UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

LA RÔLE DES BRYOPHYTES DANS LES MÉCANISMES D'ENTOURBEMENT DES FORÊTS D'ÉPINETTE NOIRE DE LA CEINTURE D'ARGILE DU QUÉBEC ET DE L'ONTARIO

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AVANT-PROPOS

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L'entourbement est le développement d'une couche épaisse de matière organique sur le sol en association avec la remontée de la nappe phréatique. L'entourbement est associé à une réduction du taux de croissance des arbres qui est potentiellement une conséquence du milieu froid et humide dans lequel poussent les racines. À cause de leurs propriétés physiques (production, décomposition, capacité d'absorber l'eau), les sphaignes ont été associées à l'accumulation de la matière organique sur le sol et à la remontée de la nappe phréatique, mais cette relation n'a pas encore été démontrée. La ceinture d'argile du Québec et de l'Ontario est une grande région affectée par l'entourbement. Malgré l'importance de ce processus pour la région, il y a peu d'études qui examinent en détail l'entourbement. L'objectif global de cette thèse est de déterminer les mécanismes d'entourbement et le rôle des bryophytes dans le processus d'entourbement des forêts d'épinettes noires de la ceinture d'argile du Québec et de l'Ontario.

Des études dans une chronoséquence de peuplements d'épinettes noires ont pu déterminer que l'accumulation avec le temps de matériel organique sur le sol minéral est causée par le climat régional, ainsi que la présence de sphaignes et de plantes éricacées. De plus, il a été démontré que la remontée de la nappe phréatique n'est pas une cause de l'accumulation de la matière organique mais une conséquence de cette dernière. Malgré des hypothèses émises il y a plus de 50 ans, la sphaigne n'a pas joué de rôle direct dans la remontée de la nappe phréatique mais plutôt un rôle indirect via sa contribution à l'accumulation de la matière organique.

Les études portant sur le phénomène de l'entourbement lui-même ont illustré l'importance de la communauté des bryophytes sur le fonctionnement de l'écosystème. La communauté de bryophytes passe d'une communauté dominée par les mousses hypnacées, à une communauté dominée par des sphaignes formant des hummocks, à une communauté dominée par les sphaignes de milieux humides. Les changements en lumière et en humidité disponible associés à l'entourbement ont été identifiés comme étant les facteurs qui causent les changements de communautés lors de la succession. La quantité de lumière disponible pour les bryophytes augmente avec l'âge du peuplement à cause de l'ouverture du couvert forestier suite à la sénescence par pied d'arbre. Le taux d'humidité disponible augmente quant à lui avec l'accumulation de la matière organique et la remontée éventuelle de la nappe phréatique. Puisque les mousses et les sphaignes sont en partie responsables de l'accumulation de la matière organique, ces résultats suggèrent que la succession dans la communauté de bryophytes s'appuie sur le modèle de facilitation.

Malgré que les changements de composition aient été expliqués par les changements dans l'environnement, l'établissement initial des sphaignes dans les jeunes peuplements n'était pas expliqué par des limitations d'habitat. La disponibilité des spores n'explique pas le manque de sphaignes dans les jeunes peuplements. Mais, les colonies de sphaignes se sont établies à plus de 70% du temps sur le bois mort, ce qui potentiellement expliquerait une restriction dans le temps et l'espace de la colonisation. Ensemble, ces résultats nous permettent de voir que les changements dans la communauté de sphaignes sont influencés

plutôt par des processus stochastiques (la colonisation) au début de la succession et par des processus dirigé par l'habitat et les processus de compétition à la fin de la succession.

Ces études mettent l'emphase sur deux lacunes dans l'aménagement forestier de peuplements et de paysages entourbés. Les forêts entourbées et les jeunes forêts non entourbées contiennent des communautés de bryophytes riches et distinctes. La coupe avec la protection des sols et de la régénération (CPRS), qui est la norme dans la forêt boréale au Québec, ne recrée pas la structure des jeunes forêts quand c'est appliqué dans les vieilles forêts. Également, la CPRS ne récréer pas la structure des vieilles forêts entourbées et le manque de ces deux types d'habitat dans le futur pourrait mettre les espèces associées avec ces stades en périls. Les coupes partielles ont le potentiel de recréer les communautés de bryophytes associées avec les vieilles forêts mais jusqu'à maintenant, uniquement les sphaignes ont été examinées, et cela à court terme.

En conclusion, une meilleure connaissance et compréhension de la communauté des bryophytes dans les forêts d'épinette noire sur les dépôts fins nous permettra de formuler une meilleure stratégie d'aménagement qui prend en compte la biodiversité des bryophytes de ces forêts extraordinaires et leur productivité.

INTRODUCTION GÉNÉRALE

0.1 LA FORÊT BORÉALE

La forêt boréale est un des biomes le plus étendu au monde. Elle couvre 6.7 millions km^2, soit un tiers des forêts mondiales (Scott, 1995), et elle joue un rôle important dans le cycle planétaire du carbone (Goulden et al., 1998). Deux caractéristiques distinguent la forêt boréale des autres biomes, la prédominance des feux de forêt comme agent de perturbation, et l'abondance des bryophytes terricoles.

0.1.1 Les feux de forêt

Le feu est l'agent de perturbation dominant dans le biome boréal (Payette, 1992; Johnson, 1992), mais son rôle varie beaucoup avec les essences présentes et le climat. Les essences présentes influencent davantage la sévérité des feux, tandis que le climat, lui, influence la fréquence. Par exemple, en Europe l'espèce dominante, le pin sylvestre (*Pinus sylvestris*), est résistante au feu. Lorsqu'un feu se produit dans des peuplements matures, il est dit non-sévère puisque la plupart des arbres ne sont pas tués et généralement uniquement le sous-bois est brûlé (Englemark et Hytteborn, 1999). Par contre, une interaction entre la sévérité et la fréquence est possible. Quand la fréquence est faible, des espèces qui ne sont pas résistantes aux feux peuvent coloniser les sites (e.g. *Picea abies* et *Betula pendula*), ce qui résulte lors d'un prochain feu à une plus grande mortalité des arbres et à une caractérisation du feu comme étant plus sévère (Englemark et Hytteborn, 1999). En Amérique du Nord les deux espèces dominantes, l'épinette noire (*Picea mariana*) et le pin gris (*Pinus banksiana*) ne sont généralement pas résistantes au feu, ainsi lors d'un feu l'impact est sévère, les arbres sont tous tués, le sous-bois est brûlé et la succession recommence (Heinselman, 1981). Comme en Europe, une interaction entre la sévérité et la fréquence des feux est possible en Amérique du Nord. Dans certain cas, quand les forêts sont vieilles et très humides, un feu peu sévère peut survenir. Les arbres y sont tués, mais le sous-bois n'est pas complètement brûlé (Lecomte et al. 2006). Ces exemples illustres que bien que le feu est une constante dans la forêt boréale, son caractère et rôle varient énormément.

De même, les variations dans la composition des forêts et du climat à travers le biome influence aussi le cycle de feu. Dans les régions continentales où l'aridité est extrême, les cycles de feu sont courts, de l'ordre de 70-80 ans (Heinselman, 1981). Dans ces systèmes, il y a très peu de succession dans la strate arborescente (Dix et Swan, 1971; Black et Bliss, 1978; Heinsleman 1981). Le temps écoulé entre deux feux par rapport à la longévité des arbres est trop court. Par contre, dans les régions océaniques l'humidité des masses d'air limite la fréquence des feux, et les cycles de feu sont plus longs. Dans ces systèmes, on assiste à une succession en espèces et en structure dans la strate arborescente (Bergeron, 2000; Harper et al., 2002; Lesieur et al., 2002; Lecomte et al. 2005). Cette succession est causée par l'effet cumulé des processus naturels (e.g. entourbement, vieillissement des arbres) et des perturbations secondaires (épidémie d'insecte, chablis), qui avec le temps depuis le dernier évènement de feu modifient la structure et la composition de la forêt.

0.1.2 Les bryophytes

Les bryophytes dominent le sous-bois de plusieurs forêts boréales. Elles se retrouvent souvent en forme de tapis continu qui recouvre entièrement le sol. Elles peuvent représenter une proportion significative de la production primaire (Longton, 1992; Bisbee et al., 2001; O'Connell et al., 2003), peuvent réduire le température du sol et peuvent absorber les nutriments lessivés des arbres par la précipitation (Van Cleve et Viereck, 1981).

La strate des bryophytes qu'on retrouve dans le biome boréal d'Amérique du Nord, subit une succession typique, où les espèces de début de succession sont remplacées par d'autres espèces, et ultimement par les mousses hypnacées (*Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis*; Black et Bliss 1978; Heinselman 1981; Foster 1985). Dans les régions de l'est où les cycles de feu sont plus longs, la succession continue et aboutit à une invasion et à une expansion des sphaignes (Foster 1985; Boudreault et al., 2002). Ce changement de composition de la strate muscinale, de mousses hypnacées à sphaignes, entraîne des changements dans le fonctionnement de l'écosystème. Comparé aux mousses hypnacées, les sphaignes ont un taux de fixation du carbone élevé (Bisbee et al., 2001; Swanson and Flanagan 2001), un plus grand effet d'isolation sur le sol (Dioumaeva et al., 2002), et un taux de décomposition réduit (Swanson and Flanagan, 2001; Turetsky, 2003). Malgré l'ampleur des effets sur l'écosystème, les causes et les mécanismes d’établissement et d’expansion des sphaignes dans le tapis de mousses hypnacées ne sont pas encore bien compris.

0.2 L’ENTOURBEMENT

L’entourbement est le développement d’une couche épaisse de matière organique sur le sol en association avec la remontée de la nappe phréatique. La cause ultime de l’entourbement est un taux de production de biomasse qui est supérieur au taux de décomposition. L’entourbement est associé à une réduction du taux de croissance des arbres (Bonan et Shugart, 1989; Glebov et Kurzukhin, 1992). Cette réduction est potentiellement une conséquence du milieu froid et humide dans lequel poussent les racines. L’entourbement est un processus qui prend place globalement mais qui est limité à des régions distinctes, où les conditions permettent un excès de production par rapport à la décomposition dans le sous-bois. Bien que la cause ultime soit commune à toutes les régions affectées par l’entourbement, soit un excès de production de biomasse, la cause proximale varie entre les régions. Par exemple, en Alaska l’entourbement est une conséquence du développement du pergélisol sous les tapis de mousses hypnacées, et en Sibérie l’entourbement est une conséquence de l’expansion des tourbières avoisinantes. À cause de leurs propriétés physiques (production, décomposition, capacité d’absorber l’eau), les sphaignes ont été associées à l’accumulation de la matière organique sur le sol, et à la remontée de la nappe phréatique (Heilman, 1966; Noble et al., 1984), mais cette relation n’a pas encore été démontrée.

La ceinture d’argile de Québec et de l’Ontario est une grande région (125 000 km^2) affectée par l’entourbement. La présence, à la fois, de sols argileux déposés par les lacs proglaciaires Ojibway-Barlow et d’une topographie dominée par des pentes faibles favorise l’entourbement dans la région. Le phénomène est aussi favorisé par la dominance de l’épinette noire, qui est une espèce produisant une litière résistante à la décomposition. Malgré l’importance de ce processus pour la région, il y a peu d’études qui examinent en détail l’entourbement (cf. Taylor et al., 1987; Boudreault et al., 2002; Jeglum et He, 1995; Groot, 2002; Lecomte et al., 2005).

0.3 L'AMÉNAGEMENT FORESTIER

Dans les forêts aménagées pour l'extraction de matières ligneuses, l'aménagement écosystémique, où les interventions forestières s'inspirent des processus naturels de l'écosystème (McRae et al., 2001), est couramment vu comme la meilleure façon de conserver la diversité biologique et structurelle des forêts à l'échelle du paysage. Cependant, afin de réussir un aménagement écosystémique, il faut comprendre les processus régionaux. Couramment en forêt boréale les coupes de faible rétention (où tous les arbres de diamètre commercial sont récoltés) qui ne perturbent pas le sol, sont l'intervention dominant. Il y a deux lacunes dans cette vision de la forêt boréale sur la ceinture d'argile : (1) les forêts subissent un cycle de feu long (Bergeron et al., 2001), et par conséquence développent, avec le temps depuis feu, une diversité de structures horizontales et verticales qui n'est pas reproduite par des coupes totales, et (2) les coupes avec protection de la régénération et des sols (CPRS), qui sont exigées par les normes au Québec, n'imitent pas les feux, parce qu'elles ne perturbent pas le sol (Bergeron et al., 1999). Pour résoudre la première problème, les coupes partielles ont été suggérées comme un outil qui permettrait l'extraction de matières ligneuses et la création de structures associées avec les vieilles forêts. Toutefois, on ne sait pas encore si ces techniques créent avec succès des structures acceptables pour les espèces associées aux vieilles forêts. Les conséquences du deuxième problème ne sont pas encore documentées, et l'ultime effet de la CPRS sur la succession des peuplements entourbés est aussi inconnu. De même, les méthodes pour mieux imiter les feux sévères sont peu testées.

0.4 OBJECTIFS

L'objectif global de cette thèse est de déterminer les mécanismes d'entourbement, et le rôle des bryophytes dans le processus d'entourbement des forêts d'épinettes noires de la ceinture d'argile du Québec et de l'Ontario. La thèse est divisée en trois sections réparties sur sept chapitres au total. La première section examine les mécanismes de l'entourbement et la remontée de la nappe phréatique (chapitres I et II). Les mécanismes de succession de la communauté des bryophytes sont traités dans la deuxième section (chapitres III, IV, V, VI) et finalement les conséquences des coupes partielles sur la communauté de sphaignes sont examinées dans la troisième section (chapitre VII).

Ces travaux ont été réalisés dans la chronoséquence principalement mise en place par Nicolas Lecomte, et le Réseau des Coupes Partielles.

CHAPITRE I

PALUDIFICATION IN BLACK SPRUCE (PICEA MARIANA) FORESTS OF EASTERN CANADA: POTENTIAL FACTORS AND MANAGEMENT IMPLICATIONS

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1.1 ABSTRACT

Over time boreal black spruce forests on fine-textured soils in western Quebec, Canada develop very thick forest floors composed of poorly decomposed litter created by the tree and understory layers. These paludified soils are typically waterlogged and cold, and in this fire-mediated landscape, are at least partially consumed by stand replacing fires, which facilitates the establishment of the next generation of trees. Within a context of ecosystem based management, forest harvest should mimic the dual effects of high severity fire on tree and forest floor biomass. This study was designed to investigate potential factors of forest floor thickness in order to determine the impact of removing only a tree layer, and to suggest strategies to limit paludification in this important forestry region. Forest floor thickness, fire severity, basal area, canopy closure, cover of *Sphagnum* spp. and ericaceous spp. were measured in black spruce stands across a chronosequence from 50 to 350 years after fire. Fire severity was determined to be a key factor in determining forest floor thickness by path analysis. After high severity fires forest floor thickness was primarily dependant on stand age, but was also positively influenced by *Sphagnum* spp. cover and negatively influenced by the presence of trembling aspen (*Populus tremuloides*). These results suggest that forest interventions that do not remove the organic layer may be mimicking low severity fires and promoting poor growth and regeneration. Forest floor thickness may be limited by avoiding interventions that open the canopy that promotes the presence of *Sphagnum* spp. and ericaceous spp., or by practicing mixed silviculture of trembling aspen and black spruce. However, a balance needs to be maintained between the application of these techniques and the preservation of paludified forests to maintain natural landscape proportions.

Dans l'ouest du Québec, Canada avec le temps depuis le dernier feu, les forêts d'épinette noire sur sols fins développent des couches épaisses de matière organique formée de la litière des arbres et du sous-bois. Ces sols entourbés sont typiquement froids et saturés d'eau et, par conséquent, leur combustion (totale ou partielle) par les feux de forêt facilite l'établissement d'un nouveau peuplement. Dans le contexte d'aménagement écosystémique, la récolte d'arbre dans ces forêts devrait imiter l'effet double des feux de forêt, soit la combustion des arbres et de la couche de matière organique. Cette étude a pour but d'investiguer les facteurs qui influencent l'épaisseur de la matière organique pour être capable d'évaluer l'impact d'enlever uniquement les arbres et de finalement suggérer des stratégies pour limiter l'entourbement dans cette région forestière. Dans une chronoséquence de sites âgés de 50 à 350 ans après feu, l'épaisseur de la matière organique, la sévérité du dernier feu, l'ouverture de la couronne et le recouvrement des sphaignes et des éricacées ont été mesurés. Une analyse par coefficient de direction a démontré que la sévérité du dernier feu est un facteur clé dans l'accumulation de la matière organique. Après un feu de haute sévérité, l'épaisseur de la matière organique est principalement déterminée par le temps depuis feu mais est aussi influencée positivement par le recouvrement des sphaignes et négativement par la présence des peupliers faux-tremble (*Populus tremuloides*). Ces résultats suggèrent que les interventions forestières qui ne réduisent pas la couche de matière organique pourraient imiter les feux de faible sévérité et pourraient ainsi promouvoir la faible croissance et établissement dans le nouveau peuplement. L'épaisseur de la matière organique pourrait être

limitée par des interventions qui gardent un maximum de recouvrement de couronne et par conséquent limiter l'étalement des sphaignes et des éricacées ou par la sylviculture mixte des peupliers faux-tremble et des épinettes noires. Toutefois, au niveau du paysage, un équilibre entre la préservation des forêts entourbées et leur remise en production est nécessaire.

1.2 INTRODUCTION

Boreal black spruce (*Picea mariana* Lamb.) forests develop thick forest floors composed of partially decomposed and un-decomposed plant matter that is a product of the understory and tree layers. The thickest forest floors occur in regions prone to paludification, such as the interior of Alaska (Viereck et al., 1993), old glacial Lake Agassiz (Heinselman, 1963), the Clay Belt of Québec and Ontario (Taylor et al., 1987), and Labrador (Foster, 1984). In these regions decomposition is considerably slower than litter production, due to low temperatures, and the presence of poor decomposition substrates in the litter (Prescott et al., 2000). As a result, very thick forest floors accumulate, and forests may develop into peatlands (Crawford et al., 2003).

While paludification is frequently discussed, the local mechanisms that result in reduced decomposition are not clear. Cited causes include *Sphagnum* spp. invasion (Lawrence, 1958), thick feather moss cover (Viereck et al., 1993), the presence of ericaceous species (DeLuca et al., 2002) and water table rise due to a variety of causes (Taylor et al., 1987; Bonan and Shugart, 1989). Regardless of the cause, the accumulation of deep forest floors has a profound negative effect on forest productivity (Bonan and Shugart, 1989;Glebov and Kurzukhin, 1992), as paludified soils tend to be water-logged, cold and have a significant proportion of nutrients locked up in the poorly decomposed organic matter that makes up the forest floor (Heinselman, 1963; Van Cleve and Viereck, 1981; Bonan and Shugart, 1989; Glebov and Kurzukhin, 1992). These changes are believed to cause a drop in the growth rate of trees (Van Cleve and Viereck, 1981), and inhibit the development of seedlings (Bonan and Shugart, 1989; Greene et al., 1999). As a result, regeneration is decreased without a stand replacing fire that burns through the forest floor.

Ecosystem based management includes the assumption that diversity (biological and structural) can be conserved when forestry interventions are modelled after natural disturbances (McRae et al., 1999). Therefore, in a landscape where forestry is applied, it is important to understand how the disturbance regime affects ecosystem processes in order to accurately mimic them. Within the boreal forest it is frequently assumed that clearcuts mimic the stand replacing fires that are the dominant disturbance factor. However, it has been suggested that without site preparation to disturb the accumulated forest floor, clearcuts do not resemble fires (Bergeron et al., 1999). Ultimately, without a better understanding of how forest floor biomass is accumulated after fire, and how this process is affected by fire characteristics (e.g. severity or depth of burn in forest floor) the potential impacts of a lack of forest floor disturbance can only be speculated on.

