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COMPRENDRE LA MÉCANIQUE DU PROCESSUS DE RECOLONISATION VÉGÉTALE DES TOURBIÈRES EXPLOITÉES

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RÉSUMÉ

La recolonisation naturelle des tourbières aspirées et abandonnées est pauvre. Dans un effort pour mieux comprendre les raisons sous-jacentes à cette situation, le processus de recolonisation fut considéré comme une série de filtres environnementaux qui laissent passer seulement les espèces avec des caractères autécologiques appropriés. Les espèces étudiées étaient les mousses et plantes vasculaires les plus communes dans les tourbières naturelles ou les tourbières aspirées et abandonnées au Québec. La première étude examina le potentiel relatif des espèces étudiées à immigrer aux surfaces exploitées. Les espèces diffèrent beaucoup selon leur fréquence en bordure, leur fécondité maximale et leur potentiel de dissémination par le vent, l'eau ou les animaux. Plusieurs espèces de mousses, d'éricacées et d'arbres sont avantagées pour immigrer vers les surfaces exploitées. Une deuxième étude avait pour objet la stabilité des surfaces exploitées. Trois aspects ont été examinés : la susceptibilité à l'érosion éolienne des tourbes de différents degrés de décomposition, la rugosité des surfaces exploitées et leur stabilité sur le terrain. Les tourbes sont très susceptibles à l'érosion lorsqu'elles sont meubles, surtout si elles sont peu décomposées, mais dès qu'une mince croûte se forme à la surface, elles restent stables. Sur le terrain, l'érosion éolienne semble négligeable par rapport au gel et dégel saisonnier pour expliquer l'instabilité d'un substrat tourbeux. La troisième étude examina le potentiel de germination et d'établissement des plantes vasculaires, en déterminant l'émergence des plantules en fonction de la profondeur d'enfouissement des graines et les taux de croissance des plantules. La masse des graines prédit leur susceptibilité à l'enfouissement ainsi que la croissance des racines, mais l'aire spécifique des feuilles prédit leur taux de croissance relatif. L'étude finale intègre ces données pour déterminer si une approche d'écologie fonctionnelle permet de prédire et de mieux comprendre la recolonisation naturelle des tourbières exploitées. Pour toutes les espèces ou les plantes vasculaires seules, leur fréquence en bordure et leur position en bordure demeurent des causes indépendantes de la recolonisation. La capacité de dissémination par le vent est secondaire. Tous ces résultats devraient nous permettre de mieux cibler les efforts de restauration.

ABSTRACT

The recolonization of abandoned milled bogs is poor. In an attempt to understand the underlying reasons, the recolonization process was considered as a series of environmental filters which selectively allows the survival of only those species with suitable autecological traits. Study species were the most common mosses and vascular plants in milled or abandoned milled bogs in Québec. A first study examined the relative immigration potential of study species to milled bogs. Study species differ markedly in terms of their populations in edges of milled bogs, maximum fecundity and dispersal potential by wind, water or animals. Overall, several species of mosses, ericaceous shrubs and trees have high potential to immigrate to milled bogs. A second study focussed on the stability of milled peat surfaces. Three aspects were examined: the wind erosion potential of peats as a function of their degree of decomposition, the surface roughness lengths of milled peatlands, and the stability of milled peat substrates in the field. Milled peats are highly prone to wind erosion when loose, especially the less decomposed peats. However, once a light crust is formed, they are all stable. Insignificant wind erosion was also observed in the field in spite of very low roughness lengths. However, milled surfaces are very unstable, apparently as a result of seasonal freeze-thaw action. A third study examined the germination and establishment potential of vascular plants, first by examining seedling emergence as a function of seed burial depth and second by measuring their seedling growth rates. Burial sensitivity and root performance were functions of seed mass while relative growth rate could be predicted by seedling specific leaf area. The final study brought elements of previous studies together to determine whether a trait-based approach could be used to predict and better understand natural recolonisation of milled peatlands. For all species and vascular plants alone, abundance of species in edges of milled bogs and edge bias relative to milled edges were independent causes of recolonisation. Propagule wing loading for all species and propagule fall time for vascular plants were also important. The restoration of abandoned milled peatlands should benefit from this better understanding of the recolonisation process.

L'AVANT-PROPOS

La thèse est présentée sous forme de quatre articles rédigés en anglais. Le premier article (Chapitre 2) sur l'immigration des plantes dans les tourbières exploitées a été rédigé avec Line Rochefort et Claude Lavoie comme co-auteurs et a été soumis pour publication au *Journal of Applied Ecology*. Le deuxième article (Chapitre 3) sur l'érosion et la stabilité du substrat a également été rédigé avec Claude Lavoie et Line Rochefort et a été accepté pour publication dans le *Canadian Journal of Soil Science*. Le troisième article (Chapitre 4) sur la germination et l'établissement des plantes de tourbières a été rédigé avec Line Rochefort et a été soumis pour publication à *Plant Ecology*. Finalement, le quatrième article (Chapitre 5) sur la prédiction de la recolonisation a été rédigé avec Line Rochefort et Claude Lavoie, mais n'a pas encore été soumis pour publication. Pour tous ces travaux, j'atteste que je suis le principal responsable de la conception des idées, de l'organisation et de l'accomplissement des travaux de terrain et de laboratoire, de l'analyse des données et de la rédaction des manuscrits. Je peux ainsi affirmer que, bien appuyé intellectuellement par ma directrice et co-directeur, cette thèse est bel et bien le fruit de mon propre travail.

Ma directrice de thèse, Mme Line Rochefort, et mon codirecteur, M. Claude Lavoie, m'ont aidé par l'entremise d'échanges d'idées stimulants et de critiques justes à tous les stades de mon doctorat. Ils méritent ainsi le statut de co-auteurs des articles issus de la thèse. Mais, je leur dois beaucoup plus. Je leur dois une reconnaissance profonde pour avoir cru en moi dès le départ et tout au long de mon doctorat. Je les remercie sincèrement pour le soutien logistique, technique, financier et parfois moral que j'ai reçu. J'espère que cette thèse n'est que le début d'une longue collaboration fructueuse.

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

LES RÈGLES D'ASSEMBLAGE COMME APPROCHE EN RESTAURATION

Le développement de modèles prédictifs est un des objectifs ultimes de toute étude en écologie (Peters 1991), et particulièrement en écologie des communautés (Keddy 1992). À cet égard, on peut se poser la question suivante: quel niveau minimum de connaissances sur les espèces de plantes et sur l'environnement doit-on atteindre pour prédire le devenir d'une communauté végétale?

Nos efforts pour comprendre et prédire la dynamique des communautés végétales datent au moins du début du XX^{e} siècle (McIntosh 1985). Parmi les premiers et les plus influents, Clements (1916) considérait une communauté végétale comme une 'super-organisme' dynamique, avec une ontogenèse spécifique de stades de succession identifiables. Ces idées ont été populaires et ont nourri une grande tradition d'écologie végétale descriptive ayant pour but d'identifier les communautés végétales et de prédire leurs stades de succession. Le désir et la nécessité de simplifier la complexité végétale fait en sorte que cette tradition continue de nos jours (exemples dans les tourbières : Godwin & Conway 1939; Sjörs 1948; Du Rietz 1949; Dansereau & Segadas-Vianna 1952; Vitt & Slack 1975; Wells 1981; Couillard & Grondin 1986; Damman & French 1987). À l'autre extrême, Gleason (1926) soutenait que l'étude des communautés végétales, de leur dynamique et leur prédiction devaient se faire à partir de travaux sur les individus et non sur les associations d'espèces. Ces idées ont tardé à être adoptées mais elles ont donné naissance à l'analyse des communautés le long de gradients végétaux (ex. Whittaker 1956; Curtis 1959), qui a par la suite dominé l'étude des communautés végétales et de leur dynamique (McIntosh 1975). Par contre, cette approche doit faire face au problème d'un grand nombre d'espèces et de la variabilité de leurs populations dans l'espace et le temps.

Plus récemment, les recherches sur l'écologie fonctionnelle des espèces essayent de comprendre et de prédire le développement de communautés végétales en étudiant non pas les espèces elles-mêmes mais plutôt les caractéristiques autécologiques des espèces (Smith, Shugart & Woodward 1997). Cette approche a été utilisée pour développer des modèles prédictifs à plusieurs échelles. Par exemple, des modèles d'écologie fonctionnelle ont été utilisée pour prédire la végétation par rapport au climat régional et ses réponses aux changements climatiques (Box 1981; Woodward 1987; Reich, Walters, & Ellsworth 1997; Smith Shugart & Woodward 1997; Díaz, Cabido & Fernando 1998), pour suivre le développement des invasions biologiques et leurs impacts sur les communautés envahies (Burke & Grime 1996; Rejmánek 1996; Rejmánek & Richardson 1996; Reichard & Hamilton 1997), pour étudier la succession végétale et l'effet des perturbations (Noble & Slatyer 1980; van der Valk 1981; Stockey & Hunt 1994; Tsuyuzaki & del Moral 1995; Leishman 1999; McIntyre *et al.* 1999; Weiher *et al.* 1999) et pour élaborer des règles d'assemblage des communautés (Keddy 1992; Weiher & Keddy 1995; Booth & Larson 2000a, b).

L'utilisation des règles d'assemblage (*sensu* Keddy 1992) semble être fort utile pour structurer les recherches sur la prédiction des communautés végétales. Selon cette approche, un habitat est constitué d'une série de filtres environnementaux. Seules les espèces qui possèdent les caractéristiques autécologiques adéquates peuvent traverser tous les filtres et donc coloniser l'habitat. Une connaissance approfondie des filtres et des caractéristiques autécologiques des espèces peut ainsi permettre à l'écologiste de développer un modèle prédictif efficace. Par exemple, advenant la modification d'un des filtres de l'habitat (une hausse du niveau d'eau, la disparition d'un herbivore, etc.), on peut prédire l'impact de cette modification sur l'ensemble des espèces en présence. L'approche des règles d'assemblage est toutefois loin de faire l'unanimité chez les chercheurs, même au niveau de la définition de l'approche (Weiher & Keddy 1999a). Pour certains, elle devrait être basée uniquement sur les interactions biotiques entre espèces (Wilson 1999); pour d'autres, tout facteur abiotique ou biotique qui influence l'organisation d'une communauté végétale devrait être considéré (Weiher & Keddy 1999b).

L'usage des règles d'assemblage pour prédire l'évolution des communautés végétales d'écosystèmes fortement perturbés constitue un défi particulier. En effet, les filtres environnementaux prédominants y sont souvent extrêmes et la gamme d'espèces colonisatrices est dans plusieurs cas peu étendue. Les recherches sur la restauration de tels écosystèmes ont non seulement pour but de déterminer quelles espèces peuvent franchir les filtres mais aussi comment modifier ces derniers pour faciliter la recolonisation végétale des écosystèmes en question. À cet égard, l'approche des règles d'assemblage offre un potentiel intéressant dans le cadre d'études sur la restauration des écosystèmes perturbés (Keddy 1999). Grâce à 1) l'identification des filtres critiques ralentissant la recolonisation végétale des sites perturbés ou favorisant des espèces indésirables, et 2) la connaissance des caractères autécologiques clés des espèces colonisatrices aux différents stades de leur vie, il est théoriquement possible, par les règles d'assemblage, de prédire la recolonisation végétale, mais aussi de mieux comprendre la dynamique de la communauté en régénération. Les filtres contraignants et les stades de vie limitatifs des espèces désirées pourraient ainsi être diagnostiqués, ce qui permettrait de mieux cibler les interventions de restauration nécessaires.

LE CAS DES TOURBIÈRES EXPLOITÉES

Les tourbières à dominance de sphaignes, exploitées par la méthode moderne d'aspiration, sont des écosystèmes fortement perturbés. Les surfaces en exploitation peuvent atteindre plusieurs kilomètres carrés (Rochefort 2001). Il n'y a aucun réservoir de graines ou de spores dans le sol (Salonen 1987). Lorsque les sites sont abandonnés, les plantes immigrent dans le milieu par dissémination à partir des zones végétées situées en périphérie (Curran & MacNaeidhe 1986; Salonen 1990; Salonen & Setälä 1992; Poschlod 1995) ou par introduction délibérée (Rochefort 2000). Au Canada, les conditions chimiques du substrat sont souvent semblables aux tourbières ombrotrophes naturelles (Wind-Mulder, Rochefort & Vitt 1996), donc très acides (pH <5) et pauvres en éléments nutritifs, quoique légèrement enrichies en azote. Par contre, les particularités physiques des sites sont très différentes de celles qui caractérisent les tourbières naturelles. L'acrotelme, la couche de sphaignes et de tourbe peu décomposée à la surface des tourbières (Ingram 1978), est absent. Le substrat peut alors présenter des conditions beaucoup plus sèches et variables que dans une tourbière non exploitée (Price 1996, 1997; Price, Rochefort & Quinty 1998). Le cycle de gel-dégel déstabilise beaucoup le substrat près de la surface du sol (E. Groeneveld, U. Laval, comm. pers.). En somme, les espèces de tourbière qui essayent de recoloniser les sites exploités sont confrontées à des filtres environnementaux aux mailles particulièrement fines.

La recolonisation naturelle des tourbières exploitées par la végétation est très lente, même après plusieurs années d'abandon (Salonen 1987; Salonen, Penttinen & Särkkä 1992; Desrochers, Rochefort & Savard 1998; Bérubé & Lavoie 2000). Sans intervention humaine, les sites aspirés retournent rarement à un état voisin des tourbières ombrotrophes naturelles à moyen terme (< 30 ans) (Lavoie & Rochefort 1996). Les espèces qui s'installent le plus souvent sur les tourbières exploitées à l'aspirateur diffèrent des espèces qui dominent les tourbières naturelles (Tableau 1.1). Les bryophytes sont rares et ne sont pas dominées par les sphaignes. Un certain nombre de plantes vasculaires colonisent les sites, mais certaines espèces typiques des tourbières ne sont pas présentes (comme *Sarracenia purpurea* et *Drosera rotundifolia*), alors que d'autres (ex. *Betula* spp.) envahissent les sites exploités après leur abandon et changent grandement le caractère de l'écosystème (Lavoie & Rochefort 1996; Lavoie & Saint-Louis 1999).

OBJECTIF PRINCIPAL DE LA THÈSE

Le but de la restauration des tourbières exploitées au Canada est le retour à un écosystème de tourbière fonctionnel et accumulateur de tourbe (Quinty & Rochefort 1997; Rochefort 2000). Il s'agit en premier lieu de favoriser le retour des espèces qui dominent dans les tourbières naturelles (Tableau 1.1), et particulièrement les sphaignes qui sont responsables de la production de la tourbe (van Breemen 1995), qui contrôlent les conditions hydrologiques des sites (Ingram 1978) et qui produisent l'acidité extrême des tourbières ombrotrophes (Clymo 1984). En second lieu, il s'agit de reconstituer les deux couches de tourbe qui régissent le régime hydrologique des tourbières non perturbées, soit l'acrotelme et le catotelme (Rochefort 2000).

Malgré les recherches récentes en matière de restauration des tourbières (Rochefort 2000), plusieurs lacunes existent concernant les connaissances sur la dissémination et la regénération des espèces de plantes qui poussent dans ces écosystèmes. Pourtant, une meilleure connaissance des filtres environnementaux qui existent dans les tourbières abandonnées, associée à une connaissance de la capacité intrinsèque de recolonisation des espèces typiques des tourbières, devraient permettre de mieux comprendre la dynamique de

Tableau 1.1. Les espèces de plantes les plus communes dans les tourbières naturelles et les tourbières exploitées à l'aspirateur au Québec (N = 31 tourbières naturelles, L. Rochefort, données non publiées; N = 11 surfaces exploitées à l'aspirateur et abandonnées, L. Rochefort et F. Quinty, données non publiées). Les fréquences d'apparition sont présentées par leur moyenne ± écart-type. La nomenclature suit Anderson, Crum & Buck (1990) pour les mousses, sauf pour les sphaignes qui suit Anderson (1990). Pour les plantes vasculaires, la nomenclature suit Scoggan (1978), sauf pour *Vaccinium oxycoccus* L.

		Tourbières naturelles		Tourbières exploitées	
Espèce	Famille	Fréquence d'apparition (%)	n	Fréquence d'apparition (%)	n
Mousses					
Dicranella cerviculata	Dicranaceae	0	0	< 1	3
Pleurozium schreberi	Hylocomiaceae	4 ± 12	5	2 ± 3	3
Pohlia nutans	Bryaceae	0	0	5 ± 17	3
Polytrichum strictum	Polytrichaceae	15 ± 21	18	3 ± 5	5
Sphagnum angustifolium	Sphagnaceae	33 ± 32	21	0	0
Sphagnum capillifolium	Sphagnaceae	55 ± 32	27	1 ± 2	2
Sphagnum fallax	Sphagnaceae	22 ± 28	17	0	0
Sphagnum fuscum	Sphagnaceae	49 ± 33	26	< 1	1
Sphagnum magellanicum	Sphagnaceae	46 ± 28	29	0	0
Herbacées					
Carex limosa	Cyperaceae	24 ± 26	20	0	0
Carex oligosperma	Cyperaceae	35 ± 31	19	0	0
Carex stricta	Cyperaceae	0	0	2 ± 8	1
Drosera rotundifolia	Droseraceae	35 ± 35	24	0	0
Eriophorum angustifolium	Cyperaceae	2 ± 5	4	2 ± 5	3
Eriophorum vaginatum	Cyperaceae	19 ± 20	21	11 ± 21	8
Rubus chamaemorus	Rosaceae	17 ± 32	9	4 ± 6	7
Sarracenia purpurea	Sarraceniaceae	17 ± 21	16	0	0
Scirpus cespitosus	Cyperaceae	17 ± 30	10	0	0
Arbustes					
Andromeda glaucophylla	Ericaceae	32 ± 22	26	0	0
Aronia melanocarpa	Rosaceae	5 ± 12	6	2 ± 2	5
Chamaedaphne calyculata	Ericaceae	71 ± 31	31	9 ± 9	10
Kalmia angustifolia	Ericaceae	39 ± 28	26	17 ± 26	8
Kalmia polifolia	Ericaceae	49 ± 33	28	< 1	4
Ledum groenlandicum	Ericaceae	36 ± 31	23	14 ± 17	10
Rhododendron canadense	Ericaceae	0	0	1 ± 2	5
Vaccinium angustifolium	Ericaceae	7 ± 12	11	14 ± 13	9
Vaccinium oxycoccus	Ericaceae	74 ± 26	31	< 1	3
Arbres					
Betula papyrifera	Betulaceae	0	0	5 ± 10	6
Betula populifolia	Betulaceae	0	0	3 ± 6	4
Picea mariana	Pinaceae	21 ± 22	20	< 1	4

recolonisation des tourbières exploitées après abandon et d'expliquer le succès ou l'insuccès de certaines espèces végétales. Ces connaissances permettraient de prescrire des interventions plus ciblées lors des activités de restauration.

L'objectif principal de cette thèse est de déterminer les règles d'assemblage qui permettent de prédire la recolonisation naturelle des tourbières exploitées par la méthode d'aspiration tôt après leur abandon. L'étude se concentre sur les tourbières exploitées dans lesquelles on trouve encore un dépôt résiduel de tourbe de sphaignes de 40 cm ou plus. En utilisant les règles d'assemblage, donc en identifiant les caractéristiques autécologiques clés des espèces colonisatrices et les filtres limitant le succès de recolonisation dans les tourbières, on espère également être en mesure de proposer des interventions qui favoriseront la restauration des sites. Autrement dit, si nous savons où, quand et pourquoi la recolonisation naturelle est inefficace, nous serions mieux en mesure de modifier l'environnement et favoriser la revégétation.

UNE APPROCHE DÉDUCTIVE

L'étude des règles d'assemblage nécessite une analyse explicite des interactions clés qui existent entre l'environnement et les espèces disponibles pour la recolonisation (Keddy 1992). Une approche déductive (*sensu* Noble & Gitay 1996) a donc été retenue pour choisir *a priori* les espèces potentiellement disponibles pour la recolonisation, les filtres environnementaux critiques et les caractéristiques autécologiques dont l'étude est pertinente.

En raison de l'absence d'un réservoir de graines ou de spores dans le sol (dorénavant appelées diaspores), la recolonisation des tourbières exploitées se fait grâce à des sources de diaspores externes, localisées en bordure des zones exploitées. Toute diaspore doit donc se disséminer, germer, s'établir, croître jusqu'au stade adulte et se reproduire à son tour (Figure 1.1). Ces stades doivent être franchis l'un après l'autre pour qu'une espèce ait une chance raisonnable de constituer une population sur les surfaces exploitées. Les stades de dissémination, de germination et d'établissement sont les étapes les plus critiques pour la

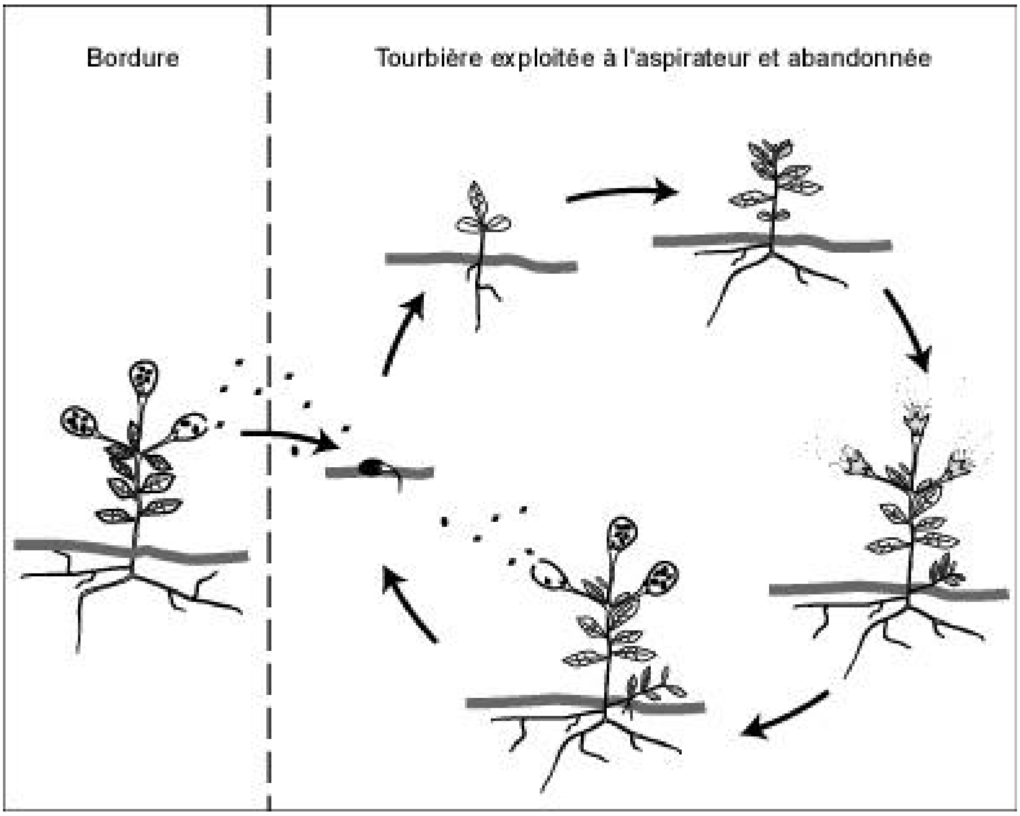

Figure 1.1: La progression de stades pour une plante qui recolonise une surface de tourbière exploitée et abandonnée.

régénération d'une communauté végétale (Grubb 1977) et sont l'objet d'un intérêt particulier dans cette thèse.

Espèces ciblées

Les espèces ciblées dans cette étude sont réparties dans deux groupes. Il s'agit, en premier lieu, des mousses et des plantes vasculaires les plus communes dans les tourbières ombrotrophes naturelles du Québec. Le second groupe d'espèces est constitué des plantes qui colonisent les tourbières exploitées à l'aspirateur au Québec (Tableau 1.1). On a inclu dans ce groupe la mousse *Dicranella cerviculata* car elle est commune dans les sites exploités à l'aspirateur, quoique peu mentionnée dans les inventaires. En tout, la liste comprend 9 espèces de mousses et 21 espèces de plantes vasculaires. Les espèces de tourbières naturelles peuvent être considérées comme des espèces désirables pour la restauration. Les espèces des tourbières exploitées et abandonnées sont les espèces qui ont franchi avec un succès plus ou moins grand les filtres environnementaux mais qui ne sont pas nécessairement typiques des tourbières ombrotrophes.

Sources de diaspores

Des plants-mères doivent être présents à proximité des surfaces exploitées et être suffisamment féconds pour fournir des diaspores pour la recolonisation. Certaines diaspores légères comme les spores pourraient être originaire d'habitats plus éloignés, mais les sources proches devraient fournir la majorité des diaspores. Les sites tourbeux non exploités à proximité immédiate des sites en restauration constituent donc les sources premières de diaspores. De tels sites ont des caractéristiques édaphiques qui leurs sont propres, ne sont pas tous au même stade successionnel et sont sous l'influence de différents régimes hydrologiques. Dans plusieurs cas, un gradient de végétation existe perpendiculairement à la bordure; les sources de diaspores ne sont donc pas réparties de manière uniforme.

Dissémination

Les diaspores doivent se disséminer sur les surfaces exploitées pour les coloniser. L'efficacité avec laquelle une espèce dissémine ses diaspores détermine son potentiel de recrutement et donc est d'une importance cruciale pour prédire la composition future d'une communauté végétale (Houle 1995; Schupp & Fuentes 1995). Les tourbières exploitées pouvant atteindre une superficie de 5 km^2, la distance séparant les sources de diaspores des sites de recolonisation peut agir comme un important filtre limitatif. Pour franchir ce filtre, les diaspores doivent posséder des adaptations facilitant leur dissémination. D'autre part, la dissémination dépend non seulement de ces adaptations, mais aussi de la présence d'un vecteur de transport approprié.

Le vecteur animal : la dissémination par vecteur animal nécessite des diaspores qui attirent l'animal ou s'y accrochent. Le potentiel de dissémination varie selon l'espèce animale, son comportement et le nombre d'individus en présence. La répartition spatiale des habitats propices aux animaux influence aussi fortement les déplacements des individus (Stiles 1992). Tous ces facteurs font en sorte qu'il est difficile de caractériser un tel vecteur de dissémination. Ceci dit, la diversité et l'abondance des petits mammifères et des oiseaux sont plus élevées en bordure des tourbières exploitées que dans les tourbières naturelles (Delage, Fortin & Desrochers 2000; Mazerolle, Drolet & Desrochers 2001), ce qui suggère que plusieurs animaux contribuent probablement avec une efficacité plus ou moins grande à la dissémination des diaspores dans les tourbières en régénération.

Le vecteur eau : la dissémination par l'eau est possible pour les diaspores qui flottent. Des nappes d'eau libre sont parfois présentes à la surface des tourbières exploitées et abandonnées, du moins dans les canaux de drainage. C'est notamment le cas lorsque les canaux sont bloqués ou si une fonte précipitée de la neige ou une chute de pluie abondante a lieu.

Le vecteur vent : le vent est probablement le plus important vecteur de dissémination primaire et secondaire dans les tourbières exploitées. Les surfaces exploitées sont vastes et planes, sans obstacle pour freiner le vent. Pour évaluer le potentiel de dissémination par le vent des espèces, ont doit tenir compte de la hauteur à laquelle les diaspores sont relâchées, de la vitesse de chute de ces dernières et de leur portance (Augspurger & Franson 1987; Greene & Johnson 1989; Johnson & Fryer 1992). Des modèles complexes ont été développés pour prédire la dissémination primaire par le vent à partir d'une source unique (Greene & Johnson 1989; Okubo & Levin 1989), d'une forêt vers une clairière (Greene & Johnson 1996) ou d'un peuplement d'arbres vers les zones environnantes (Nathan *et al.* 2001). Par contre, l'hétérogénéité de la structure végétale des bordures rend l'environnement éolien variable et difficilement descriptible avec précision, ce qui empêche l'application de tels modèles. D'autre part, la dissémination secondaire par le vent est souvent plus importante que la dissémination primaire dans les milieux ouverts à surface lisse, ce qui est le cas des tourbières exploitées (Matlack 1989; Johnson & Fryer 1992; Greene & Johnson 1997; Fort & Richards 1998).

Germination

Une fois parvenue à sa destination finale, une diaspore doit être en mesure de germer. Pour germer durant les périodes favorables, les graines de plantes vasculaires doivent souvent mettre fin à un état de dormance (Baskin & Baskin 1998). Par contre, les spores de mousses peuvent germer dès que les conditions environnementales sont appropriées (Clymo & Duckett 1986; Hartmann & Weber 1990; Cronberg 1993). Le bris de dormance et la germination varient entre les espèces et dépendent de plusieurs facteurs, tels que la lumière, les températures, les conditions hydriques, l'environnement gazeux (O_2, CO_2) et l'environnement chimique (Hartmann & Weber 1990; Baskin & Baskin 1998). Comme la chimie du substrat tourbeux des tourbières exploitées ne diffère guère de celle des tourbières naturelles (Wind-Mulder, Rochefort & Vitt 1996), elle ne devrait pas être un filtre critique pour la germination des diaspores des plantes de tourbière. L'environnement physique constitue probablement le principal filtre à la germination. Plusieurs facteurs physiques, surtout la température et les conditions hydriques, sont plus variables et extrêmes en zones tourbeuses perturbées que dans les tourbières naturelles (Price 1996, 1997; LaRose, Price & Rochefort 1997). Il se peut que des conditions physiques propices à la germination des diaspores soient réunies pour de courtes périodes, mais la durée pendant laquelle ces conditions persistent n'est peut-être pas assez longue pour plusieurs espèces.

L'instabilité de la surface dans les tourbières exploitées est un filtre potentiellement fort important au cours de la période de germination. Dans les tourbières exploitées à l'état d'abandon, le couvert végétal minime ne peut empêcher l'érosion du substrat et le déplacement des particules de tourbe par le vent et la pluie. Il ne peut non plus modérer les effets du soulèvement gélival près de la surface du sol. Les diaspores sont en outre susceptibles d'être enfouies par les particules de tourbe érodées, ce qui minimise leur probabilité de germination. En effet, la transmission de la lumière, essentielle à la germination de plusieurs diaspores, est presque nulle au-delà d'une couche de sol de texture fine de plus de 2 mm d'épaisseur (Kasperbauer & Hunt 1988; Mandoli *et al.* 1990; Benvenuti 1995), avec un grand déclin dans le ratio rouge à rouge lointain (Bliss & Smith 1985; Mandoli *et al.* 1990). Les plantes formant des graines de plus petite taille seront particulièrement affectées par ce phénomène (Jurado & Westoby 1992; Vázquez-Yanes & Orozco-Segovia 1992; Reader 1993; Jurik, Wang & van der Valk 1994; Milberg, Andersson & Thompson 2000).

Établissement des plantules

Les diaspores doivent non seulement germer, mais les plantules qui en sont issus doivent ensuite s'établir sur la surface exploitée. Les plantules sont particulièrement sensibles aux stress environnementaux durant leurs premiers jours, semaines ou mois (Harper 1977; Larcher 1995). Les conditions physiques dans les tourbières exploitées et abandonnées semblent être particulièrement défavorables à ce stade de vie (Salonen 1992, 1994; Salonen & Setälä 1992; Grosvernier, Matthey & Buttler 1995; Rochefort 2000; Tuittila *et al.* 2000). En premier lieu, l'albédo de la tourbe nue étant très faible, la surface absorbe la majorité de l'énergie solaire (Oke 1987, p. 79). Les conditions microclimatiques sont alors extrêmes à la surface de la tourbe durant l'été quand la tourbe s'assèche (Price 1996, 1997; Price, Rochefort & Quinty 1998, Marcoux 2000), ce qui provoque potentiellement des stress hydriques et thermiques élevés chez les plantules. Celles ayant accès à suffisamment d'eau peuvent éviter ces stress grâce à l'évapotranspiration. Les plantules de mousses doivent tolérer ces stress extrêmes à la surface ou périr. Pour leur part, les plantules de plantes vasculaires avec système racinaire bien développé peuvent puiser l'eau dans le sol pour éviter la dessiccation. En effet, les conditions d'humidité s'améliorent de façon substantielle à seulement quelques centimètres sous une surface tourbeuse exploitée (Price 1997; Price, Rochefort & Quinty 1998). Étant donné que la masse des graines et le taux de croissance définissent la taille des plantules, incluant les racines (Causton & Venus 1981; Jurado & Westoby 1992), ces deux caractères autécologiques et surtout leur interaction seront déterminants pour évaluer le taux de survie des plantules d'espèces vasculaires à travers des périodes de sécheresse.

