples	pH		EC (µS)		Ca		Mg		Na		K		N/NH_4^+		N/NO_3^-		P total		PO_4^{3-}	
							mg l^{-1}															
Pre-rewetting [b]	RP1	4	6.6		330														0.1	(0.05)		
	R10	1																	0.4			
	REF (gram) [c]	1																	0.9			
Post-rewetting [b]	UNR	5	6.2	(0.2)	334	(61)	35.7	(7.2)	14.7	(3.6)	2.1	(0.4)	4.7	(1.8)	1.9	(1.5)	0.20	(0.35)	0.4	(0.4)	0.45	(0.29)
	R10	5	7.5	(0.2)	259	(35)	33.9	(6.1)	12.2	(1.3)	1.4	(0.3)	0.8	(0.4)	0.0	(0.0)	0.01	(0.00)	0.1	(0.0)	0.10	(0.09)
	R1	5	6.5	(0.2)	424	(143)	47.5	(15.4)	19.9	(5.1)	3.4	(2.2)	3.5	(0.4)	0.4	(0.5)	0.03	(0.01)	0.2	(0.2)	0.13	(0.20)
	RP1	8	7.9	(0.5)	231	(44)	26.5	(4.8)	11.6	(2.1)	1.3	(0.2)	1.2	(0.6)	0.0	(0.0)	0.02	(0.01)	0.1	(0.0)	0.01	(0.01)
	REF (gram) [c]	4	7.1	(0.5)	270	(42)	33.1	(7.9)	12.2	(1.4)	1.3	(0.2)	0.5	(0.2)	0.0	(0.0)	0.01	(0.01)	0.2	(0.0)	0.01	(0.02)
	REF (forest) [c]	4	7.3	(0.3)	360	(63)	42.6	(14.4)	18.4	(10.6)	3.1	(1.1)	1.2	(0.6)	0.0	(0.0)	0.01	(0.01)	0.1	(0.0)	0.00	(0.01)

[a] *UNR*: unrestored; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: surrounding reference ecosystem.

[b] Pre-rewetting: samples collected in August 2015 in sectors to be rewetted in September 2015. Post-rewetting: mean water chemistry data from samples collected in May, June, July and August 2016.

[c] Water samples collected from the open graminoid fen area and the forested fen area of the reference ecosystem.

Means ± (SD) of peat chemistry data for each sector of the experimental site.

	Sector [a]	# samples	pH		EC (µS)		Ca		Mg		Na		K		N/NH_4^+		NO_3^-		P (available)	
							mg g^{-1}													
Pre-rewetting [b]	R1	1	4.7																	
	RP1	6	5.2	(0.4)																
Post-rewetting [b]	UNR	2	6.3	(1.5)	224	(136)	18.8	(8.8)	2.4	(0.5)	0.0	(0.0)	0.2	(0.1)	0.0	(0.0)	0.12	(0.07)	0.0	(0.0)
	REF (gram) [c]	2	6.7	(0.1)	137	(25)	15.8	(0.9)	1.7	(0.1)	0.1	(0.0)	0.6	(0.3)	0.1	(0.0)	0.06	(0.01)	0.0	(0.0)
	R10	3	6.7	(0.2)	123	(57)	24.8	(0.7)	2.5	(0.4)	0.0	(0.0)	0.4	(0.1)	0.1	(0.0)	0.04	(0.01)	0.1	(0.0)
	R1	3	6.0	(0.4)	101	(20)	16.1	(2.8)	2.6	(0.5)	0.0	(0.0)	0.1	(0.0)	0.0	(0.0)	0.05	(0.03)	0.0	(0.0)

[a] *UNR*: unrestored; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: surrounding reference ecosystem.

[b] Pre-rewetting: samples collected in August 2015 in sectors to be rewetted in September 2015. Post-rewetting: samples collected in August 2016.

[c] Peat samples collected from the open graminoid fen area of the reference ecosystem

Annexe B Regression equations between carbon flux component and environmental factors for each sector of the study site

Relation between carbon flux component and environmental factors. Only statistically significant simple regressions are shown. UNR: unrestored; R1: first growing season after rewetting; R10: ten growing seasons after rewetting; REF: surrounding reference ecosystem.