The objectives of this study are to examine some of the factors that are believed to influence the accumulation of thick forest floors in boreal black spruce stands on fine textured soils on the Clay Belt of Québec and Ontario. Factors included in the analyses are fire severity, stand density, degree of crown closure, density of trembling aspen, and *Sphagnum* spp., and ericaceous spp. cover. High fire severity, stand density and trembling aspen presence are expected to decrease forest floor thickness, while low canopy closure, and high cover of ericaceous and *Sphagnum* spp. are expected to increase forest floor thickness. With a better understanding of these factors, it may then be possible to suggest silvicultural solutions to either better mimic high severity, stand replacing fires, or to limit forest floor accumulation.

1.2.1 Study Area

The study was conducted in the western boreal forest of Québec, within the black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin 1996). Specifically, the study took place within the Clay Belt of Québec and Ontario, a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsonian (Vincent and Hardy 1977). The Clay Belt is an excellent area in which to study forest floor accumulation because it is prone to paludification (Boudreault et al. 2002), and supports a large forestry industry. Average annual temperature is 0.8°C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Québec (Environment Canada 1993). The dominant disturbance types are large fires that kill all above ground vegetation. Between 1850 and 1920 the fire cycle was ca 135 years, and it has since increased to ca 398 years; mean stand age is 148 years (Bergeron et al. 2004).

1.3 MATERIALS AND METHODS

1.3.1 Data Collection

During the summer of 2003, 18 black spruce dominated sites ranging from 50 to 350 years since fire (see Appendix A for a full description) were sampled. A stand initiation map (Bergeron et al., 2004) and an ecoforestry map (Harper et al., 2002) were used to choose sites on a slight incline with fine-textured deposits. Slope and soil textured were both verified at the site, and time since fire was established by either dating of dominant trees, or verification of fire map dates by dating of a few dominant trees. The severity of the last fire on the forest floor was established by determining the position of the uppermost charcoal layer within numerous forest floor profiles. While strictly speaking more fuel may have been consumed in the low severity fires, severity of fire on the forest floor may be most accurately measured by the amount of forest floor not-consumed by fire (Alexander, 1982; Nguyen-Xuan, 2000). If the charcoal was situated at the interface between the forest floor and the mineral soil, the last fire was designated as high severity. If however, the charcoal layer was within the forest floor layer, the last fire was designated as low severity. For further details on the methods used, see Lecomte et al. (2006). Among the stands sampled, 13 sites were established after high severity fire and five sites after low severity fire.

Within each site, five quadrats of 100 m^2 were installed, with four nested quadrats of 25 m^2. Within each 25 m^2 quadrat, forest floor thickness was determined by measuring the depth to mineral soil in a randomly chosen location, including therefore the entire organic layer. The clay A horizon provided a clear end point to forest floor depth. A densiometer reading was taken (a concave mirror scored with a grid to allow estimation of canopy cover), and the diameter at breast height (dbh) of all trees greater than 8 cm was measured. Basal area per hectare was calculated for all species together, and for trembling aspen alone. Both stand density and canopy openness were included as variables as stand density also includes the effect of the trees on the soil. Covers (%) of *Sphagnum* spp. and ericaceous spp. (primarily *Ledum groenlandicum,* and *Kalmia angustifolia*) were estimated. The 25 m^2 quadrats were assumed to be independent, as soil processes tend to vary on the scale of a few meters, therefore analyses were performed on the values for the 25 m^2 quadrats.

1.3.2 Statistical Analyses

Forest floor thickness was natural log transformed in all analyses for normality. All other variables were normally distributed.

Pearson correlations were calculated between transformed forest floor thickness and potential explanatory variables [basal area, open canopy, trembling aspen (PET) basal area, *Sphagnum* spp. and ericaceous spp. cover] for each data set. Spearman's correlation coeffecient was used for fire severity. Because many of the potential explanatory factors examined were auto-correlated, partial correlation and path analysis, rather than multiple regression, were used to determine the potential structure (including direction) of the relationships among the variables. A d-sep test (Shipley, 2000) was used to determine the likelihood that an a-priori structure was correct. Partial correlation coefficients (or path coefficients) among the variables allowed the determination of the magnitude of direct and indirect effects among variables. The variables included in each path analysis were selected from the list of potential variables based on strong partial correlation with forest floor thickness, indicating they were related when the other variables were held constant. The percent of variation in forest floor thickness explained by the selected explanatory variables was calculated with linear regression using SPSS 10.0. A p of 0.05 was used in all analyses, except the Pearson correlations where a p of 0.01 was used, due to the large number of correlations calculated.

1.4 RESULTS

Forest floor thickness was negatively correlated with fire severity (i.e. thinner forest floors after high severity fires), total basal area, and trembling aspen (PET) basal area, and positively correlated with cover of ericaceous spp. and *Sphagnum* spp., canopy openness, and time since fire (TSF; Table 1.1). The importance of fire severity is visible in the different curves for sites after high and low severity fires (Figure 1.1). After a high severity fire, a 50 year old site had only approximately 17 cm of forest floor on average, while in a neighbouring site, 50 years after a fire of low severity there was approximately 40 cm of forest floor.

Table 1.1 Pearson correlation coefficients (Spearman for severity) among factors influencing forest floor thickness, in all sites, and after high and low severity fires. Values in bold are significant at p 0.01.

All sites	Severity	Basal area	Open canopy	*Sphagnum* cover	Ericaceous cover	PET basal area	TSF
Forest floor thickness	**-0.358**	**-0.547**	**0.573**	**0.584**	**0.640**	**-0.169**	**0.738**
Severity		**0.309**	**-0.260**	**-0.201**	**-0.341**	0.093	0.000
Basal area			**-0.577**	**-0.451**	**-0.607**	**0.249**	**-0.506**
Open canopy				**0.414**	**0.561**	-0.108	**0.580**
Sphagnum cover					**0.557**	**0.147**	**0.526**
Ericaceous cover						**-0.145**	**0.605**
PET basal area							-0.099

High severity	Basal area	Open canopy	*Sphagnum* cover	Ericaceous cover	PET basal area	TSF
Forest floor thickness	**-0.489**	**0.565**	**0.661**	**0.634**	**-0.177**	**0.802**
Basal area		**-0.551**	**-0.501**	**-0.585**	**0.261**	**-0.618**
Open canopy			**0.449**	**0.591**	-0.103	**0.685**
Sphagnum cover				**0.644**	**-0.150**	**0.724**
Ericaceous cover					-0.139	**0.770**
PET basal area						-0.122

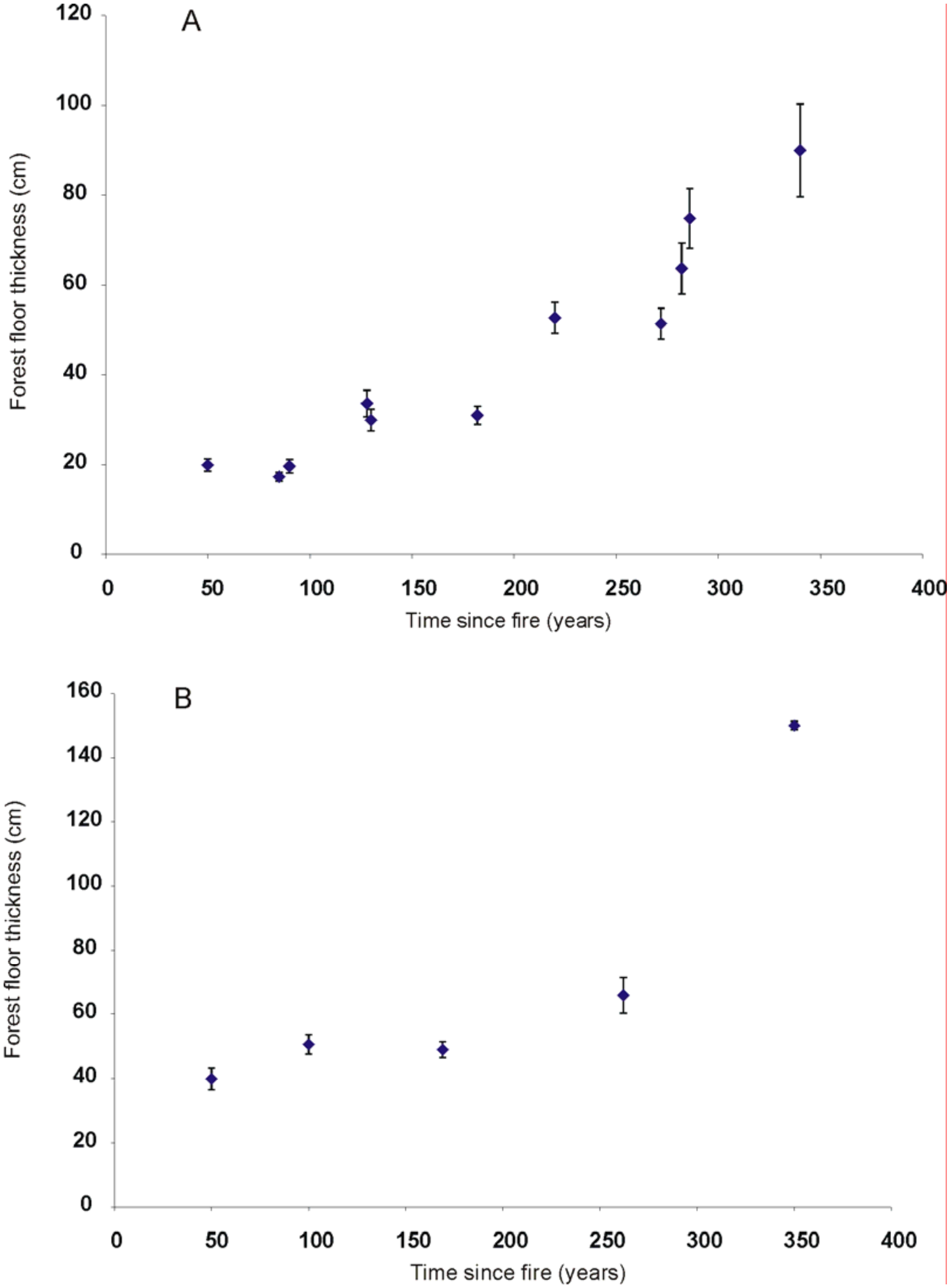

Figure 1.1 Development of forest floor with time since (A) high and (B) low severity fires as mean thickness with standard error. Each point represents the mean of 20 values for each site.

As most of the potential factors were auto-correlated, partial correlations were calculated to determine which would be retained for path analysis. TSF, fire severity, cover of *Sphagnum* spp. and ericaceous spp. were retained, as they had a significant partial correlation, even when the other factors were taken into consideration (Table 1.2). The structure determined by path analysis (Figure 1.2), which was not rejected by d-sep analysis (p= 0.2989; Shipley, 2000), indicated that TSF and fire severity were the two dominant factors on forest floor thickness, with the largest direct effects, 0.606 and –0.295 respectively. The cover of *Sphagnum* spp. and ericaceous spp. also had statistically significant direct effects, although with less influence than TSF and fire severity. In fact the majority of the correlation between forest floor thickness and *Sphagnum* spp. and ericaceous spp. cover is due to shared correlation with TSF and fire severity. In turn, *Sphagnum* spp. cover was positively influenced by cover of ericaceous spp., and TSF. Cover of ericaceous species was influenced negatively by fire severity and positively by TSF.

Table 1.2 Direct effect, indirect effect and error terms for path analysis of forest floor thickness in all sites, and after high and low severity fires. Total value represents the Pearson correlation coefficient (R^2).

	Variable	Direct	Indirect	Error	Total
All sites	Time since fire	0.606	0.307	0.0711	0.738
	Severity	-0.295	-0.123	0.047	0.371
	Sphagnum cover	0.164	0.324	0.0960	0.584
	Ericaceous cover	0.079	0.513	0.0481	0.640
High severity	Time since fire	0.489	0.284	0.0273	0.800
	Sphagnum cover	0.198	0.288	0.174	0.659
	PET basal area	-0.116	0.0235	-0.0845	-0.177
	Ericaceous cover	0	0.621	0.0100	0.631
	Open canopy	0	0.519	0.0460	0.565

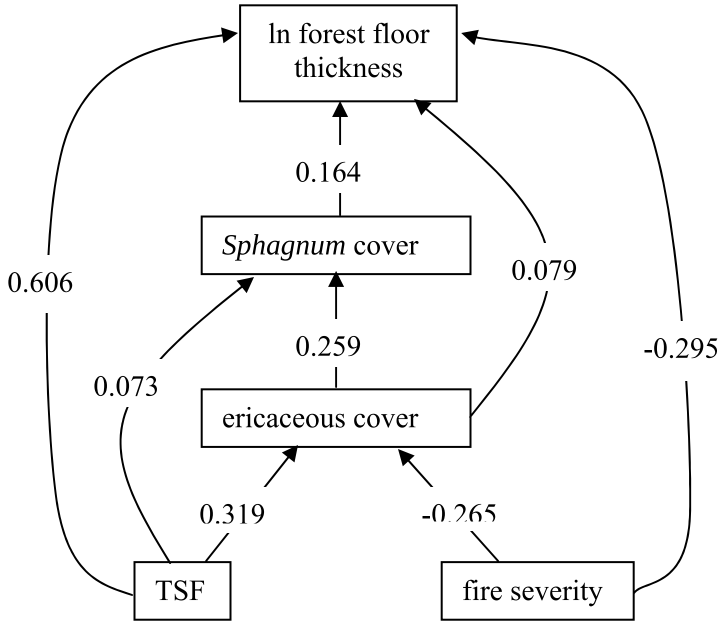

Figure 1.2 Path analysis of factors affecting forest floor thickness after high and low severity fires combined. The structure was not rejected by d-sep analysis (Shipley, 2000), p = 0.2989. Multiple regression indicated that 70% of the variability was explained by the included variables. Arrows and numbers indicate the direction of causality and the path coefficient between two variables.

As fire severity was a dominant factor, the high severity sites were analysed separately. After severe fires, forest floor thickness was highly correlated with the amount of open canopy, cover of *Sphagnum* spp., cover of ericaceous spp., amount of trembling aspen and TSF, which were all also auto-correlated (Table 1.1).

TSF, amount of trembling aspen, cover of *Sphagnum* spp. and ericaceous spp., and canopy openness all had significant partial correlations when the other factors were accounted for. The structure suggested by path analysis, indicated that only TSF, *Sphagnum* spp. cover and amount of trembling aspen had direct effects on forest floor thickness (Table 1.2; Figure 1.3). The cover of ericaceous spp. and the amount of open canopy had an indirect effect via *Sphagnum* spp. cover. The presented model explains 65% of the variability ($p<0.0001$), as indicated by multiple regression, and the structure was not rejected by a d-sep test (Shipley, 2000) with a p of 0.725.

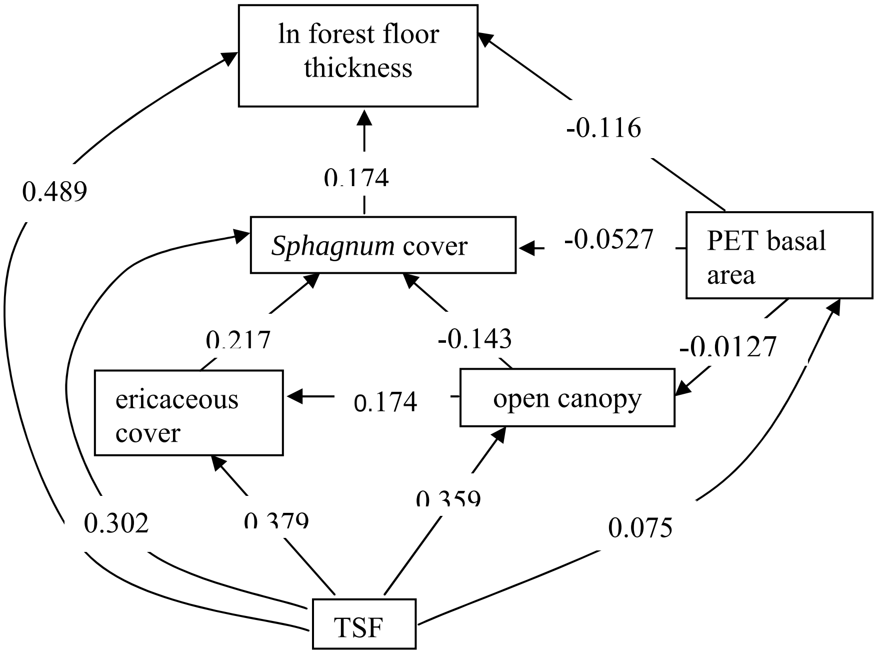

Figure 1.3 Path analysis of factors affecting forest floor thickness after high severity fires. The structure was not rejected by d-sep analysis (Shipley, 2000), p = 0.725. Multiple regression indicated that 65% of the variability was explained by the included variables. Arrows and numbers indicate the direction of causality and the path coefficient between two variables.

1.5 DISCUSSION

1.5.1 Time since fire and fire severity

Time since fire (TSF) was the most important factor influencing forest floor thickness within both the entire data set and the analyses restricted to the high severity fire sites. This is only logical, as the matter within the forest floor takes time to accumulate. However the strong relationship with TSF also indicates that on fine-textured soils on the Clay Belt, no additional initiative process is required. This is in contrast to other geographical areas where a non-linear relationship exists, and thick forest floors are developed after the creation of an impermeable layer by an external factor such as the development of permafrost, a chemical change in the soil, or the expansion of neighbouring peatlands (Bonan and Shugart, 1989; Glebov and Korzukhin, 1992; Viereck et al., 1993).

From TSF it is possible to calculate the rate of accumulation of forest floor matter. However, the true rate of accumulation in the oldest stands cannot yet be accurately determined, as these sites may be older than indicated by dendrochronological age alone. Carbon 14 tests on similar stands in the same region have indicated that the oldest trees currently found were actually established a long time after the last fire (Cyr et al., 2005), resulting in an underestimation of stand age. While a change in stand age would affect the interpretation of the rate of forest floor accumulation and potentially the relative importance of each mechanism, it would not affect the mechanisms investigated here.

After TSF, fire severity was the most important factor in explaining variation in forest floor thickness in the complete data set. This is reflected in the very different forest floor thicknesses in young stands after high and low severity fires, and in the relationship between forest floor thickness and time (Figure 1.1). This may be due to two causes. The intuitive cause is that residual matter left by a low severity fire gives the forest floor a head start. However, the presence of residual matter may also accelerate the rate of accumulation by affecting the function of factors suggested here, primarily *Sphagnum* spp. and ericaceous spp. For example, the residual layers of the forest floor left after non-severe fires may facilitate *Sphagnum* spp. establishment, and growth (Dyrness and Norum, 1983; Purdon et al., 2004). For this reason, a separate analysis was completed for the high severity fire sites.

A similar detailed analysis of the low severity sites was not possible with the data from this study, as too few low severity fires were sampled. Therefore, future studies should focus on understanding the influence of low fire severity and residual matter on the factors influencing the development of forest floors proposed here. This may be of particular importance, as the long fire cycles found in the eastern boreal forests permit the accumulation of a significant forest floor. This may cause a self-perpetuating cycle as forests with a thicker forest floor are moister and lose less organic matter during subsequent fires (Foster, 1985; Kasischke et al., 2000).

1.5.2 Forest floor thickness after high severity fires

While TSF was overwhelmingly the most important factor influencing forest floor thickness, there was variation in the thickness of the forest floor within and among sites, particularly at later stages in the chronosequence (Figure 1.1). Within this analysis, the factors explaining this variation were the cover of *Sphagnum* spp., the amount of trembling aspen, the openness of the canopy and the cover of ericaceous spp.

The presence of *Sphagnum* spp. in the understory has frequently been implicated as a key factor in the development of thick forest floors. They are believed to have a negative effect on decomposition through the development of a cold, wet and acidic environment for decomposers (Turetsky, 2003). In addition they also affect decomposition rates through their rapid production of biomass, which has a high C:N ration, and is resistant to decomposition (Hobbie, 1996; Turetsky, 2003). However, while our results indicate that they are a direct factor in determining forest floor thickness, the magnitude of effect is comparatively weak.