Le microclimat extrême des surfaces exploitées favorise aussi le gel et le dégel de la surface du sol au cours du printemps et de l'automne (E. Groeneveld, U. Laval., comm. pers.). En milieux agricoles, les sols organiques sont particulièrement sensibles à la formation de cristaux de glace à la surface qui causent beaucoup de mortalité chez les plantules de plantes vasculaires (Brink *et al.* 1967). Un système racinaire bien développé permettra à une plantule de survivre à l'action du soulèvement gélival en surface (Roach & Marchand 1984).

L'instabilité de la surface causée par l'érosion par le vent et la pluie semble aussi être problématique pour les jeunes plantules qui risquent un déracinement. Le vent est un agent érosif potentiellement important à cause de la grande superficie des sites exploités, de l'absence d'obstacle ou de végétation, des surfaces relativement lisses et de la faible densité de la tourbe sèche. L'érosion éolienne peut être extrême sur les sols organiques en milieux agricoles (Lucas 1982). Ceci dit, peu d'études ont évalué son ampleur et les conditions propices à un tel agent érosif dans les tourbières exploitées (McNeil *et al.* 2000).

Stades juvénile et adulte

Si une plante colonisatrice peut se rendre à maturité, elle peut alors se propager de façon végétative ou se reproduire sexuellement pour créer une colonie dans le site perturbé. Des caractéristiques autécologiques agissant au cours de la croissance et de la reproduction, telles qu'une courte période juvénile, une capacité de propagation végétative, un système de reproduction simple et une haute fécondité, ont été associées au succès des espèces envahissantes dans différents milieux (Thompson *et al.* 1995; Rejmánek 1996; Rejmánek & Richardson 1996). Il est alors possible que les meilleurs colonisateurs des tourbières exploitées aient des caractéristiques similaires.

HYPOTHÈSES PRINCIPALES

Trois hypothèses principales sont testées dans cette thèse:

H1) Un modèle simple construit à partir d'une connaissance des filtres écologiques critiques existant dans les tourbières exploitées à l'aspirateur et des caractéristiques autécologiques clés des principales espèces de tourbière peut réussir à prédire la recolonisation des tourbières exploitées dans le Québec méridional.

H2) Le succès de recolonisation des tourbières exploitées à l'aspirateur est déterminé principalement à un seul stade durant la recolonisation des tourbières, soit au stade des sources de diaspores, durant la dissémination, la germination, l'établissement ou les stades juvéniles et adultes des plantes.

H3) Parmi tous les filtres environnementaux, la stabilité du substrat de tourbe en surface est le filtre critique qui empêche la recolonisation des tourbières exploitées par les plantes de tourbière.

ORGANISATION DE LA THÈSE

La thèse est composée de chapitres qui correspondent à une série d'articles indépendants où sont testées les différentes hypothèses énoncées ci-dessus. Les chapitres se succèdent dans l'ordre logique de la colonisation des espèces dans les tourbières exploitées (Figure 1.1).

Le Chapitre 2 aborde le début du processus de recolonisation, soit la caractérisation des sources de diaspores au pourtour des tourbières exploitées ainsi que la dissémination des espèces ciblées.

Il analyse la capacité relative des espèces de plantes vasculaires et de mousses à atteindre les surfaces tourbeuses exploitées. Au sens plus large, il propose une approche générale qui devrait être utile pour déterminer les espèces disponibles pour la recolonisation après une perturbation majeure quelconque.

Le Chapitre 3 examine de près la question de la stabilité de la surface des tourbières exploitées, surtout l'ampleur de l'érosion éolienne dans ces surfaces et le potentiel d'érosion par rapport aux différents substrats tourbeux. Il permet de vérifier l'importance de ce filtre environnemental et prépare le terrain pour l'étude des étapes successives de germination et d'établissement des espèces ciblées dans les tourbières exploitées.

Le Chapitre 4 évalue le potentiel de germination et d'établissement des plantules d'espèces vasculaires ciblées à l'aide d'expériences en milieux contrôlés traitant du potentiel de germination, des effets de l'enfouissement sous la tourbe et de la mesure des taux relatifs de croissance des plantules sous conditions optimales. Il essaie aussi de déterminer si des mesures simples telles que la masse des graines peuvent prédire de façon efficace le comportement des plantules à ces stades.

Le Chapitre 5 regroupe les données, surtout celles des Chapitres 2 et 4, et cherche à savoir si la recolonisation peut être prédite par les caractéristiques autécologiques mesurées. Il tente aussi de formuler les règles d'assemblage qui existent dans les tourbières exploitées et abandonnées.

Enfin, ces articles sont suivis par le Chapitre 6 où des conclusions générales sont énoncées. Dans ce chapitre, les répercussions de la recherche sur la restauration des tourbières sont abordées.

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CHAPITRE 2

DETERMINING THE IMMIGRATION POTENTIAL OF PLANTS COLONIZING DISTURBED ENVIRONMENTS : THE CASE OF MILLED PEATLANDS, QUÉBEC[1]

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[1] Campbell,. D.R., Rochefort, L. & Lavoie, C. (article soumis) Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands, Québec.

RÉSUMÉ

Une méthode a été développée pour évaluer le potentiel relatif des plantes à immigrer vers des sites tourbeux en régénération après perturbation. Le but était de déterminer quelles sont les espèces pour lesquelles le filtre de l'immigration ne représente pas un problème. La méthode est basée sur l'identification des espèces potentielles pour la recolonisation, des inventaires des populations localisées dans les bordures des sites exploités et la caractérisation de leur fécondité maximale et de leur capacité de dissémination par le vent, l'eau ou les animaux. La méthode a été appliquée au cas des tourbières exploitées à l'aspirateur et abandonnées au Québec. Trente-deux espèces de mousses et de plantes vasculaires les plus communes, soit dans les tourbières naturelles ou dans les tourbières aspirées et abandonnées, ont été sélectionnées comme espèces recolonisatrices potentielles. Selon cette méthode, les mousses, les arbustes et les arbres possèdent en général un fort potentiel pour immigrer sur les tourbières aspirées. Les plantes herbacées ont un potentiel d'immigration relativement faible, en partie en raison de leur rareté dans les bordures. Cette méthode est flexible et pourrait être appliquée à d'autres écosystèmes fortement perturbés. Elle permet de porter un jugement sur les espèces qui auront de la difficulté à franchir le filtre de l'immigration.

ABSTRACT

A method was developed to evaluate the comparative ability of plants to immigrate to sites after severe disturbance. The goal was to establish baseline knowledge of the species pool in severely disturbed sites prior to restoration. The method was based on the identification of potential colonists, inventories of populations in surrounding vegetation and autecological information on their maximum fecundity and dispersal by wind, water or animals. An index was developed to determine relative immigration potential. The method was applied to milled peatlands in southeastern Québec, Canada, after the cessation of peat extraction activities. Thirty-two species, ranging from mosses to trees, were selected as potential colonists using vegetation inventories of natural and abandoned milled peatlands in southern Québec. Populations of study species differ markedly in edges of milled peatlands in terms of their abundance, presence and fertile plants. An edge effect is apparent where the populations of many species vary as a function of distance from milled surfaces. It is caused, in part, by drainage. Mosses have relatively high potential to immigrate to milled bogs because of their high fecundity and the wind dispersal ability of their spores. The scarcity of mosses in abandoned milled bogs, especially *Sphagnum* spp., does not appear to be a result of the lack of immigrant propagules. Herbs have relatively low immigration potential, due to their rarity in edges, but herbs such as *Eriophorum vaginatum* succeed to recolonize milled bogs in spite of this low potential. Shrub species generally have high immigration potential because of their abundance in edges and high dispersal ability of propagules by wind, water or animals. Trees have high immigration potential due to their importance in edges and wind dispersal abilities. The determination of immigration potential provides information on probable species pools after severe disturbance. Its flexibility and applicability to varied life forms should make it useful for diagnosing recolonization bottlenecks in a wide variety of disturbance situations prior to restoration.

INTRODUCTION

The main goal of most projects in ecosystem restoration is to shorten the successional pathways towards plant communities which are functionally similar, if not structurally similar, to the pre-disturbance state (Lockwood & Pimm 1999). One approach taken to achieve this goal is similar to that proposed for determining assembly rules of plant communities (Keddy 1992, 1999). Managers must first define the species pool available for recolonization, secondly determine the main abiotic and biotic filters operating during the recolonization process, thirdly determine how species respond to these filters, and finally manipulate these filters in an efficient manner until the community is restored. The initial information required is the composition of the post-disturbance species pool available for recolonization. This species pool consists of adult plants and propagules which persist through the disturbance and propagules which immigrate from surrounding sites (Noble & Slatyer 1980). Following a severe disturbance, the species pool is entirely dependent on the immigration of propagules, and recolonization, in the absence of introductions, is propagule-limited and proceeds by primary succession (e.g. industrial waste sites: Ash, Gemmel & Bradshaw 1994; volcanic eruptions: del Moral & Wood 1993). The dispersal capacity of species consequently acts as a major control on natural recolonization.

Milled peatlands are examples of severely-disturbed environments which rely entirely on immigration or active introductions for recolonization. Ombrotrophic peatlands in eastern Canada are exploited for their peat over several decades using the method of milling and vacuum collection (Crum 1988). Once abandoned, milled surfaces are flat and large (up to 5 km^2), with a dense network of ditches. Fibric to sapric, *Sphagnum* peat substrates usually remain (>1 m thick), which are acid (pH 3-5) and nutrient-poor (Wind-Mulder, Rochefort & Vitt 1996). There is no residual plant cover nor a seed bank (Salonen 1987). Subsequent recolonization is slow, and many typical ombrotrophic peatland species are absent, notably *Sphagnum* species (Curran & MacNaeidhe 1986; Salonen 1987, 1990; Salonen, Penttinen & Särkkä 1992; Salonen & Setälä 1992; Desrochers, Rochefort & Savard 1998; Bérubé & Lavoie 2000). The poor recolonization has been attributed to the paucity of immigrant propagules and harsh edaphic conditions for plant establishment (Salonen & Setälä 1992), but the relative importance of each is poorly understood.

The immigration of plants into disturbed ecosystems can be determined in a straight-forward manner by trapping the diaspore rain. However, such determinations are labour-intensive and forcibly site-specific (Salonen 1987; Poschlod 1995). Furthermore, traps in milled peatlands are often filled by peat (pers. obs.). Immigration may also be quantified using physical models such as those developed for determining wind dispersal of tree seeds from forest edges to clearings (Greene & Johnson 1997) or from isolated stands (Nathan, Safriel & Noy-Meir 2001). But, if the vegetation structure surrounding the disturbed area is variable, as is the case for milled peatlands, the consequent wind environments will be as well, making predictions difficult. Such models are sensitive to variability in the wind environment (Nathan, Safriel & Noy-Meir 2001). A more general approach has been proposed to define local and regional species pools of target communities, which in effect defines immigration potential (Pärtel *et al.* 1996; Zobel, van der Maarel & Dupré 1998). A series of key autecological factors for immigration are considered for each species: ecological similarity with the target community, proximity of populations, fecundity, abundance, dispersal capacity, availability of dispersal agent, germinability and seed longevity. A factor with a low value reduces the overall probability of a species of belonging to a species pool of a particular target community (Zobel, van der Maarel & Dupré 1998). The approach cannot provide quantitative information on dispersal distances, but it allows for a general determination of probable immigrants to a community from a large suite of potential species.

In this study, a method was developed to assess the comparative immigration potential of plants colonizing milled peatlands based on the approach proposed for determining local and regional species pools (Zobel, van der Maarel & Dupré 1998). Immigration is considered strictly as the arrival of potential colonists to a milled surface. A comparative approach is used, and an index of immigration potential is determined for each species relative to the remainder of the species considered. Unlike previous work, this method is relatively simple yet is applicable to many disturbance situations. It allows managers to evaluate probable immigrants, and thereby limit species introductions to poor-dispersers and concentrate efforts on providing suitable edaphic conditions. Natural dispersal processes can thus be harnessed to complement restoration practices. Moreover, poor recolonization success despite good immigration potential would suggest that other steps after immigration control recolonization. Although this approach can easily be applied to individual sites, it is applied here to the general case of milled peatlands in southeastern Québec to determine the general immigration potential of plants into milled peatlands in this entire region.

METHODS

Identification of potential colonists

Study species were chosen *a priori* as the most frequent species of vascular plants and mosses occurring in abandoned milled peatlands or natural ombrotrophic peatlands in southern Québec (Table 2.1). Similar substrate, pH and nutrient conditions are found in

Table 2.1 Most frequent species of mosses and vascular plants in natural ombrotrophic peatlands or abandoned milled peatlands in Québec (natural peatlands: N = 31, L. Rochefort, unpubl. data; abandoned milled peatlands : N = 11, abandoned for 6 to 20 years, L. Rochefort & F. Quinty, unpubl. data).

		Natural peatlands		Milled peatlands	
Species	Family	Percent occurrence (mean ± SD)	n	Percent occurrence (mean ± SD)	n
Mosses					
Dicranella cerviculata	Dicranaceae	0	0	< 1	3
Pleurozium schreberi	Hylocomiaceae	4 ± 12	5	2 ± 3	3
Pohlia nutans	Bryaceae	0	0	5 ± 17	3
Polytrichum strictum	Polytrichaceae	15 ± 21	18	3 ± 5	5
Sphagnum angustifolium	Sphagnaceae	33 ± 32	21	0	0
Sphagnum capillifolium	Sphagnaceae	55 ± 32	27	1 ± 2	2
Sphagnum fallax	Sphagnaceae	22 ± 28	17	0	0
Sphagnum fuscum	Sphagnaceae	49 ± 33	26	< 1	1
Sphagnum magellanicum	Sphagnaceae	46 ± 28	29	0	0
Herbaceous plants					
Carex limosa	Cyperaceae	24 ± 26	20	0	0
Carex oligosperma	Cyperaceae	35 ± 31	19	0	0
Carex stricta	Cyperaceae	0	0	2 ± 8	1
Drosera rotundifolia	Droseraceae	35 ± 35	24	0	0
Eriophorum angustifolium	Cyperaceae	2 ± 5	4	2 ± 5	3
Eriophorum vaginatum	Cyperaceae	19 ± 20	21	11 ± 21	8
Rubus chamaemorus	Rosaceae	17 ± 32	9	4 ± 6	7
Sarracenia purpurea	Sarraceniaceae	17 ± 21	16	0	0
Scirpus cespitosus	Cyperaceae	17 ± 30	10	0	0
Shrubs					
Andromeda glaucophylla	Ericaceae	32 ± 22	26	0	0
Aronia melanocarpa	Rosaceae	5 ± 12	6	2 ± 2	5
Chamaedaphne calyculata	Ericaceae	71 ± 31	31	9 ± 9	10
Kalmia angustifolia	Ericaceae	39 ± 28	26	17 ± 26	8
Kalmia polifolia	Ericaceae	49 ± 33	28	< 1	4
Ledum groenlandicum	Ericaceae	36 ± 31	23	14 ± 17	10
Rhododendron canadense	Ericaceae	0	0	1 ± 2	5
Vaccinium angustifolium	Ericaceae	7 ± 12	11	14 ± 13	9
Vaccinium oxycoccus	Ericaceae	74 ± 26	31	< 1	3
Trees					
Betula papyrifera	Betulaceae	0	0	5 ± 10	6
Betula populifolia	Betulaceae	0	0	3 ± 6	4
Larix laricina	Pinaceae	5 ± 9	12	1 ± 1	6
Picea mariana	Pinaceae	21 ± 22	20	< 1	4
Pinus banksiana	Pinaceae	0	0	< 1	1

milled peatlands and natural ombrotrophic peatlands, although milled peatlands are substantially drier (Price 1996; Wind-Mulder, Rochefort & Vitt 1996). Study species from natural peatlands were chosen based on vegetation surveys of 31 natural peatlands (L. Rochefort, unpublished data). Vegetation was surveyed in ten 1 m^2 quadrats placed across open habitats in each peatland. The mean number of quadrats per peatland where each species was present was determined, and species occurring above an arbitrary limit of 15% of quadrats were selected as study species (Table 2.1). Study species from milled peatlands were chosen based on surveys of 11 milled peatland surfaces abandoned for 6 to 20 years (L. Rochefort & F. Quinty, unpublished data). Each survey consisted of ten transects of equal length placed perpendicularly across the peat field and equidistant from each other. Along each transect line, vegetation at ten equidistant points was surveyed. The average number of points per species was tabulated for each transect, and species occurring above an arbitrary limit of 1% of points were selected as study species (Table 2.1). The moss *Dicranella cerviculata* and the trees *Pinus banksiana* and *Larix laricina* were also included as study species because they are more frequent on abandoned milled surfaces than surveys indicated. In total, 23 species of vascular plants and nine species of mosses were included for study. Nomenclature for mosses follows Anderson, Crum and Buck (1990), except for *Sphagnum* which follows Anderson (1990). Nomenclature for vascular plants follows Scoggan (1978-1979), except for *Vaccinium oxycoccus* L..

Source populations in edges of milled peatlands

Populations of study species in edges of milled peatlands were evaluated in the summer of 1998 through random surveys of edges of twelve active or abandoned milled peatlands in southeastern Quebec (Table 2.2). For each milled surface, the perimeter of the milled surfaces was identified, and sections adjacent to processing mills and recently cut-over areas were excluded. The remaining perimeter was divided into four equal segments, and a starting point for the transects was randomly determined within each perimeter segment (Figure 2.1a). In total, four transects were surveyed per peatland. Each transect ran perpendicular to the edge and began where vegetative cover began (Figure 2.1b). Study species were surveyed at distances of 2, 5, 10, 20, 30, 40, 50 and 60 m from the edge using

Table 2.2. The location, area and edge perimeter of milled peatland surfaces surveyed. Where milled peatlands consisted of several separate milled surfaces, one was chosen as the sampled surface.

Milled peatland	Location	Milled area (ha)	Milled perimeter (km)
Ascension	48º44' N 71º42' W	61	4.1
Bois-des-Bel	47º58' N 69º26' W	11	1.3
Chemin-du-Lac	47º46' N 69º31' W	236	6.7
Escoumins	48º18' N 69º26' W	83	6.0
Milot	48º51' N 71º49' W	95	5.7
Rivière-Ouelle	47º27' N 69º57' W	38	2.6
Saint-Charles	46º45' N 71º00' W	56	2.9
Saint-Fabien	48º16' N 68º57' W	29	2.3
Saint-Henri	46º42' N 71º05' W	107	5.3
Saint-Modeste	47º51' N 69º27' W	59	2.6
Saint-Paul-du-Nord	48º27' N 69º18' W	48	3.2
Verbois	47º50' N 69º27' W	236	8.9

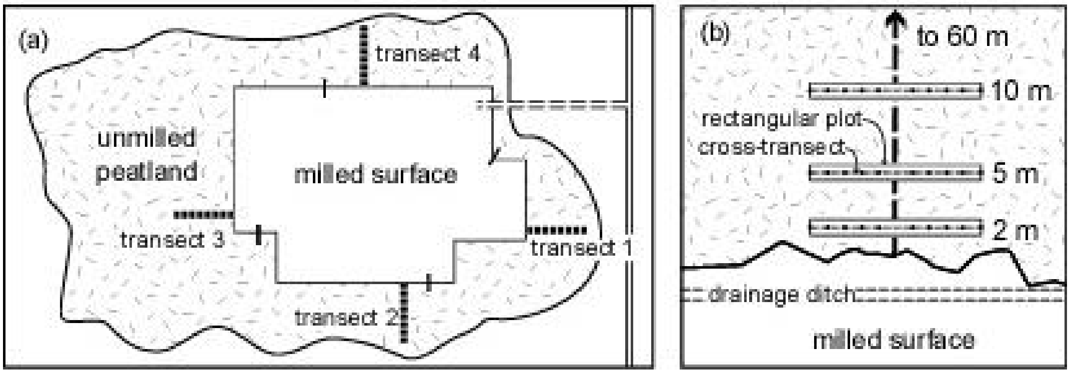

Figure 2.1. Placement of main transects in the edges of milled bogs (a), and a close-up plan view of a portion of a transect (b).

three techniques. First, a 10-m long cross-transect was placed perpendicular to the main transect at each distance, and the presence of study species touching a 2-cm diameter point were noted at ten 1-m distant points. This technique allowed for quantitative estimations of percent cover of most study species, but was inadequate to detect small or infrequent species. In order to census all species, 1 × 10 m rectangular plots were placed perpendicular to the main transect at each distance and the presence of each study species was determined. Third, the presence of flower- or fruit-bearing individuals was evaluated in the same rectangular plots. Sampling was arbitrarily limited to 60 m from edges, based on the impact of drainage on edges studied by Poulin, Rochefort & Desrochers (1999). Propagules may disperse from longer distances, but they should be rare relative to those originating close to milled edges.

Aerial photographs (1948–1994) were examined to estimate the age of the closest drainage ditch to the sampling point. Age of drainage was set as the midpoint age between the aerial photograph when a ditch appears and the previous photograph. If a ditch was present at the date of the earliest photograph, this date was taken as the drainage age.

Maximum fecundity

The fecundity of a given species varies widely in space and time, making its estimation difficult. The maximum fecundity of a species is however more easily determined and allows for a discrimination between species at least on a log scale. The maximum fruiting body density of each species was therefore determined in the 1999 growing season by deliberately searching peatlands in southeastern Québec for individuals with large concentrations of fruiting bodies. Fruiting bodies were considered as berries, drupelet aggregates, spikes, cones or capsules, depending on the species. Maximum density was determined at two separate sites for most species. Habitats searched included edges of milled peatlands, as well as natural peatlands and abandoned milled peatlands for species which fruited infrequently in edges. Counts were made by placing quadrats of 50 x 50 cm for vascular plants or 25 x 25 cm for mosses over areas of high concentration and counting the number of fruiting bodies. Five quadrats were counted per species per site, and where possible, quadrats were placed more than 2 m apart. Four undispersed fruiting bodies were collected per quadrat for a total of twenty fruiting bodies per species per site.

For vascular plants, the number of propagules in twenty fruiting bodies was counted in the laboratory under a dissecting microscope. Propagules with aborted or predated seeds were not counted. For mosses, spore number in five capsules was determined using the haemacytometer technique of Sundberg & Rydin (1998), except that spore aggregates were separated by repeated shaking of the vial in a wide arc. Spores in four 1 mm^2 squares on the diagonal of the Fuchs-Rosenthal haemacytometer were counted, and four subsamples were counted for each vial. The total number of spores per capsule was calculated from the spore count and the ratio of the counted volume to the sample volume. For vascular plants and mosses, the number of propagules per dm^2 was determined by multiplying the density of fruiting bodies by the average seed or spore counts. The highest number of propagules per dm^2 was selected as the maximum fecundity for that species.

Wind dispersal ability

Three variables were used to estimate the wind dispersal ability of study species: 1) propagule release height, 2) fall time (propagule release height / settling velocity), and 3) propagule wing loading (mass / area). Propagules released from higher elevation are generally exposed to greater wind velocities (Greene & Johnson 1996) and consequently have greater probability of being carried further by wind. Likewise, propagules with a longer fall time (higher release height and/or slower settling velocity) are also more likely of being exposed to wind and carried away. Wing loading is an key dispersal variable because its square root predicts settling velocity and hence horizontal dispersal distance of wind-dispersed species (Augspurger 1986; Augspurger & Franson 1987). It also predicts entrainment wind velocity during secondary dispersal (Johnson & Fryer 1992; Greene & Johnson 1997). Only dispersal ability of moss spores was evaluated. Dispersal by vegetative fragments is also possible (Poschlod 1995), however they are not adapted to long distance dispersal as are spores (Kimmerer 1991; Sundberg 2000) and should therefore contribute little to the post-milled species pool.

Propagule release height: The median propagule release height for each species was measured along transects in edges of milled peatlands, described above. Individuals were chosen randomly within rectangular plots closest to the milled edge, for a maximum of three individuals per species per transect. Because *Sphagnum* species possess an air gun release mechanism which shoots their spores 15 cm or more above the capsules (Ingold 1965), this height was taken as the release height.

Fall time: Fall time was determined by dividing propagule release height by settling velocity. For vascular plants, propagules were first collected in the field and air-dried in the laboratory for at least two weeks prior to testing. Settling velocity was evaluated by dropping them in a room with still air from a height of 2 m and measuring settling time with a stopwatch (Thompson 1993). The settling velocity for small-seeded species, namely *Kalmia* spp., *Ledum groenlandicum* and *Drosera rotundifolia*, was measured from a release height of 1 m. Except for trees, these release heights were much greater than actual release heights for these species in the field, therefore measured settling velocity should closely approach terminal velocity (Thompson 1993). For tree species, most propagules rapidly began to spin and attain a constant velocity. Settling velocity measurements were taken following a random complete block experimental design. For moss spores, terminal velocity was calculated from spore diameter using Stokes' law for spheres at low Reynolds numbers and assuming spores to be unit density spheres (Gregory 1973, pp. 19-20). Although few measurements of spore density are available for bryophytes, this assumption generally holds for most pollen and fungi spores (Gregory 1973, pp. 21). Spore diameter was taken from the literature (Crum & Anderson 1981; Daniels & Eddy 1985).

Wing loading: Wing loading was calculated by dividing propagule mass by plan area (silhouettte) of the entire seed, following Augspurger (1986), Matlack (1987) and Greene & Johnson (1997). For vascular plants, propagules were dried at 70 ºC for 48 hours then weighed to 10 µg precision. For species with large propagules, twenty propagules were weighed individually. For species with smaller propagules, ten groups of 20-100 propagules were weighed. To determine plan area of the propagules, smaller propagules were photographed digitally, larger propagules were scanned with an image scanner, and for *Eriophorum* species, photographs were taken then digitized. The area of propagules was then determined using Scion image analysis software (Scion Corporation 2000). For *Eriophorum* species, effective propagule area was estimated by measuring bristle length in four directions and calculating the area of a circle using mean bristle length as the radius. For mosses, spores were again considered to be unit density spheres. Spore diameter was used to calculate sphere area and volume. From volume, mass was then determined. Spore diameter was taken from the literature, as indicated above.

Floatability

The ability of propagules of vascular plants to float was evaluated by placing air-dried propagules of each species individually in microcentrifuge tubes or beakers of distilled water at 21° C for 72 hours and shaking containers at each 8-12 hours. The proportion of ten viable propagules which remained afloat were then determined for each species. The floatability of moss spores was not evaluated.

Capacity for animal dispersal

Dispersal ability of propagules of vascular plants by animals was evaluated by simply determining the presence of fleshy fruit. Fleshy-fruited propagules will be actively sought for their pulp and not their seeds. Therefore, their seeds are likely to survive the ingestion and digestion processes. Propagules of remaining species may be sought by animals, but the seeds themselves would be food sources, and consequently would be largely predated. No species had any obvious adaptations to adhere to animals (hooks or barbs). Such structures are not necessarily required for epizoochory to occur (Fischer, Poschlod & Beinlech 1996; Kiviniemi & Telenius 1998), although dispersal distances are usually shorter. Neither did species have propagules with elaiosomes. The dispersal capacity of moss spores by animals was not evaluated.

Data analyses

Multiple logistic regression analyses were performed using the GENMOD procedure of SAS statistical analysis software (SAS Institute 1996-1999) to determine the effects of distance from edge and drainage age on presence or presence of fertile plants of study species. Because adjacent plots within a main transect may have been autocorrelated, repeated analyses were used within main transects using the autocorrelation option. Similarly, simple Poisson regression analyses were performed with GENMOD to determine the effects of these same variables separately on species abundance, again using repeated analyses and the autocorrelation option. In all regressions, Type 3 contrasts were used and the dispersion parameter was scaled to deviance.

A composite variable for 'importance in edges' was calculated for each species from 1) its mean presence across all distances, 2) its mean abundance, 3) its mean presence of fertile plants; and 4) a trend variable indicating its bias with respect to the distance from the edge. This fourth variable was constructed using the regression slopes with respect to distance from the edges as determined from the three regression analyses above. Species whose regression slopes were significantly positive with respect to distance (more abundant or present further from the edge) were given a score of 0, while those with a significantly negative slope with respect to distance (more abundant or present closer to the edge) were given a score of 2. Those without a significant slope were given a score of 1. Scores were added for the three regressions (abundance, presence and fertile plants) for a possible total score of 6. All variables were then rescaled using the technique of ranging (Sneath & Sokal 1973) to values between 0 and 1 in the following manner,

$$x_i' = \frac{(x_i - x_{\min})}{(x_{\max} - x_{\min})}$$

where x_i' is the ranged value of variable x, x_i is the original value, x_{min} is the minimum value for that variable and x_{max} is the maximum value. The arithmetic mean of these four variables was taken. This composite variable was again rescaled from 0 to 1 using the same ranging technique.

A composite variable for 'dispersal ability by wind' was also constructed for each species from: 1) release height, 2) fall time, and 3) log wing loading. Log_{10} wind loading was used instead of square root wing loading because a far greater range of values were obtained in this study than those in previous studies (e.g. Augspurger & Franson 1987; Greene & Johnson 1997), as a result of the inclusion of species with heavy propagules (wingless seeds, berries). Each variable was again rescaled using the ranging technique, but wing loading was rescaled inversely so that smaller wing loading had greater value. As such, species with a combination of high release height, long fall time and small wing loading were considered as the best wind dispersers. The composite wind dispersal ability was determined from the arithmetic mean of these three variables which was rescaled again using the ranging technique.

Remaining variables (log maximum fecundity, floatability and fleshy fruits) were also rescaled using the ranging techniques. The relative immigration potential of each species by wind, water or animals was then calculated as the geometric mean of 1) their importance in edges of milled peatlands, 2) their maximum fecundity and 3) their dispersal ability by either wind, water or animals. This value was again rescaled using the ranging procedure. The geometric mean was used because overall immigration ability is the product and not the sum of these three variables. To avoid over-penalizing species that fell last for edge importance, fecundity or dispersal ability, 0.01 was added to all ranged values prior to geometric averaging. Consequently, such species may have low but non-negligible immigration potential.

RESULTS

Populations in edges of milled peatlands

Populations of study species differed markedly in the edges of milled peatlands either in terms of abundance, presence or fertile plants (Table 2.3). Many species also varied with distance from the edges (Figure 2.2 for presence and fertile plants). Among mosses, *Polytrichum strictum* was widespread and showed no significant trend with distance. The

Table 2.3. Populations of study species in the edges of milled bogs in terms of abundance, presence and presence of fertile plants, and their trends as functions of distance from the edge (dist) and drainage age (age). For abundance data, the number of cross-transects (n) where a species was found is shown along with its percent occurrence (%) across all cross-transects (N = 380). For presence and fertile plants, the number and percent of all plots where present is shown (N = 380). Trends for distance or age were determined from signs of significant slopes from multiple Poisson and logistic regression analyses (*P* < 0.05, N = 48 main transects; see text for details).