Sector [a]	C flux component	Effect	Equation	F	P
UNR	ER	Vegetation volume	0.544 (Vol_veg) +7.12	33.65	<0.0001
		Air temperature	0.611 (T_{air}) -7.60	19.14	<0.0001
	GEP	Vegetation volume	-1.22 (Vol_veg) -4.20	130.72	<0.0001
		Water table level	-0.507(WTL) -18.0	16	0.0002
	NEE	Vegetation volume	-681 (Vol_veg) +3.0	51	<0.0001
		Water table level	-0.481 (WTL)-6.747	44	<0.0001
R1	ER	Vegetation volume	0.637(Vol_veg) +3.08	53.67	<0.0001
		Water table level	-0.536 (WTL)+13.67	41.37	<0.0001
		Air temperature	0.703 (T_{air})-6.81	13.08	0.0006
	GEP	Vegetation volume	-1.71(Vol_veg) -3.06	116	0.0006
		Water table level	1.15(WTL) -31.708	34	<0.0001
		Air temperature	-1.09(T_{air}) -0.044	5.43	0.0232
	NEE	Vegetation volume	-1.07 (Vol_veg) +0.027	65.9	<0.0001
		Water table level	0.616 (WTL)-18.03	15.8	0.0002
	CH_4	Water table level	0.0154(WTL) +1.8	5.2	0.0257
R10	GEP	Vegetation volume	-0.459(Vol_veg) -21.106	4.17	0.0466
	ER	Vegetation volume	0.366 (Vol_veg) +2.86	19.05	<0.0001
	CH_4	Water table level	0.0294(WTL) +1.646	43.76	<0.0001
		Soil temperature	0.0476(T_5) +1.19	28.9	<0.0001
REF	ER	Vegetation volume	0.214 (Vol_veg) +4.29	4.82	0.033
		Water table level	-0.128 (WTL)+9.37	3.92	0.0534
		Air temperature	0.285 (T_{air})+0.1646	16.54	0.0002
	GEP	Vegetation volume	-0.817 (Vol_veg) -6.276	21.24	<0.0001
		Water table level	0.2789(WTL) -23.73	4.33	0.043
	NEE	Vegetation volume	0.603 (Vol_veg)-1.98	12.82	0.0008
		Air temperature	0.429 (T_{air}) -25.09	9.82	0.003
	CH_4	Soil temperature	0.044(T_5) +0.682	20.02	<0.0001
RP1	ER	Water table level	-0.106(WTL) +5.55	7.16	0.013
	CH_4	Water table level	-0.06(WTL) +4.11	35.05	<0.0001

[a] *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

Annexe C Cover of vegetation strata and complete list of vascular and bryophyte species inventoried at the study site

		Sector [a]			
		UNR	R1	R10	REF
Sampling effort	Number of vascular sampling units (1 m^2)	10	35	40	45
	Number of bryophyte sampling units (900 cm^2)	100	350	400	450
Total vegetation cover		13 (7)	26 (11)	39 (28)	73 (18)
Total vascular plant cover		13 (7)	26 (11)	28 (8)	40 (12)
Total bryophyte cover		<1	1 (1)	18 (18)	57 (19)
Vegetation strata	Pref. Habitat [b]				
Trees and shrubs		<1	8 (7)	3 (4)	18 (13)
Alnus incana subsp. rugosa (Du Roi) R.T. Clausen	Facultative			<1	
Betula pumila Linnaeus	Peatland		<1	1 (3)	7 (8)
Dasiphora fruticosa (Linnaeus) Rydberg	Facultative		<1	<1	5 (8)
Larix laricina (Du Roi) K. Koch	Facultative		<1		6 (11)
Lonicera villosa (Michaux) Roemer & Schultes	Peatland				<1
Picea mariana (Miller) Britton, Sterns & Poggenburgh	Facultative				<1
Populus balsamifera Linnaeus	Facultative		1 (1)		
Populus tremuloides Michaux	Facultative	<1	<1		
Salix arctophila Cockerell ex A. Heller	Peatland				<1
Salix bebbiana Sargent	Facultative		1 (1)	<1	
Salix discolor Muhlenberg	Facultative		1 (2)	1 (1)	
Salix interior Rowlee	Facultative				<1
Salix pedicellaris Pursh	Peatland			<1	1 (2)
Salix serissima (L.H. Bailey) Fernald	Wetland		2 (3)	<1	
Thuja occidentalis Linnaeus	Facultative				2 (6)
Ericaceae				1 (1)	5 (7)
Andromeda polifolia Linnaeus	Peatland		<1	1 (1)	1 (2)
Rhododendron groenlandicum (Oeder) Kron & Judd	Wetland			<1	2 (6)
Vaccinium oxycoccos Linnaeus	Peatland		<1	<1	2 (4)
Carex		2 (2)	8 (6)	22 (11)	12 (6)
Carex aquatilis Wahlenberg	Peatland	<1	<1	2 (3)	3 (5)
Carex aurea Nuttall	Facultative			<1	
Carex chordorrhiza Linnaeus	Peatland			1 (2)	<1
Carex disperma Dewey	Wetland				<1
Carex echinata Murray	Wetland				<1
Carex gynocrates Wormskjold ex Drejer	Peatland			<1	<1
Carex interior L.H. Bailey	Peatland	<1	3 (4)	<1	
Carex lasiocarpa Ehrhart	Peatland	1 (2)	1 (1)	17 (10)	9 (7)
Carex leptalea Wahlenberg	Peatland			<1	
Carex limosa Linnaeus	Peatland			<1	<1