The direct negative effect of the presence of trembling aspen on forest floor thickness is inferred to be due to the presence of a high quality litter on the forest floor, which results in higher decomposition rates overall. Légaré et al. (2005) found increasing decomposition rates of popsickle sticks, in the forest floor with increasing presence of trembling aspen in the forest composition. In addition to this direct effect, the presence of trembling aspen diminished the cover of *Sphagnum* spp. This effect is particularly interesting when canopy openness is accounted for and implies that there is a relationship that is not directly related to shade. It has been suggested that deciduous leaves have a negative effect on the growth of forest floor mosses, either through a chemical interaction or through shading (Frego and Carleton, 1995; Saetre et al., 1997).

Canopy openness had only an indirect effect on forest floor depth, via *Sphagnum* spp. cover. The negative interaction between these two factors is surprising, as *Sphagnum* spp. is generally considered to be shade intolerant, and dependent on full sunlight for maximum growth (Bisbee et al., 2001; Ohlson et al., 2001). However, *Sphagnum capillifolium*, a highly shade tolerant species (Hayward and Clymo, 1983), dominates in young stands (Fenton and Bergeron, 2006). As a result, total *Sphagnum* cover does not display the expected relationship with canopy openness. The negative relationship may be due to improved growth of *Sphagnum* spp. in the less illuminated sites in the older sites, which allows them to avoid desiccation and photoinhibition.

The cover of ericaceous species had only an indirect effect on forest floor depth, via *Sphagnum* spp. However, in Europe *Empetrum nigrum,* has been shown to have a strong direct impact on ecosystemic processes (Wardle et al., 1997, 2003) through the production of phenols that retard decomposition (DeLuca et al., 2002). In this study, while *Kalmia angustifolia* and *Ledum groenlandicum* litter have been shown to produce phenols (Inderjit and Malik 1997, 2002), their effect on forest floor thickness after high severity fires was solely through their effect on the abundance of *Sphagnum* spp., and probably not a direct effect on decomposition rate. Ericaceous species, and vascular plants in general, may stimulate *Sphagnum* spp. growth through a “scaffolding” effect, where the *Sphagnum* spp. use vascular plants to physically support fast vertical growth (Malmer et al., 2003). The high level of variability in forest floor depth within sites, particularly in the older sites (Figure 1.1A), indicates the importance of very local factors, such as small canopy openings, and *Sphagnum* spp. and ericaceous spp. cover.

1.5.3 Management implications

Ecosystem based management requires an understanding of regional disturbance and stand dynamics in order to be successfully applied. The development of thick forest floors on the Clay Belt of Québec and Ontario is an excellent example. Because on the Clay Belt black spruce stands on fine textured soils accumulate thick forest floors over time, which have a negative effect on tree growth (Heinsleman, 1981; Glebov and Kurzhkin, 1992), any management technique that wishes to emulate a stand replacing fire must also remove at least a part of the forest floor. The very thick forest floors, and low stand density of stands established after low severity fires illustrate potential consequences of failing to do so. Further research is required in order to determine which method is most efficient at removing forest floor and creating favourable sites for black spruce.

The factors affecting forest floor thickness determined in this study suggests several potential solutions for limiting the development of the forest floor within a stand, which should be further tested. The importance of *Sphagnum* spp. and ericaceous spp. in forest floor depth suggest that stands with these mostly shade intolerant species in the understory should be opened up only with caution, to prevent an acceleration of forest floor accumulation. Furthermore, to limit their establishment, stands should be re-established at high density, to limit light and therefore their establishment sites. The influence of trembling aspen on forest floor thickness, and the more detailed analyses completed by Légaré et al. (2005) suggest that the inclusion of moderate component of trembling aspen may limit the development of a thick forest floor. However, further research is required to determine optimal densities.

1.5.4 Conclusions

While within managed stands the accumulation of thick forest floor needs to be mitigated for continued sustainability of harvests, these stands are an important part of the natural forest mosaic. As such, they are important for conserving the diversity of a variety of taxonomic groups. Therefore, rather than suggesting that all these stands should be harvested, scarified and planted, we suggest that fire be more accurately mimicked within the component of the landscape which is managed for timber.

1.6 ACKNOWLEDGMENTS

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CHAPITRE II

SOIL OXYGEN WITHIN BOREAL FORESTS ACROSS AN AGE GRADIENT

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2.1 ABSTRACT

Globally, soil anoxia and water table rise play a role in the development of peatlands from forests. Cited causes have included a diversity of internal and external mechanisms, including *Sphagnum* and feather mosses, hardpan development, and peatland expansion. The objectives of this study were to examine water table depth in black spruce stands of the Clay Belt of Quebec and Ontario, and to associate changes with potential stand scale causal factors. A methodological issue, the link between oxygen zone and water table, was also addressed. Within stands less than 100 years post fire, oxygen zone and water table position were only loosely related, and no other potential factors were significantly correlated. Across a chronosequence of stands, while oxygen zone thickness in the soil profile was relatively constant, its position relative to the mineral soil changed, as it rose from the mineral soil into the organic forest floor. Forest floor thickness was the dominant explanatory factor in oxygen zone position, suggesting that in these forests other postulated mechanisms are less important. At the landscape level, the movement of the oxygen zone into the organic forest floor has important consequences for the long-term productivity of this intensively exploited forest region.

Généralement, l'anoxie du sol et la remontée de la nappe phréatique jouent des rôles dans la transformation des forêts en tourbières. Les causes invoquées pour expliquer la remontée de la nappe inclus les sphaignes, les mousses hypnacées, le développement d'une couche imperméable et l'expansion des tourbières avoisinantes. Les objectifs de cette étude sont d'examiner la nappe phréatique dans les pessières de la Ceinture d'argile du Québec et de l'Ontario et d'associer les changements observés dans la position de la nappe phréatique avec des facteurs potentiels à l'échelle du peuplement. Une question méthodologique, le lien entre la zone oxydée et la nappe phréatique, est aussi investiguée. Dans les peuplements âgés de moins de 100 ans depuis le dernier feu, la zone oxydée et la nappe phréatique sont faiblement corrélées et aucun autre facteur explicatif n'a été trouvé. Dans une chronoséquence de peuplements, malgré que l'épaisseur de la zone oxydée soit relativement constante, la position de la nappe phréatique relative au sol minéral change car elle monte dans la couche de matière organique. L'épaisseur de la matière organique est le facteur explicatif le plus important dans la position de la nappe phréatique, ce qui suggère que les autres mécanismes postulés sont moins importants. Au niveau du paysage, la remontée de la nappe phréatique a des conséquences importantes pour la productivité à long terme des forêts de cette région forestière intensivement exploitée.

2.2 INTRODUCTION

Water table rise and associated anoxic conditions in boreal forest successional sequences have been associated with slowed tree growth, tree death and ultimately the development of bogs (Crawford et al., 2003, Vygodskaya et al,. 2002, Viereck et al., 1993, Zobel, 1990, Heilman, 1966, Lawrence, 1958).

Cited causes for water table rise are numerous and include internal factors such as the development of a hard pan in podzolic soils (Bonan and Shugart, 1989), the development of permafrost under moss insulated soils (Viereck et al., 1993), the establishment of *Sphagnum* mosses (Lawrence, 1958), the accumulation of moisture retaining organic matter (Heinselman, 1981; Heilman, 1966), the reduction in evapo-transpiration with stand structural changes (Taylor et al., 1987), and external factors, such as the influence of the raised water table of neighbouring wetlands (Glebov and Korzukhin, 1992; Neiland, 1971).

Compared to forests in Alaska, Siberia, and Minnesota, the paludifying black spruce (*Picea mariana*) forests of the Clay Belt of Quebec and Ontario are relatively little studied. Within this context, the overall objective of this study was to document water table depth within the boreal forest, at the stand scale. Few studies have taken an interdisciplinary approach and looked at forest stand scale factors that play a role in water table and soil oxygen dynamics, and we wanted to examine their potential role across an age and paludification gradient. However, a methodological issue was also addressed; the negative impacts on plants of water table rise are more truly due to a lack of oxygen, but oxygen zone depth is rarely measured. Therefore, the specific objectives of this study were twofold: (1) to compare variations in oxygen zone depth to water table depth and other potential biologic explanatory factors, and (2) to document changes in oxygen zone depth with time since fire and associate these changes with potential causal factors suggested from the literature, including tree density, organic forest floor depth, and *Sphagnum* spp. abundance.

2.3 STUDY AREA

The study area is located at the border of the Abitibi-Témiscamingue and Nord du Quebec regions, in the southeastern boreal forest of Canada, which is part of the black spruce (*Picea mariana* (Mill.) BSP) - feathermoss (*Pleurozium schreberi* (Brid.) Mitt.)) forest of western Quebec (Grondin, 1996). This bioclimatic domain extends over the Clay Belt of Quebec and Ontario, a major physiographic region resulting from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expansion, in the Wisconsinan (Vincent and Hardy, 1977). The average annual precipitation totals 856.8 mm and average annual temperature is 0.8°C (Environment Canada, 1993) recorded at the closest weather station (La Sarre). This ecosystem is dominated by large fires that kill most of the trees and aboveground vegetation (Bergeron et al., 2001). Mean stand age is 139 yrs and fire cycle length has increased from 141 years between 1850 and 1920, to 326 years since 1920 (Bergeron et al., 2001).

2.4 MATERIALS AND METHODS

2.4.1 Experimental design

Potential mechanisms causing variations in oxygen zone depth, such as water table depth, stand basal area (as an indirect measure of leaf area), organic forest floor depth, and abundance of *Sphagnum* spp., are often correlated with time since last fire. Thus, two observational studies were set up in order to describe variations in oxygen zone and their potential causes. Sites were chosen with none to slight slopes, and clay dominated soil to facilitate comparison between stands. Stand selection included a laborious assessment of soil properties and slope. From this we can feel confident that soil properties were relatively constant between sites and that water movement was down the soil profile and not horizontal. The fire origin of all stands was verified by identification of charcoal horizons in the forest floor. All stands had only a single charcoal layer immediately above the mineral soil, indicating that these stands were established after a severe stand replacing fire (Lecomte et al. 2005). Time since fire was established from the fire map elaborated by Bergeron et al. (2004), and confirmed by dating and analysis of cross sectional tree discs from each site.

The first study was installed in stands that originated after fires that took place around 1920 with a heterogeneous distribution of aspen. More precisely sites 1, 2 and 3 originated from fires in 1926, 1916 and 1916 respectively. This study was principally set up to compare oxygen zone depth and water table depth but also to test the potential influence of other stand level factors suggested from the literature without the influence of time. In the second study, a chronosequence of seven black spruce stands was established (Table 2.1), which allowed us to document changes in oxygen zone depth with time since fire and associate changes with potential causal factors suggested from the literature. Oxygen zone depth in both studies was measured with steel rods, approximately 120 cm long, which were driven into the soil and recuperated after 5 weeks. Two zones of rust form on the metal rods: a zone of orange/brown rust indicating the interface between the zones of abundant and scarce oxygen in the soil and a zone of black rust that indicates places where oxygen has diffused into a previously anaerobic zone (Bridgham et al., 1991; Carnell and Anderson, 1986). As the oxygen zone and water table are not static across a growing season, their positions measured here apply uniquely to the season during which it was measured. However, as the study occurred during the period where water availability declines rapidly with the development of deciduous leaves, (i.e. late May to late June), we think that this is a key period in the growing season.

Table 2.1 Description of sites used in Study II. All values are means ± standard errors.

Site	Time since fire (yrs)	Mean basal area (m^2 /ha)	Thickness of organic forest floor	% cover *Sphagnum*
N23	85	44.08±10.60	16.6±13.3	9.7±4.9
S1	90	41.94±16.82	19.7±1.5	21.8±4.4
W1	130	43.74±14.28	29.9±2.4	11.0±3.2
N50	220	20.67±6.35	50.4±5.6	68.5±4.6
L22	272	22.89±11.71	51.4±3.5	55.0±4.1
N6	282	21.31±7.82	60.9±6.5	62.7±2.9
N20	340	7.19±5.50	90±10.3	62.0±4.21

2.4.1.1 Study I

In each of three stands twelve units of three steel rods were set in a triangle shape around an approximately 1m long PVC tube with small holes drilled in it. PVC tubes and steel rods were driven into the soil and left for a period of 5 weeks. The twelve units were at a distance of at least 20 m from each other in each 2 to 3 hectare stand. As the water table and soil processes are variable at the scale of meters and the sampling points were all 20 m apart, we consider them to be individual sampling points. Water table depth in the PVC tubes was measured every three days from May 26th to June 19th 2003 with a graduated stick with an open electronic circuit at one end attached to an electronic bell. Steel rods were removed with locking pliers and instantly taped with different colours to identify the zone with orange/brown and black rust. Distance from the soil surface to the bottom of the orange/brown zone was measured to assess oxygen zone depth. Basal area of each tree was determined in a 14 m diameter circular plot centred on the small unit of steel rods. Cover of *Sphagnum* spp. was assessed on a 2 m^2 square plot centred on the unit of 1 m^2. From another study, mineral soil was collected, pooled, air dried, ground and analysed for texture by granulometric analyses (McKeague, 1976) for 18 of the 36 1m^2 units of the sampling design. Organic forest floor thickness was measured at three different locations for each 1 m^2 unit.

2.4.1.2 Study II

In July 2003, metal rods were installed in 7 black spruce dominated sites in a chronosequence. Within each site, five quadrats of 100 m^2 were installed, each containing four nested quadrats of 25 m^2. Within each 100 m^2 quadrat four metal rods (as described above) were installed on July 17, one in each 25 m^2 quadrat in either *Sphagnum* spp. or feather mosses *(Pleurozium schreberi, Ptilium crista-castrensis, Hylocomium splendens*; two each per 100 m^2). Again, as the rods were all greater than 10 m apart, and soil processes vary at the scale of meters we consider these points to be individual samples, and not sub-samples. Organic forest floor thickness (the LFH layer to the mineral soil), basal area of all species, and % ground cover of *Sphagnum* spp. was also measured in each 25 m^2 quadrat. The rods were removed 40 days later, and immediately taped, as in Study I.

2.4.2 Statistical analyses

2.4.2.1 Study I

To test the predictability of oxygen zone depth by water table depth, we performed a linear regression analysis for the full sampling period. Moreover, to explore the importance of a possible delay between conditions favourable for oxidation and newly formed rust on the rods, Pearson correlations were performed between maximum oxygenated layer depth and the mean water table depth at different times during the sampling period. With the aim of testing the relationship between oxygen zone depth and environmental variables, Pearson correlations were performed between oxygen zone depth and water table depth, sand percent, silt percent, clay percent, total plot basal area, organic forest floor thickness and *Sphagnum* spp. cover.

2.4.2.2 Study II

In order to account for the change in apparent soil surface position (due to increased organic forest floor thickness with age) an index was created, where orange/brown rust depth was subtracted from organic forest floor thickness. Therefore, values less than 0 indicated that the oxygen zone was in the mineral soil, while values greater than zero indicated that the oxygen zone was in the organic forest floor. Samples within a site were treated as independent replicates due to the variation of soil characteristics at the scale of a meter (Boettcher and Kalisz, 1991; Rhoades, 1997). As such there were 140 sample points included in the study. A one-way analysis of variance (ANOVA) was used to determine whether oxygen zone thickness and oxygen index varied among 5 approximate age groupings (<100, 100-150, 150-250, 251-300, >300). These ages are based on dendrological ages (age of oldest tree), however they are an estimate as recent C^{14} dates suggest that the oldest trees were established a considerable period after stand replacing fire. While the C^{14} dates suggest that the stands are considerably older than first believed (300-1000 years) they did not alter the order or the groupings of the sites. For this reason an ANOVA test was used rather than a regression. A t-test was used to examine the difference in oxygen zone depth between *Sphagnum* spp. and feather mosses.

In order to examine factors that potentially influenced oxygen zone thickness and oxygen index, correlations, and subsequently path analysis (which includes direction of relationship) were performed. Factors included were organic forest floor thickness, total basal area (m^2/ha), total *Sphagnum* spp. cover (%) and time since fire. A d-sep test (Shipley, 2000) was used to determine the likelihood that an a-priori structure is correct. Partial correlation coefficients (or path coefficients) among the variables allow determination of the magnitude of direct and indirect effects among variables.

2.5 RESULTS

2.5.1 Relationship between oxygen zone and water table

According to Figure 2.1, the water table dropped during the sampling period, with occasional increases that suggest the influence of precipitation. This figure illustrates that the formation of orange rust could be delayed in time until favourable oxidation conditions occur. However, Pearson correlation coefficients between oxygen zone depth and water table depth or mean water table depth for different intervals of time were similar (Table 2.2). The relationship between oxidation zone depth and mean water table depth for the full sampling period was significant at the 0.05 threshold according to the regression analysis, with a coefficient of determination of 0.2325 (Figure 2.2).

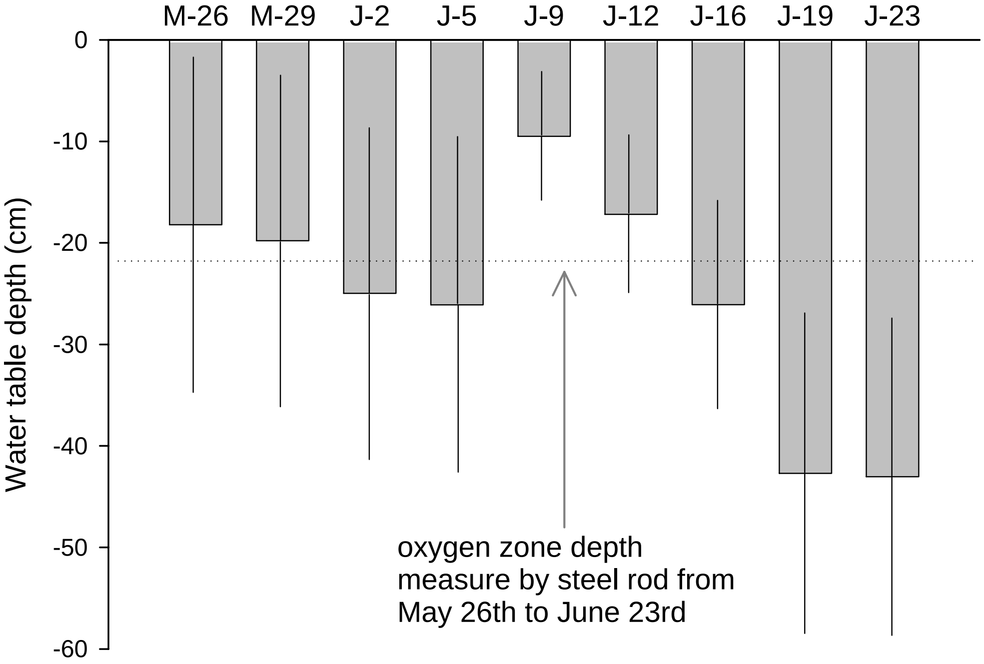

Figure 2.1 Water table depth (columns) and oxygen zone depth (dotted line) during the sampling period. Mean water table depth was calculated using all 32 sampling units for each sampling days, bars indicate standard deviation.

Table 2.2 Pearson's correlation coefficients between oxygen zone depth and water table depth or mean water table depth for different intervals of time. Probabilities for significance test are in parentheses, H_0: Rho =0, N=32.