Species	Abundance				Presence				Fertile plants			
	n	%	dist	age	n	%	dist	age	n	%	dist	age
Mosses												
Dicranella cerviculata	7	0.3	–	–	18	5	–	–	9	2	–	–
Pleurozium schreberi	98	6.5	+		123	33	+		13	3	+	
Pohlia nutans	48	2.7			70	18		–	12	3		
Polytrichum strictum	84	6.6			131	34			44	12		
Sphagnum angustifolium	43	2.9	+	–	61	16	+	–	0	0		
Sphagnum capillifolium	124	10.2	+	–	167	44	+	–	19	5		–
Sphagnum fallax	3	0.1			6	2			0	0		
Sphagnum fuscum	83	6.8	+	–	122	32	+	–	23	6	+	–
Sphagnum magellanicum	47	2.1	+	–	83	22	+	–	2	1		
Herbaceous plants												
Carex limosa	20	1.1		–	23	6		–	6	2		
Carex oligosperma	16	1			26	7			9	2		
Carex stricta	9	0.6		+	12	3			3	1		
Drosera rotundifolia	12	0.5			31	8	+	–	13	3		
Eriophorum angustifolium	6	0.2		–	11	3		–	3	1		
Eriophorum vaginatum	25	1.3		–	50	13		–	20	5		–
Rubus chamaemorus	20	0.7			50	13			6	2		
Sarracenia purpurea	4	0.1			20	5			1	0		
Scirpus cespitosus	4	0.2			6	2			6	2		
Shrubs												
Andromeda glaucophylla	29	1.1		–	55	14		–	30	8		–
Aronia melanocarpa	37	2.1			57	15			18	5	–	
Chamaedaphne calyculata	191	16.3		–	224	59		–	205	54		–
Kalmia angustifolia	219	26.7			260	68		–	207	54		–
Kalmia polifolia	79	3.3		–	135	36		–	102	27		–
Ledum groenlandicum	196	17.1			237	62		–	191	50		
Rhododendron canadense	67	4.6			93	24			72	19		
Vaccinium angustifolium	155	11.1	–		202	53			58	15	–	
Vaccinium oxycoccus	78	5	+	–	97	26	+	–	35	9	+	–
Trees												
Betula papyrifera	51	4.6	–		67	18	–		21	6	–	
Betula populifolia	37	2.8	–		40	10	–		30	8		
Larix laricina	86	5.5			112	29			50	13		
Picea mariana	144	17.2	+	–	173	46	+	–	101	27	+	
Pinus banksiana	30	1.9			39	10			35	9		

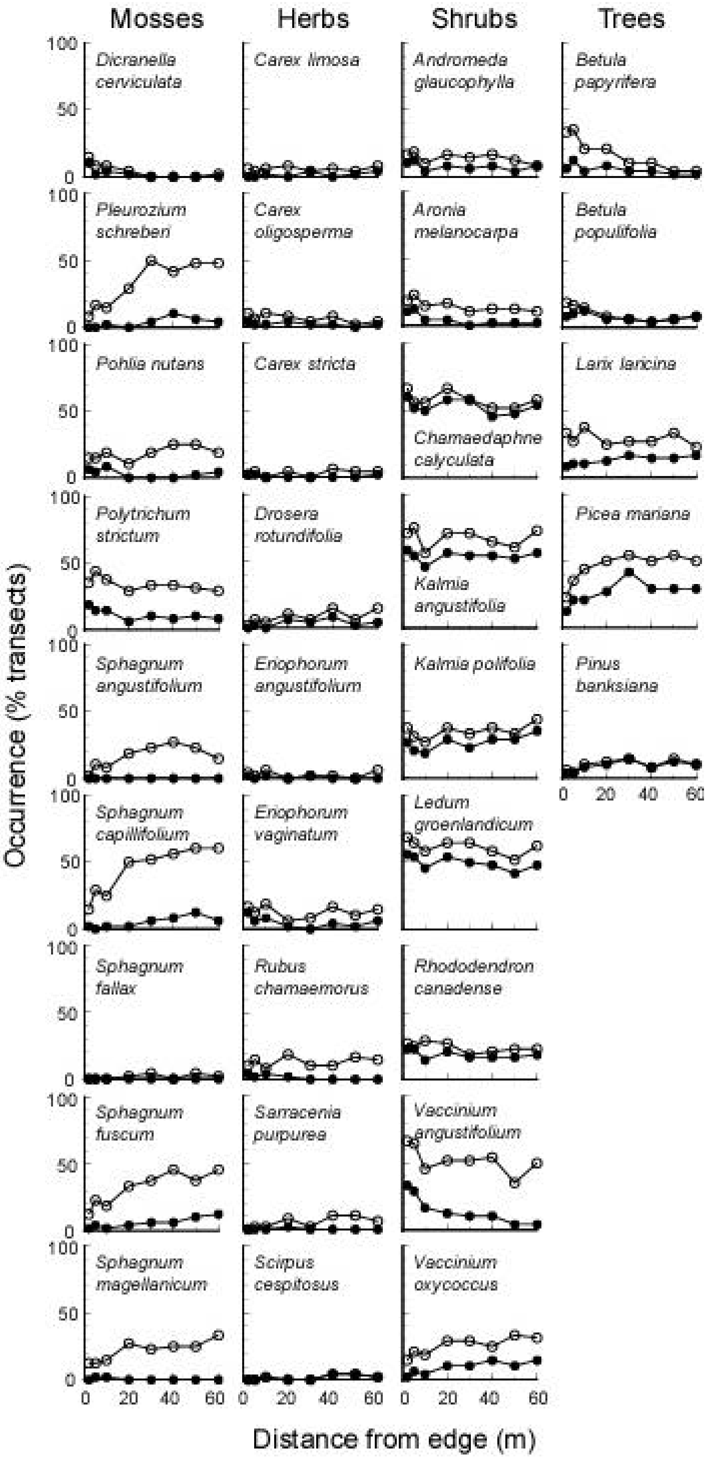

Figure 2.2. Percent presence (open symbols) and presence of fertile plants (solid symbols) of study species in edges of milled peatlands as a function of distance from the edges (N = 48 transects in 12 peatlands).

mosses *Pleurozium schreberi*, *Sphagnum capillifolium* and *S. fuscum* only became frequent at greater distances, and edge effects were still apparent at distances of 30, 50 and 60 m, respectively. Other *Sphagnum* species were less abundant but showed similar patterns with respect to distance from edges. *Dicranella cerviculata* was generally infrequent, but contrary to other mosses, increased within 10-20 m from edges. Herbaceous plants were uncommon in general, with few fertile plants. *Eriophorum vaginatum* was the most common herb. Shrubs, especially *Chamaedaphne calyculata*, *Kalmia angustifolia*, *Ledum groenlandicum* and *Vaccinium angustifolium*, were by far the most frequent species in edges of milled peatlands. Relatively few trends with respect to distance were found amongst shrubs, although *Aronia melanocarpa* and *Vaccinium angustifolium* increased in abundance or presence of fertile plants near edges, while *Vaccinium oxycoccus* declined. *Picea mariana* was the most frequent tree species, but declined in importance within 30 m of edges. Conversely, *Betula papyrifera* and *B. populifolia* were present more often within 30 m of edges. *Larix laricina* was common in edges but showed no trends with respect to distance. The overall frequency of study species in edges appears to be well summarized by the composite variable of importance in edges (Figure 2.3).

Drainage ditches were 1.7 ± 1.1 m (mean ± SD) deep with respect to cross-transects and plots. Distance to the nearest drainage ditch was only moderately correlated with the distance to milled edges ($r = 0.72$), because many ditches occurred further from edges or ran parallel to main transects. Most ditches were dug in the 1970s and 1980s, although some sites were drained earlier in the 1930s to 1950s, and a few sites in the early 1990s. Many of the older drainage ditches were dug for agricultural drainage of adjacent lands and not for peat extraction purposes. On average, drainage occurred 26.8 ± 12.8 years ago (mean ± SD) across all sampling points and with a range from 5.5 to >50 years. Drainage age is not correlated with distance from edges ($r = 0.04$). The abundance, presence or presence of fertile plants of most species decreased with increasing drainage age (Table 2.3). Consequently for most species, changes in abundance or presence appear to take place over the longer term.

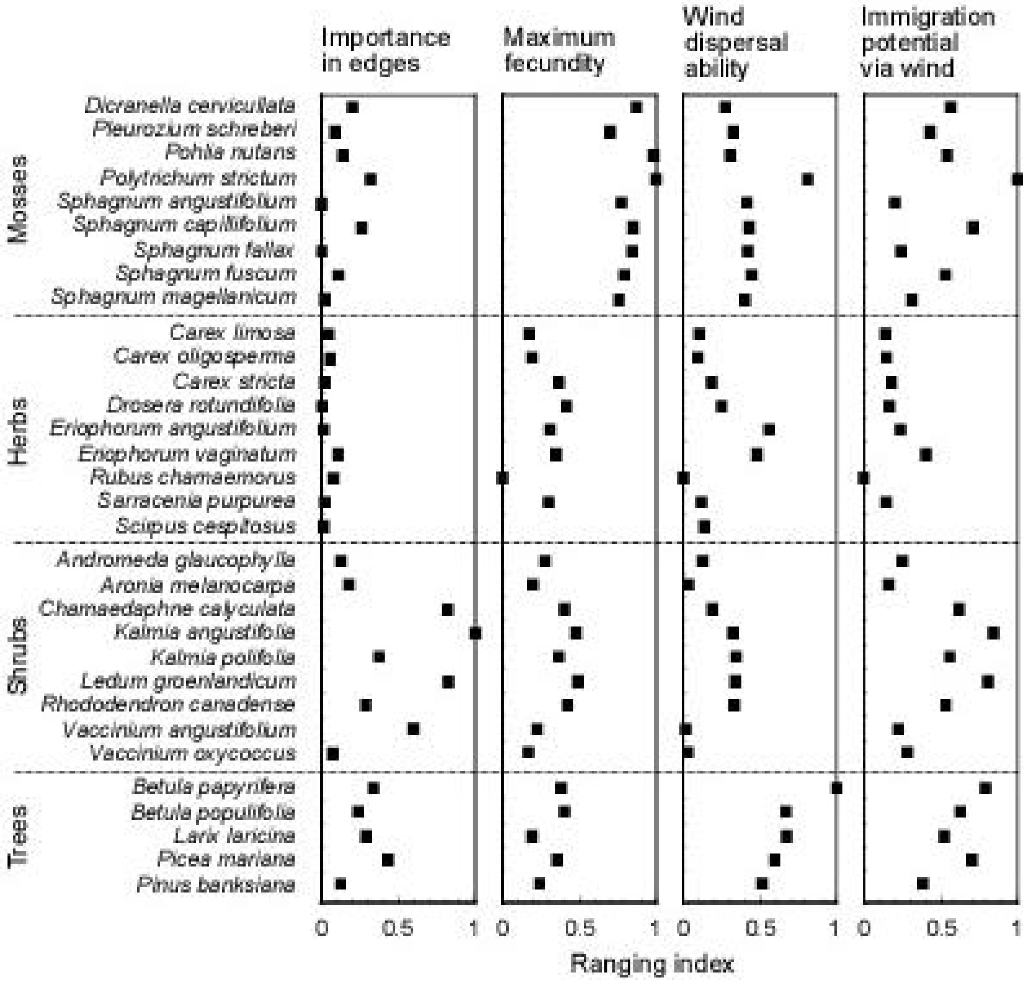

Figure 2.3. Importance in edges, log maximum fecundity, wind dispersal ability and overall immigration potential via wind dispersal by study species of mosses and vascular plants. The axes were rescaled to set the range for each variable between 0 and 1 (see text for details). The overall immigration potential via wind dispersal is the geometric mean of importance in edges, maximum fecundity and wind dispersal ability.

Maximum fecundity

Mosses, especially *Polytrichum stricum* and *Pohlia nutans*, were by far the most fecund of the study species (Figure 2.3; Appendix 2.1). Amongst vascular plants, the shrubs *Kalmia angustifolia* and *Ledum groenlandicum* were the most fecund. *Rubus chamaemorus* was by far the least fecund species. Maximum fecundity was not determined for *Scirpus caespitosus* because of the lack of fruiting plants in 1999.

Dispersal ability

Study species have a wide variety of propagule types, ranging from spores (mosses), variously winged seeds, seeds with long pappus, fleshy fruits and others (Appendix 2.1). Many species have obvious adaptations favouring wind dispersal. Tree species under study had the highest release heights as well as winged seeds with low wing loading. Consequently they had the highest composite wind dispersal abilities, especially *Betula papyrifera* (Figure 2.3). Mosses had low release heights, except for *Sphagnum* species. However, they also had very low wing loadings and long fall times as a result of the small size of spores, allowing them to take full advantage of any wind turbulence for dispersal. As a result, the composite wind dispersal ability of mosses was also high, especially for *Polytrichum strictum* which has very small spores. Amongst herbaceous plants, both species of *Eriophorum* have high wind dispersal ability, because propagules had abundant long pappus bristles which favoured very low wing loading. Several shrub species, including both *Kalmia* species, *Ledum groenlandicum* and *Rhododendron canadense*, have small, winged propagules with low wing loading favouring their dispersal by wind.

All propagules of *Carex* species, *Drosera rotundifolia*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Kalmia polifolia* and to a lesser extent *Kalmia angustifolia* remained afloat as a result of trapped air bubbles. The large berries of *Vaccinium oxycoccus* and to a lesser extent *Vaccinium angustifolium* also remained afloat, but fleshy fruits of other shrubs did not. Amongst trees, only a small proportion of *Betula* seeds remained afloat.

The only species of vascular plants with fleshy fruits were *Rubus chamaemorus*, and the shrubs *Aronia melanocarpa*, *Vaccinium oxycoccus* and *Vaccinium angustifolium* (Appendix 2.1). As such, only these species were considered to have high potential for animal dispersal.

Immigration potentials

Immigration via wind dispersal: The moss *Polytrichum strictum* showed the highest overall potential as a result of moderate frequency in edges and high fecundity and dispersal ability by wind (Figures 2.3). Other mosses had relatively high immigration potential because of their fecundity and dispersal ability. Herbaceous plants showed lower immigration potential via wind dispersal, largely as a result of their rarity in edges. *Eriophorum vaginatum* was the most likely herbaceous species which would immigrate by wind to milled peatlands. The ericaceous shrubs *Kalmia angustifolia* and *Ledum groenlandicum* were the vascular plants with the highest immigration potential, closely followed by *Betula papyrifera* and *Picea mariana.*

Immigration via water dispersal: Many species of shrubs showed a high potential of immigrating to milled peatlands via water dispersal (Figure 2.4). This was the case for *Chamaedaphne calyculata* and *Kalmia angustifolia*, and to a lesser degree, *Andromeda glaucophylla*, *Kalmia polifolia* and *Ledum groenlandicum*. The immigration potential of herbaceous plants via water dispersal was higher than via wind dispersal, yet still remained low relative to other species, as a result of their rarity in edges. Trees showed low potential of being dispersed by water.

Immigration via animal dispersal: Only shrub species with fleshy fruits showed higher potential of immigrating to milled peatlands via animal dispersal (Figure 2.4). *Vaccinium angustifolium* showed the highest potential, followed by *Aronia melanocarpa* and *Vaccinium oxycoccus. Rubus chamaemorus* was the herbaceous species with the highest potential of immigration via animal dispersal, but although it has fleshy fruits, it had a low overall score because of its rarity in edges and low fecundity. Several species without fleshy

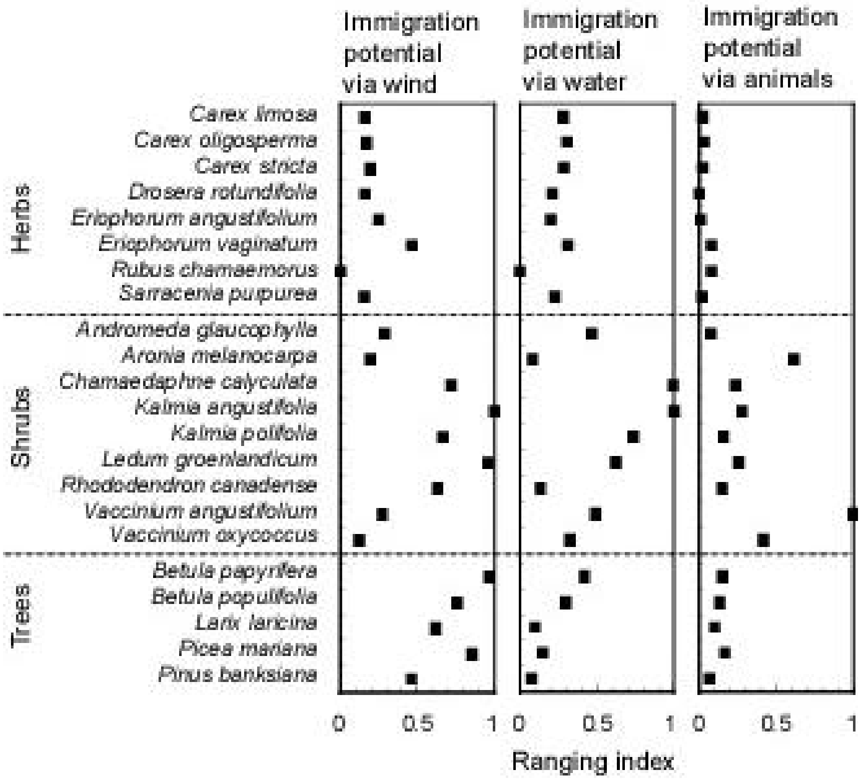

Figure 2.4: Overall relative immigration potential via wind dispersal, water dispersal and animal dispersal for study species of vascular plants. The axes were rescaled as in Fig. 2.3.

fruits had low but non-negligible potentials to be dispersed by animals (e.g., *Kalmia*) because they were frequent in edges and fecund.

Immigration potentials versus actual recolonization

The estimation of immigration potentials can be compared to survey data of frequent colonists of abandoned milled peatlands in Québec (Table 2.1) to determine the role of immigration on actual recolonization. The comparison is crude because successful colonists differ in their ability to survive and spread in milled peatlands, but it permits an evaluation of the role of immigration in determining actual recolonization.

Although mosses have high immigration potential by wind, mosses are greatly under-represented on abandoned milled peatlands as compared to vascular plants (Figure 2.5a). Mosses with higher immigration potential by wind are generally more frequent colonists on milled peatlands. However, *Sphagnum capillifolium* and *S. fuscum* are rare on milled peatlands (<1% occurrence) even though they have relatively high immigration potential. For vascular plants, species which have high immigration potential by either wind, water or animal dispersal are generally the most frequent colonists on abandoned milled peatlands (Figure 2.5b). Several exceptions exist, as is the case for *Kalmia polifolia* which shows high potential to immigrate via both wind and water dispersal but has very low presence on milled surfaces. Conversely, *Rubus chamaemorus* and *Eriophorum vaginatum* are both more frequent in milled peatlands than predicted by their immigration potential.

DISCUSSION

Immigration of plants to milled peatlands

Immigration of potential colonists depends on the occurrence of residual populations in edges, their fecundity and their ability to disperse by an available vector. The disparity between species is evident just from the residual populations in milled edges. The species composition of edges is also substantially different from natural ombrotrophic peatlands. Many typical peatland species are rare (e.g. herbs), while other species which are absent

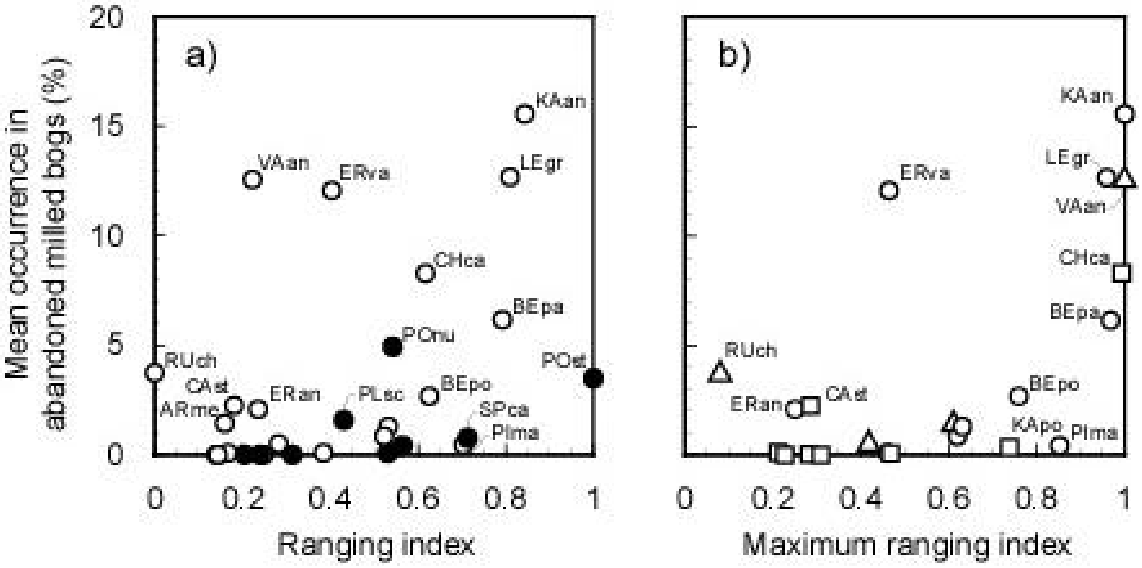

Figure 2.5. Comparison of the mean occurrence of study species in abandoned milled peatlands in Québec versus (a) the immigration potential of all species by wind dispersal (mosses : solid circles; vascular plants : hollow circles), and versus (b) the mean immigration potential of vascular plant species by wind (circles), water (squares) and animal dispersal (triangles). Mean occurrences of study species in abandoned milled peatlands are from Table 2.1. Species codes are constructed using the first two letters of the genus and the species (see Appendix 2.1 for a species list).

from natural peatlands have become frequent in edges (e.g. birches). A pronounced edge effect is also evident where many species vary in abundance as a function of distance from the edge. The dissimilarity of the vegetation between milled edges and natural peatlands in part reflects decades of disturbance on many species from drainage and extraction activities. Direct drainage effects appear to have an impact because drainage age predicts the occurrence of several species. Drainage in peatlands changes species composition as a result of changed hydrologic conditions and consequent effects on soil aeration and nutrient dynamics (Laine, Vassander & Laiho 1995; Price 1996; Poulin, Rochefort & Desrochers 1999). However, it is unclear to what extent drainage versus other disturbances associated with peat extraction are responsible for this edge effect. For instance, the decline of *Picea mariana* near edges may not be caused by drainage, but rather by the practice of clearing of trees prior to exploitation.

Differences in immigration ability between study species become even more evident when edge populations are coupled with their maximum fecundity and dispersal ability by wind, water and animals. Species differ dramatically in their ability to disperse by a particular dispersal agent. Several species are not limited to dispersal by a single agent. However, wind is the key dispersal agent in all milled peatlands because of their large, open and aerodynamically-smooth substrates (Campbell, Lavoie & Rochefort 2002). Several studies have determined the prevalence of wind-dispersed diaspores in the seed rain and the importance of long-distance dispersal in milled peatlands (Curran & MacNaeidhe 1986; Salonen 1987; Salonen, Penttinen & Särkkä 1992; Poschlod 1995). For instance, *Betula* species are known to be entrained long distances over smooth surfaces (Matlack 1989; Greene & Johnson 1997). In Europe, *Betula pubescens* dispersed up to 1061 viable seeds m^2 yr^{-1} in milled peatlands from a distance of 250 m from closest vegetated edges (Salonen 1987).

Surface water is present in milled peatlands during snow melt and for longer periods in parts of the drainage ditch network. Water can therefore act as a seasonal dispersal agent for diaspores. However in comparison to wind dispersal, water dispersal is more site-specific, and depends on the duration, location and flow direction of surface water in the drainage network with respect to the edges of the milled zones.

Remnant peatland fragments in milled peatlands have more abundant and diverse assemblages of songbirds than in natural peatlands (Delage, Fortin & Desrochers 2000). Small mammals are also more diverse in these fragments than in natural peatlands (Mazerolle, Drolet & Desrochers 2001). Their effectiveness as seed dispersal agents is however unknown. Certainly, the lack of vegetation and consequent habitat on milled peatlands restricts the use of milled surfaces by animals and any consequent seed dispersal. However, the prevalence of *Vaccinium angustifolium* in abandoned milled surfaces appears to indicate that animals do disperse their seeds on milled peatlands. Occasional tracks of large mammals in milled bogs indicate that epizoochory of propagules may occur, but it is likely less important than observed in grazed ecosystems (Fischer, Poschlod & Beinlich 1996).

This study provides evidence that the potential for mosses to immigrate by spores is relatively important on milled surfaces. Moss species are only moderately common and fertile in edges of milled peatlands but are very fecund and have great wind dispersal abilities. Previous studies have shown that dispersal of moss spores is concentrated within short distances of adult plants (1-2 m: McQueen 1985; Kimmerer 1991; Miles & Longton 1992). However, only one study compared spore release versus observed deposition patterns (Miles & Longton 1992). Less than 13% of released spores were deposited within 2 m in forested and less in open habitats. Mosses therefore have highly leptokurtic dispersal distributions with long, fat tails (*sensu* Clark *et al.* 1998) which favours long-distance dispersal. Furthermore, spore release, including that for *Sphagnum* species with their air gun release mechanism, is favoured under dry conditions (Ingold 1965). Wind will favour dessication, therefore dispersal should be promoted during windy periods.

The discrepancies between immigration potential and the actual recolonization for several species suggest that other factors after immigration controls their colonization success. The recolonization failure of mosses must primarily be a result of problems during establishment on milled peat surfaces. *Sphagnum* species are especially vulnerable to drought and substrate instability during the establishment phase (Rochefort 2000). *Picea mariana* is also frequent in edges, relatively fecund and has high wind dispersal ability, but is a rare component of the vegetation in abandoned milled peatlands. Harsh substrate conditions, possibly summer drought or needle ice, must prevent their establishment and survival on milled peatlands. Conversely, *Eriophorum vaginatum* is relatively fecund and has high wind dispersal ability, but is infrequent in edges of milled peatlands. Similarly, *Rubus chamaemorus* is infrequent in edges, has low fecundity and only disperses by animals, yet is more frequent in milled peatlands than many species. Their frequency in abandoned milled peatlands infers that the remainder of their life cycle, namely their germination, establishment, growth and reproduction, is favoured on milled peatlands relative to the other species.

The immigration potential approach

Determining the immigration potential of a species is relatively simple given a list of potential colonists, data on source populations of propagules, and autecological information on fecundity and dispersal characteristics of species. It is also possible to compare species with a wide range of life forms, from mosses to trees. With this information, a restoration manager should be able to pinpoint bottlenecks during the immigration sequence. Restoration efforts may then be tailored to encourage desired or discourage undesirable species. This approach is also flexible. The general case of immigration potential in milled peatlands in Québec was considered here, but immigration could also be considered on a site-specific basis if local surveys of edge populations are conducted, although higher sampling effort may be needed to better characterize individual sites. Different weight may also be given to dispersal by wind, water or animals on a site-specific basis. Furthermore, this approach should be applicable to many disturbance scenarios beyond that of milled bogs.

The main disadvantage of this approach is the lack of quantitative determinations on dispersal distance. Probable concentrations of diaspores on disturbed sites at different distances from edges cannot be determined. However, considering that many factors control actual immigration, including site history and layout, wind speed, direction and turbulence, topography, populations of animal vectors, flooding regime, as well as their seasonal and interannual variation, actual immigration should vary greatly between sites and years. Any quantitative determinations of actual immigration would vary likewise. A qualitative determination of immigration potential using a relative index does not suffer from this problem, yet provides simple, useful determinations of the likely initial species pools following disturbance.

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Appendix 2.1: Detailed data on maximum fecundity and dispersal variables for study species.

Species	Propagule type	Maximum fruiting body density (dm^{-2})	Number of propagules		Log maximum fecundity	Maturity period[a]	Median release height (m)	
			n	mean ± SE			n	mean ± SE
Mosses								
Dicranella cerviculata	spore (16 - 21 µm)	581	5	35300 ± 13100	7.31	?	39	0.008 ±
Pleurozium schreberi	spore (11 - 20 µm)	9	5	81900 ± 26900	5.87	Jul-Aug?	7	0.019 ±
Pohlia nutans	spore (16 - 21 µm)	432	5	416000 ± 18000	8.26	Jul-Aug	37	0.022 ±
Polytrichum strictum	spore (8 - 9 µm)	60	5	4240000 ±	8.41	Jul-Sep	65	0.046 ±
Sphagnum angustifolium	spore (22 - 24 µm)	33	5	89300 ± 13100	5.47	Jul-Aug	0	0.15
Sphagnum capillifolium	spore (24 - 28 µm)	182	5	71600 ± 12400	7.12	Jul-Aug	42	0.15
Sphagnum fallax	spore (25 - 28 µm)	176	5	73100 ± 22900	7.11	Jul-Aug	0	0.15
Sphagnum fuscum	spore (23 - 27 µm)	54	5	81600 ± 15000	6.64	Jul-Aug	38	0.15
Sphagnum magellanicum	spore (26 - 30 µm)	26	5	89300 ± 14000	6.36	Jul-Aug	8	0.15
Herbaceous plants								
Carex limosa	achene in periginium	2	20	14 ± 1	1.34	Aug-Sep	20	0.20 ± 0.02
Carex oligosperma	achene in periginium	5	20	7 ± 1	1.49	Aug-Sep	6	0.49 ± 0.05
Carex stricta	achene in periginium	5	16	177 ± 9	2.98	Jul-Sep	3	0.41 ± 0.02
Drosera rotundifolia	seed with fusiform tips	23	8	111 ± 8	3.41	Aug-Sep	29	0.09 ± 0.01
Eriophorum	achene with silky	17	20	18 ± 3	2.49	June-July	6	0.47 ± 0.04
Eriophorum vaginatum	achene with silky	19	20	37 ± 2	2.84	June-July	24	0.30 ± 0.01
Rubus chamaemorus	large fleshy drupe	1	20	1	-0.15	July-Aug	15	0.09 ± 0.01
Sarracenia purpurea	wingless seed	0	18	1330 ± 78	2.42	Sep-Oct	1	0.25 ± 0.00
Scirpus caespitosus	short-bristled seed	ns[d]	0	ns[d]	ns[d]	July-Aug	8	0.20 ± 0.01
Shrubs								
Andromeda glaucophylla	wingless seed	9	20	20 ± 1	2.24	Sep-Nov	30	0.21 ± 0.02
Aronia melanocarpa	berry-like pomes	34	20	1	1.53	Aug-Sep	28	0.85 ± 0.05
Chamaedaphne	wingless seed	32	20	60 ± 2	3.29	Sep-Oct	118	0.44 ± 0.02
Kalmia angustifolia	terminally-winged seed	69	20	130 ± 15	3.95	Sep-Oct	122	0.48 ± 0.02
Kalmia polifolia	terminally-winged seed	5	20	176 ± 20	2.98	Jul	84	0.39 ± 0.02
Ledum groenlandicum	terminally-winged seed	83	20	133 ± 11	4.04	Sep-Oct	106	0.47 ± 0.02
Rhododendron	terminally-winged seed	17	20	184 ± 15	3.48	Oct-Nov	48	0.58 ± 0.02
Vaccinium angustifolium	berry	64	16	1	1.81	Jul-Sep	62	0.30 ± 0.02
Vaccinium oxycoccus	berry	20	20	1	1.3	Sep-Oct	39	0.01 ± 0.00
Trees								
Betula papyrifera	bilateral winged seed	5	20	264 ± 20	3.13	Aug-Oct	23	6.45 ± 0.56
Betula populifolia	bilateral winged seed	5	20	392 ± 11	3.31	Aug-Oct	27	3.13 ± 0.27
Larix laricina	asymetrical winged seed	1	-	32[e]	1.51	Aug-Sep	49	4.83 ± 0.36
Picea mariana	asymetrical winged seed	16	20	51 ± 4	2.91	Aug-Nov	62	3.85 ± 0.25
Pinus banksiana	asymetrical winged seed	3	20	30 ± 3	1.93	Sep-Nov?	27	2.86 ± 0.24

Appendix 2.1 (continued)

Species	Settling velocity (m s^{-1})		Fall time (s)	Propagule area (mm^2)		Propagule mass[b] (mg)		Wing loading (mg cm^{-2})	Floatability (%)	Fleshy fruits[c]
	n	mean ± SE		n	mean ± SE	n	mean ± SE			
Mosses										
Dicranella cerviculata	-	0.012	0.69		0.0011	-	2.7x10^{-5}	2.5	-	-
Pleurozium schreberi	-	0.009	2.19		0.00075	-	1.6x10^{-5}	2.1	-	-
Pohlia nutans	-	0.012	1.86		0.0011	-	2.7x10^{-5}	2.5	-	-
Polytrichum strictum	-	0.003	17.38		0.00023	-	3.0x10^{-6}	1.1	-	-
Sphagnum angustifolium	-	0.026	5.70		0.0017	-	5.1x10^{-5}	3.1	-	-
Sphagnum capillifolium	-	0.023	6.44		0.0021	-	7.4x10^{-5}	3.5	-	-
Sphagnum fallax	-	0.024	6.20		0.0022	-	7.8x10^{-5}	3.5	-	-
Sphagnum fuscum	-	0.022	6.94		0.002	-	6.5x10^{-5}	3.3	-	-
Sphagnum magellanicum	-	0.027	5.57		0.0025	-	9.2x10^{-5}	3.7	-	-
Herbaceous plants										
Carex limosa	20	2.03 ± 0.01	0.10	20	4.5 ± 0.1	20 (1)	1.42 ± 0.1	31.7	100	0
Carex oligosperma	20	2.64 ± 0.01	0.19	16	9.7 ± 0.5	16 (1)	5.47 ± 0.15	58.4	100	0
Carex stricta	20	1.48 ± 0.01	0.27	20	3 ± 0.2	20 (1)	0.4 ± 0.06	13	100	0
Drosera rotundifolia	20	0.39 ± 0.00	0.23	20	0.26 ± 0.01	10	0.008	3.1	100	0
Eriophorum angustifolium	20	0.24 ± 0.00	1.94	20	1262 ± 78	20 (1)	0.95 ± 0.07	0.08	60	0
Eriophorum vaginatum	20	0.26 ± 0.00	1.14	20	1119 ± 51	20 (1)	1.84 ± 0.07	0.17	30	0
Rubus chamaemorus	20	3.43 ± 0.02	0.03	20	31.4 ± 2.3	20 (1)	50.51 ± 5.72	149.7	0	1
Sarracenia purpurea	20	2.14 ± 0.02	0.11	16	1.8 ± 0.1	16 (1)	0.52 ± 0.03	28.4	60	0
Scirpus caespitosus	20	1.15 ± 0.01	0.17	20	1.2 ± 0.1	10 (20)	0.24	19.8	0	0
Shrubs										
Andromeda glaucophylla	20	1.87 ± 0.02	0.11	20	0.75 ± 0.03	10 (20)	0.18	23.8	100	0
Aronia melanocarpa	20	3.72 ± 0.02	0.23	20	30.8 ± 1.1	20 (1)	73.11 ± 3.86	238.9	0	1
Chamaedaphne calyculata	20	1.09 ± 0.01	0.41	20	0.51 ± 0.02	10 (20)	0.071	13.9	100	0
Kalmia angustifolia	20	0.33 ± 0.00	1.46	20	0.17 ± 0.01	10	0.0047	2.7	70	0
Kalmia polifolia	20	0.23 ± 0.00	1.69	20	0.29 ± 0.01	10	0.0059	2	100	0
Ledum groenlandicum	20	0.31 ± 0.01	1.51	20	0.27 ± 0.01	10	0.0057	2.1	20	0
Rhododendron canadense	20	0.39 ± 0.01	1.49	20	0.65 ± 0.03	10	0.0177	2.7	0	0
Vaccinium angustifolium	20	3.45 ± 0.02	0.09	20	14.1 ± 0.7	20 (1)	21.32 ± 1.86	148.1	30	1
Vaccinium oxycoccus	20	3.46 ± 0.02	0.003	20	79 ± 3.6	20 (1)	63.69 ± 4.27	80.2	100	1
Trees										
Betula papyrifera	20	0.72 ± 0.01	9.01	20	6.9 ± 0.5	20 (1)	0.22 ± 0.02	3.4	20	0
Betula populifolia	20	0.58 ± 0.01	5.37	20	5 ± 0.3	10 (20)	0.096	1.9	10	0
Larix laricina	20	1.34 ± 0.04	3.60	19	22.8 ± 0.9	20 (1)	1.5 ± 0.1	6.5	0	0
Picea mariana	20	0.86 ± 0.01	4.47	20	15.1 ± 0.8	20 (1)	1.49 ± 0.09	10.1	0	0
Pinus banksiana	20	0.73 ± 0.00	3.94	20	39.6 ± 1.7	20 (1)	3.32 ± 0.26	8.3	0	0

a: Approximate period of fruit maturity and propagule dispersal based on field notes.

b: The number of propagules from which each mass determination is measured is shown in parentheses. For species whose propagules were measured in groups, only the mean mass per propagule is given.

c: For fleshy fruits, 0 = no; 1 = yes.

d: Fecundity for Scirpus caespitosus was not sampled. *e*: From Young and Young (1992).