Carex tenuiflora Wahlenberg	Peatland		1 (2)	<1	<1
Carex trisperma Dewey	Peatland	<1	1 (4)		
Herbaceous species		14 (5)	18 (12)	7 (6)	13 (10)
Agrostis scabra Willdenow	Facultative	4 (5)	2 (2)		
Alopecurus aequalis Sobolewski	Wetland		<1		
Bidens cernua Linnaeus	Wetland	1 (2)	<1		
Caltha palustris Linnaeus	Wetland				<1
Calamagrostis stricta (Timm) Koeler	Facultative		<1	1 (1)	<1
Campanula aparinoides Pursh	Wetland			<1	<1
Cirsium arvense (Linnaeus) Scopoli	Other	1 (1)	<1		
Cirsium discolor (Muhlenberg ex Willdenow) Sprengel	Other	<1	<1		
Comarum palustre Linnaeus	Peatland			<1	1 (2)
Drosera rotundifolia Linnaeus	Peatland		<1	<1	<1
Eleocharis acicularis (Linnaeus) Roemer & Schultes	Wetland		1 (4)		
Eleocharis elliptica Kunth	Wetland			<1	<1
Epilobium ciliatum Rafinesque	Facultative	1 (1)	<1	<1	
Equisetum fluviatile Linnaeus	Wetland	<1	<1	1 (1)	<1
Eriophorum angustifolium Honckeny	Peatland				<1
Euthamia graminifolia (Linnaeus) Nuttall	Facultative	<1	<1	<1	
Fragaria vesca Linnaeus	Other	<1	<1		<1
Galium aparine Linnaeus	Other			<1	
Glyceria striata (Lamarck) Hitchcock	Wetland			<1	<1
Hordeum jubatum Linnaeus	Other	4 (4)	<1		
Juncus alpinoarticulatus Chaix	Wetland			<1	
Juncus brevicaudatus (Engelmann) Fernald	Wetland		1 (3)		
Juncus bufonius Linnaeus	Facultative		<1		
Juncus nodosus Linnaeus	Wetland		<1		
Lobelia kalmii Linnaeus	Wetland		<1	<1	<1
Lysimachia thyrsiflora Linnaeus	Wetland			<1	<1
Maianthemum trifolium (Linnaeus) Sloboda	Wetland			<1	1(3)
Menyanthes trifoliata Linnaeus	Peatland			2 (3)	5 (8)
Muhlenbergia glomerata (Willdenow) Trinius	Facultative			<1	<1
Parnassia palustris Linnaeus	Wetland			<1	<1
Pedicularis lanceolata Michaux	Wetland			<1	<1
Persicaria pensylvanica (Linnaeus) M. Gómez de la Maza	Facultative				1 (3)
Petasites frigidus var. sagittatus (Pursh) Cherniawsky	Facultative				<1
Phragmites australis (Cavanilles) Trinius ex Steudel	Facultative			<1	<1
Potentilla argentea Linnaeus	Other	<1			
Potentilla norvegica Linnaeus	Other			<1	<1
Rhynchospora alba (Linnaeus) Vahl	Peatland		<1		<1
Rorippa palustris (Linnaeus) Besser	Wetland	<1	<1		
Rubus arcticus Linnaeus	Peatland			<1	1 (2)
Sarracenia purpurea Linnaeus	Peatland				1 (2)
Scirpus cyperinus (Linnaeus) Kunth	Wetland		1 (3)		
Thypa sp.	Wetland	<1	<1	<1	