Variables	Rho (*p*)
Water table depth May 26th	0.47 (0.0065)
Mean water table depth from May 26th to May 29th	0.46 (0.0089)
Mean water table depth from May 26th to June 2nd	0.44 (0.0110)
Mean water table depth from May 26th to June 5th	0.44 (0.0110)
Mean water table depth from May 26th to June 9th	0.45 (0.0104)
Mean water table depth from May 26th to June 12th	0.44 (0.0120)
Mean water table depth from May 26th to June 16th	0.44 (0.0127)
Mean water table depth from May 26th to June 19th	0.51 (0.0026)
Mean water table depth from May 26th to June 23rd	0.47 (0.0080)

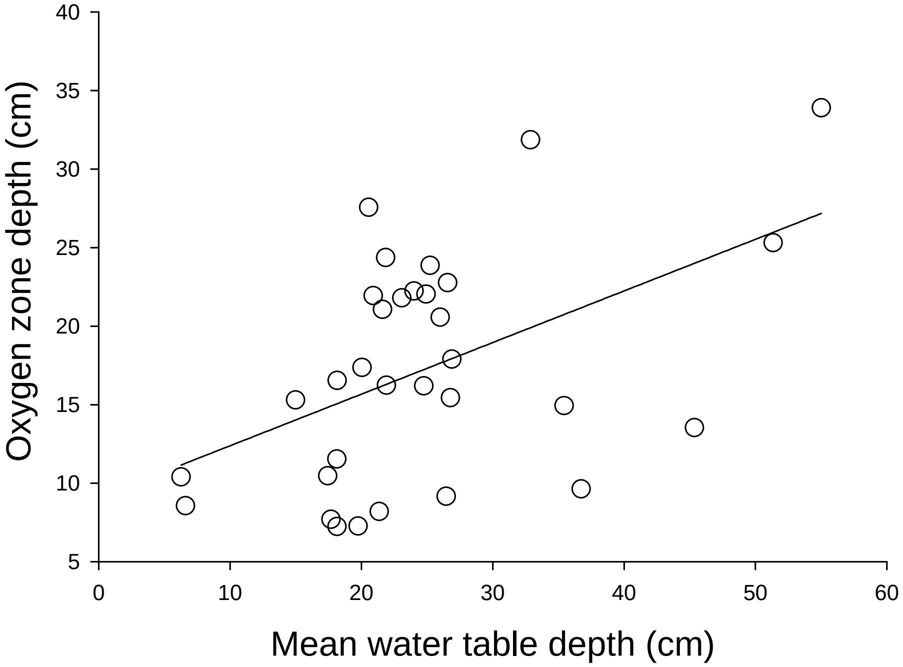

Figure 2.2 Relationship between oxygen zone depth and mean water table depth for the full sampling period (oxygen zone depth = 9.10 + 0.33 (mean water table depth), $R^2 = 0.2325$, F value = 9.09, p = 0.0052, N = 32).

Table 2.3 Pearson's correlations coefficients between oxygen zone depth and other variables. Probabilities for significance test are in parentheses, H_0: Rho =0.

Variables	N	Rho (*p*)	Mean ±S.E.	Min - Max
Sand percent	18	-0.32 (0.1980)	21.39 ± 16.47	9.12 – 71.03
Clay percent	18	0.14 (0.5686)	36.07 ± 16.38	8.82 – 56.75
Silt percent	18	0.22 (0.3790)	42.55 ± 13.06	20.14 – 71.13
Mean water table depth (May 26th – June 23rd)	32	0.48 (0.0052)	24.90 ± 10.64	6.28 – 55.01
Total local basal area	32	0.01 (0.9722)	42.59 ± 8.02	26.40 – 65.21
Organic forest floor thickness	32	0.16 (0.3731)	10.86 ± 3.53	4.94 – 20.33
Sphagnum cover	32	-0.31 (0.0811)	5.81 ± 17.99	0.00 – 75.00

The oxygen zone depth was significantly correlated with mean water table depth for the full sampling period, however sand percent, clay percent, silt percent, local basal area, organic forest floor thickness and *Sphagnum* spp. cover were not significantly related to oxygen zone depth (Table 2.3).

2.5.2 Relationship between oxygen zone and age

Oxygen zone depth varied among age groups (F = 15.31, p <0.001), with the deepest oxygen zones in sites between 150 and 275 years after fire (Figure 2.3). The position of the oxygen index had a linear relationship with time since fire increasing from 12.8 cm below to 65 cm above the mineral soil-organic interface. Oxygen zone depth did not vary between *Sphagnum* spp. and feather mosses (F= 0.718, p = 0.398).

The oxygen zone depth was not correlated with any of the explanatory variables, but the oxygen index was highly correlated with organic forest floor thickness, total basal area, total *Sphagnum* spp. cover and time since fire (Table 2.4). Because these variables were highly inter-correlated, path analysis rather than multiple regression was used. The structure determined by path analysis (p=0.86) indicated that organic forest floor thickness had not only the greatest total relationship with oxygen index, as would be expected, but also the largest direct effect (Figure 2.4, Table 2.5). While time since fire was highly correlated with oxygen index, this was entirely due to indirect effects via organic forest floor thickness, *Sphagnum* spp. cover and total basal area. Perhaps more importantly, while *Sphagnum* spp. cover and total basal area were highly correlated with oxygen index, this was almost entirely due to indirect effects.

Figure 2.3 Changes in position of oxygen zone in soil profile with increasing tree age. Grey bars indicate the thickness of the organic forest floor, while white bars indicate the position of the oxygen zone (i.e. oxygen index). Letters indicate statistical differences, capital letters differences in oxygen zone thickness (relative to the profile surface), and lower case letters differences in the position of the oxygenated layer relative to the mineral soil – organic interface.

Table 2.4 Correlation matrix of oxygen zone, oxygen index and potential explanatory factors. Variables in bold are significant.

	Oxygen zone	Oxygen index	Organic forest floor thickness	Total basal area	Total *Sphagnum* cover	Time since fire
Oxygen zone	1.00	**0.437**	-0.044	-0.026	0.039	0.008
Oxygen index		1.00	**0.918**	**-0.469**	**0.442**	**0.618**
Organic forest floor thickness			1.00	**-0.535**	**0.510**	**0.687**
Total basal area				1.00	**-0.627**	**-0.722**
Total *Sphagnum* cover					1.00	**0.708**
Time since fire						1.00

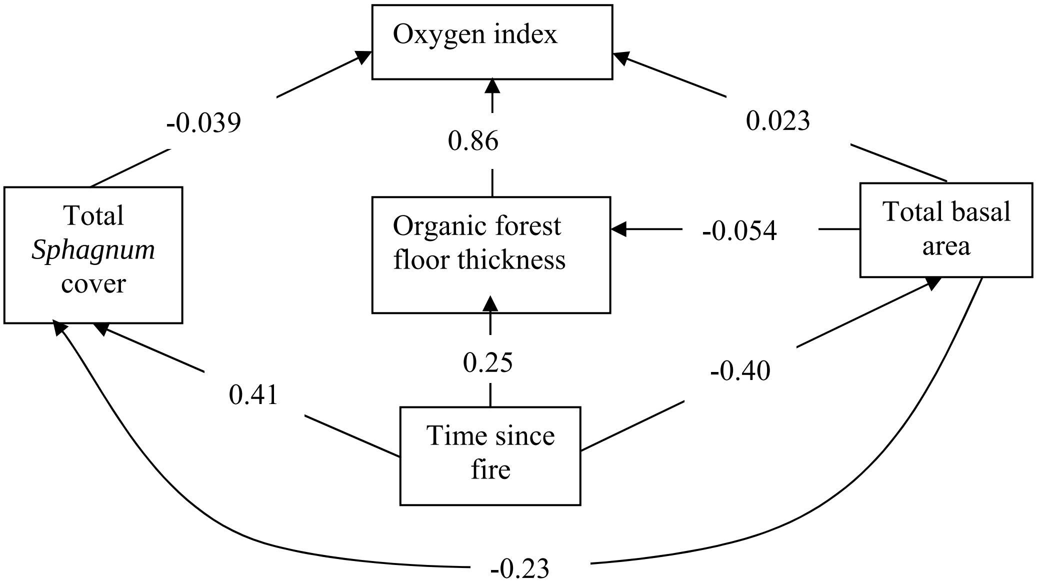

Figure 2.4 Path analysis of factors influencing oxygen index in black spruce chronosequence. Values are path coefficients (partial correlations) of individual factors. The structure was tested with a D-Sep test based on Shipley (2000) and has a 0.86 probability of being the correct structure.

Table 2.5 Direct, indirect, error and total of explanatory factors used in path analysis to explain variations in oxygenated index.

Variable	Organic forest floor thickness (cm)	*Total* Sphagnum *cover (%)*	Total basal area (m^2)	Time since fire (years)
Direct	0.863	-0.0390	0.0231	
Indirect	0.992	0.288	-0.297	0.628
Error	-0.0737	0.154	-0.172	-0.00997
Total (R^2)	0.918	0.442	-0.469	0.618

2.6 DISCUSSION

2.6.1 Relation between oxygen zone and water table

The amount of oxygen present in a soil is dependant on many factors, but is ultimately the result of empty soil space, which is a function of soil texture and structure (Scanlon et al., 2000). Soil oxygen is reduced by increases in soil water volume, and strong correlations between oxygen zone depth and water table depth have been observed (Belyea, 1999; Groot, 1998; Carnell and Anderson, 1986). Despite a significant relationship between oxidation zone depth and water table depth, assumption of a close correlation between these variables or predictability of one variable by another are inappropriate in this study, because of the low coefficient of determination (R^2=0.2325). This result contrasts with Belyea (1999) who found a strong correlation (R=0.95) between water table depth and reducing condition assessed in a mire environment. Bridgham et al. (1991) found optimal accuracy of steel rods in organic soil with a relatively constant hydrology and a low accuracy on mineral soil with frequent fluctuations of the water table. The low potential of predictability obtained in our study could be attributed to the high variability of the capillarity fringe that is associated with the soil structure at the micro scale, which depends on the activity of the root network and soil fauna. Delay between the favourable oxidation conditions and rust formation has been suggested to explain the lack of correlation, however it does not seem to be a major factor in our study. An alternate explanation may be that there is a poor correlation between the water table and the oxygen zone during the spring and early summer (May-July) period when the water table is generally falling from its spring maximum. We may have found a higher correlation between the oxygen zone and the water table if we had sampled during the late summer (August - September) period when the water table is presumably less temporally variable.

2.6.2 Factors influencing oxygen zone depth within a stand age

The absence of a significant correlation between oxygen zone depth and soil texture, local basal area and *Sphagnum* spp. cover was surprising as it is generally accepted in the literature (Dubé et al., 1995; Noble et al., 1984; Heikurainen, 1967). Air diffusion rate should be higher in coarse soil texture, however presence of soil organic forest floor (SOM) could change porosity and well-structured clay within a mineral soil could hide the expected correlation. In this case, soil porosity would be a more appropriate variable to measure than soil texture.

Local basal area varied from 26.40 to 65.21 m^2/ha in our study design. This is a different range from the comparison between forests and clear-cuts where the relationship between basal area and oxygen zone or water table depth is generally tested, and natural variation in stand density would undoubtedly have different effects on the oxygen layer than an artificial variation created by harvest. Regardless, our results suggest that a local variation in basal area of 60% within a stand is not a large enough reduction in evapo-transpiration to induce a change in oxygen zone depth in our study area. An alternate explanation may be that the opening of the canopy can result in an increase of understory layer cover (Légaré et al., 2002) and consequently understory evapo-transpiration, which can contribute considerably to stand evapo-transpiration (Ovhed, 1995; Kelliher et al., 1990; Spittlehouse and Black, 1982). Therefore a trade-off between tree and understory evapo-transpiration may exist, resulting in no effect on the oxygen layer.

Development of a thick organic forest floor layer is believed to induce a rise of the water table through capillarity (Clymo, 1984). Thus, the relationship between oxygen zone depth and organic forest floor depth was tested to explore the relationship on non-organic soil. The maximum organic forest floor depth observed in the study 1 which was 20.33 cm was obviously too low to induce an increase of the water table through capillarity. We hypothesize that a threshold of organic forest floor depth should be reached to induce a rise of water table.

The absence of a significant correlation between oxygen zone depth and *Sphagnum* spp. cover in our sites suggest that sphagna, without the development of a thick organic forest floor layer, could not induce a rise in the water table and thus reduce the depth of the oxygenated layer. However, the low p-value associated with the correlation suggests that sphagna could be associated with the process in later forest stages.

2.6.3 Changes in soil oxygen in association with time since fire

The position of the oxygen zone, as indicated by the oxygen index, moved from the mineral soil in young stands up to 60 cm above the mineral soil in the organic forest floor in the oldest stand. The oxygen index was also highly correlated with several of the environmental variables, however path analysis indicated that organic forest floor thickness was the dominant factor in determining the relative position of the oxygen zone, among stand ages. As the organic forest floor forms on the surface of the soil, peat at depth is compressed and continues to decompose. The large pores are the first to collapse resulting in increased capillarity in the peat, which in turn increases its capacity for water retention (Silins and Rothwell, 1998). This peat with high capillarity and water retention capacity may act like a sponge on the surface of the soil resulting in the water table and oxygen zone moving from the mineral soil into the organic layer (Clymo, 1984).

There was relatively little correlation between oxygen zone depth and age, and in fact it was deepest in the 150-275 age groups. Furthermore there was no correlation between oxygen zone and any of the measured variables. The lack of trend with age is in opposition to what would be predicted based on the literature, as several studies suggested that the water table, and by assumption the oxygen zone, approach the surface with increasing paludification (e.g. Hartshorn et al., 2003; Zobel, 1990). We suggest two potentially interacting hypotheses to explain this anomalous result. (1) Changes in the bryophyte community composition with time since fire (Fenton and Bergeron, 2006a) may increase bryophyte production, allowing accumulation of organic forest floor in excess of the rate of creation of small pores via peat decomposition, resulting in a lag between increases in the position of the soil surface and the water table position. Additional compositional changes to slower growing species as the soil surface moves away from the water table may explain the reduction in oxygen depth in the extremely old group. (2) Alternatively, it has been suggested that the herb layer may have a significant impact on the water table (and therefore, some impact on the oxygenated layer ; (Ovhed, 1995; Kelliher et al., 1990; Spittlehouse and Black, 1982)). Therefore, a trade off may exist between the evapo-transpiration of the trees and the understory layer of shrubs and small black spruce (Lecomte et al., 2005).

Sphagnum spp., which have been suggested to be driving factors in paludification through water table rise (Klinger, 1990; Noble et al., 1984; Heilman, 1966; Lawrence, 1958), were weakly correlated with oxygen index within a stand age in this study (Table 2.4), and did not have a significant direct effect on the oxygen index. These results were confirmed by the lack of a difference in oxygen depth beneath *Sphagnum* spp. and feathermoss across the age gradient. *Sphagnum* spp. do have a role to play in organic forest floor accumulation (Fenton et al., 2005), and may perpetuate paludification once it has begun but organic forest floor, regardless of origin, appears to be the main driving factor.

As in the first study, total basal area was not a dominant factor explaining variation in oxygen index. This is also surprising, suggesting that evapo-transpiration has little effect on the position of the oxygen layer within the soil profile in this system. This may be due to the low evapo-transpiration rates of black spruce, the dominant tree in these stands, or the inherently poor drainage of the clay soils. Alternatively, the effect of evapo-transpiration by the trees may be masked by the effect of the understory (Ovhed, 1995; Kelliher et al., 1990; Spittlehouse and Black, 1982), which is inversely correlated with basal area.

2.6.4 Rate of oxygen zone rise

The high speed at which the oxygenated zone seems to have risen in this chronosequence may seem alarming, as the dendrochronology indicates a change from a dry forest to a relatively open bog in less than 400 years. This rate differs dramatically from the approximate 800 years that has been suggested in Siberia by Glebov and Kurzukhin (1992). However, recent C^{14} dates of charcoal and organic forest floor immediately above mineral horizon in the research area established by Cyr et al. (2005) indicate that dendrochronology dates may substantially underestimate the age of the forest. Spruce trees were able to establish in the understory of the forest in the absence in fire, and the initial cohort died out, resulting in a maximum tree age that in some cases significantly underestimates time since fire. Therefore, the forests that we have dated as being approximately 250 years since fire may in fact be closer to 1000 or even 2000 years since fire, and the process of paludification on the Clay Belt would proceed at a pace similar to that found in Siberia.

2.6.5 Conclusions

This study suggests that the water table and oxygenated layer move from the mineral soil into the organic forest floor within a soil profile at approximately 250 years after fire, and when roughly 40-50 cm of organic forest floor or peat is present. This is a key turning point at a stand and landscape level. Within a stand, this forces tree roots into the organic forest floor, which alters their nutritional balance, and growth rate. Furthermore, at the landscape scale, as Glebov and Kurzukhin (1992) indicate, it is at this stage that the forests becomes "bogged", and decomposition and removal of the accumulated organic forest floor is unlikely within the current climatic context.

2.7 ACKNOWLEDGMENTS

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CHAPITRE III

FACILITATIVE SUCCESSION IN A BOREAL BRYOPHYTE COMMUNITY DRIVEN BY CHANGES IN AVAILABLE MOISTURE AND LIGHT

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3.1 ABSTRACT

Question: What are the drivers of bryophyte succession in paludifying boreal black spruce forests?
Location: The Clay-Belt of Québec and Ontario, Canada.
Methods: The bryophyte community and habitat variables (forest floor thickness, water table, stand density, canopy openness micro-climate and presence of ericaceous species) were analysed in a chronosequence of 13 stands from 50 to more than 350 years since fire.
Results: Across the chronosequence, feather mosses were replaced by shade and desiccation tolerant slower growing hummock sphagna and then by faster growing hollow sphagna. These changes were linked with both increasing light availability and the movement of the water table into the forest floor.
Conclusions: As water table rise is dependent on forest floor thickness, which is in turn influenced by the presence of sphagna, this successional sequence represents an example of facilitation. Furthermore, it emphasizes the importance of water table rise in determining stand level, and landscape level variables such as carbon balance.

Question : Quelles sont les facteurs dirigeant la succession dans les forêts d'épinette noire propices à l'entourbement?
Localisation: La Ceinture d'Argile du Québec et de l'Ontario
Méthodes : La communauté des bryophytes et les variables environnementales (épaisseur de la couche de matière organique, nappe phréatique, densité du peuplement, ouverture de la couronne, microclimat et présence des espèces éricacées) ont été analysées dans une chronoséquence de 13 sites âgés de 50 à 350 ans depuis le dernier feu.
Résultats : Avec le temps depuis le dernier feu, les mousses hypnacées ont été remplacées par les sphaignes de butte à faible croissance tolérantes à l'ombre et à la dessiccation et ensuite par des sphaignes de creux à forte croissance. Ces changements ont été liés avec une augmentation dans la disponibilité de la lumière et le mouvement de la nappe phréatique dans la couche de matière organique.
Conclusions : Étant donné que la remontée de la nappe phréatique dépend de l'épaisseur de la matière organique, qui est elle même influencée par l'abondance des sphaignes, cette succession représente un exemple de facilitation. De plus ces résultats mettent l'emphase sur l'importance de la remontée de la nappe phréatique sur la détermination des variables intervenant à l'échelle du peuplement et à l'échelle du paysage tel que la balance de carbone.

3.2 INTRODUCTION

Boreal forests are distinguished from many other biomes by the importance of the bryophyte layer in ecosystem function. The bryophyte layer constitutes an important component of the biomass, and influences total net primary production (Gower et al., 1997; Bisbee et al., 2001) and soil respiration (O'Connell et al., 2003). An example of the influence of the bryophyte layer is paludification of boreal forests, a phenomenon by which a forest on mineral soil is transformed into a treed peatland (Crawford et al., 2003) via the accumulation of a thick forest floor and a rising water table (Glebov and Korzukhin, 1992). Associated with these changes in the soil is the establishment and subsequent expansion of *Sphagnum* spp. mosses into the previously feather moss (*Pleurozium schreberi, Ptilium crista-castrensis, Hylocomium splendens*) dominated bryophyte layer (Reiners et al., 1971; Foster, 1985; Boudreault et al., 2002), at approximately 100 years post fire. The ecosystemic consequences of this change in bryophyte functional group can be dramatic; as compared to feather mosses, sphagna have a greater carbon fixation rate (Bisbee et al., 2001; Swanson and Flanagan, 2001), a greater buffering effect on soil temperature (Dioumaeva et al., 2002) and a slower decomposition rate (Swanson and Flanagan, 2001; Turetsky, 2003). Furthermore, wetter black spruce-*Sphagnum* spp. stands have a longer fire cycle and because of their greater humidity they lose less carbon when they are burned [figures of 12 vs. 33% of Net Primary Productivity were indicated by Harden et al. (2000)].