CHAPITRE 3

WIND EROSION AND SURFACE STABILITY IN ABANDONED MILLED PEATLANDS[2]

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[2] Campbell, D. R., Lavoie, C. & Rochefort, L. (2002) Wind erosion and surface stability in abandoned milled peatlands. *Canadian Journal of Soil Science*, **82**: 85-95.

RÉSUMÉ

Les tourbières exploitées par la méthode d'aspiration sont recolonisées très lentement par les plantes après leur abandon. Une cause possible de la lenteur du processus est l'instabilité du substrat pendant la période de germination et d'établissement des plantules, instabilité causée par l'érosion éolienne. Quatre études ont été menées pour évaluer l'importance du phénomène de l'érosion éolienne. Une première expérience en soufflerie a été effectuée pour déterminer le potentiel d'érosion de la tourbe sèche et meuble en fonction de son degré de décomposition. Une deuxième expérience en soufflerie a été effectuée pour réévaluer ce potentiel, mais pour des tourbes sèches avec une mince croûte à la surface. Troisièmement, des profils de vent ont été dressés pour déterminer la rugosité des surfaces exploitées. Finalement, la stabilité et l'érosion éolienne ont été mesurées sur le terrain sur des surfaces exploitées et abandonnées. Dans la soufflerie, l'érosion de la tourbe meuble est importante et inversement reliée à la décomposition de la tourbe. Par contre, une fois qu'une croûte se forme en surface, les tourbes sont très stables. Les surfaces des tourbières exploitées sont lisses en terme aérodynamique, donc les plantules sont probablement exposées à d'importantes forces érosives lors des périodes de grands vents. Sur le terrain, les surfaces aspirées et abandonnées sont instables, mais surtout au printemps, avant le début du mouvement des particules sur la surface, et peu durant l'été. L'instabilité des surfaces est un facteur contraignant pour la restauration des tourbières aspirées.

ABSTRACT

Peatlands exploited for their peat by the method of milling are poorly recolonized by plants after the cessation of extraction activities, in part due to unstable peat substrates. Wind erosion has been suspected to play a role in this instability. Four studies were conducted to investigate the role of wind erosion in abandoned milled peatlands. A wind tunnel experiment was performed to evaluate the erodibility of dry, loose peat as a function of its degree of decomposition. A second wind tunnel experiment was conducted to determine how crusted peats differ in their resistance to erosion as a function of their degree of decomposition, without the input of abraders. Third, wind profiles were measured in milled, revegetated and natural peatlands in southeastern Québec to determine their aerodynamic roughness length. Finally, field measurements were made at three abandoned milled peatlands through two field seasons to characterize substrate stability and particle movement. In the wind tunnel, the erodibility of loose surface peat decreased with increasing decomposition and was predicted by their equivalent diameter to mineral particles 0.84 mm in diameter. However, once surface crusts formed, peats were all resistant to erosion. Surfaces of abandoned milled peatlands were aerodynamically smooth, therefore exposed surface elements are subject to strong erosive forces during wind events. The greatest subsidence on abandoned milled peatlands occurred in the spring, prior to the surface movement of particles. Erosion during the summer could not be clearly detected. The instability of the peat surface remains a constraint for the restoration of abandoned milled surfaces.

INTRODUCTION

Peatlands in Canada and northern Europe have been drained and cleared over extensive areas for agricultural production or peat extraction (Lappalainen 1996). After drainage has ceased, subsidence of these peatlands continues (Mirza and Irwin 1964; Millette 1976; Irwin 1977; Schothorst 1977; Parent, Millette & Mehuys 1982; McLay, Allbrook & Thompson 1992; Price and Schlotzhauer 1999; McNeil *et al*. 2000). This subsidence is usually attributed to shrinkage, compression and biochemical oxidation of the peat (Schothorst 1977). However, wind erosion can also be an important cause of subsidence, at least in agricultural settings when the soil is dry and broken by farm machinery (Irwin 1977; Lucas 1982; Parent, Millette & Mehuys 1982). By comparison to mineral soils, wind erosion of organic soils has received scant attention. It has only recently been considered in milled peatlands (McNeil *et al.* 2000).

Peat is usually extracted from peatlands using the modern method of milling (Crum 1988, pp. 182-188; Frilander, Leinonen & Alakangas 1996). A peatland is first drained by ditching at 20-40 m intervals and the surface vegetation is removed. The soil surface is repeatedly harrowed to a depth of 5 to 20 cm to break up and dry the peat. In North America, the milled peat is then collected using vacuum collectors. In this manner, 5 to 10 cm of peat may be removed per year over several decades. In Canada, once milled peatlands are abandoned, fibric to sapric, sphagnum or sedge peat deposits remain (usually <1 m deep), often with a surface layer of harrowed peat. Milled surfaces are large (up to 5 km^2), flat and bare of vegetation. Their subsequent recolonization by plants is very slow (Salonen 1987; Desrochers, Rochefort & Savard 1998). Several barriers have been invoked to explain this problem, including the paucity of propagules (Salonen, 1987; Salonen & Setälä 1992; Poschlod 1995; Rochefort 2000), surface drought and inhospitable microclimate at the peat surface (Price 1996; Price, Rochefort & Quinty 1998; Rochefort 2000; Tuittila *et al.* 2000) and low concentrations of mineral nutrients (Salonen 1994). However, the instability of the abandoned substrate also appears to be a critical factor (Rochefort 2000). Wind erosion has been suspected to cause, in part, this surface instability. First, the lack of vegetation, long fetches and relatively smooth surfaces should allow strong erosive forces near the surface during high winds. Peat is also very light when dry (Puustjarvi and Robertson 1975), and crusted organic soils are fragile as compared to mineral soils (Zobeck 1991a). Furthermore, we have observed particle movement over abandoned milled surfaces when conditions were especially dry. Finally, thicker deposits of loose peat have been found near forest edges downwind of a milled bog, possibly due to deposition of wind-eroded peat (McNeil *et al.* 2000).

Wind erosion involves the interplay between the atmosphere and the ground surface. Wind decreases in velocity near the surface due to frictional drag of the air over the surface elements (Oke 1987, p. 54). This produces a shearing stress, the strength of which depends on wind velocity, air density and surface roughness. Each rigid and homogeneous surface has a characteristic roughness length (z_0), determined from the wind profile. Smooth surfaces have small roughness lengths and consequently steep velocity gradients above the surface during wind events. An exposed particle on such a surface is subjected to the combined atmospheric forces of drag in the direction of the wind, rotation about the particle's axis and lift upwards (Greeley and Iversen 1985, p. 71). Particle movement begins when these forces exceed particle weight and cohesive forces bonding it to other particles. Particles move by suspension, saltation (lift-off and return to the surface) or surface creep. Those in saltation collide with others on the surface and accelerate erosion downwind (Chepil and Milne 1941). However, after rainfall, soil particles bind together forming thin surface crusts once dry, which are much more resistant to wind erosion (Zobeck 1991b).

Surface stability is important for the establishment of vascular plants and mosses in abandoned milled peatlands. The general objective of this study was therefore to evaluate the role of wind erosion in the surface instability of abandoned milled peatlands. Four studies were conducted. First, a wind tunnel study was conducted to evaluate how the erodibility of loose, dry peat varies as a function of the degree of decomposition of the peat. The degree of decomposition is the primary parameter determining the physical properties of peat, including particle size and density (Puustjarvi and Robertson 1975). A second wind tunnel study was conducted to determine how dry, crusted peats resist wind erosion as a function of their degree of decomposition. Third, the characteristic roughness length (z_0) was measured in milled peatlands, as well as in revegetated and natural peatlands, to evaluate the potential for strong erosive forces. Finally, the surface stability and particle movement was measured in abandoned milled peatlands over two summers in order to quantify the role of wind erosion in their subsidence.

METHODS

Wind tunnel experiments

Samples of milled surface peat were collected during July 1999 from actively milled peatlands in the Rivière-du-Loup bog in eastern Québec (47°48'N, 69°31'W). Their degree of decomposition was determined on the von Post scale from peat just below the milled layer. In the von Post test, the decomposition of peat is evaluated along a nine-point scale by squeezing peat in the hand and determining water colour, quantity of extruded material, fibre content and distinctiveness of plant fragments (Parent and Caron 1993). Three replicate samples of milled peat of von Post 3, 4, 5 and 6 were collected for a total of 12 samples. A poorly decomposed peat of von Post 3 is light brown in colour with many long fibres, while a more decomposed peat of von Post 6 is almost black and has low fibre content (Puustjarvi and Robertson 1975). Milled peat was collected with a garden rake and placed in large plastic bags for transport to the wind tunnel facility. Replicate samples were collected in different milled peatlands where possible, and if not, at least 50 m apart on different peat fields.

Gravimetric water content and fresh and dry bulk density were measured for 170 cm^3 samples of milled peat by weighing them fresh and after being dried at 105 °C for 24 hours (Parent and Caron 1993). A particle size distribution of each peat sample was determined using a wet sieving method which allowed for the gentle separation of peats into their smallest component particles. Peat samples were rewetted with the help of a detergent, stirred for over 2 hours, then sifted under water using a series of flat sieves with openings of 6.35, 4.00, 2.36, 1.68, 0.84, 0.36 and 0.15 mm. The size distribution of aggregates was also determined for each sample using a dry sieving technique. Samples were gently sifted dry using a series of flat sieves with openings of 9.50, 6.35, 4.75, 4.00, 2.80, 2.36, 1.68, 0.84, 0.36 and 0.15 mm. For both sieving techniques, fractions were dried at 105 ºC for 24 hours, and expressed as percentages of the pre-sieved dry total.

Wind tunnel tests were conducted at the Trent Wind Tunnel in Peterborough, Ontario. The facility consists of an open loop, suction-type wind tunnel with a 13 × 0.71 × 0.76 m working section designed for simulation of boundary layer flow (for specifications see: http://www.trentu.ca/geography/featuresNet4.html). The exit of the wind tunnel was fitted with a stainless steel mesh with 0.129 mm openings to capture all larger particles in a settling chamber. For each experiment, trays were first prepared in the following manner. Peat samples were dried for 3 days in a glasshouse. Each peat sample was then placed in a tray 200 × 35 × 2.7 cm in size, and the surface was smoothed. For the loose peat experiment, peat-filled trays were left to air dry for 36 hours prior to testing. For the crusted peat experiment, peat-filled trays were sprayed with 2 L water in a fine mist (2.8 mm precipitation), and left to air dry for 36 hours. This treatment produced a thin (2-3 mm) dry crust at the peat surface.

Both the loose peat and the crusted peat experiments followed a random complete block design with four peat types and three blocks. To test each sample, a peat-filled tray was placed in the wind tunnel so that the sample surface was level with the floor of the wind tunnel. Each run at a particular wind velocity lasted 180 s. The sample was subjected to an initial run at a freestream velocity of 2.8 m s^{-1}, as measured at 40 cm height. Freestream velocity was increased by ~2 m s^{-1} in subsequent runs to maxima of 10.4 ± 0.7 m s^{-1} and 12.4 ± 0.1 m s^{-1} (mean ± SD) in the loose and crusted peat experiments, respectively. Lower maximum wind speeds were attained during the loose peat experiment due to the clogging of the exit filter by eroded peat. After each run, eroded peat was carefully collected from the settling chamber, and its weight was determined after drying at 105 °C for 24 hours. Following the final run of each experimental tray, a 155 cm^3 subsample was collected to determine gravimetric moisture content and fresh and dry bulk density, as above. Measurements of eroded peat were converted to a volume basis using the dry bulk density in order to compare the volume of eroded peat between the different peat types.

Following the loose peat experiment, aggregate size distributions were determined for peat eroded at the maximum set velocity (10.4 ± 0.7 m s^{-1}; mean ± SD), using the same dry sieving method used above. This attained velocity is close to that of 11.2 m s^{-1} used by Chepil (1950) to determine the erodibility limit of 0.84 mm in diameter for particles of mineral soil. The equivalent diameter to mineral soil particles of 0.84 mm size was calculated for each peat sample following Chepil and Woodruff (1963) by multiplying the actual diameter of a peat aggregate by the ratio of the bulk density of the peat to that of quartz sand (2.65 g cm^{-3}). Fresh bulk density of each peat sample was used to approximate apparent aggregate density (Chepil and Woodruff 1963, p. 237).

Data for the wind tunnel experiment were analysed using the GLM procedure of SAS statistical software (SAS Institute 1996-1999). Fresh and dry bulk density, and water content of field and experimental peats were analysed together as a function of their degree of decomposition on the von Post scale using analyses of variance (ANOVA) with *a priori* polynomial contrasts. Roughness lengths were analysed versus their degree of decomposition using separate ANOVA with *a priori* polynomial contrasts and repeated measures ANOVA. For both experiments, volumes of eroded peat per wind tunnel run were log-transformed ($\log_{10} x + 0.1$), then analysed versus their degree of decomposition using repeated measures ANOVA. All tests were considered significant at $P < 0.05$.

Field studies

Study area

Field measurements were made at four sites near Rivière-du-Loup in eastern Québec. The Saint-Modeste (SM) site (47°52'N, 69°27'W) was a 23 ha milled peatland abandoned since 1987, adjacent to a 36 ha actively-milled peatland (Figure 3.1). A fringe of forest 5 to 15 m high surrounded the milled peat surface. The site was flat with widely-spaced ditches and almost bare of vegetation (<1% cover). The surface peat in the abandoned section consisted of fibric sphagnum peat (von Post 3 to 4), and peat thickness exceeded 1.2 m. A wind profile was measured at one station in 1998. Stability was measured at two stations in 1998 and at eight stations in 1999 to obtain a better idea of stability across the abandoned milled surface. Maximum fetch was 0.7 to 1.2 km from the south.

The Bois-des-Bel (BB) site (47°48'N, 69°31'W) was a 11 ha milled peatland abandoned since 1980 (Figure 3.1), and surrounded by forested peatland with ~10 m tall trees. The milled surface was flat with a considerable amount of woody debris. Fibric sphagnum peat (von Post 3 to 4) was present at the surface, and peat thickness was over 1 to 3.5 m. Vegetation was sparse (<1 to 3%) and dominated by birch (1 to 3 m tall), ericaceous shrubs and cottongrass (*Eriophorum vaginatum*) tussocks. Maximum fetch was 0.25 km from the south.

The Chemin-du-Lac (CL) site (47°45'N, 69°31'W) was a small abandoned milled surface located along the periphery of a large actively-milled peatland (>3 km^2; Figure 3.1). The surface peat varied from fibric to hemic sphagnum and sedge peat (von Post 4 to 6), and peat thickness was as little as 0.2 m over clay. Surface stability was measured in 1998 and 1999 on abandoned sedge peat 15 m from the edge of actively-milled peatland. This station was protected from the wind to the east by herbs 20 m away (<1 m tall), but had fetches of over 2.5 km from the north and 0.25 to 0.5 km from the south and west before reaching

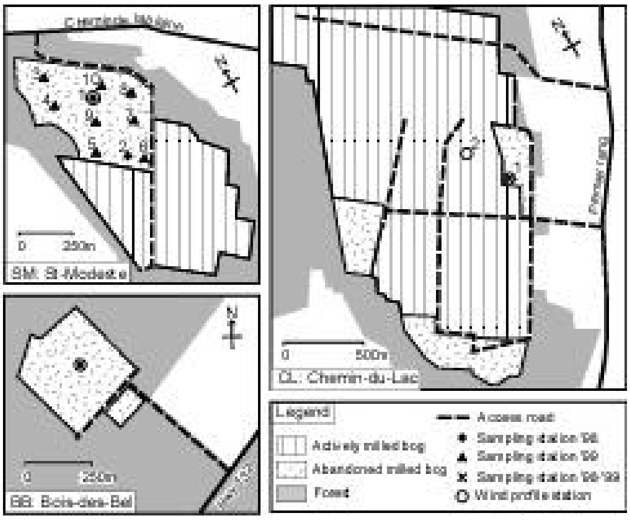

Figure 3.1: Study sites near Rivière-du-Loup, Québec, showing stability and wind profile measurement stations.

elevated access roads (1-3 m tall). Wind profiles were measured over the abandoned surface (CL1) and in a large flat section of the actively milled peatland (CL2).

Wind profiles were also measured at two stations at the Président Ouest (PO) site (47°48'N, 69°31'W). The first station was in a 19 ha section of abandoned milled peatland, well-recolonized (90% cover) with *Eriophorum angustifolium*, *E. vaginatum* and *Carex canescens*. The last two species are tussock-formers, producing scattered dense obstacles around 15 cm tall. The second station was located nearby in a 21 ha open natural bog remnant with 10-15 cm tall hummock-hollow topography and 100% cover by *Sphagnum* mosses and ericaceous shrubs.

Temperature and precipitation data are available up until 1998 for the Saint-Arsène meteorological station (47°57'N, 69°23'W; 1961-1990 normals: Atmospheric Environment Service (AES) 1993; detailed data: Environment Canada, unpublished) and for 1999 from the Bois-des-Bel study site (M. Waddington, McMaster University, unpublished data). Highest monthly mean temperatures were attained in July 1998 (17.6 °C), and June 1999 (17.4 °C). In both years, August was the driest summer month (57.7 and 32.7 mm in 1998 and 1999 respectively). Normals of wind data (1951-1980) are available for the Rivière-du-Loup airport (47°48'N 69°33'W; AES 1982). Prevailing wind direction in May is from the north and in June to September from south to southwest. Mean wind speeds at 10.1 m height from May to September are 12 to 13.5 km hr^{-1} (3.3 to 3.8 m s^{-1}), and maximum sustained hourly speeds are 45 to 58 km hr^{-1} (12.5 to 16.1 m s^{-1}).

Wind profiles

Wind profiles were measured in September 1998 on cloudy days with temperatures of 11 to 17 °C and mean wind speeds of 3.5 to 6.8 m s^{-1} at 2.23 m height. As a result of the windy, cloudy conditions, profiles were considered to have been measured under neutral atmospheric conditions (Oke 1987, pp. 51-55). Wind speeds were measured using five Gill three-cup anemometers installed on a mast at log heights of 0.449, 0.670, 1.000, 1.492 and 2.226 m above the surface. These were connected to a datalogger (model 23X, Campbell Scientific Inc.), and simultaneous wind velocity measurements were taken at 15 s intervals for 39 to 74 minutes, depending on the site (Table 3.1). Mean wind speeds were calculated over the entire measurement period. Wind profile parameters were then calculated from the logarithmic equation (Oke 1987, p. 116):

$$u_z = (u_* / k)\ln[(z - d)/z_0] \qquad (1)$$

where u_z = mean wind velocity at a given height z; u_* = friction velocity; k = Von Karman's constant (0.40); d = zero plane displacement height; and z_0 = roughness length. Parameters u_*, d and z_0 were chosen using a least squares fit technique (Stearns 1970). Values of these parameters were substituted into equation 1 and those that produced the highest R^2 between calculated and measured mean wind speeds were chosen as the best solution.

Surface stability

Stations were sampled in 1998 at approximately one-month intervals from June 16 to October 3, and in 1999 at approximately two-week intervals from May 14 to September 29. Five measurements were taken at each station and sampling date: 1) gravimetric water content of surface peat, 2) dry bulk density, 3) change in surface elevation and microtopography, 4) amount of saltating particles, and 5) amount of wind blown dust. Gravimetric water content and dry bulk density were measured twice at each station by taking two 170 cm^3 samples of surface peat to a depth of 4.3 cm. Changes in surface elevation and microtopography were determined after all ground frost had melted using a horizontal wire installed parallel to the peat surface. The horizontal wire consisted of a 30 cm section of stiff wire elevated ~10 cm above the peat surface. The wire was attached to supports on both ends that rested on the peat surface. The base of each support consisted of a rectangular frame of stiff wire covered with cloth to prevent undercutting erosion, and was firmly anchored to the surface with 10 cm long pins. Bases of each support remained flush with the initial, cloth-covered surface throughout the field season. Height to a 3 mm diameter point on the surface was measured to 1 mm precision at ten 3 cm distant points along the wire. At each measurement station in 1998, four horizontal wires were installed 6 m apart across the width of a peat field. In 1999, only two horizontal wires were installed per station and located 20-30 m apart.

Table 3.1 : Wind profile parameters measured in actively milled, abandoned and natural peatlands near Rivière-du-Loup, Québec. The R^2 values indicate the fit between the mean measured and calculated wind speed profile.

Station	Surface characteristics	Plant cover (%)	Fetch (m)	Duration (min)	Zero plane displacement (d) (mm)	Roughness length (z_0) (mm)	Friction velocity (u_*) (m s^{-1})	R^2
CL1	abandoned, but 15 m from milled zone	<1	250	43	-3	3.6	0.40	0.98
CL2	actively milled	0	300	45	4	5.2	0.45	0.99
SM1	abandoned with little woody debris	0	250	71	4	2.1	0.32	0.98
BB	abandoned with much woody debris and scattered birches, cottongrasses and ericaceous shrubs	<1-3	180	74	-3	18.8	0.38	0.99
PO1	abandoned with rhizomatous and tussocky cottongrasses and sedges	90	370	53	14	41.3	0.60	0.99
PO2	natural bog with *Sphagnum* hummocks, low ericaceous shrubs	100	330	39	14	40.9	0.65	0.99

Deposition of particles transported by saltation was measured between sampling periods using pitfall traps. They consisted of 1 L plastic containers sunk into the peat surface with 1 cm protruding above the surface to prevent the capture of peat during rain events. The mouth of these containers was 10 cm in diameter and a baffle was placed inside the trap to prevent the escape of deposited peat. In 1998, four pitfall traps were placed 6 m apart at each station, while in 1999 only two pitfall traps were installed 20 to 30 m apart at each station.

Wind-blown dust was captured between sampling dates using Fryrear traps (Fryrear 1986), modified with rain hoods (Shao *et al.* 1993). Air and particles enter these traps through a 10 cm^2 opening directed windward by a weather-vane. The air exits via a 60 µm screen, capturing larger dust particles. Their efficiency compares favourably to other dust trapping devices (Shao *et al.* 1993). In 1998, three traps were placed at each station on a mast with the base of their openings at heights of 0.15, 0.37 and 1 m in order to determine the optimal trap height. This height was found to be 0.15 m, and in 1999 only one Fryrear trap was installed per station at this height.

RESULTS

Wind Tunnel Experiments

Peat characteristics

Fresh and dry bulk densities increased linearly with increasing degree of decomposition (Figures 3.2a and 3.2b). Bulk densities of field peat were however always lower than those of peat in experimental trays. Water content of the peat decreased linearly with increasing degree of decomposition (Figure 3.2c). Water content of peats of tray peats were not significantly different from each other, but were significantly drier than field peats. Particle size distributions of peat samples as determined by wet sieving varied with the degree of decomposition (Figure 3.3). More decomposed peats had a higher proportion of finer particles, especially those less than 0.15 mm in size. One sample of von Post 6 was composed of strong aggregates that could not easily be broken down to the finest particles,

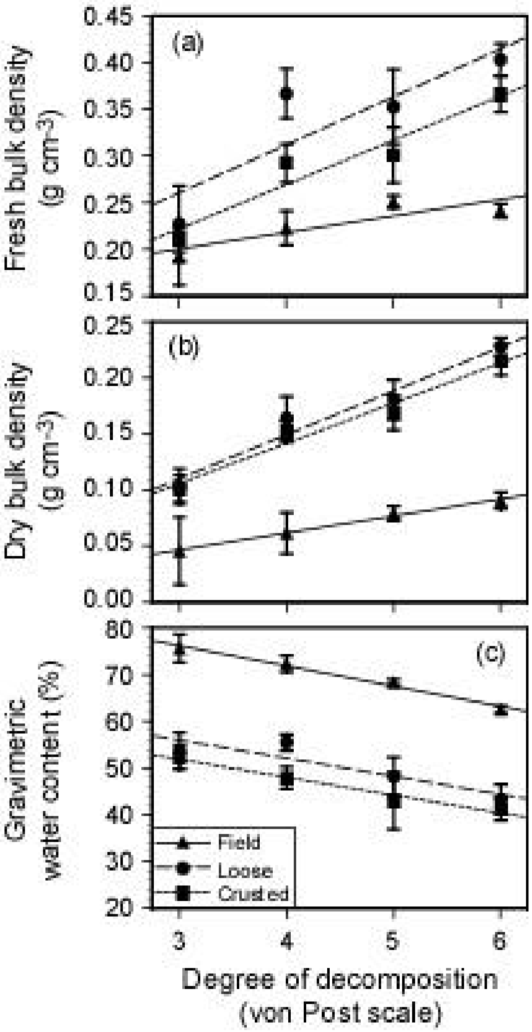

Figure 3.2: Mean values of a) fresh bulk density, b) dry bulk density and c) gravimetric water content of peats of increasing degree of decomposition as measured on the von Post scale for samples of milled field peat (triangles), loose peat in experimental trays (circles) and crusted peat in experimental trays (squares). Standard errors are shown.

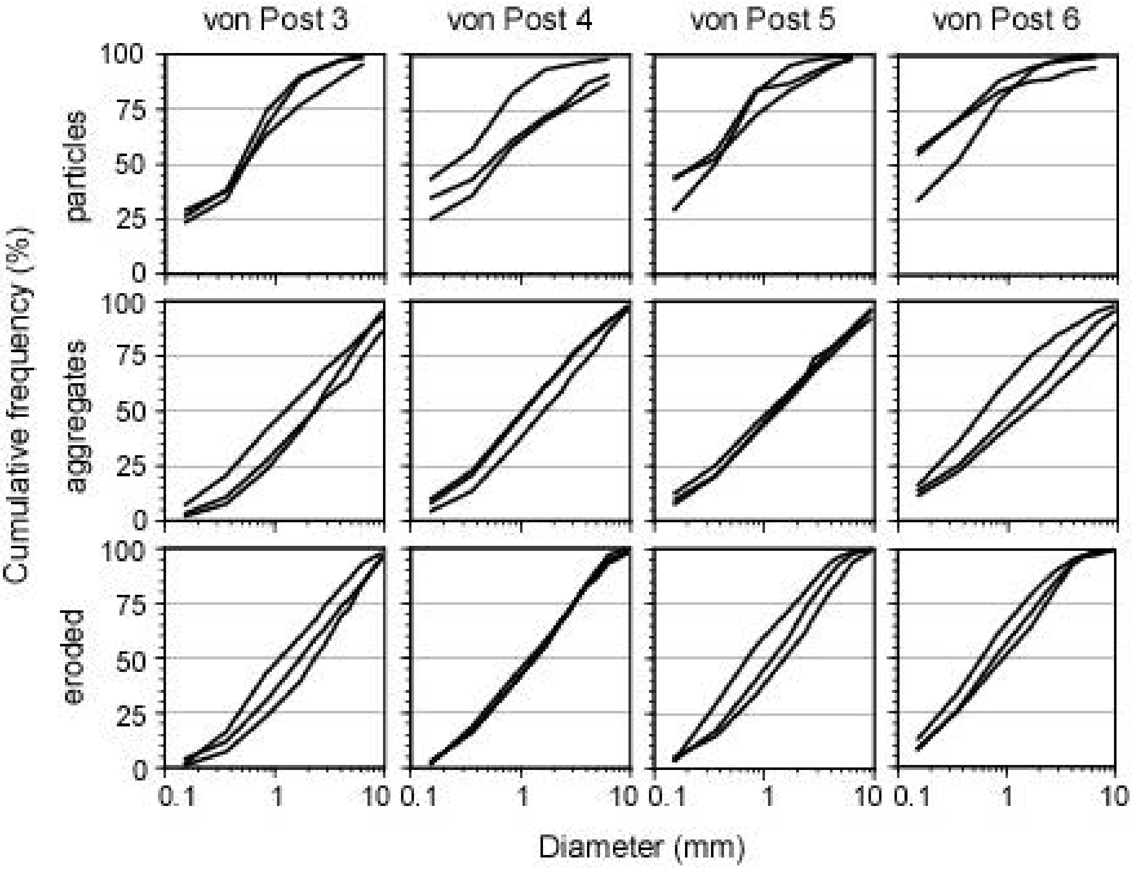

Figure 3.3: Cumulative size distributions of particles of milled peat (top row), aggregates of milled peat (middle row) and aggregates of peat eroded during the loose peat wind tunnel experiment at an attained velocity of 10.4 ± 0.7 m s-1 (mean ± SD; bottom row), for peats of increasing degree of decomposition on the von Post scale. The three replicate samples are shown.

and as such, the particle size distribution of this peat appears coarser. Only slight differences were observed in size distributions of aggregates between peats of increasing degree of decomposition, as determined from dry sieving (Figure 3.3).