Trichophorum alpinum (Linnaeus) Persoon	Wetland		<1	<1	
Trichophorum cespitosum (Linnaeus) Hartman	Peatland			<1	<1
Triglochin maritima Linnaeus	Peatland				<1
Utricularia intermedia Hayne	Peatland			<1	
Utricularia vulgaris Linnaeus	Wetland			<1	<1
Bryophytes		<1	<1	18 (18)	57 (19)
Aulacomnium palustre (Hedw.) Schwägr	Peatland		<1	<1	2 (4)
Brachythecium acutum (Mitt.) Sull	Peatland				4 (12)
Bryum pseudotriquetrum (Hedw.) G. Gaertn., B. Mey. & Scherb	Peatland	<1	<1	1 (2)	
Calliergonella cuspidata (Hedw.) Loeske	Peatland			<1	
Calliergon giganteum (Schimp.) Kindb	Wetland				1 (4)
Straminergon stramineum (Dicks. ex Brid.) Hedenäs	Peatland				<1
Campylium stellatum (Hedw.) C.E.O. Jensen	Peatland		<1	12 (12)	18 (13)
Climacium dendroides (Hedw.) F. Weber & D. Mohr	Other				<1
Dicranum undulatum Schrad. ex Brid	Peatland				1 (3)
Fissidens adianthoides Hedw	Other			<1	
Fissidens osmundoides Hedw	Other				<1
Helodium blandowii (F. Weber & D. Mohr) Warnst. var. blandowii	Wetland				<1
Hypnum lindbergii Mitt	Facultative			<1	<1
Marchantia polymorpha Linnaeus subsp. Polymorpha	Other			<1	
Plagiomnium ellipticum (Brid.) T.J. Kop	Peatland			<1	
Pleurozium schreberi (Willd. ex Brid.) Mitt	Other				1 (5)
Polytrichastrum longisetum (Sw. ex Brid.) G.L. Sm	Other	<1			
Polytrichum commune Hedw. var. commune	Facultative				<1
Polytrichum strictum Menzies ex Brid	Peatland		<1	<1	<1
Pseudocalliergon trifarium (F. Weber & D. Mohr) Loeske	Peatland			<1	
Scorpidium cossonii (Schimp.) Hedenäs	Wetland		<1	4 (6)	22 (15)
Scorpidium scorpioides (Hedw.) Limpr	Peatland			<1	1 (4)
Sphagnum angustifolium (Warnst.) C.E.O. Jensen	Peatland				1 (5)
Sphagnum fallax H. Klinggr	Peatland			<1	
Sphagnum fuscum (Schimp.) H. Klinggr	Peatland				3 (13)
Sphagnum papillosum Lindb	Peatland				<1
Sphagnum russowii Warnst	Peatland				1 (6)
Sphagnum warnstorfii Russow	Peatland				1 (4)
Tomenthypnum nitens (Hedwig) Loeske	Peatland			<1	<1

[a] *UNR*: unrewetted; *R1*: first growing season after rewetting; *R10*: ten growing seasons after rewetting; *REF*: reference ecosystem.

[b] *Peatland*: species preferentially found in peatlands (Sphagnum peatlands or fens), *Wetlands*: species preferentially found in wetlands, *Facultative*: species that can occur in wetlands, but not preferentially, *Other*: species preferentially found in other types of ecosystem (e.g. upland habitats).

Note: Vascular plant nomenclature according to Brouillet et al. (2010+); bryophyte nomenclature according to Faubert (2012; 2014). Vascular plant species classified following classifications by Payette and Rochefort (2001), Jeglum (1991), USDA (2018), Gignac et al. (2004). Moss species classified following classifications by Payette and Rochefort (2001), Vitt (2014), Faubert (2012; 2014) and FNA (1993+). See section *Methods* for details on categorization of species.