The replacement of species along a successional gradient can be viewed as being driven either by the population life span of individual species, or by interactions among species and habitat conditions (Bazzaz, 1990). Bryophyte colonies in forest floors may have almost unlimited life spans due to their continual upward growth as long as conditions remain unchanged, therefore it is unlikely that the shift observed is due to death of the feather moss colonies. In light of this, the shift in bryophyte functional groups represents a replacement where the sphagna are capable of overtopping the feather mosses and gain access to an important limiting factor in the boreal forest floor, space (Slack, 1990). Replacement by overtopping is a strongly asymmetric (neutral, negative) interaction which, however, may also occur in the reverse direction (sphagna are overtopped by feathermosses in approximately 30% of recorded cases in young forests; Fenton unpublished data).

Interactions like this have been referred to as asymmetric competition (Rydin, 1997) and as amensalism (Burkholder, 1952; Økland, 2000). The question that has not been addressed in previous studies is: what environmental change alters the habitat and allows the sphagna to gain an advantage over the feather mosses? Based on the physiology of the functional groups, two main environmental gradients within ageing forests have been suggested as the causes of change in the bryophyte layer; sphagna growth is favoured by (1) increases in available light (Bisbee et al., 2001), and (2) increases in available moisture (Taylor et al., 1987; Van Cleve and Viereck, 1981). However, while these hypotheses have been discussed, their true role in driving successional changes has not been tested. In addition, these environmental gradients have been suggested for successional sequences more than 150 years post-fire, and in general have been based uniquely on differences in functional groups (i.e. feather mosses versus *Sphagnum* spp.) and not on the behaviour of individual species. Therefore the objectives of this study are to document the changes in dominant species composition with increasing time since fire in black spruce forests, and to determine whether changes in light and/or moisture drive successional changes in paludifying black spruce forests across an extended time gradient. The role of ericaceous species was also investigated as they may have allelopathic interactions with trees and other species (Inderjit and Malik, 1997; Wardle et al., 1998) that may favour *Sphagnum* spp. growth.

3.3 STUDY AREA

The Clay Belt of north-east Ontario and north-west Québec (Figure 3.1) is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent and Hardy, 1977). In its northern portion, it is dominated by black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forests (Grondin, 1996), and is particularly prone to paludification between fires due to its poorly drained clay dominated soil, low topographic relief, and moderately humid and cold climate [889.9mm of precipitation annually; annual mean temperature 0.7^0C (Environment Canada, 2004)]. The dominant disturbance types are large fires that kill all above ground vegetation. Between 1850 and 1920 the fire cycle was ca 135 years, and it has since increased to ca 398 years (Bergeron et al., 2004), as a result the average age of the forests is in excess of 100 years. It lies just south of the Hudson Bay-James Bay Lowlands, the second largest peatland complex on the globe.

3.4 METHODS

3.4.1 Sampling

A chronosequence approach was used to address successional changes. The main weakness of this approach is the possibility that initial conditions were not identical for all stands. While this is a valid argument, the chronosequence used here has been extensively validated. This study is part of a larger project, investigating the causes and consequences of paludification on the Clay Belt of Québec and Ontario. A previous study indicated that as older forests have escaped fire by chance they are as likely to burn as other forests on the landscape, and as such represent a true end point to succession and are not topographical escapes (Cyr et al., 2005). The established chronosequence has been validated via stem analysis (Lecomte et al. in press), and *in situ* analysis of the forest floor (Lecomte et al. in press; Fenton unpublished data). In addition site selection included a detailed analysis of

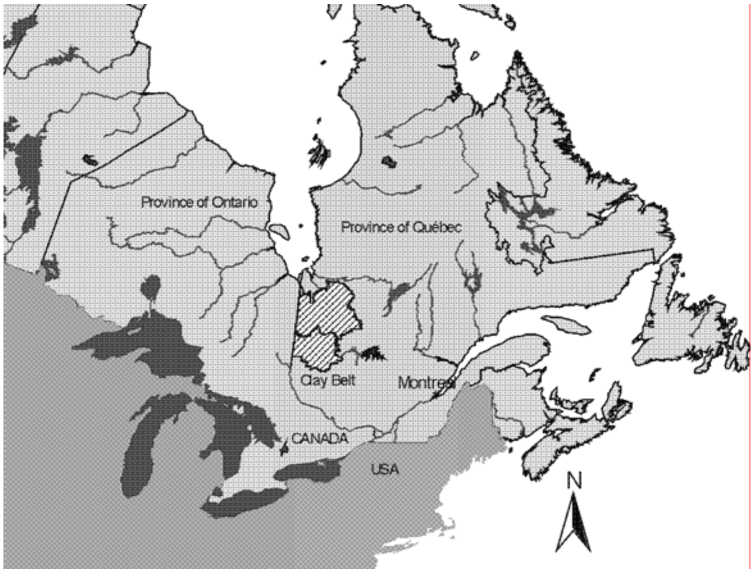

Figure 3.1 Location of study area within in the province of Québec. The ecoregions where the ClayBelt occurs is indicated, and may slightly overestimated the actual area.

slope and soil texture to determine that the sites were established in similar edaphic conditions. Similarly, the presence of charcoal uniquely at the interface between the mineral and organic layers of the soil was verified to establish that the forests issued from a high severity fire (i.e. a fire that affected the ground and not only tree crowns). However, it is conceivable that there were small patches of *Sphagnum* remaining after the previous fire that were not detected by our methods. We believe that their influence on our results would be minimal. A more detailed description of site selection procedures is given by Lecomte et al. (in press).

During the summer of 2003, 13 black spruce dominated sites ranging from 50 to 350 years since fire were sampled. Sites were chosen based on a stand initiation map of the area (Bergeron et al., 2004) and were selected in the field on the basis of proximity to road, and presence of a mild slope and clay dominated soil. Time since fire (TSF) was established by verification of stand initiation map dates by dating basal cross-sections of a few dominant trees (for more details see Lecomte et al. in press). However, in the oldest stands (>200 years TSF) C^{14} dating of charcoal particles in a few of the sites suggest that the oldest trees were established a considerable period after stand replacing fire. While the C^{14} dates suggest that the stands are considerably older than first believed (300–1000 years) they did not alter the order or the groupings of the sites. For this reason dendrochronology dates were used as they are consistent across the sites.

Within each site, five quadrats of 100 m^2 were installed, with four nested quadrats of 25 m^2. The initial 100m^2-quadrat was randomly placed at least 50 m from the nearest road, and subsequent quadrats were placed at least 10m apart along a randomly chosen bearing. Within each 25 m^2 quadrat, all bryophyte species were identified and their percent cover visually estimated. Samples of all non-easily identifiable species were collected for identification in the lab. A representative collection of voucher specimens is stored at the Université du Québec en Abitibi-Témiscamingue. While all of the species data were included in the ordination, only the patterns of the dominant forest floor mosses and *Sphagnum* spp. are analyzed in detail.

A series of habitat variables (both abiotic and biotic) affecting substrate availability and microclimate were measured in each 25 m^2 quadrat in order to interpret the bryophyte pattern (Table 3.1).

Table 3.1 Abiotic and biotic variables measured within 25 m^2 quadrats in order to interpret patterns in bryophyte species composition. Variables marked with an * were significant when tested individually in the partial canonical correspondence analysis. Classes of coarse woody debris decomposition were modified from Söderström (1987)

Code	Full variable name	Description
	Forest floor*	Depth from the moss surface to the organic-mineral interface, which is clearly defined on the Clay Belt
	Water table*	The position of the water table in a randomly chosen location within the 25m^2 quadrat.
	Water table index*	The position of the water table relative to the organic matter-mineral soil interface. Values <0 are in the mineral soil, values >0 are in the organic matter.
Coniferous canopy	% coniferous canopy cover	% canopy cover occupied by coniferous trees, measured on a densiometer
Deciduous canopy	% deciduous canopy cover	% canopy cover occupied by deciduous trees, measured on a densiometer
Open canopy	% cover without canopy *	% of canopy that is not covered by coniferous or deciduous trees, and is therefore open to the sky.
CWD 1	% cover of coarse woody debris, decay class 1	% of the forest floor covered by coarse woody debris >5cm in diameter (CWD) of decay class 1 – freshly fallen
CWD 2	% cover of coarse woody debris, decay class 2	% of the forest floor covered by coarse woody debris >5cm in diameter (CWD) of decay class 2 – bark loosening
CWD 3	% cover of coarse woody debris, decay class 3 *	% of the forest floor covered by coarse woody debris >5cm in diameter (CWD) of decay class 3 bark falling, softening of wood
CWD 4	% cover of coarse woody debris, decay class 4	% of the forest floor covered by coarse woody debris >5cm in diameter (CWD) of decay class 4 very soft, shape collapsed
% leaves	% cover of deciduous leaves	% cover of the forest floor covered by deciduous leaves
% pits	% cover peat pits *	Deep water holes formed in the organic matter

% mineral	% cover mineral soil	Mineral soil exposed on the forest floor
BA bS	Basal area black spruce (m^2/ha)	Basal area of all black spruce (*Picea mariana*) in the quadrat >8cm in diameter
BA jP	Basal area jack pine (m^2/ha)	Basal area of all jack pine (*Pinus banksiana*) in the quadrat >8cm in diameter
BA bF	Basal area balsam fir (m^2/ha) *	Basal area of all balsam fir (*Abies balsamea*) in the quadrat >8cm in diameter
BA tam	Basal area tamarack (m^2/ha)	Basal area of all tamarack (*Larix laricinia*) in the quadrat >8cm in diameter
BA tA	Basal area trembling aspen (m^2/ha)	Basal area of all trembling aspen (*Populus tremuloidies*) in the quadrat >8cm in diameter
Tot BA	Total basal area (m^2/ha)	Basal area of all stems >8cm in diameter in the quadrat
Mean tree size	Mean tree diameter *	Mean diameter of all trees >8cm in the quadrat
LCR bS	% live crown ratio black spruce *	Mean % of black spruce stems with living foliage, measured as a visual estimate
LCR jP	% live crown ratio jack pine	Mean % of jack pine stems with living foliage, measured as a visual estimate
LCR bF	% live crown ratio balsam fir	Mean % of balsam fir stems with living foliage, measured as a visual estimate
LCR tam	% live crown ratio tamarack	Mean % of tamarack stems with living foliage, measured as a visual estimate
LCR Ta	% live crown ratio trembling aspen	Mean % of trembling aspen stems with living foliage, measured as a visual estimate
# tip ups	# of tree tip ups	# of tree tip ups per quadrat, which creates variability in the quadrat
# snap offs	# of trees snapped off	# of trees snapped off (rather than tipped up) per quadrat

% ericaceous	% cover of ericaceous species *	% of the forest floor covered by the canopy of ericaceous species, primarily *Rhododendron groenlandicum, Kalmia angustifolia*

Steel rods 120 cm long were used to measure the depth of water table in the soil. The rods were placed in the soil for several weeks during which orange-brown rust formed at the interface of the oxygenated and non-oxygenated zones of the soil profile (Carnell and Anderson, 1986), which approximated the position of the water table. The width of the rusted surface indicates the variation in the water table level during the 40-day period caused by rainfall, drought and seasonal variation. In a previous article (Fenton et al. 2006) we demonstrated that the highest point (i.e. closest to the forest floor surface) had the closest relation to the mean actual water table position (which was simultaneously measured in water wells). Therefore in this study the depth to the beginning of the heavily rusted area was used in analyses. In July 2003, 7 of the 13 chronosequence sites were chosen for further study and one steel rod was randomly installed in each 25-m^2 quadrat. The rods were removed 40 days later with locking pliers and the distance from the forest floor surface (i.e. directly above the moss) to the zone of orange-brown rust was immediately identified with colour tape and later measured in the lab. While the randomly placed rods may not have always captured the fine scale spatial variation within quadrats, these measurements were nevertheless considered to give appropriate indication of relative positions of the water table among quadrats. In order to account for the change in apparent soil surface position (due to increase in forest floor thickness with age), the interface between mineral soil and forest floor was used as a reference point for measurements. This was achieved by subtracting forest floor thickness from depth to the zone of orange/brown rust. Values less than 0 indicate that the water table was in mineral soil, while values greater than zero indicate that the water table was in the forest floor. For more details see Fenton et al. (2006).

In addition to the indirect measures of microclimate explained above, the microclimate of *Sphagnum capillifolium, S. magellanicum* and *Pleurozium schreberi* habitats were measured directly in 2004 in 2 sites (85 and 270 years after fire) between the months of April and September. While equipment limitations restricted the sampling to two sites, these data provide detailed information on the actual microclimate experienced and created by the bryophytes in the two forest types (young and old). Two replicate microclimatic stations were installed in each site. Each microclimatic station (Campbell Scientific Dataloggers CR10) was equipped with two photosynthetically active radiation probes (PAR Lite Kipp and Zonen) and two shielded temperature and humidity sensors (CS500 Vaisala 50Y). One PAR and one temperature-humidity probe were installed at moss level in a patch of *Pleurozium schreberi* and *S. capillifolium* and *S. magellanicum* respectively. Therefore, four probe pairs were placed in the young stand and four probe pairs in the old stand. Temperature (^{0}C), relative humidity and PAR density (µmol $s^{-1}m^{-2}$) were recorded as hourly averages, as well as daily maxima and minima. PAR was also recorded as daily totals (µmol m^{-2} day^{-1}). Moss level precipitation, in partially buried rain gauges, was also measured for each species patch, in ml. Relative humidity was converted to vapour pressure deficit (VPD in hPA) by the following formula:

$$VPD = (6.1078)\{\exp[17.269T/(273.3+T)]\}(1-RH) \qquad (1)$$

where T is temperature in Celsius and RH is relative humidity as a decimal (modified from Tanner 1972).

3.4.2 Analyses

Species were grouped into two taxonomic and functional guilds (true mosses and *Sphagnum* spp.) in order to facilitate interpretation. Similarly, sites were separated into five age groups: 100 TSF (85-95 TSF, 4 sites, 80 quadrats), 150 TSF (130-150 TSF, 2 sites, 40 80 quadrats), 200 TSF (180-220 TSF, 3 sites, 60 80 quadrats), 275 TSF (260-300 TSF, 3 sites, 60 80 quadrats) and >350 TSF (1 site, 20 80 quadrats). The cover of a few species was examined in quadrats where the water table was above or below the water table, with the non-parametric Kruskal-Wallis test. Tests with p value of 0.05 or less are referred to as significant.

In order to summarise overall gradients in species composition, a detrended correspondence analysis (DCA; Hill, 1979, Hill and Gauch, 1980) was carried out. Only species occurring in a total of 5 or more quadrats, and only quadrats in which ≥ 5 or more such species were present, were included in the ordination. CANOCO ver. 4 (ter Braak and Šmilauer, 1998) was used for DCA ordination. The ordinated matrix contained 97 species in 253 quadrats (out of 260). Strictly speaking the 20 quadrats from a site are pseudoreplicates, but the variation within sites, and indeed within 100 m^2 quadrats, was very high (Table 3.2). This justified our treatment of the quadrats as separate samples in exploratory multivariate analyses. Habitat variables were passively fitted to the ordination axes as vectors in the ordination diagram (indirect gradient analysis). As water table depth was measured in only 7 of the 13 sites, the mean value of oxygen depth and oxygen index of the measured sites for each age group was included in the sites where it was not measured directly. A non-metric multidimensional scaling (NMDS) analysis was carried out, using PC-Ord (v.4; McCune and Mefford, 1999). As the resultant structure was very similar to that of the DCA, only the DCA is presented.

In order to determine the amount of variation in the species pattern explained by the measured habitat variables, a variation partitioning approach (Borcard et al., 1992; Økland, 2003) was undertaken, using (partial) canonical correspondence analysis (CCA; ter Braak, 1986). A subset of uncorrelated habitat variables was chosen for each of four categories (see below) through forward selection, using default settings in CANOCO (ter Braak and Šmilauer, 1998). Variables were included in analysis if they explained amounts of residual variation, individually significant at the $\alpha = 0.05$ level. The ten selected variables (Table 1) fell into 4 categories: canopy (lcr black spruce, % open canopy, basal area of balsam fir, mean tree size), amount of paludification (organic matter thickness, oxygenated zone thickness, oxygen index), pocket sites (coarse woody debris 3 and % peat pits) and % ericaceous spp. cover. Contributions of categories and their interactions to bryophyte community variation were approximated as a proportion of the sum of Canonical Eigenvalues (the total variation explained), as recommended by Økland (1999).

Table 3.2 Mean and standard error of first and second axis scores from the DCA analysis at different spatial scales. The mean and standard error was calculated for each 100 m^2 plot (from the four component quadrat scores), and then the mean was taken of the plot means and standard errors. A similar analysis was completed for individual sites and age groups.

Scale	Axis 1	Axis 2
100m^2 plot	1.45 (0.24)	1.85 (0.32)
Site	1.47 (0.35)	1.89 (0.46)
Age group	1.63 (0.43)	1.84 (0.54)

Spearman's correlations between individual species abundance and canopy openness and water table index were calculated (SPSS v.10), and the relationships were graphed for 6 key species present along the gradient: *Pleurozium schreberi, Ptilium crista-castrensis, Sphagnum capillifolium, S. russowii, S. magellanicum, S. fuscum*.

Microclimatic variables were analyzed by comparing the frequency of values recorded in sphagna and *P. schreberi* habitats in young and old stands. Because the duration of extreme values are biologically important, in addition to mean values, the duration of high values (upper decile = 90% percentile) were calculated. Values and durations were compared using GLM with age and species as the two factors, and the Julian date as a co-variate (SPSS v. 10). A full factorial model was used, with the default settings.

3.5 RESULTS

3.5.1 Variation in species composition

The dominant pattern in community composition, represented by the first DCA axis [Total inertia (TI) = 4.859; EV = 0.554; gradient length = 3.41 S.D. units; Figure 3.2], was the successional change associated with increasing forest age. Along this gradient, a gradual replacement of a feather moss dominated community by a sphagna dominated community took place (Figure 3.2). Feather mosses (*Pleurozium schreberi, Ptilium crista-castrensis, Hylocomium splendens*) and *Dicranum polysetum* dominated the youngest sites, resulting in little variation among these plots in the DCA ordination (Figure 3.2). While its cover decreased gradually with increasing age, *P. schreberi* remained the most frequent species overall.

The composition of *Sphagnum* spp. experienced distinct shifts over time. *S. subtile* and *S. girgensohnii* were distinctly associated with young stands (Figure 3.2), and larger patches of sphagna contained exclusively *S. capillifolium* and *S. russowii*. With increasing age, *S. capillifolium* and *S. rubellum* or *S. russowii* became more common and abundant (Figure 3.2). In the 275 TSF group *S. magellanicum* and *S. fallax* (sensu lato.) became more abundant. By 350 TSF *Sphagnum fuscum,* and *S. fallax* were the dominant Sphagna, while *S. magellanicum* was still frequent, although not abundant (<5% cover).

The second DCA axis (EV = 0.440, gradient length = 3.383 S.D. units) was more difficult to interpret, but mainly reflected differences between quadrats with *S. capillifolium, S. rubellum, S. fuscum*, and *Cladina rangiferina* versus those dominated by *S. russowii, S. magellanicum,* and *S. fallax*.