Loose peat experiment

During initial runs at the lowest wind speed (2.8 m s^{-1}), roughness length (z_0) of the trays decreased linearly with increasing degree of decomposition of the peats. However, in all following runs (>4.6 m s^1), there was no difference in roughness between peats. Roughness lengths in all trays decreased with increasing wind speed, likely due to deflation of the peat surface by erosion. Peat in this experiment easily eroded from the trays (Figure 3.4). Eroded volume increased with increasing wind speed, but the overall erosion patterns as determined by repeated measures analyses were not significantly different between peats of increasing degrees of decomposition. Neither are differences apparent between peat types in the threshold velocities of initial particle movement (Figure 3.4). However, dry sieving shows that size distributions of aggregates eroded at the highest wind velocity differed from aggregates of milled peat in experimental trays (Figure 3.3). A size limit of erosion is apparent for each peat type, above which little peat was eroded. The 99% percentile size limit decreases with increasing decomposition on the von Post scale (Figure 3.5). Loose particles of poorly-decomposed peats are lighter, consequently larger particles are eroded as compared to more decomposed peats. These actual size limits closely follow the limits of erodibility of the peats predicted by their equivalent diameter to particles of mineral soil 0.84 mm in size, as calculated from their bulk densities relative to mineral soil (Figure 3.5).

Crusted peat experiment

At all wind speeds, roughness length (z_0) of the trays decreased linearly with increasing degree of decomposition of the peats. The roughness length also decreased with increasing wind speed, even though little or no deflation was observed, possibly due to elastic compression of the peat at high wind speeds. Throughout this experiment, the crusted peat surfaces were very resistant, with very little erosion of peat, even at attained freestream velocities over 12 m s^{-1} (Figure 3.4). Eroded peat volumes were fifty to a hundred-fold less

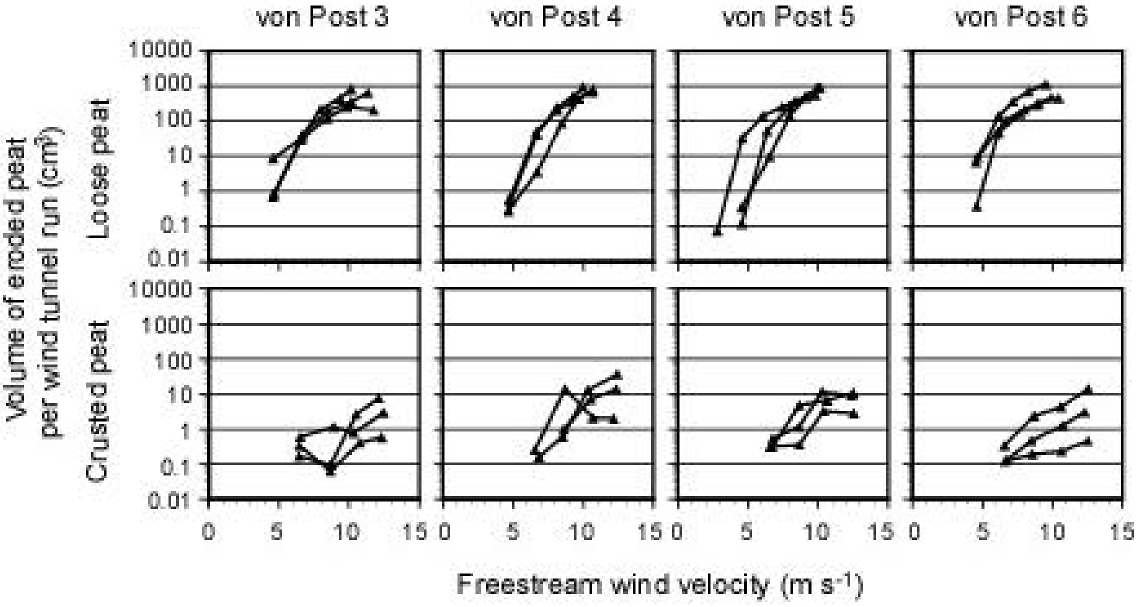

Figure 3.4: Loss of volume sequences as a function of freestream velocity in the wind tunnel for loose peats (top row) and crusted peats (bottom row) of increasing degree of decomposition on the von Post scale. The three replicate samples are shown.

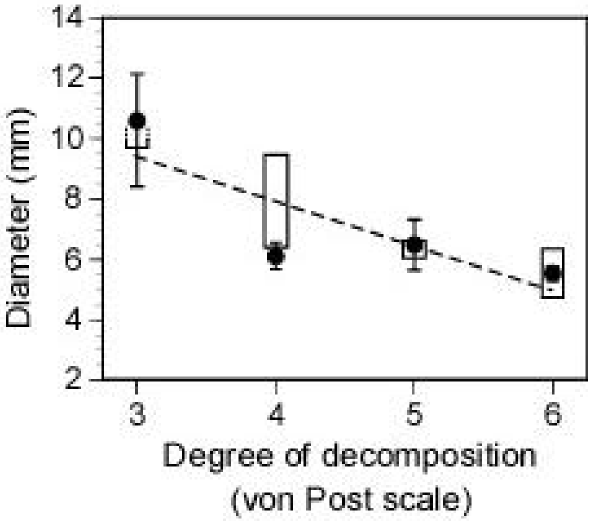

Figure 3.5 : Largest predicted (circles) and actual (rectangles) aggregate sizes of peat eroded in the loose peat experiment as a function of their degree of decomposition on the von Post scale. Predicted largest aggregates were determined by calculating the equivalent diameter for each peat corresponding to mineral soil particles of 0.84 mm in diameter (mean ± SE). Fresh bulk density values from the loose peat experiment were used in the calculations. Actual largest peat aggregates were determined from the 99% percentile of aggregate size distributions for peats eroded in the wind tunnel at 10.4 ± 0.7 m s-1 (mean ± SD, n = 12; Figure 3.3). The rectangles show the range of largest particle sizes for the three replicates. For peats of von Post 3, only one of the three samples reached this 99% limit at 9.5 mm.

than in the loose peat experiment. Peat eroded mostly from the leading edge of the trays as plaques, due to edge effects of the trays. The overall erosion pattern as determined by repeated measures analyses was not significantly different between peat types. Neither were there differences in threshold velocities of initial particle movement nor in volumes eroded at the highest wind velocity tested. Particle size distributions of eroded aggregates could not be determined due to insufficient volumes of eroded peat.

Field wind profiles

Wind profiles measured in milled peatlands closely matched the expected linear relationship between wind speed and the natural logarithm of height ($R^2 > 0.97$; Table 3.1). Actively milled surfaces had similar roughness lengths (z_0) as unvegetated, abandoned milled peatlands with little woody debris. Roughness length was much higher over rougher surfaces, as seen at Bois-des-Bel, which had considerable woody debris. At the revegetated milled peatland and natural peatland at Président Ouest, the profile was displaced upwards by 14 cm as a result of the vegetation cover. The roughness length of the revegetated milled peatland was remarkably similar to that of natural peatlands, even though there was considerable difference in the vegetation (rhizomatous and tussocky cottongrasses and sedges versus *Sphagnum* hummocks with low ericaceous shrubs).

Stability of milled surfaces

The 1999 data for Saint-Modeste illustrate the general patterns observed of surface stability. In mid-May, the surface was initially smooth to, more commonly, bumpy in appearance (Figure 3.6). This roughness is also reflected in the initial within-wire standard deviation (Figure 3.7). The seasonal progression of the surface can be divided into a ‘spring’ phase from May to mid-June and a ‘summer’ phase from mid-June to the end of September (Figure 3.7). During the spring phase, the mean elevation of the peat surface dropped by 4.2 mm. However, moisture remained unchanged at around 80%, and almost no material was caught in pitfall or Fryrear traps. During the summer phase, there was a smaller drop in the peat surface of 2.7 mm. The surface became smoother as the season progressed (Figure 3.6), which is also reflected by the reduction of the within-wire standard deviation

Table 3.2 : Changes and rates of change of surface elevations of milled peatlands near Rivière-du-Loup, Québec, during the 1998 and 1999 field seasons (mean ± SD), as measured using several horizontal wires placed parallel to the surface. Measurements are made with respect to the initial surface. For 1999, overall values are shown as well as values for the spring period (Julian day 134 to 161, i.e., May 14 to June 10) versus the summer period (Julian day 161 to 272, i.e., June 10 to September 29).

		Saint-Modeste			Bois-des-Bel			Chemin-du-Lac		
Year	Julian date	n	Change (mm)	Rate (mm week^{-1})	n	Change (mm)	Rate (mm week^{-1})	n	Change (mm)	Rate (mm week^{-1})
1998	167-283	8	-3.1 ± 10.8	-0.18 ± 0.65	4	-6.5 ± 2.5	-0.39 ± 0.15	4	-2.0 ± 1.2	-0.12 ± 0.07
1999	134-161	16	-4.2 ± 1.9	-1.09 ± 0.50	2	-7.1 ± 0.4	-1.83 ± 0.09	2	-2.0 ± 1.9	-0.51 ± 0.49
1999	161-272	16	-2.7 ± 3.0	-0.17 ± 0.19	2	-5.0 ± 2.5	-0.31 ± 0.16	2	-7.5 ± 1.1	-0.47 ± 0.07
1999	134-272	16	-6.9 ± 2.9	-0.35 ± 0.15	2	-12.0 ±2.1	-0.61 ± 0.11	2	-9.5 ± 3.0	-0.48 ± 0.15

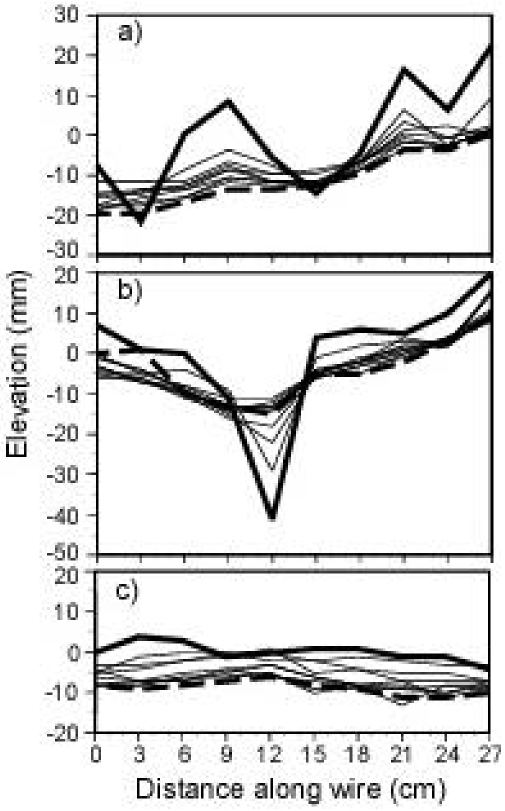

Figure 3.6: Three microtopographic profiles of milled peat surfaces found at the Saint-Modeste site, Québec, in 1999 showing a range of typical surface changes: a) subsidence and smoothing of bumpy microtopography; b) subsidence and filling of cracks; c) subsidence of a flat surface. The thick solid line is the initial surface profile in mid-May (Julian day 134), and the thick dashed line is the surface profile in late September (Julian day 272). Thin solid lines are profiles at intermediate dates.

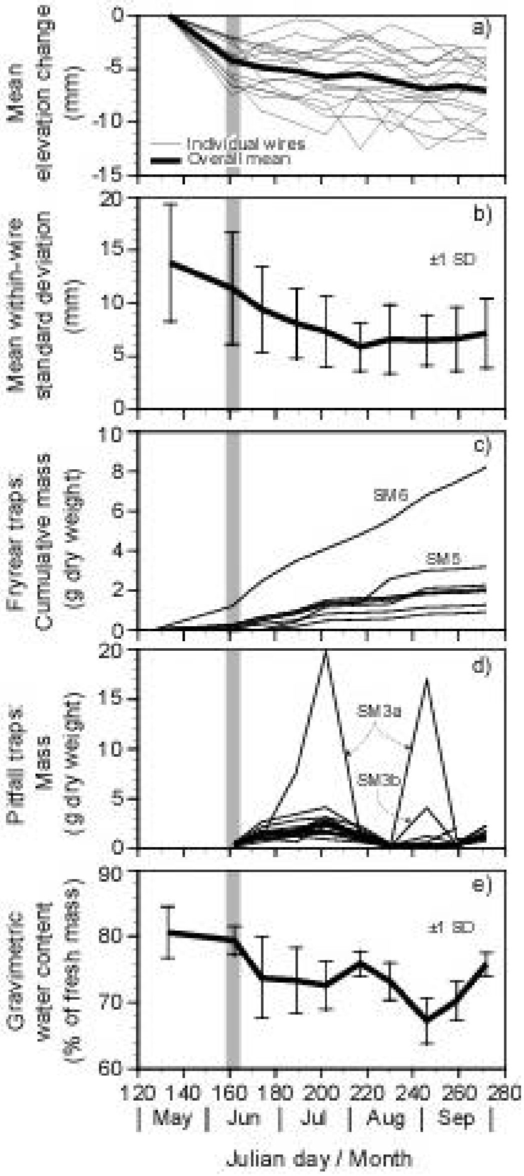

Figure 3.7: Summary of surface stability data for the Saint-Modeste site, Québec, in 1999. Shown are a) the mean elevation changes of the surface as measured from individual horizontal wires (n = 16) and the overall mean elevation change; b) the overall within-wire standard deviation of surface elevation (n = 16; mean ± SD); c) the cumulative dry mass of dust collected in Fryrear traps at sampling stations (n = 8); d) the dry mass of peat collected in pitfall traps (n=16); and e) the gravimetric water content of the surface peat (n = 16; mean ± SD). The broad gray line indicates the transition between the spring phase when no peat movement is observed and the summer phase when peat movement begins.

(Figure 3.7). The surface dried, reaching a mean water content of 68% by early September. Dry bulk density of surface peat remained unchanged throughout both phases (0.14 ± 0.01 g cm^{-3}, mean ± SD). Dust and larger particles were captured at most stations during this period. Most dust was collected in Fryrear traps adjacent to the actively milled sites (stations SM5 and SM6), but larger particles were mostly collected in pitfall traps furthest from the milled area (station SM3). Overall, the weekly rate of subsidence in 1999 during the 'spring' phase was over six-fold greater than during the 'summer' phase (Table 3.2). In 1998 and 1999, rates of subsidence in the summer were similar although more variable due to deposition at some sites. In 1998, less peat was captured in the Fryrear and pitfall traps than at most stations in 1999. The moisture content of the surface peat in 1998 reached a minimum of 65 ± 12 % (mean ± SD), similar to that in 1999.

At Bois-des-Bel, the general patterns were similar to Saint-Modeste in 1999, with definite spring and summer phases of surface subsidence (not shown), but rates of subsidence were approximately double those at Saint-Modeste for both years (Table 3.2). Rates of subsidence during the summer were similar in 1998. For both years however, little peat was caught as dust or larger particles (0.25 g cumulative total in Fryrear trap, 2 g biweekly maximum in pitfall traps in 1999). The moisture content of the surface peat reached a minimum of 50 ± 9% and 60 ± 11% (mean ± SD) in 1998 and 1999 respectively. Dry bulk density remained unchanged (0.15 ± 0.00 g cm^{-3}, mean ± SD).

At Chemin-du-Lac, the patterns of stability were different than at other sites. In 1999, there was no difference in the rate of subsidence between spring and summer (Table 3.2), but subsidence was four-fold higher than in 1998. For both years, there was a great deal of peat trapped as dust or as larger particles. In 1998 and 1999 respectively, there were totals of 16 g and 11 g caught in the Fryrear traps, and maxima of 125 g (monthly, 1998) versus 16 g (biweekly, 1999) caught in pitfall traps. In both years, ditches were partly filled with peat after mid-summer windstorms. This site also was the driest with water content of surface peat dropping to 40% and 55% in 1998 and 1999, respectively. Dry bulk density remained unchanged throughout the season (0.22 ± 0.00 g cm^{-3}, mean ± SD).

DISCUSSION

Erodibility of milled peats

The wind tunnel experiments show that loose and dry milled peat is easily eroded by wind. However, differences in threshold velocity of initial particle movement were not found between peats of increasing degree of decomposition. Differences may exist, but more samples and smaller incremental increases in wind velocity would be required to detect them. Differences between peats did become evident at high wind speed. The concept of a 0.84 mm equivalent diameter limit for erodible particles (Chepil 1950; Woodruff and Siddoway 1965) appears to apply well to light aggregates such as peats, even though they are six to ten-fold lighter than mineral soils. Their erodibility at high wind speeds decreases with increasing degree of decomposition, as a result of the increasing particle density. The erodibility of loose peats at high wind speed can be evaluated simply by measuring their fresh density. However, problems may exist in scaling-up this conclusion to the field situation. Roughness lengths over the peat surfaces in the wind tunnel were two to three orders of magnitude lower than those observed in the field, and wind velocities were very high. Consequently, smaller peat particles may erode in the field situation.

Once even a thin crust is formed after being rewetted and dried, all peats become very resistant to erosion by wind in the wind tunnel. Since crust strength increases with rainfall intensity (Farres 1978), crusted peats in the field should be even more resistant to wind erosion since they periodically receive more intense rainfall than that applied in the wind tunnel experiment. It is expected that fibric peats would be more resistant to erosion by abrasion due to their higher fibre content.

Roughness of milled surfaces

In term of roughness lengths (z_0), milled peatlands with little woody debris more closely resemble agricultural fields tilled by disks (z_0 = 1.6 to 2.7 mm; Saleh, Fryrear & Bilbro 1997) or fallow ground (z_0 = 1-4 mm; Wieringa 1993) than natural bogs with their hummock-hollow topography. Steep wind velocity gradients consequently occur near the surface of milled peatlands during wind events, producing strong erosive forces. Climate normals for wind (AES 1982) show that strong wind events do periodically occur during the summer. Particles on the surface would be subject to strong drag and lift during windstorms, favouring their movement.

Woody debris increases the roughness length substantially and should provide protection against wind erosion. However, once milled peatlands are revegetated with rhizomatous and tussocky cottongrasses and sedges, their roughness length essentially returns to values that characterize natural bogs, at least at high wind speeds. In sufficient density and aerial extent, rhizomatous and tussock-forming species therefore act to restore wind velocity gradients and consequent momentum and energy transfer over milled surfaces. This may explain in part their efficiency as companion plants for the restoration of bog plant communities (Grosvernier, Matthey & Buttler 1995).

Role of wind erosion in subsidence

Surfaces of milled peatlands near Rivière-du-Loup subsided during spring and summer 1998 and 1999, but this phenomenon could not be clearly linked to wind erosion. The subsidence during the spring phase in 1999 at Saint-Modeste and Bois-des-Bel occurred prior to any movement of particles on the surface and was greater than during the summer. This subsidence may have been even greater since measurements only began in late spring. The peat surface did not dry substantially during this spring period, indicating that shrinkage of the peat upon drying did not play a major role in the subsidence process, as is sometimes observed (Schothorst 1977). The initial bumpy appearance of the peat surface appears to have been caused by needle ice that is commonly observed in milled peatlands during the spring and fall (E. Groenveld, Université Laval, pers. comm.). Organic soils are especially prone to disturbance by needle ice formation (Brink *et al.* 1967). It is possible that the spring subsidence is related to the consolidation of surface peat after the melting of needle ice, although further study is required to test this hypothesis.

During the summer phase when the surface dried, there was no strong evidence of wind erosion of abandoned surfaces. No sudden changes in surface elevation were observed as would be expected if erosion occurred during strong wind events. Wind speed was not monitored during field seasons, but windstorms did occur. At Bois-des-Bel, the summer subsidence (6.5 mm in 1998; 5.0 mm in 1999) was similar to the mean subsidence rates measured at that site in 1999 using different techniques (5.8 to 6.8 mm yr^{-1}; McNeil *et al.* 2000). Carbon oxidation was apparently sufficient to explain subsidence observed at Bois-des-Bel. This may also be the case for Saint-Modeste. However, the observed accumulation of loose peat at the downwind edge of the Bois-des-Bel peatland (up to 3.8 mm), suggests that displacement of surface peat by wind has taken place, at least over the long term. The Chemin-du-Lac site was the driest and had by far the most captured peat particles, yet there is no clear pattern of subsidence by wind erosion. Inputs of particles from adjacent actively milled fields were certainly plentiful at this site, and deposition of particles may have compensated for any wind erosion that might have occurred.

Several factors may have helped to stabilize the surface during both summers. Surface crusts most likely played a key role, since they dramatically reduce the erodibility of dry peat, as observed in the wind tunnel experiment. Surface moisture was also likely important. Peat is very absorbent (Puustjarvi and Robertson 1975), therefore regular precipitation would increase peat density and reduce its erodibility. Furthermore, moist soils have stronger cohesion than dry soils as a result of adsorbed water films (Chepil 1956). It is therefore possible that wind erosion only becomes important in abandoned milled peatlands during drought years. Greatest particle movement was observed when surface peat was driest.

CONCLUSIONS

This study demonstrates that peat is highly erodible when loose and dry. The erodibility of different peats can be evaluated by determining their fresh density and proportion of aggregates less than 0.84 mm in equivalent diameter. Abandoned milled surfaces are also aerodynamically smooth with consequent steep velocity gradients above the surface during wind events. However despite these favourable conditions, wind erosion during the summer was not an important cause of subsidence in milled peatlands. This was probably due, in part, to the crusting of the surface that makes them very resistant to wind erosion. It is possible that wind erosion takes on a more important role during drought years. Nevertheless, surfaces of abandoned milled peatland still appear to be unstable, especially during the spring, but due to causes other than wind erosion.

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CHAPITRE 4

GERMINATION AND SEEDLING GROWTH OF BOG PLANTS IN RELATION TO THE RECOLONIZATION OF MILLED PEATLANDS[3]

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[3] Campbell, D.R. & Rochefort, L. (article soumis) Germination and seedling growth of bog plants in relation to the recolonization of milled peatlands.

RÉSUMÉ

Deux expériences ont été effectuées pour évaluer le potentiel des plantes vasculaires à germer et s'établir dans les tourbières aspirées et abandonnées et pour déterminer si des caractères autécologiques facilement mesurables peuvent prédire leur succès. Vingt espèces d'herbacées, d'arbustes ou d'arbres communes soit dans les tourbières exploitées et abandonnées ou dans les tourbières naturelles du Québec ont été étudiées. Une première expérience en serre avait pour but de tester l'effet de l'entourbement sur le potentiel de germination et d'émergence des espèces. Une deuxième expérience en chambre de croissance a été effectuée pour mesurer la croissance des plantules sous conditions optimales entre une et trois semaines après leur germination. Dans l'expérience sur l'entourbement, l'émergence pour la plupart des espèces diminue de façon exponentielle en fonction de la profondeur d'enfouissement. La pente de cette relation exponentielle est fortement corrélée avec la masse des graines et les graines plus petites que 0.1 mg sont les plus sensibles au phénomène. Dans l'expérience de croissance, le taux relatif de croissance n'est pas corrélé avec la masse des graines, mais plutôt avec l'aire spécifique des feuilles, sauf pour les espèces avec des graines de moins de 0.01 mg. L'évaluation de la masse des graines et de l'aire spécifique des feuilles devraient aider à déterminer le taux de survie des plantules dans les tourbières exploitées. Des interventions plus ciblées pourraient alors être entreprises pour faciliter la restauration des espèces désirées dans de telles tourbières.

ABSTRACT

Two controlled experiments were conducted to evaluate the potential for vascular plants to germinate and establish in milled peatlands and to assess whether easily measured plant traits can be used to predict their probable success. Study species included twenty species of perennial herbs, shrubs and trees occurring frequently in undisturbed bogs or abandoned milled bogs in Québec, Canada. First, a glasshouse experiment was performed to test the effect of burial under peat on germination and seedling emergence. Second, a growth chamber experiment was conducted to measure relative growth rate and other growth parameters of seedlings between 1 and 3 weeks of age. In the burial experiment, seedling emergence decreased exponentially with peat depth for most species examined. The slope of the exponential decline varied between species and was strongly correlated with seed mass. Seeds less than 0.1 mg in mass were most sensitive to burial. In the seedling growth experiments, *Betula* species had the highest absolute and relative growth rates, which may help to explain their prevalence in milled bogs. Relative growth rate (RGR) was not correlated with seed mass, however it was strongly correlated with leaf area ratio (LAR) and especially specific leaf area (SLA) of seedlings, except for species with seed mass less than 0.01 mg. Screening of species for seed mass and SLA should help predict their germination and establishment success or failure in milled peatlands and allow more directed interventions to favour the establishment of desirable species in milled bogs.

INTRODUCTION

Plants recolonizing severely disturbed sites are faced with numerous challenges. Seeds or other diaspores must disperse to the site. Once settled, they must break dormancy, germinate, and sequester sufficient resources to establish and grow. During the restoration of disturbed plant communities, desirable species are actively introduced, and environmental conditions are selectively ameliorated to promote their establishment and growth. Prediction of the responses of desirable and undesirable species to critical environmental conditions is consequently essential to the prescription of suitable restoration techniques. One approach to this problem is the identification and screening of plant traits required for species to survive critical environmental filters (Keddy 1992, 1999). A list of easily measured traits would be especially useful for the prediction of successful species at different stages through the recolonization process.

Milled bogs are examples of severely disturbed ecosystems that have been the subject of restoration attempts (Wheeler & Shaw 1995; Rochefort 2000). In North America, peat is usually extracted from bogs using the modern method of milling and vacuum collection (Crum 1988, pp. 182-188). Once abandoned, milled peat surfaces are large (up to 5 km^2), flat and bare of vegetation. Fibric to sapric, *Sphagnum* peat substrates usually remain (<1 m thick), which are acid (pH 3 to 5) and nutrient-poor, although slightly enriched with nitrogen as compared to natural bogs (Wind-Mulder, Rochefort & Vitt 1996). There is no seedbank (Salonen 1987), and natural recolonization after the cessation of extraction activities is very slow (Desrochers, Rochefort & Savard 1998; Bérubé & Lavoie 2000). Dispersal is a major constraint to natural recolonization of milled bogs; species which are abundant in edges, fecund and with good dispersal abilities are favoured (Curran & MacNaeidhe 1986; Salonen 1987; Salonen & Setälä 1992; Poschlod 1995; Chapter 2, this thesis). However, microclimatic and substrate conditions in milled bogs also appear to be harsh and limiting to the subsequent germination of seeds and seedling establishment (Salonen & Setälä 1992; Tuittila *et al.* 2000).

Seed burial in milled bogs appears to be a critical filter for some species that impedes the release of seed dormancy and germination. Seeds may be buried under water- or wind-deposited loose peat and litter, or burial may result from the instability of milled peat substrates (Campbell, Lavoie & Rochefort 2002). Small-seeded species are in general more dependent on light for germination than large-seeded ones (Milberg, Andersson & Thompson 2000), and the emergence of buried seeds has repeatedly been correlated with seed size (old field herbs : Reader 1993; emergent macrophytes : Jurik, Wang & van der Valk 1994; arid woodland species: Jurado & Westoby 1992; rainforest trees : Vázquez-Yanes & Orozco-Segovia 1992). However, the application of this relationship to bog species and the seed size limit for emergence under peat are not known.

Once emerged, seedlings in milled bogs will be subject to surface instability and strong winds (Campbell, Lavoie & Rochefort 2002), hot and dry surface conditions in mid-summer (Price 1997; Price, Rochefort & Quinty 1998), needle ice which forms near the peat surface in spring and fall and damages roots (Quinty & Rochefort 2000; E. Groeneveld, Université Laval, pers. comm.), and low pH, nutrient-poor conditions (Salonen 1994; Wind-Mulder, Rochefort & Vitt 1996). Seedling mortality is consequently high (C. Lavoie, Université Laval, pers. comm.). Seedlings must rapidly attain sufficient size and extend roots to sequester nutrients and especially water to avoid summer drought and heat stress. Large root mass also improves seedling survival after damage from frost heaving (Roach & Marchand 1984). The size of a seedling at any particular time after germination depends on both seed size and its relative growth rate (RGR : growth in mass per unit mass; Causton & Venus 1981). Larger seeds produce larger seedlings soon after germination, and large seed size alone increases early seedling survival in drought-prone or nutrient-poor habitats (Leishman & Westoby 1994; Milberg & Lamont 1997). However, species with higher RGR eventually outperform others if suitable conditions for growth persist. Smaller-seeded species generally have greater RGR (Fenner 1983; Shipley & Peters 1990; Marañon & Grubb 1993; Swanborough & Westoby 1996). Easily measured sub-components of RGR, especially specific leaf area (leaf area per unit leaf mass, SLA) also predict RGR (Lambers & Poorter 1992; Reich, Walters & Ellsworth 1992; Saverimuttu & Westoby 1996; Hunt & Cornelissen 1997).

In this study, two controlled experiments were conducted to evaluate the germination and establishment potential of bog plants and to identify simple traits that predict their responses in milled bogs. A first experiment was conducted to: 1) determine the response of bog plants to burial by peat; 2) evaluate whether seed mass was a good indicator of burial response; and 3) determine the size limit of seeds sensitive to burial. A second experiment on the same species was conducted to : 4) measure relative growth rate and especially root performance of these bog plants; 5) evaluate how seed mass predicts growth parameters; and 6) if RGR can be predicted by easily measured sub-components of RGR.

METHODS

Plant species

Study species were chosen as the most frequent vascular plants occurring in either natural bogs or abandoned milled bogs in Québec (Appendix 4.1). The former species are desirable species for restoration, while the latter species actually recolonize milled bogs but include undesirable species not usually found in undisturbed bogs (e.g., *Betula* species). In total, 21 species were chosen, including polycarpic perennial herbs, shrubs and trees. Fruiting bodies of all species except *Rubus chamaemorus* were collected in the summer and fall of 1997 and 1998 from milled and natural peatlands near Rivière-du-Loup (47°45'N, 69°30'W), Rivière-Ouelle (47°27'N, 69°57'W) and Québec City (46°47'N, 71°03'W). Fruiting bodies were always collected from multiple individuals at each site and pooled. Seeds were cleaned, dried at room temperature for 2 to 3 weeks then stored at 8 °C under dry, dark conditions until the start of stratification treatments. *Rubus chamaemorus* fruits were collected in summer 1995 from Havre Saint-Pierre (50°16'N, 63°35'W) and frozen until 1997 when they were cleaned, dried, then stored as above. Single populations of seeds were used for each species, therefore intraspecific genetic variation was not considered in this study. Nomenclature follows Scoggan (1978-1979), except for *Vaccinium oxycoccus* L.

A subsample of seeds of each species was taken to determine seed dry mass. Seed appendages were removed prior to weighing, except for small-seeded, winged species (*Drosera*, *Kalmia*, *Ledum* and *Rhododendron* spp.). Seeds were dried at 70 °C for 48 hours, then weighed to 0.01 mg precision. For large-seeded species, 20 seeds were weighed individually, while for smaller-seeded species, ten batches of 4, 20 or 100 seeds were weighed.

Experiment 1 : Seed burial and germination

A preliminary experiment on the effects of burial on seedling emergence of study species was conducted in spring 1998 from seed collected in 1997 and stratified, but germination for several species was poor or nil, apparently caused by a fungal infestation during stratification. The experiment was repeated in spring 1999 using mostly seeds collected in 1998 with modifications of pre-treatment conditions. Germination was acceptable for all species, except for *Carex limosa*, *C. stricta* and *Scirpus cespitosus* which had low seed viability. Consequently, the 1999 experiment is reported here for all species except for *C. limosa* and *S. cespitosus*, for which data from the preliminary experiment is presented, since both germinated well in 1998. *Carex stricta* did not germinate well in either year and is not reported.

All species received a stratification pre-treatment. Seeds were placed in Petri dishes on filter paper, wetted with distilled water and allowed to imbibe for 24 hours. Excess water was removed and seeds were spread evenly. Petri dishes were sealed with parafilm, covered in foil and placed at 4 °C for 20 weeks until the beginning of the experiment. Seeds of *Carex oligosperma* and

Rubus chamaemorus were treated differently since no germination was found in the preliminary experiment, although seeds were viable and scarified. Both species have hard, thick seed coats. Their seeds were first stratified in nylon bags in moist peat at 4°C for 54 weeks prior to being removed and stratified as above in Petri dishes for 20 weeks.

Burial treatments were prepared in early May 1999 in the following manner. The substrate was a fibric *Sphagnum* peat, medium-brown in colour when moist (von Post scale 2; pH 3.8; Munsell colour 10YR 4/4). The peat was first passed dry through a 2.36 mm sieve, then wetted with distilled water. Square pots 8-cm wide and 9-cm deep were filled to 2 cm from the rim and levelled. Peat-filled pots were then refrigerated until seeds were sown. Seeds were counted in a room illuminated only by dim incandescent bulbs covered by a green gelatin lighting filter with a red to far red ratio (660: 730 nm) of 0.18, and efforts were made to limit their exposure to this light. Either 25 or 50 seeds were counted per pot, depending on the species, and evenly spread in each pot, except within 1 cm of their edge. Seed coats of *Carex oligosperma* and *Rubus chamaemorus* were scarified with a file. Seeds were buried under one of four depths of sifted peat: 0, 5, 10 or 15 mm, determined on a mass basis and corrected for peat subsidence during watering based on preliminary tests. Peat was added in 2 to 3 mm thick layers and wetted with a fine mist between layers to ensure full hydration of the peat. Seeded pots were refrigerated at 8 °C in the dark for 1-3 days prior to the experiment.

Pots were placed on a single table in a glasshouse and arranged in a two factor (species x burial depth), random complete block design with five blocks. Pots were the randomized experimental unit. Blocks were rotated twice monthly. Pots were watered with a fine mist of deionized water (pH 4.9; conductivity: ~5 $\mu S \cdot cm^{-1}$) every 1 to 3 days from early May to mid-August to maintain the peat surface moist. From mid-August through September when seedling emergence was infrequent, the experiment was watered at 3 to 5 day intervals, and the peat surface dried out between waterings. Mean minimum and mean maximum air temperatures in the glasshouse ranged from 15 and 26 °C in May to 18 and 29 °C in July. Every 2 to 3 days and less frequently in August and September, emerged seeds were noted and carefully removed with forceps. After sowing, seed viability of each species was determined on a subsample of 100 stratified seeds. The viability of small-seeded species (< 1 mm diameter) were tested by cutting them open and examining for firm, healthy-looking tissues, while that of larger seeds was evaluated using the tetrazolium test (International Seed Testing Association 1985).

For *Carex limosa* and *Scirpus cespitosus*, the preliminary 1998 experiment was conducted in the same manner as in 1999, with the following differences. Seeds were collected in 1997 and stratified in nylon bags buried in moist *Sphagnum* peat at 4 °C for 22 weeks. Fifty seeds of each species were sown and only three burial treatments were used, namely 0, 5 and 10 mm. The experiment began in early May, but lasted only 43 days until mid-June. Mean minimum and maximum air temperatures in the glasshouse were 16 and 27 °C in May and 15 and 26 °C in June. Seed viability was not determined.

Linear regressions were performed separately for each species on $\ln(x + 1)$ transformed final emergence percentages to test the effect of burial depth. Once emergence for a species was zero across all replicates, subsequent depths were not included in the regression analyses. Correlation analyses were performed to determine how log mean seed mass of species is correlated to the slopes of these negative exponential models and with seedling growth parameters below. Statistical analyses were conducted using the GLM and CORR procedures of SAS statistical software (SAS Institute 1996-1999) and were considered significant at $P = 0.05$.

Experiment 2 : Seedling growth rates

For most species, 1998 seeds were placed in stratification for 25 weeks prior to the experiment, using the same technique as in experiment 1. For *Carex oligosperma* and *Rubus chamaemorus*, 1997 and 1995 seeds were used, respectively, which were first stratified in nylon bags in moist peat at 4 °C for 70 weeks prior to being removed and stratified as above. *Carex limosa* seeds were only collected in summer 1999 and stratified for 6 weeks prior to the experiment.

Square pots 6-cm wide and 155-mL in volume were filled with the same sieved *Sphagnum* peat used in the burial experiment and wetted with a nutrient solution (see below). Between 10 and ~100 seeds were sown per pot on the peat surface, then pots were refrigerated at 4 °C until the start of the experiment. Pots were placed in two growth chambers in a random complete block experimental design with 8 blocks (2 pots per species per block). Pots were the randomized experimental unit. Pots received 14 hours of daylight, minimum and maximum temperatures of 13 and 26 °C, and 242 µmol m^{-2} s^{-1} of photosynthetically active radiation (PAR) provided by 160 W cool white fluorescent tubes and 40 W incandescent bulbs. Pots were watered every 2 to 3 days with 50 mL of a nutrient solution, consisting of a 20% Rorison solution (Booth *et al.* 1993) with NH_4-N and only 5% of the calcium in the full Rorison solution. This solution had nutrient concentrations similar to maxima found in natural and milled bogs in eastern Canada, with slightly elevated levels of phosphorus (Table 4.1). Once germinated, seedlings were carefully thinned to one per pot.

Seedlings were harvested at 7 and 21 days after germination and were carefully removed from pots while immersed in water. Seedlings were scanned digitally using an image scanner at a resolution of 177 pixels cm^{-1}. Leaf area and maximum rooting depth were measured using Scion Image software (Scion Corporation 2000). Rooting depth was defined as the length of the longest root. Seedlings were weighed whole during the first harvest due to the small size of many species, but were separated into component parts (roots, shoot, leaves) at the second harvest and weighed. Mass was determined by drying plant parts at 70 °C for 48 hours, then weighing to 0.01 mg precision.

The following growth parameters were calculated based on means and variances at both harvests of seedling dry weight (W), leaf dry weight (L_W) and leaf area (L_A) (Causton & Venus 1981, p. 21-22 and 30-32): absolute growth rate (AGR, mg day^{-1}), defined as dW/dt where t is time; relative growth rate (RGR, day^{-1}), defined as $(dW/dt)(1/W)$; unit leaf rate (ULR, µg mm^{-2} day^{-1}), defined as $(dW/dt)(1/L_A)$; and leaf area ratio (LAR, mm^2 mg^{-1}), defined as L_A/W. RGR is the product of ULR and LAR. Both components of LAR, specific leaf area (SLA, mm^2 mg^{-1}), defined as L_A/L_W, and leaf weight ratio (LWR, mg mg^{-1}), defined as L_W/W, were only calculated from the second harvest. Three other parameters

Table 4.1 : The composition of the modified Rorison solution used in the seedling growth rate experiment as compared to means (and ranges) of water chemistry of milled and undisturbed bogs in eastern Canada (Wind-Mulder *et al.* 1996). Micronutrients in the Rorison solution (Fe, Mo, Mn, Zn, Cu and B) are not shown. Concentrations are in mg L^{-1}.

	pH	NH_4^+	NO_3^-	P [a]	K	Ca	Mg	S
Modified Rorison solution	3.6 [b]	11.2	0	6.2	15.6	4.0	4.8	12.8
Milled bogs	3.9	3.8	0.1	< 0.1	0.8	0.8	1.0	2.6
	(3.7–5.6)	(0.0–15.8)	(0.0–0.9)	(< 0.1–0.4)	(0.1–4.2)	(< 0.1–8.3)	(0.0–4.9)	(< 0.1–8.4)
Natural ombrotrophic bogs	3.8	1.1	<0.1	< 0.1	0.3	0.8	0.7	0.9
	(3.7–4.0)	(< 0.1–2.8)	(< 0.1–< 0.1)	(< 0.1–0.2)	(0.2–0.4)	(0.2–4.6)	(0.3–3.1)	(0.2–3.2)

[a] Phosphorus in the modified Rorison solution is phosphate, while in bogs it is measured as total phosphorus.

[b] pH of solution after addition to peat-filled pots.

were calculated to assess root performance based on mean values and variances of rooting depth (R_L) at both harvests: the absolute root penetration rate (ARPR, mm day^{1}), defined as dR_L/dt; the root length ratio (RLR, mm mg^{-1}) defined as (R_L/W), and calculated in a manner analogous to the leaf area ratio; and the root length to leaf area ratio (R_L/L_A, mm mm^{-2}). This last ratio was calculated to provide an index of seedling desiccation tolerance (Hendrix *et al.* 1991). Root weight ratios were not calculated because of the extremely low root mass of many species, even at the second harvest. Correlation analyses between growth parameters and mass or RGR were performed with SAS statistical software (SAS Institute 1996-1999). P values were adjusted to experiment-wise error rates using the stepwise Bonferroni adjustment with the MULTTEST procedure of SAS.

RESULTS

Experiment 1 : Seed burial and germination

The timing of germination of unburied seeds varied substantially among species (Figure 4.1), with median germination times ranging from 6 days (*Picea mariana*) to 39 days (*Vaccinium angustifolium*). Buried seeds showed similar patterns as unburied seeds. They generally emerged 2 to 7 days later depending on the species and burial depth, except for *Vaccinium angustifolium* and *V. oxycoccus* which lagged by up to 26 and 14 days, respectively, with 15 mm burial (data not shown). For most species, seedling emergence declined with burial depth (Figure 4.2), and followed negative exponential functions of the form:

$$E = a\,e^{-B_E\,Z} \qquad (1)$$

where E is the percent emergence of viable seeds, ln a is the intercept, B_E is the slope of emergence (mm^{-1}), and Z is the burial depth (mm). However, four species of herbs, namely *Carex oligosperma, Eriophorum angustifolium*, *E. vaginatum*, and *Scirpus cespitosus*, did not show any significant effect of burial on germination, at least within the range of burial

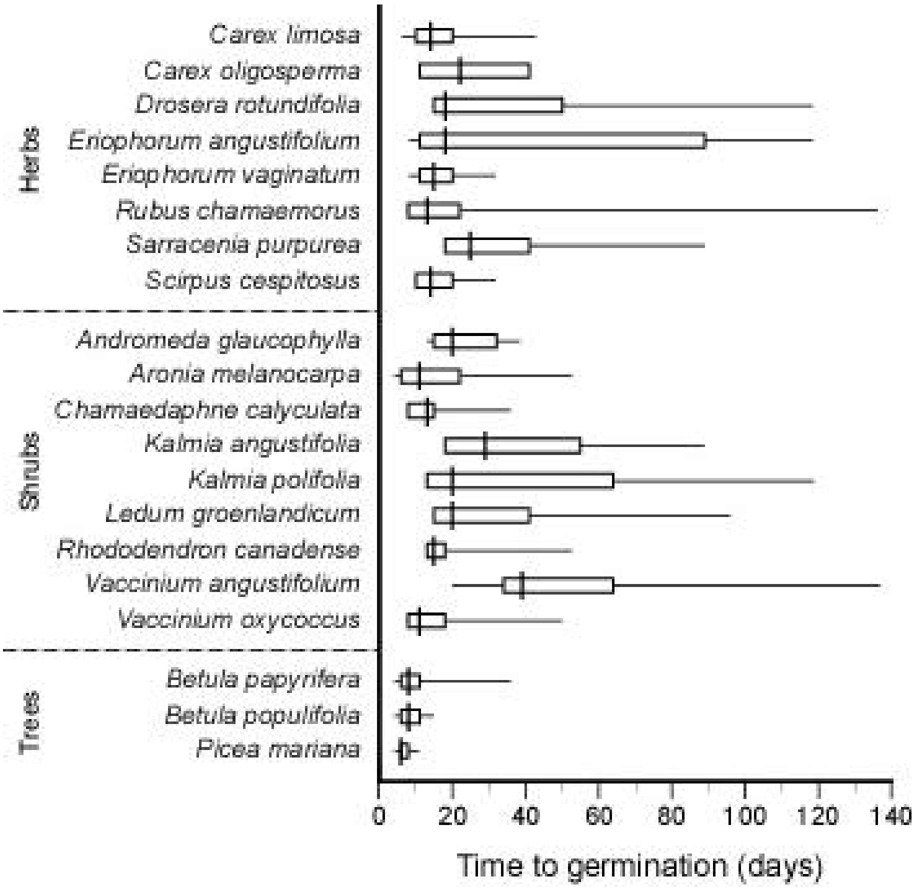

Figure 4.1: Germination timing of surface-sown seeds of herbaceous, shrub and tree species. Horizontal lines show initial and final germination, boxes show 10% to 90% germination and the vertical line shows 50% germination.

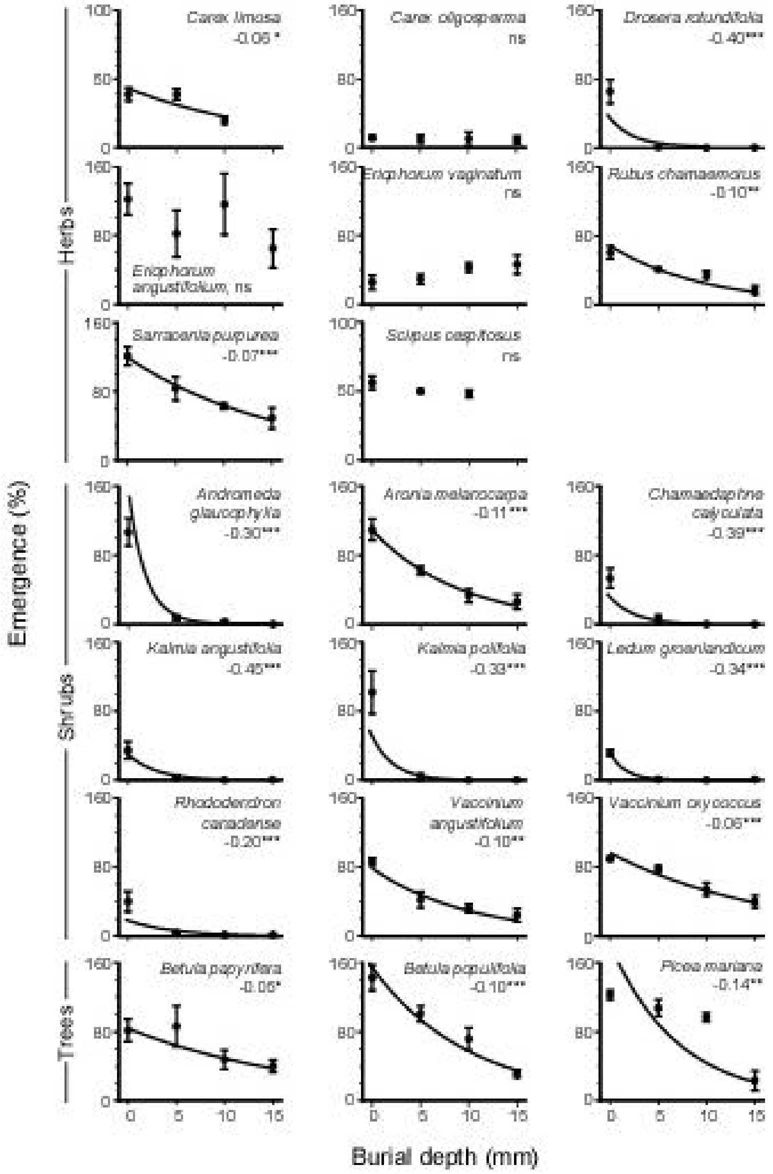

Figure 4.2 : Seedling emergence of study species as functions of seed burial depth (mean ± SE). Emergence is expressed as percent of viable seed sown, corrected using separate seed viability tests, except for Carex limosa and Scirpus cespitosus, which are expressed as percent seed sown. Percent emergence occasionally have values in excess of 100% as a result of seed viability corrections. Curves are fitted to species with significant negative exponential functions between mean emergence and burial depth. Values of significant slopes are given below the species name. Significance of slopes: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

depths tested (0 to 15 mm). The slopes of seedling emergence differed significantly between species ($F_{15, 257} = 11.77$, $P < 0.0001$).

The strength of the decline of seedling emergence with burial varied dramatically among species and was most was most marked in small-seeded species (*Andromeda*, *Chamaedaphne*, *Drosera*, *Kalmia*, *Ledum* and *Rhododendron* spp.), which hardly germinated at just 5 mm depth. Seed mass was strongly correlated with the negative exponential slopes of log emergence (B_E) versus burial depth (Figure 4.3a). Species with seeds lighter than approximately 0.1 mg were most affected by burial.

Experiment 2 : Seedling growth rates

Growth parameters could not be determined for *Carex stricta* due to poor germination and for *Kalmia angustifolia* that had small seedlings that were frequently too light to be weighed even at the second harvest. The remaining species showed wide variation in growth parameters (Appendix 4.2). Their absolute growth rate (AGR) ranged over almost three orders of magnitude and was positively correlated to log seed mass (Figure 4.3b). However both species of *Betula* were outliers, with greater AGR than predicted by seed mass. *Betula* species and *Aronia melanocarpa* had the highest relative growth rate (RGR), while *Carex* species had the lowest. However, log seed mass was not correlated with RGR of study species (Figure 4.3c). None of the sub-components of RGR was correlated with RGR either (Figure 4.4). However, the three smallest-seeded species, *Drosera rotundifolia*, *Kalmia polifolia* and *Ledum groenlandicum*, were outliers, especially for correlations of RGR with LAR or SLA. These small-seeded species have especially high SLA. If these three species were excluded, RGR was strongly correlated with LAR and especially with SLA at day 21, but remained uncorrelated with ULR or LWR (Figure 4.4).

In terms of root performance, *Drosera rotundifolia* barely formed a root system while at the other extreme, *Aronia melanocarpa*, *Betula* spp., *Carex* spp., *Eriophorum* spp. and *Rubus* *chamaemorus* had good root penetration with root lengths of 4 to 9 cm after three weeks (Appendix 4.2). Large-seeded species in general had greater ARPR (Figure 4.3d). High root

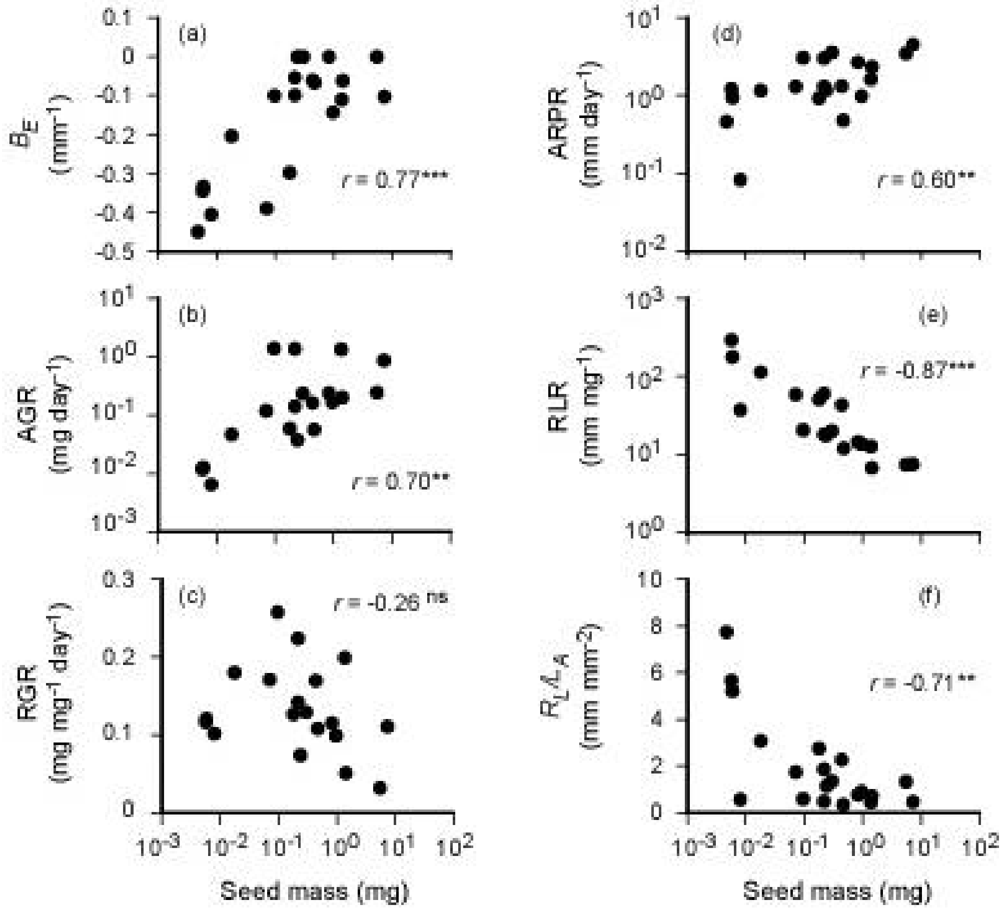

Figure 4.3 : Correlations between log seed mass of bog plants and (a) the slope of the negative exponential functions of seed emergence versus burial (BE), (b) seedling absolute growth rate (AGR, log scale), (c) seedling relative growth rate (RGR), (d) absolute rate of root penetration (ARPR, log scale), (e) overall root length ratio (RLR, log scale), and (f) the ratio of maximum root length to leaf area (RL/LA). Significance of correlations: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. P values were adjusted using the stepwise Bonferroni procedure based on k = 6 tests.

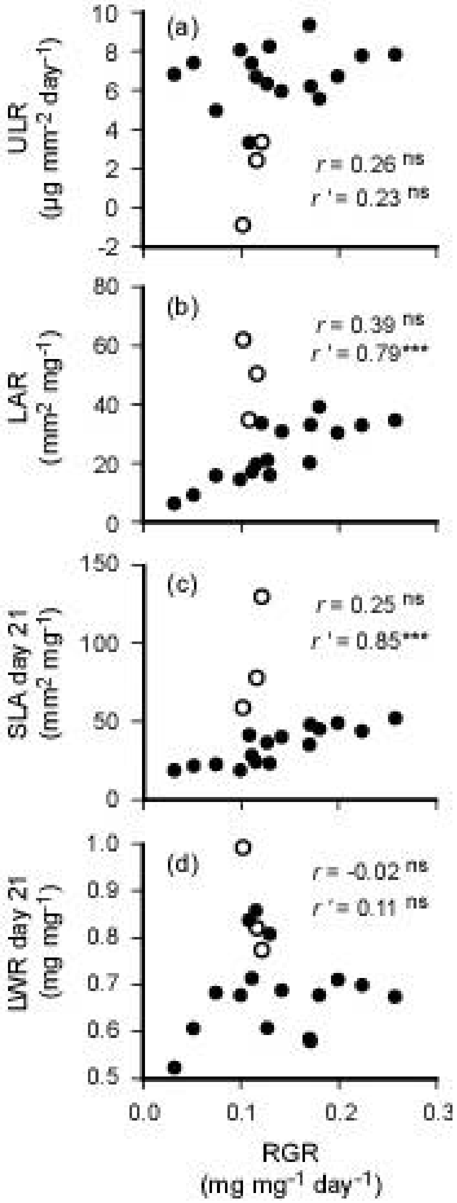

Figure 4.4 : Correlations between relative growth rate (RGR) of bog plant seedlings and (a) unit leaf rate (ULR), (b) overall leaf area ratio (LAR), (c) specific leaf area at day 21 (SLA) and (d) leaf weight ratio at day 21 (LWR). Correlations coefficients are given for the entire data set (r) and without the three smallest-seeded species (r'), which are shown by hollow circles. Significance of correlations: ns, not significant; * P < 0.05; ** P < 0.01; *** P < 0.001. P values were adjusted using the stepwise Bonferroni procedure based on k = 4 tests.

penetration was also associated with high absolute growth rates (log scales, $r = 0.74$, $P = 0.0003$). However, root length ratio (RLR) on log scale was strongly and negatively correlated with log seed mass (Figure 4.3e), indicating that small-seeded species tended to produce much longer and thinner roots in relation to total seedling mass than larger-seeded species. This was especially true for ericaceous shrub species. Small-seeded species also tended to have much higher root length to leaf area ratios (Figure 4.3f), especially species with seeds less than 0.1 mg, except for *Drosera rotundifolia* which was an outlier. Small-seeded species therefore appear to be more tolerant to desiccation than large-seeded species under similar conditions of low soil water tension.

DISCUSSION

Seed burial delays and reduces seedling emergence of most species. The slope of the negative exponential relationship between burial depth and emergence appears to be a useful and innovative measure to quantify the burial response. Light transmission through litter or soil follows a similar negative exponential function with depth, known as the Beer-Lambert extinction law (Facelli & Pickett 1991). But light transmittance is essentially nil beyond 2 mm of dark-coloured, fine-textured soils or litter (Kasperbauer & Hunt 1988; Mandoli *et al.* 1990; Benvenuti 1995), with strong declines in red to far red ratios (Bliss & Smith 1985; Mandoli *et al.* 1990). Although a light extinction curve for the peat used in the experiment was not measured, it was dark-coloured and relatively fine-textured, therefore light transmission should be nil by 5 mm depth. Since light can only act as a cue for germination within the first few millimetres of peat, other factors must cause the observed exponential declines of emergence at deeper burial depth, possibly inhibitory CO_2/O_2 ratios or the death of buried seed and seedlings (Baskin & Baskin 1998, p 149).

The burial response was strongly predicted by seed mass, as in other habitats (Jurado & Westoby 1992; Vázquez-Yanes & Orozco-Segovia 1992; Reader 1993; Jurik, Wang & van der Valk 1994). Burial under peat is especially serious for species with seed mass less than approximately 0.1 mg. Buried seeds may subsequently move to the surface and germinate through processes such as freeze-thaw action or peat decomposition and subsidence. However the ability of study species to survive in the seedbank is poorly known (Moore & Wein 1977; Huopalainen *et al.* 2000). Species with viable seedbanks usually have small and compact seeds (Thompson, Band & Hodgson 1993), which should favour species such as *Andromeda glaucophylla* and *Chamaedaphne calyculata.*

The dormancy syndromes of study species are poorly known, making it difficult to assess their probable germination timing in the field. However, many germinate better after cold stratification (*Aronia*, *Betula*, *Kalmia*, *Picea mariana* and *Rhododendron* spp., Young & Young 1992; *Chamaedaphne calyculata*, Densmore 1997; *Drosera rotundifolia*, Crowder *et al.* 1990; *Rubus chamaemorus*, Taylor 1971; *Sarracenia purpurea*, Ellison 2001; *Vaccinium oxycoccus*, Jacquemart 1997), therefore spring germination likely predominates. Whether in spring or fall, any window for germination and establishment in milled bogs will be constrained by needle ice events in spring and fall (E. Groeneveld, Université Laval, pers. com.) and by hot and dry surface conditions in mid-summer (Price 1997; Price, Rochefort & Quinty 1998), the importance of which varies between sites and years. Differences in germination timing among species suggest that species emerge at different times during these windows and consequently differ in age at which they are confronted with unfavourable conditions. For instance in spring, species with rapid germination (e.g., *Picea mariana*) would be more prone to needle ice damage while those with slow germination (e.g., *Vaccinium angustifolium*) may avoid needle-ice but may only partially germinate before the onset of summer surface drought.

Once emerged, successful establishment of seedlings in milled bogs will depend primarily on their ability to rapidly attain sufficient size, especially their roots, during favourable growth windows. Survival thresholds of seedling size or root length are not known, and would likely vary between sites and years depending on microclimatic conditions. However, the relative survival ability of species can be judged by their absolute growth rate (AGR) and root penetration rate (ARPR). Large-seeded species generally had higher AGR and ARPR. On the short term, seed size is consequently of major importance in determining probable seedling survival. Large-seeded species will be able to extend long and robust roots deeper into the milled peat substrates and thereby avoid drought stress near the surface (Price 1997). Smaller-seeded species which have greater root length to leaf area ratios will be drought-tolerant (Hendrix *et al.* 1991; Marañon & Grubb 1993), but will be faced with greater drought stress near the surface in mid-summer than large-seeded species which can avoid surface drought by extending their roots to greater depth. Absolute growth rate is a function of both seed size and RGR. Given favourable conditions and sufficient time, large-seeded species will be surpassed by smaller-seeded species with higher RGR. Among study species, *Betula papyrifera, B. populifolia* and *Aronia melanocarpa* had the highest absolute growth over three weeks as a result of their high RGR and in spite of their smaller seed size. Actual RGR depends on the intrinsic maximal RGR of the species and on growing conditions. Species were supplied with nutrients at concentrations close to the maximum values observed in milled bogs, therefore RGR and related measures can be considered as maximum values encountered in these environments. However, nutrient concentrations in milled bogs are often up to an order of magnitude lower than in the nutrient solution used in this study. The growth of species with high maximum RGR is more strongly depressed by reduced resources than those with low maximum RGR, and RGR in fertile conditions is not correlated to that in infertile conditions. (Shipley & Keddy 1988; van der Werf *et al.* 1993). Therefore, species with high RGR (e.g. *Aronia melanocarpa*, *Betula* spp., *Rhododendron canadense, Vaccinium oxycoccus*) may have greater reductions in growth under the average nutrient conditions found in milled bogs than those with low RGR (e.g. *Carex* spp., *Drosera rotundifolia, Picea mariana*, *Rubus chamaemorus*, *Sarracenia purpurea*, *Scirpus cespitosus*). However, nutrient concentrations in this study are similar to those used for infertile conditions in previous studies (Shipley & Keddy 1988; van der Werf *et al.* 1993), therefore reductions in RGR may not be severe.

No relationship was found between RGR and seed mass, in contrast to other studies (Fenner 1983; Shipley & Peters 1990; Marañon & Grubb 1993; Swanborough & Westoby 1996). However, this general relationship is relatively weak with lots of scatter (Shipley & Peters 1990) and depends on the species assemblage as well as growth conditions. LAR and especially SLA were the best indicators of RGR, consistent with other studies (Lambers & Poorter 1992; Reich, Walters & Ellsworth 1992; Saverimuttu & Westoby 1996; Hunt & Cornelissen 1997), except for very small-seeded species. . However, these studies and the present one were all conducted at lower light levels relative to full sunlight (this study: 242 vs 1500 µmol m^{-2} day^{-1}). Recent research has shown that at higher irradiance, ULR better predicts RGR than SLA or LAR (McKenna & Shipley 1999; Poorter 1999, 2001; Ryser & Wahl 2001). In the field, SLA may therefore be useful as a predictor of RGR only under slightly shaded conditions. Species with seeds less than 0.01 mg did not follow the correlation between SLA and RGR. These outliers may be a result of greater error associated with their measurement (Appendix 4.2). Alternatively, the larger SLA may reflect a strategy of these very small-seeded species to maximise light capture during early seedling growth. Increases in leaf water content is one strategy used by species to increase SLA without investing in leaf biomass (Shipley 1995).

A few simple traits therefore help to predict the probable germination and establishment performance of species recolonizing milled bogs. Seed mass is a good indicator of burial response, early seedling growth and root performance, while SLA is a better indicator of RGR, at least under lower light conditions and except for very small-seeded species. No effort was made to separate possible phylogenetic constraints from these relationships, as attempted in other studies (Saverimuttu & Westoby 1996; Swanborough & Westoby 1996), therefore care should be taken in extrapolating these results to other species. However, these relationships were strong and in agreement with previous work. Consequently, seed mass and SLA should provide good indications of the germination and establishment potential of other species.

Seed mass and relative growth rate alone do not necessarily predict overall recolonization success in milled bogs. For instance, although high RGR helps to explain the prevalence of *Betula* species and *Aronia melanocarpa*, small-seeded species (*Kalmia angustifolia*, *Chamaedaphne calyculata* and *Ledum groenlandicum*) are relatively frequent recolonizers in spite of being sensitive to burial and having low RGR (Appendix 4.1). Besides germination and establishment, actual recolonization also depends on differential dispersal, subsequent growth and reproduction of species (Salonen 1987; Salonen 1990; Salonen, Penttinen & Särkkä 1992, Salonen & Setälä 1992). However, the screening of species for these traits permits judgements on probable success of naturally-dispersed or introduced species during germination and establishment phases.