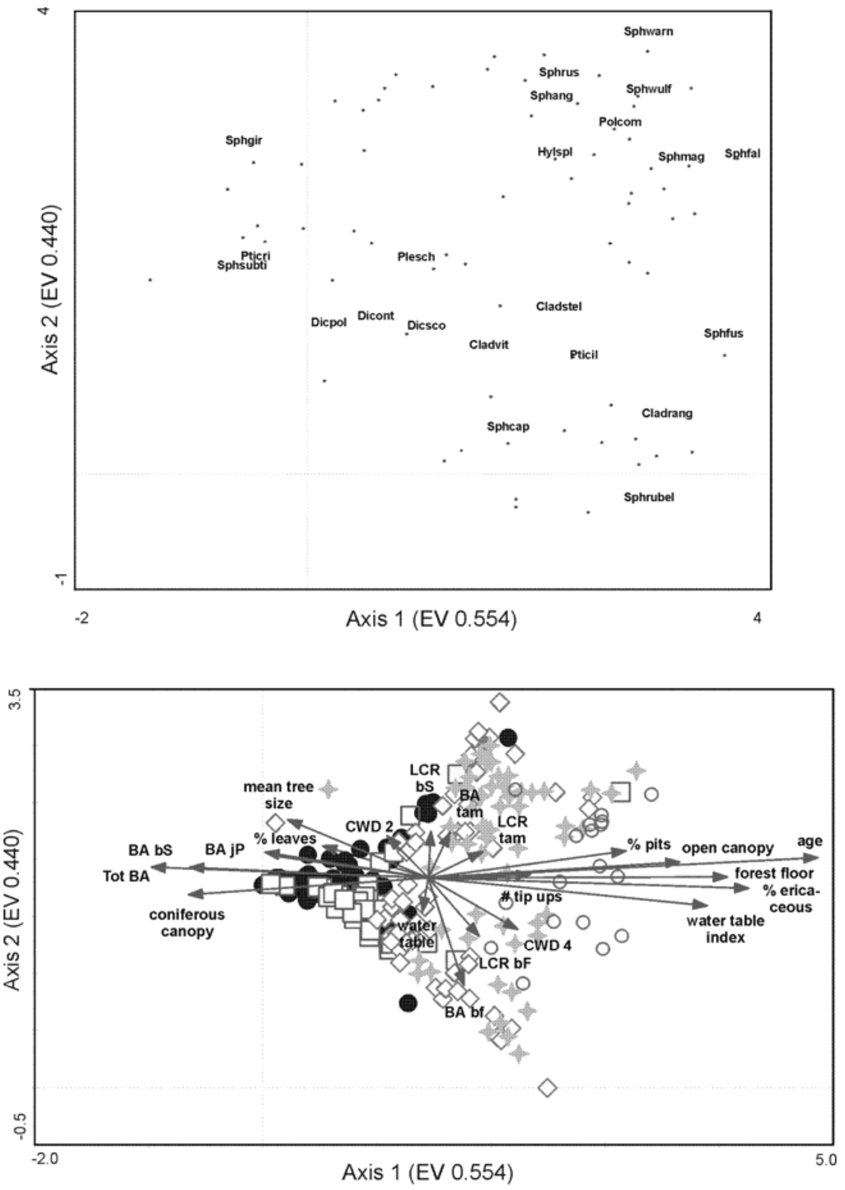

Figure 3.2 Detrended Correspondence Analysis of the total matrix of 253 quadrats; axes 1 and 2. (A) Species plot. Only dominant species are indicated, positions of other species are indicated by *. For complete names see Appendix B. (B) Quadrat plot with age classes indicated as follows: <100 TSF closed circles, 150 TSF squares, 200 TSF diamonds, 275 TSF stars, >350 TSF open circles. Vectors for environmental variables were passively fit into the diagram. The arrows indicate strength of relationship with axes and direction of maximum change in the variable in question. Abbreviations are as follows : BAbF – basal area balsam fir, BAbS - basal area black spruce, BAjP - basal area jack pine, total BA – total basal area, LCR bF – live crown ratio balsam fir, LCR bS – live crown ratio black spruce, CWD 2 – coarse woody debris 2, CWD 4 – coarse woody debris 4. See Table 3.1 for a complete description of variables.

3.5.2 Relationship between community change and habitat variables

The relationship of habitat variables to the DCA axes (Figure 3.2) indicated that the first axis was correlated with increasing forest floor thickness, position of the water table, canopy openness and cover of ericaceous species (primarily *Rhododendron groenlandicum* and *Kalmia angustifolia*: Table 3.3). DCA axis 2 was correlated with variables indicating variability in the habitat, such as live crown ratio of black spruce, and cover of peat pits.

The relative importance of these habitat variables in shaping the species pattern, as assessed by variation partitioning by CCA, were as follows: The analysis accounted for 22.35% of the variability in the species pattern and of this proportion, canopy cover (lcr black spruce, % open canopy, basal area of balsam fir, and mean tree size) and paludification (forest floor thickness, water table depth, and water table index) were dominant (19.24 and 14.00% respectively). Cover of ericaceous species, and pocket sites accounted respectively for 8.75 and 10.41% of the explained variation. Interestingly, the interaction (variability explained in addition to the sum of the individual categories) between canopy, paludification and ericaceous species was also important (6.08%).

Table 3.3 Correlation coefficients (Spearman's Rho) between DCA axes 1 and 2 and environmental variables. Variables in italics indicate that they are significant.

Environmental variable	DCA axis 1	DCA axis 2
Forest floor thickness	*0.697 (<0.001)*	*0.181 (0.004)*
Water table	0.051 (0.418)	*-0.140 (0.026)*
Water table index	*0.650 (<0.001)*	*0.138 (0.029)*
Canopy openness	*0.544 (<0.001)*	0.112 (0.072)
Cover of ericaceous species	*0.680 (<0.001)*	0.087 (0.165)
LCR black spruce	0.017 (0.782)	*0.125 (0.047)*
Cover of peat pits	*0.535 (<0.001)*	*0.209 (0.001)*

3.5.3 Species-habitat relationships

In light of the strong relationships indicated by the pCCA between community composition and ericaceous species, water table position and light, these factors were examined in greater detail. The cover of ericaceous species was strongly correlated with forest floor thickness ($R^2 = 0.528$; $p < 0.001$) and position of the water table ($R^2 = 0.362$; $p < 0.001$). Similarly the cover of *S. rubellum* ($R^2 = 0.19$; $p = 0.03$) and *S. russowii* ($R^2 = 0.19$; $p = 0.02$) were positively, and *P. schreberi* was negatively partially correlated with ericaceous cover ($R^2 = –0.291$; $p < 0.001$), even when forest floor thickness, water table position and canopy cover were accounted for. Interestingly, the abundances of sphagna found in more illuminated habitats (*S. magellanicum*, *S. fallax*) were uncorrelated with ericaceous species cover when forest floor thickness, water table position and canopy opening had been accounted for (not shown).

The relationship between canopy cover, water table index and species abundance was investigated for key species along the successional gradient (Table 3.4; Figure 3.3). The abundance of *P. schreberi* and *P. crista-castrensis* was generally negatively related to canopy openness and water table index (Figure 3.3) and these species were more common in quadrats where the water table was in the mineral soil (Table 3.4). However, *P. schreberi* was found in a variety of habitats as is indicated by the wide spread of points in Figure 3.3. *S. capillifolium* did not have a significant correlation with canopy ($R^2 = –0.133$) or water table index ($R^2 = –0.035$), and was found both in quadrats under closed and open canopies. *S. russowii* showed an intermediate pattern, present in quadrats with the water table in the mineral soil, but predominantly where the canopy was relatively open, and also present in quadrats where the water table was in the forest floor. *S. magellanicum* and *S. fuscum* were significantly less frequent in quadrats where the water table was not in the forest floor, and were restricted to quadrats with high levels of open canopy cover.

Table 3.4 Cover of selected species in sites where the water table is present in the mineral soil, compared to sites where it is present in the forest floor. Values are means and standard error, and letters indicate significant differences; a<b.

Species	Water table mineral	Water table forest floor
Feather mosses:		
Pleurozium schreberi	46.20 ± 1.50 b	24.70 ± 1.99 a
Ptillium crista-castrensis	11.37 ± 1.21 b	2.35 ± 0.54 a
Hylocomium splendens	1.48 ± 0.31 a	2.71 ± 0.54 b
Ptilidium ciliare	4.46 ± 0.52 a	5.02 ± 0.62 b
Sphagna		
Sphagnum capillifolium	6.45 ± 1.02	6.35 ± 1.41
Sphagnum russowii	10.10 ± 1.59 a	13.06 ± 2.44 b
Sphagnum rubellum	2.82 ± 0.84 a	6.56 ± 1.83 b
Sphagnum magellanicum	1.00 ± 0.40 a	8.33 ± 1.61 b
Sphagnum fallax	2.30 ± 0.78 a	12.06 ± 2.31 b
Sphagnum fuscum	0.0017 ± 0.00058 a	4.40 ± 1.20 b

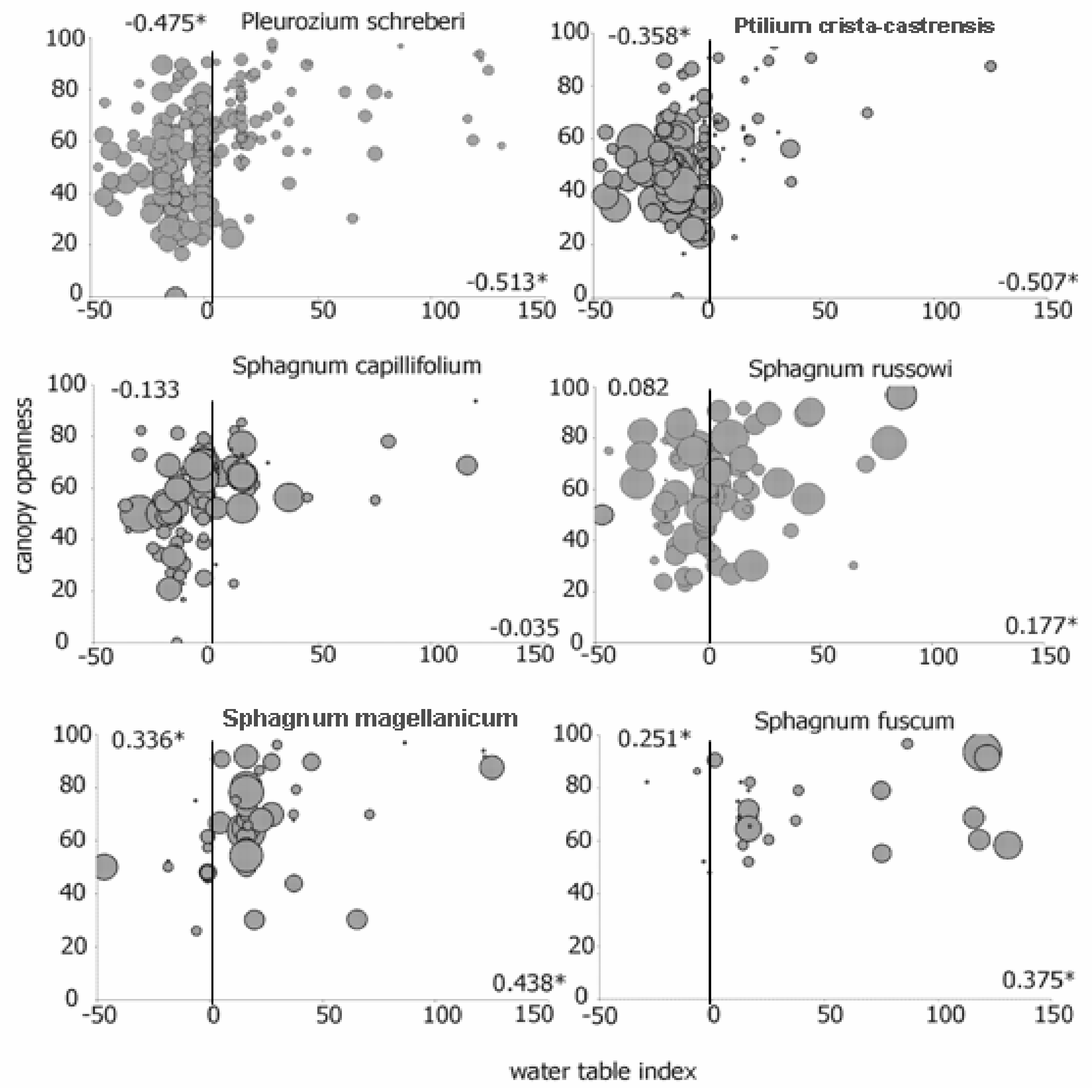

Figure 3.3 Abundance of 6 species in response to canopy openness and water table index. Circles indicate abundance and the Spearman correlation between species abundance and canopy openness and water table index are indicated in the corners of the respective axes. Significant relationships are indicated with an *. The dotted line indicates where the water table moves from the mineral soil to the organic forest floor.

The difference between habitats indicated above was confirmed with direct microclimate measurements made in one young and one old stand. The microclimate (mean total daily PAR, temperature, and vapour pressure deficit or VPD; Table 3.5) measured in the habitats of *P. schreberi* and *S. capillifolium* in the young stand and in the habitats of *P. schreberi* and *S. magellanicum* in the old stand were significantly different for total daily PAR while only subtle differences in the frequencies of temperature and VPD were observed (data not shown). Interestingly, precipitation was greater in *Sphagnum* spp. patches in both young and old stands.

Table 3.5 Means and standard error for microclimatic variables in young (85 years) and old (270 years) stands, for *Sphagnum* spp. and *Pleurozium schreberi* patches. Significant differences ($p<0.05$) between species are indicated with capital letters, while differences between age classes are indicated with lower case letters ($a<b$). GLM model for rows in italics are significant, as is the interaction term between age and species; for more details on the model, see the methods section. The N for high values indicates the number of times values exceeded the cut-off point. Values are means ± standard error.

Variable	Young		Old	
	S. capillifolium	P. schreberi	S. magellanicum	P. schreberi
Daily total PAR	*2540.0±98.9*	*2876.7±119.3*	*8319.7±334.5*	*12157.3±602.1*
Temperature	*12.9±0.079*	*12.92±0.079*	*12.96±0.13*	*13.38±0.14*
VPD	*2.78±0.044*	*2.73±0.043*	*2.82±0.068*	*3.56±0.086*
Precipitation	3335±245Ba	2985±297Aa	3932±113Ba	3083±308Aa
High PAR (N)	37±3.5	48.5±31.5	84	84
Duration (hours)	2.12±0.13Aa	2.09±0.11Aa	6.35±0.23Ab	6.37±0.21Ab
Mean value ($\text{Mmolm}^{-2}\text{s}^{-1}$)	*230.50±6.23*	*274.70±11.18*	*284.11±9.15*	*462.80±23.25*
High temperature (N)	63±7.0	52.5±4.5	34±12.0	38.5±14.0
Duration (hours)	*10.01±1.57*	*7.68±0.39*	*7.69±0.39*	*7.68±0.41*
Mean value (^{0}C)	21.663±0.13Aa	21.61±0.15Aa	22.83±0.23Ab	23.22±0.25Ab
High VPD (N)	36±2.0	34.5±4.5	32.0±16.5	40.0±18.0
Duration (hours)	6.40±0.35Ab	6.61±0.35Ab	4.52±0.32Aa†	5.33±0.27Aa†
Mean value (KPa)	*11.18±0.26*	*11.16±0.26*	*11.02±0.30*	*12.28±0.33*

†The p value for the difference between these two values when tested with a t-test is 0.0

While mean conditions give a general picture of the microclimate in these habitats, extreme conditions, and their duration may be more relevant for the performance of the species (Table 3.5). Duration of high PAR followed a similar pattern as the mean while a different pattern was observed for temperature, with longer duration of extreme temperatures in the *Sphagnum* patches in the young stand, while actual temperatures were greater in the older stand. Interestingly, while incident light and temperature were consistently higher in the older stand, duration of high VPD values was greater in the younger stand, and higher in *Pleurozium schreberi* compared to the *Sphagnum* spp. in the older stand.

3.6 DISCUSSION

3.6.1 The role of the environment in changes in community composition

Even though the species composition varies considerably within each age group, our results reveal a consistent gradient of change in the bryophyte community from feather mosses to hummock sphagna (*S. capillifolium, S. rubellum*) and then to hollow sphagna (*S. magellanicum, S. fallax*) along the first DCA ordination axis. This compositional gradient may be brought about by changes in available light due to the opening of the forest canopy and/or by changes in available moisture due to the rising water table; both of these variables are correlated with the first DCA axis (Figure 3.2) and both are shown directly to explain variation in species' presence and abundance (Figure 3.3, Tables 3.2, 3.4). Results of this study are thus consistent with both of the main hypotheses concerning the driving forces in the successional community changes in paludifying forests. The abundance of ericaceous species (*Rhododendron groenlandicum* and *Kalmia angustifolia*) is also strongly correlated with the main compositional gradient and may thus be an additional driving force for successional changes in the bryophyte community.

3.6.2 Available light

Light availability triples between young dense stands and old open stands (Table 3.5). A possible explanation for the observed successional replacement is that changes in light availability results in altered growth rates of both groups, allowing the sphagna to overtop the feathermosses and therefore claim their space. In dark young forests, feather mosses with maximum photosynthetic capacity at low light levels dominate (Williams and Flanagan, 1998). The sphagna present in these forests are capable of tolerating shade [*S. capillifolium, S. subtile, S. russowii*; Figure 3.3, (Hayward and Clymo, 1983; Gignac, 1992)] and are, accordingly, found in habitats not significantly more illuminated than those of the feather mosses. With increasing light availability due to canopy break-up, the established sphagna are likely to take advantage of the newly available light resource, as their maximum photosynthetic rate is higher than that of the feather mosses and is reached at a higher illumination level (Silvola, 1991; Williams and Flanagan, 1998). This may facilitate an increase in growth rate, allowing them to physically overtop the feathermosses and occupy their space. Once abundant light levels are reached species that are not tolerant of shade, such as *S. magellanicum, S. fallax,* and *S. fuscum* [Figure 3; (Gignac, 1992)] became dominant. The continued presence and even importance of *P. schreberi* in the older stands is interesting, and may be due to its tolerance of high light levels and temperatures (and associated desiccation, see below), as the light levels are significantly higher in the *P. schreberi* habitat than in the *S. magellanicum* habitat in the old forest.

3.6.3 Available moisture

Along with changes in light availability, moisture increases strongly along the age gradient. In young stands the water table is in the mineral soil and the soil environment is dry with a high vapour pressure deficit (VPD; Table 3.5). The species composition consists of species tolerant or resistant to desiccation. Feather mosses are capable of tolerating desiccation and of reactivating their photosynthetic apparati in a relatively short period (Silvola, 1991; Williams and Flanagan, 1998; Bisbee et al., 2001). In contrast sphagna are less tolerant of desiccation (Silvola, 1991, Gerdol et al., 1996), but more capable of resisting desiccation, by means of their colonial structure, particularly in hummock species, such as *S. capillifolium* and *S. subtile*, with tight interlacing branches and densely packed individuals (Hayward and Clymo, 1983; Schipperges and Rydin, 1998). While the habitats of *P. schreberi* and *S. capillifolium* are not significantly different in the young stands, more precipitation is collected in *S. capillifolium* patches than in *P. schreberi* carpets. This may indicate that the sphagna establish in micro-habitats that are slightly more humid than the surrounding matrix.

With increasing time since fire the forest floor thickness increases and eventually the pore size of the basal layers of the forest floor decreases during decomposition. This is likely to bring about a gradual upward movement of the water table into the forest floor via capillary action (Fenton et al., 2006), whereby the immediate environment of the forest-floor bryophytes becomes more humid. Position above water table has been shown to be one of the main structuring features in peatlands (Hayward and Clymo, 1983; Rydin, 1987; Gignac et al., 1991) and in swamp forests (Jeglum, 1991; Økland et al., 2001).

Despite the relative coarseness of the measures of water table position (one observation per 25 m^2 plot), we are able to document that a number of hollow sphagna (*S. magellanicum, S. rubellum, S. angustifolium* and *S. fallax*), that are less efficient at resisting desiccation because they form looser colonies (Schipperges and Rydin, 1998), are most likely able to colonize and expand after, or immediately before the movement of the water table into the forest floor. Once established these species may be able to overtop feather mosses and hummock *Sphagnum* species due to their higher growth rates (Moore, 1989;Rochefort et al., 1990; Vitt, 1990). Furthermore, feather mosses such as *P. schreberi* (Mulligan and Gignac, 2002) and *Hylocomium splendens* (Busby et al., 1978) have been found to be intolerant of very high water tables. A deviant pattern is shown by *P. ciliare* as it is equally abundant in quadrats with low and high water tables. The ultimate dominance of *S. fuscum* and *S. fallax* in very old stands may be due to their relatively broad tolerance of water table position compared to *S. magellanicum* and the other hollow species present (Gignac, 1992), as the height above water table increased dramatically over time, and organic material continued to accumulate in the forest floor.