Furthermore, it allows for diagnoses of the causes of recolonization failure. In a restoration context, this is valuable information. Desirable species that are vulnerable during germination and establishment can be targeted and suitable restoration procedures can be implemented to aid in their establishment. Similar screening processes should aid in the restoration planning of other disturbed environments.

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Appendix 4.1 : Selected plant species, their rank frequency in natural and milled bogs and their seed mass. Study species are the most common species in natural bogs (31 bogs surveyed, 76 species in total; L. Rochefort, unpublished data) or in abandoned milled bogs (11 bogs surveyed, 132 species in total; L. Rochefort and F. Quinty, unpublished data) located in Québec. .

Species	Family	Rank frequency in natural bogs	Rank frequency in milled bogs	Seed mass (mg) [a]
Herbs				
Carex limosa	Cyperaceae	9	Absent	1.42 ± 0.10
Carex oligosperma	Cyperaceae	7	89	5.47 ± 0.13
Carex stricta	Cyperaceae	Absent	9	0. 40 ± 0. 06
Drosera rotundifolia	Droseraceae	6	64	0.008
Eriophorum angustifolium	Cyperaceae	46	10	0.30 ± 0.03
Eriophorum vaginatum	Cyperaceae	11	4	0.83 ± 0.05
Rubus chamaemorus	Rosaceae	13	7	7.30 ± 0.16
Sarracenia purpurea	Sarraceniaceae	12	115	0.47 ± 0.03
Scirpus cespitosus	Cyperaceae	14	Absent	0.238
Shrubs				
Andromeda glaucophylla	Ericaceae	8	81	0.179
Aronia melanocarpa	Rosaceae	27	11	1.37 ± 0.09
Chamaedaphne calyculata	Ericaceae	2	5	0.071
Kalmia angustifolium	Ericaceae	4	1	0.005
Kalmia polifolia	Ericaceae	3	31	0.006
Ledum groenlandicum	Ericaceae	5	2	0.006
Rhododendron canadense	Ericaceae	Absent	12	0.018
Vaccinium angustifolium	Ericaceae	21	3	0.216
Vaccinium oxycoccus	Ericaceae	1	21	0.436
Trees				
Betula papyrifera	Betulaceae	Absent	6	0.22 ± 0.02
Betula populifolia	Betulaceae	Absent	8	0.096
Picea mariana	Pinaceae	10	22	0.96 ± 0.10

a: Large seeds were weighed individually (n = 20) and are shown with mean ± SE.

Appendix 4.2 : Growth parameters of bog plant species between 7 and 21 days of age (mean ± SE).

Species	AGR [a] (mg day^{-1})	RGR (day^{-1})	ULR (µg mm^{-2} day^{-1})	LAR (mm^2 mg^{-1})	SLA day 21 (mm^2 mg^{-1})	LWR day 21 (mg mg^{-1})
Herbs						
Carex limosa	0.20 ± 0.06	0.051 ± 0.016	7.40 ± 0.99	9.2 ± 2.0	22 ± 4	0.61 ± 0.09
Carex oligosperma	0.25 ± 0.10	0.032 ± 0.012	6.83 ± 1.53	6.4 ± 1.8	19 ± 3	0.52 ± 0.11
Drosera rotundifolia	0.01 ± 0.00	0.102 ± 0.036	-0.89 ± 2.09	62.0 ± 21.7	59 ± 8	0.99 ± 0.10
Eriophorum angustifolium	0.24 ± 0.03	0.129 ± 0.010	8.25 ± 0.72	15.9 ± 1.5	23 ± 1	0.81 ± 0.04
Eriophorum vaginatum	0.24 ± 0.04	0.115 ± 0.011	6.70 ± 0.63	19.7 ± 2.2	24 ± 2	0.86 ± 0.07
Rubus chamaemorus	0.88 ± 0.17	0.111 ± 0.013	7.37 ± 0.69	17.2 ± 1.6	29 ± 3	0.71 ± 0.06
Sarracenia purpurea	0.06 ± 0.01	0.108 ± 0.021	3.34 ± 0.48	34.7 ± 5.7	41 ± 3	0.84 ± 0.06
Scirpus cespitosus	0.04 ± 0.01	0.074 ± 0.010	4.96 ± 1.11	15.9 ± 2.3	23 ± 2	0.68 ± 0.04
Shrubs						
Andromeda glaucophylla	0.06 ± 0.01	0.127 ± 0.010	6.34 ± 0.71	21.0 ± 2.8	37 ± 4	0.61 ± 0.06
Aronia melanocarpa	1.33 ± 0.14	0.199 ± 0.013	6.71 ± 0.41	30.4 ± 2.6	49 ± 5	0.71 ± 0.05
Chamaedaphne calyculata	0.12 ± 0.02	0.171 ± 0.016	6.21 ± 0.57	33.1 ± 6.1	48 ± 4	0.58 ± 0.05
Kalmia angustifolia	–	–	–	–	–	–
Kalmia polifolia	0.01 ± 0.00	0.121 ± 0.031	3.35 ± 2.64	33.5 ± 8.6	130 ± 63	0.77 ± 0.42
Ledum groenlandicum	0.01 ± 0.00	0.116 ± 0.033	2.42 ± 1.40	50.5 ± 17.0	78 ± 16	0.82 ± 0.13
Rhododendron canadense	0.05 ± 0.01	0.180 ± 0.034	5.58 ± 1.16	39.1 ± 15.7	45 ± 6	0.68 ± 0.09
Vaccinium angustifolium	0.14 ± 0.03	0.141 ± 0.029	5.95 ± 0.77	30.8 ± 12.2	40 ± 6	0.69 ± 0.10
Vaccinium oxycoccus	0.16 ± 0.02	0.170 ± 0.015	9.33 ± 0.74	20.2 ± 2.0	35 ± 3	0.58 ± 0.05
Trees						
Betula papyrifera	1.36 ± 0.14	0.224 ± 0.016	7.78 ± 0.52	33.0 ± 5.2	44 ± 4	0.7 ± 0.04
Betula populifolia	1.40 ± 0.14	0.257 ± 0.013	7.83 ± 0.44	34.6 ± 3.9	52 ± 3	0.68 ± 0.03
Picea mariana	0.17 ± 0.02	0.099 ± 0.009	8.06 ± 0.52	14.4 ± 1.0	19 ± 1	0.68 ± 0.04

Appendix 4.2 (continued).

Species	R_L day 7 (mm)	R_L day 21 (mm)	ARPR (mm day^{-1})	RLR (mm mg^{-1})	R_L/L_A (mm mm^{-2})
Herbs					
Carex limosa	8 ± 2	41 ± 9	2.36 ± 0.62	7 ± 2	0.73 ± 0.14
Carex oligosperma	23 ± 4	72 ± 10	3.47 ± 0.76	7 ± 2	1.35 ± 0.21
Drosera rotundifolia	1 ± 0	2 ± 0	0.08 ± 0.02	37 ± 18	0.59 ± 0.10
Eriophorum angustifolium	14 ± 1	64 ± 4	3.61 ± 0.32	20 ± 2	1.37 ± 0.18
Eriophorum vaginatum	13 ± 1	50 ± 5	2.67 ± 0.35	15 ± 1	0.78 ± 0.07
Rubus chamaemorus	26 ± 3	89 ± 10	4.52 ± 0.77	8 ± 1	0.47 ± 0.05
Sarracenia purpurea	3 ± 1	10 ± 1	0.48 ± 0.07	12 ± 3	0.36 ± 0.06
Scirpus cespitosus	2 ± 1	19 ± 3	1.17 ± 0.21	17 ± 4	1.15 ± 0.25
Shrubs					
Andromeda glaucophylla	12 ± 1	25 ± 2	0.94 ± 0.16	51 ± 5	2.78 ± 0.50
Aronia melanocarpa	25 ± 1	48 ± 7	1.63 ± 0.54	13 ± 2	0.47 ± 0.08
Chamaedaphne calyculata	15 ± 1	33 ± 3	1.30 ± 0.25	59 ± 11	1.75 ± 0.23
Kalmia angustifolia	4 ± 0	11 ± 1	0.46 ± 0.09	–	7.74 ± 2.42
Kalmia polifolia	6 ± 1	19 ± 2	0.95 ± 0.17	179 ± 106	5.22 ± 0.92
Ledum groenlandicum	9 ± 1	26 ± 3	1.22 ± 0.21	296 ± 179	5.67 ± 0.73
Rhododendron canadense	7 ± 1	23 ± 3	1.17 ± 0.24	113 ± 51	3.08 ± 0.83
Vaccinium angustifolium	20 ± 4	38 ± 4	1.30 ± 0.41	61 ± 35	1.87 ± 0.28
Vaccinium oxycoccus	15 ± 2	33 ± 3	1.33 ± 0.23	43 ± 9	2.29 ± 0.51
Trees					
Betula papyrifera	24 ± 2	65 ± 9	2.99 ± 0.65	18 ± 5	0.51 ± 0.06
Betula populifolia	18 ± 1	61 ± 7	3.05 ± 0.47	20 ± 4	0.61 ± 0.07
Picea mariana	13 ± 2	27 ± 4	0.99 ± 0.31	14 ± 2	0.92 ± 0.12

a: Column abbreviations: AGR, absolute growth rate; RGR, relative growth rate; ULR, unit leaf rate; LAR, leaf area ratio; SLA, specific leaf area; LWR, leaf weight ratio; R_L, root length: ARPR, absolute root penetration rate; RLR, root length ratio; and R_L/L_A, root length to leaf area ratio.

CHAPITRE 5

A TRAIT-BASED APPROACH FOR PREDICTING THE RECOLONIZATION OF ABANDONED MILLED BOGS AND ITS IMPLICATIONS FOR RESTORATION [4]

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[4]. Campbell, D.R., Rochefort, L. & Lavoie, C (article à soumettre)

RÉSUMÉ

La recolonisation naturelle des tourbières exploitées par les plantes est pauvre. Une approche basée sur les caractères autécologiques des espèces a été utilisée pour mieux cerner les raisons sous-jacentes de cet échec. Les espèces étudiées étaient les mousses et plantes vasculaires les plus communes soit dans les tourbières aspirées et abandonnées ou dans les tourbières naturelles du Québec. Pour chaque espèce, leurs populations en bordures ainsi que les caractères autécologiques aux stades de dissémination, de germination, d'établissement et au stade adulte ont été inventoriés et décrits de façon quantitative ou semi-quantitative. Les espèces ont d'abord été classifiées en groupes fonctionnels. La modélisation des équations structurales a ensuite été utilisée pour évaluer la capacité de chaque caractère à prédire la recolonisation naturelle. Les plantes vasculaires ont pu être classifiées en six groupes fonctionnels. Pour toutes les espèces ou pour les plantes vasculaires seules, la recolonisation est prédite par l'importance des espèces en bordures des tourbières exploitées (abondance, présence ou présence de plantes fructifères) ainsi que par la tendance des espèces à croître près des surfaces exploitées. La dissémination par le vent était aussi déterminante car la recolonisation est favorisée pour les espèces qui ont une faible portance de leurs diaspores (toutes les espèces) ou un temps de chute supérieur à 1 s (plantes vasculaires seulement). Ces causes sont indépendantes les unes des autres. Le taux de croissance potentiel relatif est indirectement lié à la recolonisation car les espèces avec un haut taux ont une tendance à croître près des surfaces exploitées. Cette étude montre l'importance des sources de diaspores dans la recolonisation naturelle et la restauration des tourbières aspirées et abandonnées.

ABSTRACT

The recolonization of abandoned milled bogs is poor. A trait-based approach was used to better understand the underlying reasons for this poor success. Study species were the most common species of mosses and vascular plants in natural and abandoned milled bogs in Québec. Characteristics of propagule sources in the edges of milled bogs were determined along with dispersal, germination, establishment and adult traits. All characters and traits were first used to classify species into broad functional groups. Structural equation modelling was then used to determine which traits best predict the recolonization of abandoned milled bogs. Vascular plants could be grouped into six functional groups. For all species together and for vascular plants alone, recolonization was best predicted by the importance of species in the edges of milled peatlands (abundance, presence or presence of fertile plants), and their bias with respect to the edge of milled surfaces. Wind dispersal ability was also important since wing loading was related to recolonization of all species together, and fall time greater than 1s predicted the recolonization of vascular plants. These causes were all independent. Relative growth rate was directly related to edge bias and therefore only indirectly related to recolonization. This study demonstrates the importance of propagule sources in the natural recolonization as well as the restoration of abandoned milled bogs.

INTRODUCTION

The recolonization of plant communities after disturbance can be considered using a trait-based approach (Noble & Slatyer 1980). The recolonization process may be viewed as a series of steps, with environmental filters at each step which selectively limit the species pool. Species with suitable traits can overcome filters and recolonize the disturbed environment. The approach is similar to that used to search for assembly rules governing plant communities (*sensu* Keddy 1992).

Recolonization relies on the persistence of adult plants and propagules on site and the immigration of propagules from surrounding areas (Noble & Slatyer 1980). However, after severe disturbance, adult plants and on-site propagules are infrequent or absent, and recolonization must proceed through primary succession (del Moral & Wood 1993; Ash, Gemmell & Bradshaw 1994). Critical environmental filters may therefore operate during either the dispersal of propagules to the disturbed site, their germination, establishment, growth to maturity or subsequent reproduction. In severely disturbed environments, active intervention and restoration is often required to overcome critical environmental filters. A mechanistic understanding of the recolonization process is therefore required to diagnose the points at which desired species succeed or fail to recolonize. Specific management techniques could then be prescribed to bypass limiting environmental filters for desired species. Such a trait-based approach offers great potential in understanding and restoring damaged ecosystems (Keddy 1999).

Milled bogs are examples of severely disturbed ecosystems that have been the subject of restoration attempts (Wheeler & Shaw 1995; Rochefort 2000, 2001). Peat is usually extracted from bogs by first milling the peat then collecting it using a variety of methods (Crum 1988, pp. 182-188; Frilander, Leinonen & Alakangas 1996). Once abandoned, milled peat surfaces are large (up to 5 km^2), flat and bare of vegetation. In North America, fibric to sapric, *Sphagnum* peat substrates usually remain (<1 m thick), which are acid (pH 3 to 5) and nutrient-poor with a slight increase in nitrogen as compared to natural bogs (Wind-Mulder, Rochefort & Vitt 1996). There is no seedbank (Salonen 1987), and natural recolonization after the cessation of extraction activities is very slow (Desrochers, Rochefort & Savard 1998; Bérubé & Lavoie 2000). Dispersal is a major constraint to natural recolonization of milled bogs, and species with good dispersal abilities are favoured (Curran & MacNaeidhe 1986; Salonen 1987; Salonen & Setälä 1992; Poschlod 1995). However, substrate and microclimatic conditions in milled bogs are also harsh and limiting for seed and spore germination and establishment (Salonen & Setälä 1992; Tuittila *et al.* 2000).

Studies have attempted to evaluate the relative abilities of peatland species to disperse, germinate and establish in milled bogs (Salonen 1987, 1994; Salonen & Setälä 1992; Chapter 2 and 4, this thesis). However, the relative importance of these stages and others during recolonization is poorly understood, both for individual species and for the species pool as a whole. The general objectives of this study were first to identify functional recolonization groups and second to search for rules which govern the 're-assembly' of plant communities in milled peat bogs. The metaphor of a filter which lets pass suitable species has been used to illustrate assembly rules (Keddy 1992). It functions as a dichotomous key. Species with a certain ability or with traits above a certain threshold can pass critical filters (e.g., van der Valk 1981; Weiher & Keddy 1995). However, thresholds may be difficult to define.

In this study, trait thresholds are defined *a priori* where possible and hypotheses of dichotomous assembly rules existing at these recolonization stages are tested against the actual recolonization of milled bogs. With continuous traits for which no thresholds are clear, correlation analyses and exploratory structural equation modelling between traits and the actual recolonization of milled bogs are used to generate probable hypotheses on the importance of different traits in determining the final recolonization. Implications for the restoration of milled bogs are then discussed.

METHODS

Study species

Two intersecting groups of mosses and vascular plants were chosen as study species (Appendix 5.1). The first group consists of species found most frequently in natural bogs. It can be considered as the 'wish list' of desirable species for recolonization, but which are not necessarily available as recolonizers. The second group consists of species that most frequently recolonize abandoned milled bogs (abandonment age: 12 ± 2 yr, mean ± SE; range 6 - 20 yr). They are by definition available as recolonizers but include undesirable species (e.g., *Betula* spp.). Partial data on propagule sources, maximum fecundity and dispersal ability were available for three other species, *Dicranella cerviculata*, *Larix laricina* and *Pinus banksiana*.

Traits measured

A deductive approach (*sensu* Noble & Gitay 1996) was used to determine critical environmental filters and measured traits. Since recolonization failure is frequent in abandoned milled bogs, efforts were concentrated at the beginning of the recolonization process, at stages of propagule sources, dispersal, germination and establishment (Table 5.1).

Table 5.1: Summary of autecological traits measured at each life stage for mosses and vascular plants found frequently in natural or abandoned milled bogs in Québec.

Life stage	Character / trait	Variable type
Propagule sources	mean abundance in edges	continuous
	mean presence in edges	continuous
	mean presence of fertile plants in edges	continuous
	edge bias	continuous
	maximum fecundity	continuous
Dispersal	release height	continuous
	fall time > 1 s	binary
	fall time	continuous
	wing loading	continuous
	floatability of seeds	continuous
	fleshy fruit	binary
Germination	median germination time (T_{50})	continuous
	sensitivity to burial – seeds < 0.1 mg	binary
	sensitivity to burial – burial slope	continuous
Establishment	seed mass	continuous
	relative growth rate (*RGR*)	continuous
Adult	vegetative spread	binary
	minimum juvenile period	continuous

Propagule sources

Importance of mother plants in edges: Mother plants must be present, fertile and preferably abundant in the edges of abandoned milled surfaces in order to supply propagules for recolonization. Four variables were used to assess the importance of mother plants in edges: 1) mean abundance, 2) mean presence, 3) mean presence of fertile plants and 4) an edge bias variable constructed so that species which tended to be significantly closer to the edge received greater weight. All four variables were determined from surveys of randomly located transects placed perpendicular to edges of milled peatlands in Québec (Chapter 2, this thesis). Mean abundance was determined from 10-m long cross-transects and mean presence and presence of fertile plants were determined from 1 x 10 m quadrats, all of which were placed perpendicular to the main transect at set distances up to 60 m from the edge. The edge bias variable was determined from regression analyses of species presence, abundance or presence of fertile plants as a function of distance from the milled edge. Species were accorded scores for negative bias (0), neutral bias (1) or positive bias (2) for presence, abundance and presence of fertile plants, for a total possible score of 6 (Chapter 2, this thesis). These variables are not autecological traits as such, but complex characters that determine the initial species pool surrounding milled peatlands.

Maximum fecundity

Species must be sufficiently fecund for propagules to disperse and colonize milled surfaces. Fecundity is variable in time and space depending on multiple factors, however species can be readily discriminated at least on a log scale using their potential maximum fecundity. Log_{10} maximum fecundity was therefore used as a trait, using maximum fruiting body densities encountered in the field and counts of propagules per fruiting body in the laboratory (Chapter 2, this thesis).

Dispersal

Wind vector: Species must be able to disperse by an available dispersal vector. Milled bogs are large, free of obstacles and aerodynamically smooth (Campbell, Lavoie & Rochefort 2002), therefore wind is an important, readily available vector for both primary and secondary dispersal. Primary dispersal depends on propagule release height, its settling velocity and the wind environment (Greene & Johnson 1989, 1996), while secondary wind dispersal depends on propagule wing loading (mass divided by plan area), the presence of smooth surfaces and winds (Johnson & Fryer 1992; Greene & Johnson 1997). The vegetation structure, and therefore the wind environment, in edges of milled bogs is heterogeneous, making any predictions of primary wind dispersal difficult using existing models (Greene & Johnson 1996; Nathan, Safriel & Noy-Meir 2001). However, propagules with greater release height will generally be subjected to greater wind velocity, and greater release height coupled with slower settling velocity will also allow longer fall time for propagules to be carried away by wind. Consequently, three traits were selected to evaluate wind dispersal ability: 1) median release height, 2) fall time (median release height divided by settling velocity) and 3) wing loading. Release height was measured in edges of milled bogs. Settling velocity and wing loading for vascular plants were determined in the laboratory, while for mosses, they were determined from spore diameter using Stoke's law (Chapter 2, this thesis). A binary trait was also defined using fall time since a long fall time will favour dispersal by wind. It was defined as those species with fall times greater than 1 s duration. This threshold was arbitrarily chosen, but it appears to group species with very short fall times (< 0.4 s) which should not be easily dispersed by wind.

Water vector: Water dispersal is possible in milled peatlands for propagules which float because water is sometimes present in drainage ditches, either when they are blocked or after snow melt and large rain events. As such, water dispersal ability was determined by measuring the floatability of vascular plant propagules in the laboratory (Chapter 2, this thesis).

Animal vectors: The diversity and abundance of birds and small mammals is greater in edges of milled bogs than in natural bogs (Delage, Fortin & Desrochers 2000; Mazerolle, Drolet & Desrochers 2001), therefore animal vectors should be present, at least near edges. However, dispersal depends on both the fruit and the animal (i.e. habitat distribution and behaviour) and is difficult to quantify (Stiles 1992). Consequently, the presence of fleshy fruits was used as a simple trait to characterize the potential for animal dispersal of vascular plant propagules. No species had apparent adaptations to disperse through adhesion to animals.

Germination

Once dispersed, propagules must be able to germinate. The chemical environment of the substrate is similar to that of natural bogs (Wind-Mulder, Rochefort & Vitt 1996), but the physical environment differs greatly. Milled peat substrates are subject to needle ice in the spring and fall (E. Groeneveld, U. Laval, pers. comm.) and surface drought in mid-summer (Price 1997; Price, Rochefort & Quinty. 1998). Furthermore, propagules may be buried as a result of needle ice or the deposition of eroded peat. Germination success will therefore depend on the germination timing of species with respect to this germination window as well as on the ability of propagules to emerge while buried. Two traits were used to evaluate germination for vascular plants: 1) median germination time (T_{50}), based on greenhouse germination trials, and 2) sensitivity to burial, determined from the slope of emergence as measured in burial trials in the greenhouse (Chapter 4, this thesis). This study also showed that seeds smaller than 0.1 mg were especially sensitive to burial. This mass threshold for propagules was used as a binary trait for all species as well as for vascular plants alone.

Establishment

Once germinated, seedlings must establish on the milled surface and grow. Physical conditions of the milled peat substrate appear to be especially critical during this stage (Salonen 1992, 1994; Salonen & Setälä 1992; Grosvernier, Matthey & Buttler 1995; Rochefort 2000; Tuittila *et al.* 2000). Microclimatic conditions are extreme in summer when peat substrates are dry (Price 1996, 1997; Price, Rochefort & Quinty 1998). Vascular plant seedlings with sufficient root penetration can access water at depth and thereby avoid heat and drought stresses since moisture increases rapidly below milled peat substrates (Price 1996; Price, Rochefort & Quinty 1998). The lack of vegetation and extreme microclimate also favours needle ice formation near the surface in spring and fall (E. Groeneveld, U. Laval, pers. comm.). The size of the root system again determines seedling survival through needle ice events (Roach & Marchand 1984). Early plant growth and hence root growth depends on seed mass and seedling relative growth rate (RGR; Causton & Venus 1981; Jurado & Westoby 1992). Consequently, both log seed mass and seedling RGR were measured in the laboratory (Chapter 4, this thesis) and used here to assess the relative establishment ability of vascular plants. Mosses were not evaluated at the sporeling establishment phase.

Adult growth and reproduction

Adult traits related to growth and reproduction may also play a role in recolonization success. Species which can spread vegetatively or which reproduce quickly will be advantaged because they will not be reliant on dispersal of propagules from edge populations to spread and recolonize milled surfaces. Two adult traits were chosen: 1) ability to spread vegetatively (binary trait), and 2) minimum juvenile period, defined as the minimum time from germination to sexual reproduction. Both traits were determined from literature sources. Species which simply split or grew in tufted growth form were not considered to have the ability to spread vegetatively.

Data analyses

Vascular plants and mosses could not be classified together into functional recolonization groups as a result of the lack of trait information for mosses. For vascular plants, all continuous traits as well as binary traits with no continuous analogue (fleshy fruits and vegetative spread) were used in the cluster analysis of functional groups. Each continuous trait was first transformed to values between 0 and 1 using the range (method 5 in Milligan & Cooper 1988). A similarity matrix between species was calculated using the Gower coefficient (Gower 1971), then transformed to a metric distance matrix (Legendre & Legendre 1998, p. 276). Species were clustered using an agglomerative average linkage approach with the CLUSTER procedure of SAS (SAS Institute 1996-1999). Clustering was also attempted using single-linkage or centroid clustering algorithms, and provided generally similar results.

Relationships between each trait and the mean occurrence of species in abandoned milled bogs (Appendix 5.1) were tested using one-tailed Wilcoxon rank tests for binary variables and Spearman rank correlation analyses for continuous variables. Analyses were conducted using the CORR and NPAR1WAY procedures of SAS statistical software (SAS Institute 1996-1999). Relationships between continuous variables were further examined using *a posteriori* exploratory structural equation modelling (Shipley 2000, p. 243) to determine possible causal relationships behind observed correlations. These analyses were conducted with the EPA2 procedure of the Causal Toolbox program (B. Shipley, Université de Sherbrooke).

RESULTS

Mosses were not classified with vascular plants as a result of the lack of data on germination and establishment (Appendix 5.2). However, based solely on their fecundity and their high wind dispersal ability, they can be considered as a general recolonization group separate from vascular plants. For vascular plants, insufficient data was available from the literature to use juvenile age as a trait in the cluster analysis. *Carex stricta* could also not be classified as a result of missing data for germination and establishment traits. Remaining vascular plants can be classified into six recolonization groups based on characters and traits (Figure 5.1).

Group 1 is somewhat heterogeneous and includes most herbs and the shrub *Andromeda glaucophylla*. All are rare in edges of milled bogs, and have low to moderate fecundity, moderate to large seeds, low sensitivity to burial and low RGR. However, they have variable dispersal modes (wind: *Eriophorum* spp; water or none: others) and abilities for vegetative spread.

Group 2 only includes the carnivorous herb *Drosera rotundifolia*. It is rare in edges, especially close to milled edges. It is fecund, water and wind-dispersed, very small-seeded and sensitive to burial. It has low RGR and no potential for vegetative spread.

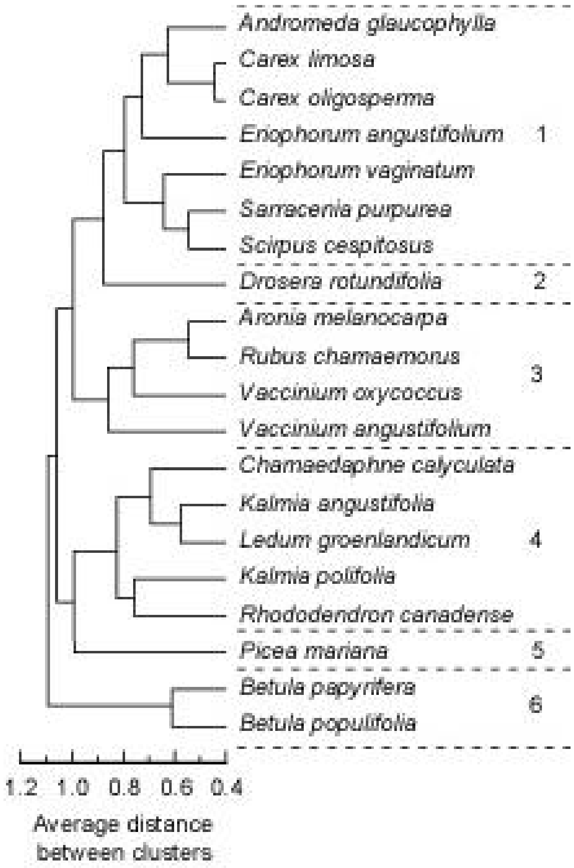

Figure 5.1 Classification of bog vascular plants into functional recolonization groups based on traits and characters.

Group 3 includes herbs and shrubs with fleshy fruits. They are moderately common in edges, but differ in their bias relative to milled edges. *Vaccinium angustifolium* is most important near edges and *V. oxycoccus* is least important near edges, while the two remaining species show little preference. However, besides having fleshy fruits, they all have low fecundity, moderate sensitivity to burial, larger seeds, moderate to higher RGR, and can spread vegetatively.

Group 4 includes the remaining ericaceous shrubs. They are frequent in edges, fecund, wind or water dispersed (occasionally both), small-seeded and sensitive to burial. They also have moderate RGR and the ability to spread vegetatively.

Group 5 includes only the tree *Picea mariana*. It is frequent in edges, although tends to occur farther from milled surfaces. It is also moderately fecund, wind-dispersed, large-seeded, moderately sensitive to burial, with low RGR and the ability to spread vegetatively.

Group 6 includes the two *Betula* species. Both are moderately frequent, but more so near milled edges. They are fecund, have high wind-dispersal ability and moderate-sized seeds which are moderately sensitive to burial. Both also have high RGR and cannot spread vegetatively.

The above classification is based on the *a priori* assumption that chosen characters and traits have equal importance in determining the natural recolonization of milled bogs. However, this is clearly not the case, as judged by the relationships of continuous and binary traits with mean recolonization (Table 5.2). If species are first all considered together, then mean abundance, mean presence, and mean presence of fertile plants in edges are all positively correlated with mean recolonization of species in milled bogs ($p < 0.01$). As well, edge bias ($p < 0.057$) and wing loading of propagules ($p < 0.089$) are close to being significantly correlated with mean recolonization. No dichotomous relationship was detected when all species were considered together. If only vascular plants are considered, then mean abundance, mean presence, and mean presence of fertile plants in edges as well as RGR are positively correlated with recolonization success in milled bogs ($p < 0.05$), and

Table 5.2 : Relationship between actual recolonization in milled bogs and autecological traits of all study species or vascular plants only. Continuous variables were evaluated using the Spearman coefficient of rank correlation (*r*), while binary variables were evaluated using a one-tailed Wilcoxon rank test (*S*).

Character/trait	All species				Vascular plants only			
	n	*r*	*S*	*P*	*n*	*r*	*S*	*P*
Propagule sources								
Mean abundance in edges	32	0.51		0.003	20	0.61		0.004
Mean presence in edges	32	0.50		0.004	20	0.64		0.002
Mean presence of fertile plants in edges	32	0.51		0.003	20	0.53		0.017
Edge bias	32	0.34		0.057	20	0.37		0.081
Maximum fecundity	31	0.07		0.711	19	0.37		0.120
Dispersal								
Median release height	32	0.21		0.244	20	0.35		0.128
Fall time > 1 s	32		184	0.127	21		125	0.032
Fall time – continuous variable	32	0.04		0.841	20	0.30		0.192
Wing loading	32	-0.31		0.089	20	-0.27		0.250
Floatability of seeds					20	-0.29		0.211
Fleshy fruit					20		52	0.182
Germination								
T_{50}					20	0.00		0.997
Sensitivity to burial – seeds < 0.1 mg					21		84	0.123
Sensitivity to burial – burial slope					20	-0.10		0.666
Establishment								
Seed mass					20	-0.30		0.204
RGR					19	0.55		0.014
Adult growth								
Vegetative spread					20		55	0.277

edge bias is close to be significant ($p < 0.081$). Furthermore, although dispersal traits are no longer correlated with mean recolonization, a dichotomous relationship does exist in which recolonization is significantly greater for species with fall times over 1 s duration.

Relationships between significant continuous traits and recolonization success were further elucidated from *a posteriori* exploratory structural equation modelling. In order to avoid type II errors, variables which correlated with mean occurrence in abandoned milled bogs at $p < 0.10$ were included in the initial exploratory analyses. Abundance, presence and presence of fertile plants in edges were strongly inter-correlated (all species: $r > 0.77$; vascular plants: $r > 0.92$). Therefore only abundance near edges was included as a representative variable of importance in edges to avoid the difficulty of cyclic graphs. The same results were obtained with either presence or presence of fertile plants in edges. When all species are considered together, the exploratory causal graph (Figure 5.2a) indicates that abundance in edges and edge bias are strong independent causes of mean recolonization in milled bogs (undirected graph obtained at $p < 0.05$, model significant at $p < 0.05$). Wing loading is also a weaker but independent cause of recolonization success (undirected graph obtained at $p < 0.15$; model significant at $p < 0.05$). In summary, the data suggest that recolonization is favoured for species which are abundant and occur closer to edges and which have lower wing loading. When only vascular plants are considered, the exploratory causal graph (Figure 5.2b) indicates that abundance in edges and edge bias are again strong independent causes of mean recolonization in milled bogs (undirected graph obtained at $p < 0.10$, model significant at $p < 0.05$). However, RGR is also a weaker direct cause of edge bias (undirected graph obtained at $p < 0.45$; model significant at $p < 0.05$) and thereby an indirect cause of recolonization success. It should be noted that *Kalmia angustifolia*, the most important species in abandoned milled bogs, could not be included in this analysis as a result of the lack of data on RGR. In summary, the data suggest that recolonization success is favoured for species that are abundant in edges and closer to milled surfaces, but edge bias is in turn favoured by higher RGR.

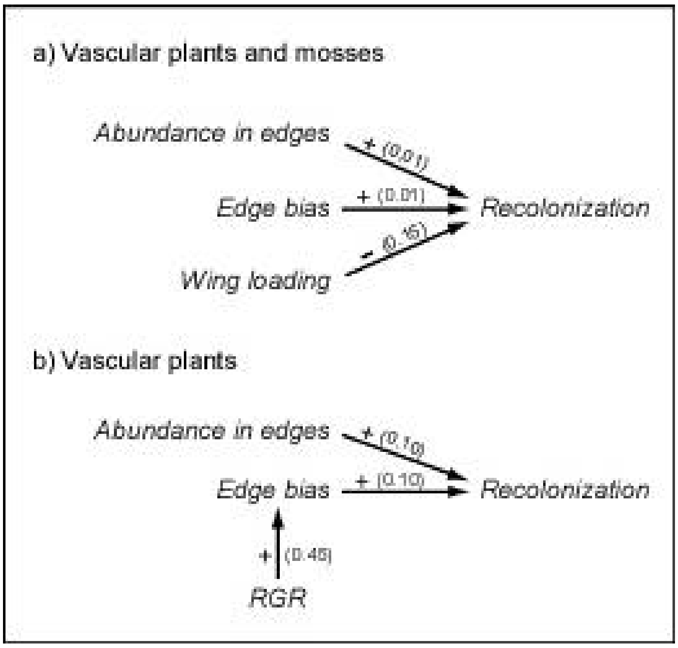

Figure 5.2. Causal hypotheses suggested from *a posteriori* exploratory structural equation modelling between measured traits and mean recolonization of species in milled bogs for a) all species and b) only vascular plants. For each arrow, the sign of the relationship is shown along with the probability level at which the variable was first included in the undirected dependency graph. Resultant models are significant at $p < 0.05$.

DISCUSSION

Overall, natural recolonization of milled bogs was predicted by traits and characters at the beginning of the recolonization sequence. Recolonization is favoured by species which 1) have frequent propagule sources in edges (abundance, presence, presence of fertile plants), or 2) grow closer to milled surfaces, or 3) have good wind dispersal ability (long fall time, low wing loading). The use of the conjunction ‘or’ is intentional since these characters and traits act independently on recolonization. Species with higher values of any one of these traits is favoured for recolonization. For instance, *Eriophorum* spp. and *Vaccinium angustifolium* are frequent colonists, yet the former are rare in edges of milled bogs but wind-dispersed, while the latter is common in edges but animal-dispersed. An additive model, in which a suite of characters is required for species to survive in an environment (Keddy 1992, 1999), does not appear to apply for the prediction of the natural recolonization of milled bogs.

The fact that species which are frequent in edges or which occur closer to edges are favoured to recolonize milled bogs seems somewhat evident. However, previous studies have not considered propagule sources as predictors of the recolonization of milled bogs (Curran & MacNaeidhe 1986; Salonen 1987; Meade 1992; Poschlod 1995). Rather, they have only considered dispersal ability to be important, especially wind dispersal ability, for controlling the recolonization of milled bogs (Curran & MacNaeidhe 1986; Salonen 1987; Poschlod 1995). RGR only appears to act indirectly by favouring faster-growing vascular plant species near edges; this indirect relationship should be confirmed with further study with a greater number of species because it is weak and based on *a posteriori* tests. These fast-growing species may take advantage of disturbances close to edges caused by machinery and drainage. Previous studies have not considered growth rates of mother-plants in edges, nor of colonists in milled peatlands, as predictors of recolonization success.

Several notable exceptions to these ‘rules’ exist. For instance, *Picea mariana* is frequent in edges and has good wind dispersal abilities, yet is a poor colonist. On the contrary, *Rubus chamaemorus*, is a relatively frequent colonist despite being rare in edges, only slightly more frequent near edges and animal-dispersed. These exceptions illustrate that these ‘rules’ are tendencies which exist over the entire species pool. Exceptional species or functional groups may successfully recolonize milled bogs using other suites of traits. It is also possible that certain key traits not measured may better predict recolonization. This may be the case for minimum juvenile period which could not be related to recolonization success as a result of lack of data.

Some traits which intuitively appeared to be key were not shown to be important predictors of natural recolonization. They may have been counterbalanced by trade-offs with other traits. For instance, with vascular plants, maximum fecundity was strongly negatively correlated to seed mass ($r = -0.83$). For natural recolonization, the advantages of being fecund and reaching many potential germination sites are perhaps countered by the disadvantages during germination and establishment of having small propagules (Chapter 4, this thesis), and vice versa. This tradeoff between germination and establishment ability has been observed previously (Ehrlén & van Groenendael 1998).

Environmental filters which operate after immigration, such as the instability of the substrate (Campbell, Rochefort & Lavoie 2002), summer surface drought (Price 1997) or needle ice formation (E. Groeneveld, U. Laval., pers. comm.) likely remain critical, but this study shows that they are secondary to immigration for determining the recolonization species pool in milled peatlands. Once a species pool is present on the milled surface, either from natural immigration or by intentional introduction, these remaining filters will become primary constraints on the recolonization success.

The testing of each filter was made by comparing measured traits and characters against the mean recolonization in 11 milled peatlands in southeastern Québec. The comparison is imperfect since only the mean condition is considered. However, edge inventories are also based on a mean condition of 12 milled peatlands in the same geographic region. Despite this comparison based on mean condition, the species pool in recolonized milled peatlands most resembles that of edges. Site-specific comparisons of actual recolonization after several years with actual edge populations and other autoecological traits may prove fruitful to confirm limiting filters.

IMPLICATIONS FOR RESTORATION

Several implications exist for the restoration of milled bogs, based on this comparison of traits with natural recolonization. They all point to the importance of propagule sources near milled surfaces under restoration. First, since species that are frequent in edges, especially near edges, are likely be the best natural recolonizers, suitable management of edges of milled bogs is important to encourage desirable species and discourage others. Edges of milled bogs are drained and frequently disturbed by heavy machinery. Although drainage cannot be avoided in milled bogs, minimizing mechanical damage of soils and vegetation in milled edges at all times during exploitation may limit opportunities for undesirable species with high RGR such as birch to establish.

Second, during restoration, the introduction of species that are either rare in edges, especially closer to edges, or not wind dispersed should be favoured in order to maximize the diversity of the recolonization species pool. Conversely, if undesirable species are abundant in edges, especially near milled surfaces, intentional introductions of desired species would be required to prevent the dominance of such species. This would apply mainly to smaller milled sites, because in large sites, immigration from the edges will likely not be sufficient for recolonization, except for species with very high immigration potential, such as *Polytrichum strictum* or *Betula* species.

Third, this study underscores the need for propagule sources of desirable species near abandoned milled peatlands to be restored. If insufficient sources are present, introductions are required. Restoration practitioners may consider the selective introduction of species on milled surfaces in a spatially heterogeneous way, such as in a patchwork or with local concentrations of selected species. If introduced species can be coaxed to reproduce, this would in effect increase their edge bias, which should favour their spread in the remainder of zones under restoration.

Finally, it is clear that when sites are being restored, the recolonization process is far from natural. Managers manipulate the process through introductions of desired species and control of microclimate, edaphic conditions and biotic interactions (e.g., in milled bogs, Rochefort 2001). Consequently, predicting natural recolonization is less important in restoration than understanding the mechanics of the entire recolonization process. Rules may exist which govern natural recolonization, but which are not important for 're-assembly' in specific restoration scenarios. For instance, introduction of diaspores (seeds, spores and plant fragments) is currently practised to restore milled peatlands in North America. The above rules for natural recolonization are all related to the immigration of species (presence, abundance, fertile plants, edge bias and wind dispersal ability) and will be less important for determining the final community. Rather, species in the introduced diaspore pool with large seeds or high RGR should be most successful. As such, examination of the complete trait matrix (Appendix 5.2) and the classification of functional recolonization groups (Figure 5.1) will provide valuable information for planning restoration projects and diagnosing failure at later stages of community development.

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Appendix 5.1: Most frequent species of vascular plants and mosses in natural or abandoned milled bogs in Québec (L. Rochefort and F. Quinty, unpublished data). Nomenclature follows Anderson (1990) for *Sphagnum*, Anderson, Crum & Buck (1990) for other mosses and Scoggan (1978-1979) for vascular plants, except for *Vaccinium oxycoccus* L.

		Natural peatlands (n = 31)		Milled peatlands (n = 11)	
Species	Family	Percent occurrence (mean ± SD)	n	Percent occurrence (mean ± SD)	n
Mosses					
Dicranella cerviculata	Dicranaceae	0	0	< 1	3
Pleurozium schreberi	Hylocomiaceae	4 ± 12	5	2 ± 3	3
Pohlia nutans	Bryaceae	0	0	5 ± 17	3
Polytrichum strictum	Polytrichaceae	15 ± 21	18	3 ± 5	5
Sphagnum angustifolium	Sphagnaceae	33 ± 32	21	0	0
Sphagnum capillifolium	Sphagnaceae	55 ± 32	27	1 ± 2	2
Sphagnum fallax	Sphagnaceae	22 ± 28	17	0	0
Sphagnum fuscum	Sphagnaceae	49 ± 33	26	< 1	1
Sphagnum magellanicum	Sphagnaceae	46 ± 28	29	0	0
Herbaceous plants					
Carex limosa	Cyperaceae	24 ± 26	20	0	0
Carex oligosperma	Cyperaceae	35 ± 31	19	0	0
Carex stricta	Cyperaceae	0	0	2 ± 8	1
Drosera rotundifolia	Droseraceae	35 ± 35	24	0	0
Eriophorum angustifolium	Cyperaceae	2 ± 5	4	2 ± 5	3
Eriophorum vaginatum	Cyperaceae	19 ± 20	21	11 ± 21	8
Rubus chamaemorus	Rosaceae	17 ± 32	9	4 ± 6	7
Sarracenia purpurea	Sarraceniaceae	17 ± 21	16	0	0
Scirpus cespitosus	Cyperaceae	17 ± 30	10	0	0
Shrubs					
Andromeda glaucophylla	Ericaceae	32 ± 22	26	0	0
Aronia melanocarpa	Rosaceae	5 ± 12	6	2 ± 2	5
Chamaedaphne calyculata	Ericaceae	71 ± 31	31	9 ± 9	10
Kalmia angustifolia	Ericaceae	39 ± 28	26	17 ± 26	8
Kalmia polifolia	Ericaceae	49 ± 33	28	< 1	4
Ledum groenlandicum	Ericaceae	36 ± 31	23	14 ± 17	10
Rhododendron canadense	Ericaceae	0	0	1 ± 2	5
Vaccinium angustifolium	Ericaceae	7 ± 12	11	14 ± 13	9
Vaccinium oxycoccus	Ericaceae	74 ± 26	31	< 1	3
Trees					
Betula papyrifera	Betulaceae	0	0	5 ± 10	6
Betula populifolia	Betulaceae	0	0	3 ± 6	4
Larix laricina	Pinaceae	5 ± 9	12	1 ± 1	6
Picea mariana	Pinaceae	21 ± 22	20	< 1	4
Pinus banksiana	Pinaceae	0	0	< 1	1

Appendix 5.2: Summary of autecological characters and traits measured for mosses and vascular plants frequently found in natural or abandoned milled bogs in Québec.

	Propagule sources[a]					Dispersal[a]				
Species	Edge abundance (%)	Edge presence (%)	Edge fertile plants (%)	Edge bias	Log max fecundity (dm^{-2})	Median release height (m)	Fall time (s)	Log wing loading (mg cm^{-2})	Ability to float (%)	Fleshy fruit
Mosses										
Dicranella cerviculata	0.3	5	2	6	7.3	0.01	0.7	0.4		
Pleurozium schreberi	6.5	33	3	0	5.9	0.02	2.2	0.3		
Pohlia nutans	2.7	18	3	3	8.3	0.02	1.9	0.4		
Polytrichum strictum	6.6	34	12	3	8.4	0.05	17.4	0.1		
Sphagnum angustifolium	2.9	16	0	1	6.5	0.15	5.7	0.5		
Sphagnum capillifolium	10.2	44	5	1	7.1	0.15	6.4	0.5		
Sphagnum fallax	0.1	2	0	3	7.1	0.15	6.2	0.6		
Sphagnum fuscum	6.8	32	6	0	6.6	0.15	6.9	0.5		
Sphagnum magellanicum	2.1	22	1	1	6.4	0.15	5.6	0.6		
Herbs										
Carex limosa	1.1	6	2	3	1.3	0.20	0.1	1.5	100	N
Carex oligosperma	1	7	2	3	1.5	0.49	0.2	1.8	100	N
Carex stricta	0.6	3	1	3	3.0	0.41	0.3	1.1	100	N
Drosera rotundifolia	0.5	8	3	2	3.4	0.09	0.2	0.5	100	N
Eriophorum angustifolium	0.2	3	1	3	2.5	0.47	1.9	-1.1	60	N
Eriophorum vaginatum	1.3	13	5	3	2.8	0.30	1.1	-0.8	30	N
Rubus chamaemorus	0.7	13	2	4	-0.2	0.09	0.0	2.2	0	Y
Sarracenia purpurea	0.1	5	0	2	2.4	0.25	0.1	1.5	60	N
Scirpus cespitosus	0.2	2	2	2		0.20	0.2	1.3	0	N
Shrubs										
Andromeda glaucophylla	1.1	14	8	3	2.2	0.21	0.1	1.4	100	N
Aronia melanocarpa	2.1	15	5	4	1.5	0.85	0.2	2.4	0	Y
Chamaedaphne calyculata	16.3	59	54	3	3.3	0.44	0.4	1.1	100	N
Kalmia angustifolia	26.7	68	54	3	4.0	0.48	1.5	0.4	70	N
Kalmia polifolia	3.3	36	27	3	3.0	0.39	1.7	0.3	100	N
Ledum groenlandicum	17.1	62	50	3	4.0	0.47	1.5	0.3	20	N
Rhododendron canadense	4.6	24	19	3	3.5	0.58	1.5	0.4	0	N
Vaccinium angustifolium	11.1	53	15	5	1.8	0.30	0.1	2.1	30	Y
Vaccinium oxycoccus	5	26	9	0	1.3	0.01	0.0	1.9	100	Y
Trees										
Betula papyrifera	4.6	18	6	6	3.1	6.45	9.0	0.5	20	N
Betula populifolia	2.8	10	8	5	3.3	3.13	5.4	0.3	10	N
Picea mariana	17.2	46	27	0	2.9	3.85	4.5	1.0	0	N

Appendix 5.2 (continued).

	Germination[b]			Establishment[b]		Adult growth		
Species	T_{50} (days)	Burial slope (mm^{-1})	Small propagules	Seed mass (mg)	RGR (day^{-1})	Ability to spread	Juvenile period (yr)	Reference[c]
Mosses								
Dicranella cerviculata			Y					
Pleurozium schreberi			Y					
Pohlia nutans			Y					
Polytrichum strictum			Y					
Sphagnum angustifolium			Y					
Sphagnum capillifolium			Y					
Sphagnum fallax			Y					
Sphagnum fuscum			Y					
Sphagnum magellanicum			Y					
Herbs								
Carex limosa	14	-0.06	N	1.42	0.051	Y		*4*
Carex oligosperma	22	0	N	5.47	0.032	Y		*4*
Carex stricta			N	1.00		Y		*4*
Drosera rotundifolia	18	-0.72	Y	0.01	0.102	N		*3*
Eriophorum angustifolium	18	0	N	0.30	0.129	Y	1	*13*
Eriophorum vaginatum	15	0	N	0.83	0.115	N	2	*16, 18*
Rubus chamaemorus	13	-0.10	N	7.30	0.111	Y	7	*15*
Sarracenia purpurea	25	-0.07	N	0.47	0.108	N		*11*
Scirpus cespitosus	14	0	N	0.24	0.074	N		*4*
Shrubs								
Andromeda glaucophylla	20	-0.41	N	0.18	0.127	Y		*4*
Aronia melanocarpa	11	-0.11	N	1.37	0.199	Y		*7*
Chamaedaphne calyculata	13	-0.65	Y	0.07	0.171	Y		*14*
Kalmia angustifolia	29	-0.51	Y	0.01		Y		*8, 12*
Kalmia polifolia	20	-0.78	Y	0.01	0.121	Y		*4*
Ledum groenlandicum	20	-0.62	Y	0.01	0.116	Y		*2*
Rhododendron canadense	15	-0.31	Y	0.02	0.180	Y		*5*
Vaccinium angustifolium	39	-0.10	N	0.22	0.141	Y	4	*9*
Vaccinium oxycoccus	11	-0.06	N	0.44	0.170	Y	6	*10*
Trees								
Betula papyrifera	8	-0.05	N	0.22	0.224	N	15	*1, 6*
Betula populifolia	8	-0.10	Y	0.10	0.257	N	8	*1, 6*
Picea mariana	6	-0.14	N	0.96	0.099	Y	10	*1, 17*

a: From Chapter 2, this thesis.

b: From Chapter 4, this thesis.

c: References for adult traits: *1*: Burns & Honkala 1990; *2*: Calmes & Zasada 1982; *3*: Crowder *et al.* 1990; *4*: Fernald 1950; *5*: Flinn & Pringle 1983; *6*: Forest Service 1948; *7*: Hall, Wood & Jackson 1978; *8*: Hall, Jackson & Everett 1973; *9*: Hall *et al.* 1979; *10*: Jacquemart 1997; *11*: Macfarlane 1908; *12*: Mallik 1993; *13*: Phillips 1954; *14*: Swan & Gill 1970; *15*: Taylor 1971; *16*: Wein 1968; *17*: Young & Young 1992; *18*: field observations.

CHAPITRE 6

CONCLUSIONS GÉNÉRALES

UNE COMPRÉHENSION DE LA MÉCANIQUE DE LA RECOLONISATION

L'objectif principal de cette thèse était de déterminer les règles d'assemblage qui permettent de prédire la recolonisation naturelle des tourbières exploitées par la méthode d'aspiration tôt après leur abandon. Il était clair dès le départ que la recolonisation naturelle est, dans la quasi-totalité des cas, insuffisante pour restaurer à court ou moyen terme les tourbières aspirées, c'est-à-dire leur redonner une structure végétale et des fonctions écologiques similaires à celles des tourbières non perturbées (Desrochers, Rochefort & Savard 1998; Bérubé & Lavoie 2000; Tableau 1.1, cette thèse). Le but ultime de la thèse était alors non seulement de prédire mais surtout de mieux comprendre la mécanique du processus de recolonisation. Cette compréhension est requise pour savoir où, quand et comment intervenir pour restaurer de tels écosystèmes grandement perturbés. L'approche utilisée a permis de décortiquer ce processus de recolonisation en le considérant comme une série de filtres environnementaux qui ne laissent passer que les espèces ayant les caractéristiques autécologiques appropriées. Cette approche a surtout été ciblée sur les premiers stades de la recolonisation, de l'immigration des diaspores jusqu'à l'établissement des plantules.

Le Chapitre 2 montre clairement que, dès la première étape de la recolonisation, durant l'immigration des espèces dans les tourbières exploitées, il y a un tri des espèces. Les espèces de plantes vasculaires et de mousses diffèrent grandement selon 1) leur abondance et la position qu'elles occupent en bordure des sites aspirés, 2) leur fécondité et 3) leur capacité de dissémination par le vent, l'eau et les animaux. Ce chapitre propose une méthode générale pour prédire le potentiel relatif d'immigration des espèces dans n'importe quel site perturbé, et ce, non pas en étudiant le phénomème *in situ*, mais plutôt en examinant si les conditions nécessaires pour une forte immigration sont réunies, soit des plants-mères abondants en bordure, une bonne fécondité et une capacité de dissémination efficace compte tenu des vecteurs présents. On peut conclure dans ce chapitre que le vent, qui est le vecteur dominant, favorise la dissémination des mousses, surtout *Polytrichum strictum*, de plusieurs éricacées, notamment *Kalmia angustifolia* et *Ledum groenlandicum*, et des arbres, surtout *Betula* spp. et *Picea mariana*. Si certaines de ces espèces sont peu fréquentes dans les tourbières aspirées (ex. : *Sphagnum* spp., *Picea* *mariana*), les causes de leur insuccès dans de tels sites doivent résider dans leur incapacité à germer, à s'établir ou à parvenir à maturité, et non pas dans leur incapacité à immigrer.

Une fois disséminée, une diaspore doit germer et croître. Plusieurs études ont déjà été réalisées pour caractériser les filtres importants qui influencent la germination et l'établissement, surtout le régime hydrique et le microclimat près du sol (Price 1997; Tuittila *et al.* 2000), mais aucune n'avait examiné la stabilité du substrat comme filtre potentiel. Le Chapitre 3 comble cette lacune et montre clairement que les surfaces tourbeuses exploitées sont des surfaces actives et instables où la microtopographie change beaucoup durant la saison de croissance. La cause principale de cette instabilité ne semble pas être l'érosion éolienne durant l'été. Le gel-dégel au printemps et à l'automne semble être un facteur plus important, ce qui a été confirmé par des études subséquentes (E. Groeneveld, U. Laval, comm. pers.). Malgré le rôle mineur du vent pour expliquer l'instabilité des surfaces tourbeuses, l'étude a pu établir que les surfaces de tourbières exploitées sont lisses en terme aérodynamique. Les plantules qui s'y établissent sont exposées à des vents qui peuvent être violents près de la surface et qui pourraient les endommager et même entraîner leur déracinement.

Le Chapitre 4 montre comment les espèces de plantes vasculaires diffèrent en terme de potentiel de germination et d'établissement dans les tourbières exploitées. La masse des graines prédit la réponse de l'entourbement sur la germination et l'émergence des plantules. Les graines ayant une masse de moins de 0.1 mg sont sensibles à l'entourbement. La masse des graines prédit aussi la croissance absolue des espèces vasculaires, ainsi que la croissance absolue des racines et la profondeur d'enracinement par unité de masse totale. Par contre, c'est l'aire spécifique des feuilles et non la masse qui prédit le mieux le taux de croissance potentiel relatif des plantules, sauf pour les espèces avec les graines les plus légères. La masse des graines et le taux de croissance potentiel relatif semblent être des facteurs clés pour évaluer la capacité des plantes à germer et à s'établir dans les tourbières exploitées une fois que les diaspores y sont disséminées.

Le Chapitre 5 intègre les données, surtout celles des Chapitres 2 et 4, de façon à répondre aux hypothèses de départ. En réponse à la première hypothèse de cette thèse, deux modèles simples ont été construits pour prédire la recolonisation des tourbières exploitées à l'aspirateur dans le Québec méridional en tenant compte d'une série de filtres environnementaux critiques et des caractères autécologiques clés des principales espèces de tourbière. Un modèle a été construit pour les mousses et les plantes vasculaires et un autre pour les plantes vasculaires seulement (Figure 5.2). Les facteurs qui favorisent la recolonisation sont : une haute fréquence des espèces en bordure, une tendance à croître tout près des bordures et une bonne capacité de dissémination par le vent. Ces facteurs étant indépendants, une espèce ayant au moins une de ces caractéristiques a plus de chances de recoloniser une tourbière aspirée qu'une espèce n'en ayant aucune.

En réponse au deuxième hypothèse de cette thèse, les premières étapes de la recolonisation, surtout celles liées à l'immigration des diaspores vers les surfaces exploitées, sont les plus importantes pour assurer un certain succès de recolonisation naturelle. Cela ne veut pas dire que les filtres environnementaux associés aux stades ultérieurs ne sont pas importants, mais ils sont secondaires par rapport au filtre de l'immigration. En réponse au troisième hypothèse de la thèse, le filtre du stabilité du substrat sur la germination et l'établissment des plantules ne semble donc pas être aussi important que les sources de diaspores.

IMPLICATIONS POUR LA RESTAURATION

Cette thèse permet de souligner l'importance de quelques pratiques actuelles de restauration, de soulever d'autres options de restauration et d'énoncer des pistes prometteuses de recherche pour mieux restaurer les tourbières exploitées. En premier lieu, elle montre que le processus de restauration débute dans les bordures, avant même que les activités d'exploitation ne soient terminées. En effet, les espèces qui recolonisent les bordures perturbées ou qui subsistent dans les secteurs non exploités sont les mieux positionnées pour recoloniser les surfaces aspirées. Une bonne gestion des bordures, favorisant les espèces désirables qui peuvent y survivre (ex. : éricacées) et nuisant aux autres (ex. : *Betula* spp.), serait profitable pour une recolonisation future des sites aspirés. Par exemple, la remise en surface du matériel minéral lors de l'excavation des canaux de drainage et le dépôt de ce matériel sur les bordures facilitent l'implantation du bouleau qui peut alors former des populations denses potentiellement nuisibles au processus de restauration naturelle (Lavoie & Rochefort 1996; Lavoie & Saint-Louis 1999).

Le rôle important des sources de diaspores dans la restauration et surtout la faible capacité de dissémination de plusieurs plantes de tourbières mettent en relief la nécessité d'introduire de façon artificielle des espèces désirables par le biais de méthodes de restauration appropriées, telles que pratiquées dans l'Est du Canada (Rochefort 2001). Ceci est particulièrement vrai lorsque la surface tourbeuse aspirée est grande ou si des espèces indésirables dominent dans les bordures. L'application de la méthode développée dans le Chapitre 2 aux sites à restaurer devrait permettre un choix éclairé des espèces à introduire.

Bien que les contraintes à la dissémination des diaspores constituent des filtres très importants pour la recolonisation des tourbières, les espèces sont tout de même exposées à d'autres filtres qui influencent la germination des diaspores, l'établissement des plantules et la croissance pour parvenir au stade adulte. Le tri des espèces de plantes vasculaires durant la germination et l'établissement se fait en fonction de la masse des diaspores et de leur taux de croissance potentiel relatif. Le rôle de ces caractères pour les mousses reste à démontrer par d'autres recherches, mais il devrait être important. Les espèces avec de très petites diaspores et un taux de croissance faible nécessitent donc une attention particulière : il importe de stabiliser le substrat et de maintenir un microclimat modéré, notamment grâce à des paillis ou des espèces compagnes, pour faciliter leur croissance. Les efforts de restauration devraient donc cibler de telles espèces. En contrepartie, les espèces avec de grosses graines ou un taux de croissance rapide nécessitent peu d'interventions pour assurer leur survie, à part l'introduction initiale et l'assurance de ressources adéquates telles que les nutriments et la lumière.

Au stade adulte, le taux de croissance potentiel relatif est aussi fortement impliqué dans la croissance des plantes et leurs interactions compétitives (Westoby 1998; Weiher *et al.* 1999). Les espèces avec un haut taux de croissance potentiel relatif peuvent utiliser avec efficacité les ressources disponibles (nutriments et lumière) en les séquestrant et en les investissant rapidement dans la croissance de leurs tissus de façon à occuper plus d'espace. Les espèces avec un taux de croissance faible poussent plus lentement mais investissent davantage leur énergie dans des tissus qui subsistent sur une plus longue période de temps; elles recyclent aussi mieux les nutriments déjà acquis. De telles espèces finissent en général par dominer dans les environnements pauvres en éléments nutritifs (Aerts & van der Peijl 1993). Le taux de croissance potentiel relatif pourrait donc s'avérer important à plus long terme pour prédire la reprise après restauration, une fois que les interactions compétitives pour la lumière et les nutriments prennent de l'ampleur. Le taux de croissance potentiel relatif est difficile à mesurer, mais il est corrélé à des mesures plus simples, comme l'aire spécifique des feuilles (Chapitre 4, cette thèse; Reich, Walters & Ellsworth 1992, 1997; Weiher *et al.* 1999), ce qui facilite son estimation pour un plus grand nombre d'espèces de tourbière.

L'APPROCHE DES RÈGLES D'ASSEMBLAGE RÉ-ÉVALUÉE

Cette thèse est basée sur l'écologie fonctionnelle des espèces et a utilisé l'approche des règles d'assemblage (*sensu* Keddy 1992) pour disséquer le processus de recolonisation et ainsi mieux cerner les filtres environnementaux actifs durant la recolonisation naturelle et la restauration des tourbières exploitées. Cette approche s'est-elle avérée avantageuse pour comprendre la recolonisation?

L'analyse de gradients de végétation et des gradients environnementaux sous-jacents est souvent utilisée pour rechercher les facteurs explicatifs de la recolonisation naturelle (ex. : Girard, Lavoie & Thériault, sous presse). Ces études se basent sur les patrons actuels de végétation et permettent une évaluation des facteurs environnementaux associés à la fréquence d'apparition des différentes espèces. Des études dendrochronologiques ou paléoécologiques permettent notamment de mieux observer cette recolonisation dans le temps (ex. : Lavoie & Rochefort 1996; Robert, Rochefort & Garneau 1999). Par contre, de telles études ne permettent pas de décrire la *mécanique* du processus de recolonisation. Or, une telle description est nécessaire pour savoir pourquoi et à quel stade le processus fonctionne ou ne fonctionne pas. À l'autre extrême, des études poussées sur une ou quelques espèces permettent une très bonne compréhension de leur capacité de recolonisation et même l'identification de seuils importants pour traverser des filtres critiques (ex.: Rochefort 2001). Par cette approche, il est toutefois difficile de placer les espèces dans un contexte de communauté car on possède de l'information sur un nombre limité d'espèces.

Par rapport aux méthodes énoncées plus haut, l'approche développée dans cette thèse est basée sur l'écologie fonctionnelle des espèces. Les filtres environnementaux critiques et les caractères autécologiques clés sont identifiés *a priori*, et les caractères sont comparés pour un grand nombre d'espèces. Les règles d'assemblage (*sensu* Keddy 1992) peuvent être élaborées en identifiant les seuils que doivent franchir les espèces pour passer outre les filtres environnementaux. Cette approche n'est pas meilleure que les autres; elle est complémentaire. Son grand avantage réside dans la comparaison de multiples espèces. Par exemple, la capacité d'immigration des mousses est difficilement quantifiable avec les autres approches, mais avec cette étude, on a pu conclure qu'elle est importante par rapport à d'autres groupes d'espèces. Le nombre élevé d'espèces a aussi permis une évaluation de l'importance de chaque caractère dans la recolonisation naturelle par l'entremise de la modélisation des équations structurelles des variables.

Il est toutefois important de noter qu'une compréhension de la mécanique de la communauté est possible avec cette méthode seulement si les caractères choisis sont déterminants pour le développement de la communauté. Le choix des caractères à mesurer doit donc se faire de façon judicieuse (McIntyre *et al.* 1999; Weiher *et al.* 1999). Ce choix est difficile et il est nécessairement subjectif. Les seuils critiques pour les caractères mesurés sont aussi des cibles floues difficilement identifiables, d'autant plus que les espèces peuvent posséder plusieurs stratégies pour contourner des filtres environnementaux contraignants. Le concept des règles d'assemblage (*sensu* Keddy 1992) reste toujours utile pour structurer les recherches sur la dynamique des communautés, mais l'élaboration de ces règles restera peut-être un but difficile à atteindre.

En somme, toutes ces approches, y compris celle utilisée dans cette thèse, permettent de mieux comprendre le processus de recolonisation des tourbières fortement perturbées. Elles sont complémentaires les unes par rapport aux autres. L'écologiste averti aura donc avantage à considérer ces approches dans leur ensemble pour faire la restauration efficace d'un écosystème.

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