3.6.4 Ericaceous species

Two different hypotheses may account for the strong correlation between ericaceous species and the successional changes in the community. Firstly, a negative effect of ericaceous species, including *Kalmia angustifolia* and *Ledum groenlandicum*, on the growth of vascular plants and decomposition of *P. schreberi* litter has been well documented (Inderjit and Malik, 1997; Wardle et al., 1998). Therefore, it is possible that the strong positive correlations of ericaceous cover with forest floor thickness and the water table is related to its effects on decomposition. However, 8.7% of the explained variation in bryophyte species composition is explained by ericaceous cover alone. This may be due to the ladder effect, described by Malmer et al. (2003), i.e. that sphagna use vascular plants as ladders and consequently they increase their annual growth. According to this hypothesis, and considering the poor ability of feather mosses to use ladders, and the presence of ericaceous species will favour the growth of sphagna over that of *P. schreberi*. This is also supported by significant partial correlation coefficients between ericaceous cover and abundances of *S. rubellum* and *S. russowii* and the negative partial correlation coefficient with *P. schreberi*.

3.6.5 The role of non-equilibrium factors in changes in community composition

This study supports the theory that equilibrial factors such as habitat changes are important drivers of successional change in this system. However, a large percentage of the variation in the community is not explained by the habitat factors examined. This may be due to stochastic factors affecting species establishment within the community. An example may be remnant patches of sphagna that have survived from the previous stand and which may influence the composition of the community in the regenerating forest. Furthermore, establishment factors may play an important role. The mechanism of establishment of sphagna patches in the feather moss carpet is still unknown, although it is believed that *Sphagnum* spores cannot germinate in the carpet (Sundberg and Rydin, 2002) because they require a specific substrate. Noble et al. (1984) observe that *S. girgensohnii* establishes in tip-ups, while Lawrence (1958) suggests that sphagna establish in holes in the carpet formed by animal urine. In our sites, sphagna seem to establish in sites with a microclimate almost identical to that of the surrounding feather mosses (Table 3.5), although the establishment substrate was not identified. The true role of establishment dynamics (e.g. availability of spores or asexual propagules and establishment sites) in driving the community pattern is as yet unknown.

3.6.7 Succession and competition theory

The sequential replacement of bryophyte species in coniferous boreal forests after fire has been described as a typical successional sequence; unlike the cyclical succession or initial floristics that frequently dominates the tree and shrub layers (Heinselman, 1981;

Foster, 1985). In this study, the type of succession appears to fit the model of facilitation as described by Connell and Slayter (1977), where later species are dependant on habitat changes produced by the initial colonizers. The hollow sphagna would be unable to establish in the older stands if the forest floor had not developed to the thickness required for the water table to rise and the accumulation of material in the forest floor is accelerated by the presence of sphagna (Fenton et al., 2005). Therefore, the presence of the hollow sphagna is dependant on the precedent group of hummock sphagna. Examples of facilitative secondary succession (as described by Connell and Slayter, 1977) are rare, and their existence in bryophyte communities has been questioned (Rydin, 1997).

It is unclear whether species displacement is due to an altered realized niche because of interactions with newly established species, or to limits of the fundamental niche. It has been suggested that habitats of hummock species are restricted by competition in poor fens and bogs (Mulligan and Gignac, 2001). The true role of competition in species displacement along this gradient can only be tested experimentally with reciprocal transplants (Rydin, 1997; Bisbee et al., 2001).

Our results demonstrate that *Sphagnum* spp. are not only structured spatially along environmental gradients (i.e. water table), but that they are also temporally structured within an evolving forest habitat. The dynamism of this system emphasizes the importance of water table movement in determining the outcome of succession, and in a landscape dominated by forests that are prone to paludification ultimately ecosystemic and landscape dynamics such as carbon balances and fire cycles.

3.7 ACKNOWLEDGMENTS

Catherine Béland, and Élise Vincent, all provided valuable field assistance. Discussions with Nicolas Lecomte and Sonia Légaré greatly enhanced the article. Bruce Bagnell provided valuable support during *Sphagnum* identification. Comments from Rune Økland greatly improved the paper. Funding for this project was provided by the UQAT-UQAM National Science and Engineering Research Council Industrial Chair (NSERC), an NSERC scholarship, the Lake Abitibi Model Forest and by an NSERC partnership grant with Forest industries and the Canadian Forest Service.

CHAPITRE IV

SUCCESSION IN A BOREAL BRYOPHYTE COMMUNITY: FACILITATION OR TOLERANCE

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4.1 ABSTRACT

Of the three models of succession (tolerance, facilitation and inhibition), the facilitative model has not yet been demonstrated experimentally in a secondary succession plant sequence. However, observational evidence suggests that facilitation may be the model that best explains species replacement in boreal forest floor bryophyte communities, because early species contribute to the accumulation of organic matter that appears to be necessary for the colonisation of late successional species. The objectives of this study were to test whether a facilitation or tolerance model best explained the successional sequence in boreal bryophytes observed in black spruce (*Picea mariana*) forests, and whether overtopping was the mechanism by which this took place. Reciprocal transplants of five species in young and old forests were used to test whether the early successional habitat was within the fundamental niche of late successional species, and that late successional habitat was within the fundamental niche of early successional species. Late successional species were unable to grow in early successional habitat, proving that their absence in that habitat is due to habitat restriction, and not other stochastic factors. In contrast, early successional species were able to grow in late successional habitat, proving that their reduction in cover or absence is not due to habitat limitation, but is most likely due to species interactions. Although the growth in height varied little among species or habitat, species that were replaced within the successional sequence were always of an inferior mass. This suggests that competitive overtopping may take place via a phalanx model, where the competitively superior species displaces the competitively inferior species via a front of invasion. These results prove that succession within this community best fits a facilitation model, and that competitive overtopping mediated via mass differential is the mechanism by which this occurs.

Des trois modèles de succession (tolérance, facilitation et inhibition), le modèle de facilitation n'a pas encore été démontré expérimentalement dans une séquence de succession secondaire. Par contre, des observations ont suggéré que la facilitation pourrait être le modèle qui explique mieux le remplacement d'espèces dans les communautés de bryophyte de sol dans la forêt boréale. Cela du au rôle que les espèces de bryophyte de début de succession jouent dans l'accumulation de la matière organique qui semble d'être nécessaire pour la colonisation des espèces de bryophyte de fin de succession. Les objectifs de cette étude sont de déterminer si le modèle de tolérance ou de facilitation explique mieux la séquence de succession des bryophytes boréales dans les forêts d'épinette noire (*Picea mariana*) et si la domination verticale est le mécanisme par lequel ce remplacement prend place. Des transplantations réciproques de cinq espèces de jeunes et vieilles forêts ont été utilisées pour tester si l'habitat du début de succession est dans la niche fondamentale des espèces de fin de succession et si l'habitat de fin de succession est dans la niche des espèces du début de succession. Les espèces de fin de succession ne sont pas capables de pousser dans l'habitat de début de succession, ce qui indique que leur absence dans cet habitat est une conséquence de restriction d'habitat et non pas une conséquence des facteurs stochastiques. À l'opposée, les espèces du début de succession sont capables de pousser dans les deux habitats, indiquant que leur restriction et/ou absence dans les vieilles forêts n'est pas due à des limitations d'habitat mais plutôt à des interactions entre espèces. Malgré que la croissance en hauteur ait peu varié entre les espèces ou les habitats, les espèces remplacées dans la séquence avaient toujours la

masse inférieure. Cela suggère que la domination verticale pourrait prendre place via le modèle de phalanx, où l'espèce supérieure remplace l'espèce inférieure par un front d'invasion. Ces résultats démontrent que la succession dans cette communauté est mieux expliquée par le modèle de facilitation et que la domination verticale via une différence de masse est le mécanisme par lequel le remplacement d'espèces prend place.

4.2 INTRODUCTION

The composition of plant communities changes through time, and the processes explaining this succession have long been a topic of debate, particularly between traditional equilibrium Clementsian theory (e.g. Drury and Nisbet, 1973) and non-equilibrium Gleasonian theory. Connell and Slayter (1977) articulated this debate into three models for succession: facilitation (Clements), tolerance (Gleason) and inhibition, where early species can only be replaced following disturbance.

With the growing acceptance that more than one model may be operating within the same community, all models are gaining acceptance (Foster, 1985; Jonsson and Esseen, 1990; Dickie *et al,*. 2005; Henriquez and Lusk, 2005). However, the role of facilitative succession remains unclear in several secondary successional sequences, as it is difficult to demonstrate concretely (Rydin, 1997). Many non-equilibrium stochastic factors (e.g. lack of propagule availability) could explain why a species is not present at an earlier point in a successional sequence. Furthermore, it is dependant on the competitive replacement of species as the mechanism to explain the change in species composition, and several studies have suggested that constant competitive hierarchies (*sensu* Keddy, 1997) are infrequently found due to fluctuating environmental conditions, stochastic disturbance events and plant density (Fowler, 1997; Dickie *et al.,* 2005; Liancourt *et al.,* 2005).

These problems are particularly true for bryophytes. Many bryophyte communities are structured only nominally by environmental factors, as propagule availability and stochastic (random and punctual) processes appear to be key factors in structuring communities (Lloret, 1994; Frego and Carleton, 1995a,b; Hurtt and Pacala, 1995; Rydin, 1997; Kimmerer and Driscoll, 2000). Furthermore, the use of the term competition in reference to bryophytes is problematic and controversial. Historically, some authors have suggested that true competition does not exist in many bryophyte communities, as they tend to have fugitive or stress tolerator life strategies and therefore exist in an environment where competition is non-existent (e.g. Slack, 1982; During, 1992). It has also been demonstrated that temporal and spatial variations in local environmental conditions can result in both species of a competitive pair being overtopped (Herben and Krahule, 1990; Fowler, 1990). However, some groups of bryophytes, particularly *Sphagnum* spp. in peatlands have been classified as competitors due to their large size, and relatively stable habitat (e.g. Økland, 1990; During, 1992; Mulligan and Gignac, 2001). Finally, authors have disagreed on the use of the word competition. Bryophytes are perennial plants that function primarily at the scale of the colony. As they have no roots they are generally believed to compete for aboveground space (Slack, 1990; Rydin, 1997) as it represents their access to resources (rainfall and light). Overtopping is consequently the main method of competitive replacement, and it is a strongly asymmetric (neutral, negative) interaction, where the species being overtopped does not have a negative effect on the overtopping species. Interactions like this have been referred to as asymmetric competition (Rydin, 1997) and as amensalism (Burkholder, 1952; Økland, 2000).

Despite the problematic nature of competition in bryophytes, and the importance of stochastic factors, there is growing evidence that changing environmental conditions can result in a shift in competitive balances and result in overtopping of bryophyte species, and ultimately in a change in community composition (e.g. Kooijman and Bakker, 1995; Sonesson *et al.,* 2002; Limpens *et al.,* 2003). One community where the change in composition is well documented are boreal forest floor bryophytes that experience a traditional relay floristic successional sequence after stand replacing fire. Pre-disturbance dominants (feather mosses *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.)BSG, *Ptilium crista-castrensis* (Hedw.) De Not.) do not immediately re-establish after a stand replacing disturbance, but re-invade later in the successional sequence when canopy cover is re-established (Foster, 1985; Taylor *et al.,* 1987). In some cases, where longer fire cycles permit, this replacement series continues as the forest evolves via succession and sphagna establish on the forest floor (Reiners *et al.,* 1977; Foster, 1985; Fenton and Bergeron, 2006a). Early successional bryophyte species change the environment, by contributing to the increasing organic layer that ultimately leads to the water table rise (Fenton *et al.* 2005, 2006) that appears to permit late successional species to establish in the community (Fenton and Bergeron, 2006a). However, definitive experimental evidence for the habitat limitation of late successional species has yet to be shown. The mechanism in the bryophyte layer is in contrast to the mechanism in the tree and shrub layers where pre-disturbance dominants frequently return immediately after fire (Heinsleman, 1981; Foster, 1985; Carleton and Maycock, 1978). While the changes in the tree layer more closely fit the tolerance model of Connell and Slayter (1977), the changes in the bryophyte layer appears to fit the facilitation model.

This study was designed to test whether the succession observed in the bryophyte community in paludifying black spruce forests follows a facilitative rather than a tolerance model (Connell and Slayter, 1977). This implies two specific hypotheses. Hypothesis 1: Late successional species are not able to survive in the early successional environment (i.e. limits of their fundamental niche), and can only invade the community after the environment has been changed by the early species, and are not absent due to chance. Furthermore, early successional species are able to grow in both habitat types, in the absence of late successional specie. Therefore, we should be able to measure a significant reduction in growth of late successional species in early compared to late habitats and an equivalent level of growth in early successional species in early and late habitats, indicating that they are not displaced due to habitat limitation. Hypothesis 2: Competition in the form of overtopping is the mechanism by which (i) species replacement takes place over the successional sequence and (ii) habitats are partitioned within forest types. This implies that in habitats that fit their fundamental niche, late successional species are able to grow bigger than early successional species, and are therefore able to out-compete them for space. Consequently the realized niche of the early species is reduced. So we should be able to measure that late successional species grow bigger, and that early successional species are able to grow in habitats currently occupied by late successional species. As we have documented two stages of species replacement within the chronosequence (Fenton and Bergeron, 2006a), we will test the second hypothesis in both a young forest where *P. schreberi* is displaced by *Sphagnum capillifolium* (Ehrh.) Hedw. and in an old forest where both of these species are displaced by low hummock and hollow species (*S. magellanicum* Brid., and *S. russowii* Warnst.) and ultimately high hummock species *S. fuscum* (Schimp.) Kilnggr.

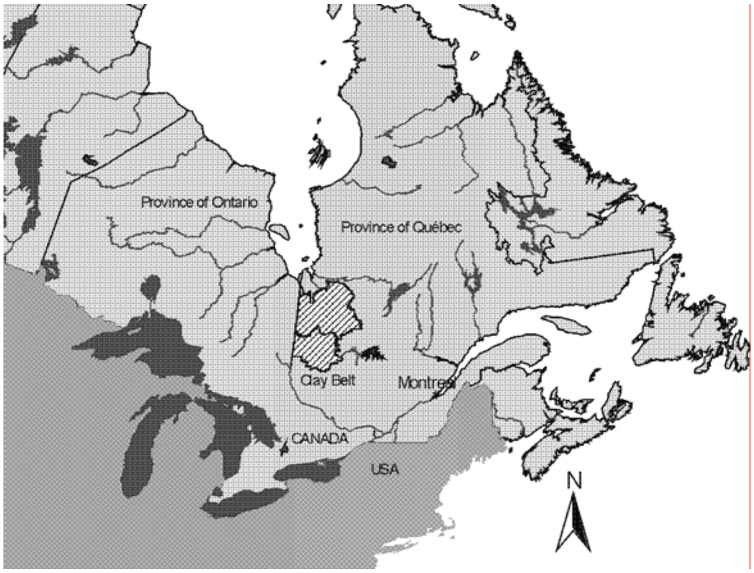

Figure 4.1 Location of study area within in the province of Québec. The ecoregions where the ClayBelt occurs is indicated, and may slightly overestimated the actual area.

4.3 METHODS

4.3.1 Study site

The study was conducted in the western boreal forest of Québec, Canada, within the black spruce (*Picea mariana* (Mill.) BSP)-feather moss (*Pleurozium schreberi*) forest type (Grondin 1996). Specifically, the study took place within the Clay Belt of Québec and Ontario (Figure 4.1), a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsinian glaciation (Vincent and Hardy, 1977). Average annual temperature is 0.8°C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Québec (Environment Canada, 2004). On the Clay Belt stands on fine textured soils with light slopes tend to paludify over time, and dips are permanent peatlands. Paludification of boreal forests is a phenomenon by which a forest on mineral soil is transformed into a treed peatland (Crawford *et al.,* 2003) via the accumulation of a thick forest floor and a rising water table (Glebov and Korzukhin, 1992). Associated with these changes in the soil is the establishment and subsequent expansion of *Sphagnum* spp. mosses into the previously feather moss dominated bryophyte layer at approximately 100 years post fire (Reiners *et al.,* 1971; Foster, 1985; Boudreault *et al.,* 2002). Two sites (spread over 50 km) were chosen to represent a young and an old stand with different bryophyte community compositions. Both had only a light slope and a similar fine soil texture and were part of a larger chronosequence for this area (see Fenton and Bergeron, 2006a). The young stand (approx. 90 years after stand replacing fire) is a dense black spruce stand with a closed canopy and the bryophyte community was dominated by feather mosses with distinct disjunct patches of sphagna, primarily *S. capillifolium*. In contrast, the old forest (approx. 600 years after stand replacing fire) was a relatively sparse stand with several layers of trees in the understory resulting in a heterogeneous light environment. The water table had moved definitively into the organic layer, and the forest floor was very uneven. The bryophyte layer was made up of generally spatially distinct patches of *S. russowii*, *S. magellanicum*, *S. fallax* (senso lato), *S. fuscum*, and *P. schreberi* that occupy different habitat conditions (Table 4.1).

Table 4.1 Mean (and standard error) values of open canopy over the habitat of each of the species in young and old forests. Differences between species in each site were tested. The t-test of the young site had a p value of 0.073, while the ANOVA for the old site was 0.054. Letters indicate differences, order a<b

Site	Species	% open canopy[1]	Forest floor thickness[2] (cm)	Water table depth[3] (cm)	Water table position[4] (cm)
Young	*Pleurozium schreberi*	19.70±1.25 a	21.56±0.98	34.62±1.06	-14.12±0.97
	Sphagnum capillifolium	23.56±1.62 b	25.40±8.80	34.47±1.90	-14.39±1.49
Old	*Pleurozium schreberi*	45.27±5.18 ab	66.37±5.29	42.83±2.88	22.54±7.05
	Sphagnum russowii	41.16±3.62 ab	57.06±4.64	46.37±4.01	12.58±8.54
	Sphagnum magellanicum	54.47±5.92 b	72.50±12.23	34.88±2.63	18.91±5.97
	Sphagnum fuscum	33.90±4.94 a	114.20±15.42	28.50±4.25	85.33±28.13

[1] Percent open canopy measured with a densiometer (scored concave mirror) over each transplant.

[2] Thickness of the organic layer lying over the mineral soil.

[3] Depth of water table below the surface, as measured by steel rods (Fenton et al., 2006)

[4] Position of the water table within the forest floor, relative to the organic:mineral interface. Negative values indicate position in the mineral soil, positive values, height above the mineral soil in the organic layer (Fenton et al., 2006).

4.3.2 Experimental design

One method used to test whether species replacement is due to species interactions or habitat limitations, is reciprocal transplants. Using *P. schreberi* as an example, if it is able to grow in the habitat space occupied by *S. capillifolium* that is gradually overtaking portions of the feather moss carpet, it can be concluded that it is being replaced due to a competitive interaction. If *P. schreberi* is unable to grow in the habitat of the sphagna, then it is not being replaced due to a competitive interaction but rather because of the limits of its fundamental niche. As such reciprocal transplants represent a method of testing the mechanism causing observed patterns in the community.

In this study, reciprocal and control transplants were performed with species between stands and within each stand. *S. russowii,* which was only present in the old stand, was transplanted into the young stand, and similarly, *S. capillifolium,* only present in the young stand, was transplanted into the old stand. Within the young stand *P. schreberi* and *S. capillifolium* were transplanted each into the habitat of the other, as well as returned to their own habitat for a control. Within the old stand *S. russowii, S. magellanicum, S. fuscum* and *P. schreberi* were transplanted into each other's habitat and into their own, although not in a fully balanced design due to logistical restrictions. Table 4.2 indicates the transplants that were performed. Five replicates of each transplant (both reciprocal and control) were performed for a total of 95 transplants.

Table 4.2 Reciprocal and control transplants performed in the young and the old stand. Site indicates which forest age is described. Old-young indicates transplants that were between sites. Transplant species indicates the species that was transplanted, while habitat species indicates the habitats into which it was transplanted

Site	Transplant species	Habitat species
Young	*Pleurozium schreberi*	*Pleurozium schreberi* *S. capillifolium*
	S. capillifolium	*S. capillifolium* *Pleurozium schreberi*
Old	*S. russowii*	*S. russowii* *S. magellanicum* *S. fuscum* *Pleurozium schreberi*
	S. magellanicum	*S. magellanicum* *S. russowii* *Pleurozium schreberi*
	S. fuscum	*S. fuscum* *S. russowii*
	Pleurozium schreberi	*Pleurozium schreberi* *S. russowii* *S. magellanicum*
Old-young	*S. russowii*	*Pleurozium schreberi* (young) *S. capillifolium* (young)
	S. capillifolium	*S. russowii* (old)

4.3.3 Transplant method

In June 2004, nearly homogeneous patches of each species were identified in the two forest sites. Plugs of each species with a diameter of approximately 30cm and a depth of at least 20 cm were cut of each species. Each plug was carefully removed and transported to the lab where a bundle of stems of a set number (that varied among species in order to achieve an adequate total weight) were identified and carefully removed from the middle of the plug. These stems were trimmed to a set length of 5 cm, were weighed at a constant hydration state, and their colour was determined, using a Munsell Color Chart for Plant Tissues (Munsell Color GretagMacbeth LLC, New Windsor, New York), in order to have a measure of health. Colours with high values and low chroma (i.e. greys) were classified as colours that indicate low vigour. All stems initially had high vigour. Once the weight of each bundle of stems was determined, they were loosely attached with a nylon cord and inserted back into the plug from which they were removed. The plugs were then returned to the forest and inserted either into their original habitat for the control, or into the habitat of a different species.

The constant hydration state was established for each species using the method described in Frego and Carleton (1995a), Mulligan and Gignac (2001), and Mulligan *et al.* (in press). Briefly, a constant weight was assured by removing all of the water from the bryophytes that is held in exterior macro-pores via centrifugation in a salad spinner. The remaining water in micro-pores and inside the plant can be said to be a constant amount. This state was determined by performing a series of standardization curves for each species, where shoots were initially soaked and weighed and then subjected to increasingly longer periods of centrifugation until a constant weight was achieved (results not shown). Once the weight of the sample does not decrease with increasing centrifugation, only tightly held water in micro-pores and internal water (inside the hyalocyst cells of the sphagna) is present. This indicates the amount of centrifugation necessary to reach a standard hydration state that is comparable between samples, and across time, and permits the comparison of wet weights. This method has the advantage of not assuming that different stems of the same species have a similar dry weight, nor does it damage the experimental stems via drying. For a complete discussion of the advantages of this method, see Mulligan *et al.* (in press).

In September 2005, after two growing seasons, the plugs were carefully removed and brought back into the lab. Each bundle of shoots were re-identified and extracted from the plug. The length of five randomly chosen shoots was measured, the bundles were soaked and centrifuged to their constant wet weight, and they were re-weighed. Their colour was also re-assessed.

4.3.4 Statistical analysis

Differences in mass (wet weight) and length among species and habitats were examined using the general linear model (GLM) in SPSS v. 10. A full factorial model was used with species and habitat as the two factors. Two separate models were run for each set of transplants in the young and old forests. In the model for the old forest, percent change in mass was used instead of change in mass (in g) because of the differences in scale among the different species. For the transplants between young and old forests species were examined individually, and different habitats were compared. A t-test was used to compare differences in mass and length in *S. capillifolium* and *P. schreberi* and a one-way analysis of variance (ANOVA) was used in the case of *S. russowii* (SPSS v.10).

4.4 RESULTS

4.4.1 Hypothesis 1: Facilitative succession

Compared to its growth in its own habitat in the old forest site, *S. russowii* grew significantly less in mass in the two young forest habitats (*S. capillifolium* and *P. schreberi*; Figure 4.2). Interestingly, growth in length varied little among the habitats, and was constant at approximately 3cm. One bundle of *S. russowii* in *S. capillifolium* habitat had a colour that indicated low vigour (Table 4.3). In contrast, *S. capillifolium* grew more in mass in the old forest habitat of *S. russowii* than in its own habitat in the young forest. The length of *S. capillifolium* did not vary between these habitats. Similarly, neither the mass nor the length of *P. schreberi* varied between the young and old forests.

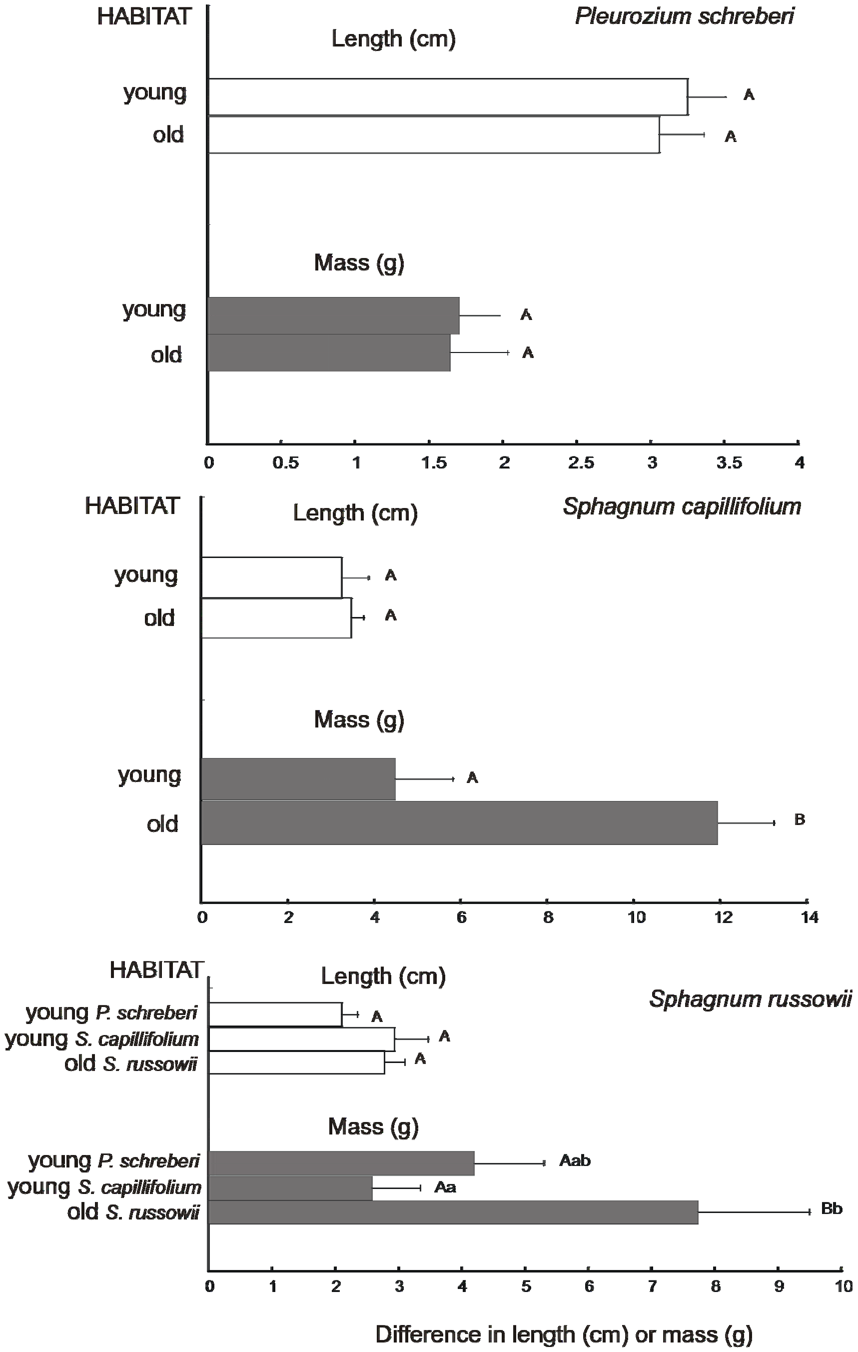

Figure 4.2 Increases in length (in cm; white) and mass (in g; black) of *P. schreberi* (top), *S. capillifolium* (middle), and *S. russowii* (bottom) when grown in their own and each other's habitats, from June 2004 to September 2005. The Y axis indicates the habitat in which the stems were grown. Letters indicate statistical differences within variables; capital letters indicate differences between forest type (young vs old), and lower case letters indicate differences among habitat types. Values indicated A are smaller than those indicated B.

Table 4.3 Number of low vigour transplants as indicated by colours with high value and low chroma (i.e. greys) in each species and habitat type.

Species	Habitat	Fraction of transplant plugs
S. magellanicum	*S. magellanicum*	1/5
	S. russowii	3/5
	P. schreberi	3/5
S. russowii	*P. schreberi*	1/5
	S. fuscum	1/5
	S. capillifolium (young)	1/5
P. schreberi	*S. magellanicum*	1/5

4.4.2 Hypothesis 2: Competitive overtopping via differential growth rates

Overall, *P. schreberi* and *S. capillifolium* both grew approximately 3.25cm in both habitats in the young forest, although each was slightly taller in their own habitat (Figure 4.3). *S. capillifolium* was heavier than *P. schreberi*, and was also heavier in the *P. schreberi* habitat than in its own. No bundle of shoots in these transplants had a colour that indicated low vigour.

There was very little variation in the growth in length of *P. schreberi* among habitats in the old forest, increasing by approximately 3 cm in all habitats (Figure 4.4). However, increase in percent mass varied among the habitats, with very little increase in *S. magellanicum* habitat, and two bundles of shoots of *P. schreberi* had a colour that indicated low vigour (Table 4.3). In its own habitat and in the *S. russowii* habitat the shoots had a percent increase of mass of approximately 30%.

S. russowii had the greatest increase in length in its own habitat and in that of *S. magellanicum* at approximately 3 cm (Figure 4.4). Growth in length was slightly reduced in the habitats of *P. schreberi* and *S. fuscum*, in both cases it was closer to 2 cm. In contrast, growth in mass was greatest in its own habitat and that of *P. schreberi*, at 60-70% and growth in mass was greatly reduced in the habitat of *S. fuscum* (~10%). In the *S. magellanicum* habitat the increase in mass of *S. russowii* was highly variable (50% to 0). Two bundles of shoots had a colour that indicated low vigour, one in the *S. fuscum* habitat, and one in *P. schreberi* (Table 4.3).

Growth in length of *S. magellanicum* was similar in its own habitat and in that of *S. russowii* (approx. 4 cm) however it was considerably reduced in the habitat of *P. schreberi* (approx. 2cm; Figure 4.4). In terms of growth in mass, % mass increase was highest in its

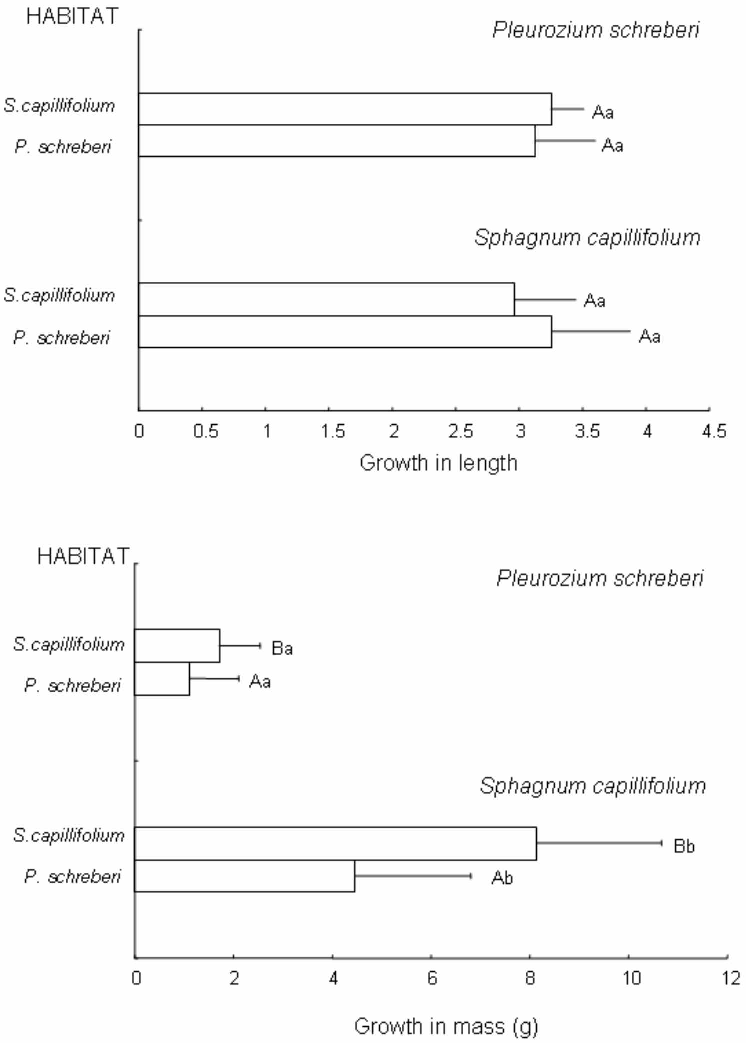

Figure 4.3 Increases in length (in cm; top) and mass (in g; bottom) of transplanted shoots in the young forest from June 2004 to September 2005. The Y axis indicates the habitat in which the shoots were grown. Letters indicate statistical differences; capital letters indicate differences in habitats (i.e. are consistent for one colour across all species) while lower case letters indicated differences in species (i.e. are consistent for a single species in all habitats). There were no differences in length among species or habitats. Values indicated A are smaller than those indicated B.

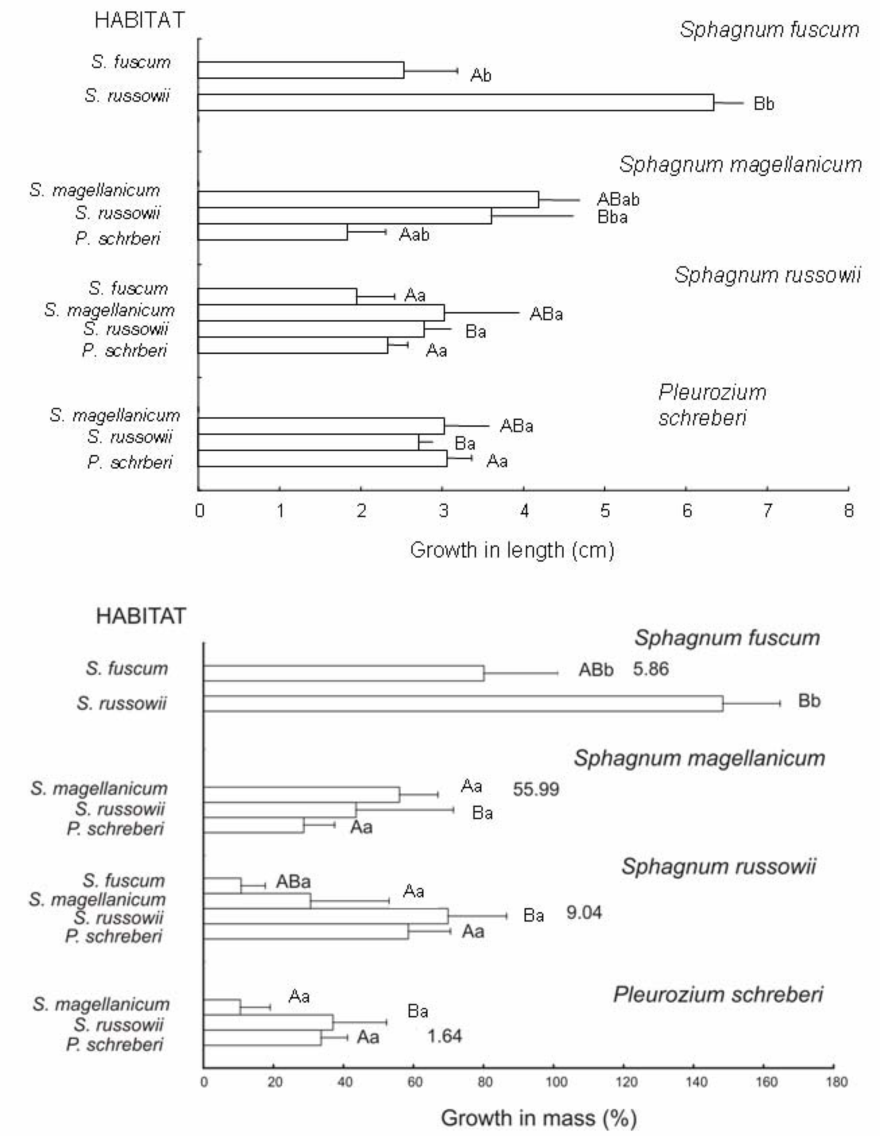

Figure 4.4 Increases in length (in cm; top) and mass (in % of initial mass; bottom) of transplanted shoots in the old forest from June 2004 to September 2005. The Y axis indicates the habitat in which species were grown. Letters indicate statistical differences; capital letters indicate differences in habitats regardless of species (i.e. are consistent for one habitat and confounds the response of all species) while lower case letters indicated differences in species (i.e. are consistent for a single species and confounds all habitats). Values indicated A are smaller than those indicated B. The numbers above the bars in the % mass graph indicate the mean mass increase in grams for each species in its own habitat.

own habitat, variable in the habitat of *S. russowii*, and low in the habitat of *P. schreberi*. *S. magellanicum* had the highest number of bundles that indicated low vigour, with a total of 7, one in its own habitat, three in *P. schreberi*, and three in *S. russowii* (Table 4.3).

S. fuscum increased its growth in both length and weight in the *S. russowii* habitat, compared to its own habitat. None of the bundles showed low vigour.

4.5 DISCUSSION

4.5.1 Hypothesis 1: Facilitative succession

At least some shoots of the late successional *S. russowii* showed low vigour in both of the habitats in the young forest (i.e. *S. capillifolium* and *P. schreberi*), supporting the first hypothesis that its absence in the young forest is due to habitat restriction (or its fundamental niche), and is probably not due to stochastic establishment or other factors. The habitat limitation may be caused by a lack of light or of humidity, as while *S. russowii* is generally considered reasonably shade tolerant and weedy (Nungesser, 2003; Slack, 1990), the young forest was very dark (see Fenton and Bergeron, 2006a). *S. russowii* is occasionally found in younger forests as a few individual shoots within a *S. capillifolium* colony (pers. obs). This presence outside its apparent fundamental niche is probably due to the capacity of *S. capillifolium* to retain water, therefore providing a wetter habitat than *S. russowii* would be able to create on its own (Rydin, 1997). These individuals may ultimately provide a nucleus from which it can expand when light and water table conditions become suitable for rapid growth.

In contrast to *S. russowii, S. capillifolium* and *P. schreberi* grew at an equal or greater rate in the old forest compared to the young forest. This also supports the facilitative succession hypothesis, indicating that their absence or limited presence in the old forest is not due to habitat limitation, and as they were present in the young forest, they must have been displaced. The increased growth rate of *S. capillifolium* in the old forest is probably due to the increased light availability. While *S. capillifolium* is very tolerant of shade (Gignac, 1992; Gerdol *et al.,* 1998), the increased light availability in the older forest would increase its photosynthetic rate, as most sphagna have reach their maxima at relatively high levels of irradiation (Williams and Flanagan, 1998). The increased light availability did not have the same effect on *P. schreberi* as it reaches its maximum rate of photosynthesis at much lower light levels (Williams and Flanagan, 1998). More interestingly, there was no reduction in the growth rate of *P. schreberi* in the old forest, despite the apparently deteriorated conditions (increased light intensity). This indicates that the species was able to adapt to the new conditions, and may suggest a sun block role for the change in colouration observed between the two habitats (data not shown).

4.5.2 Hypothesis 2: Competitive overtopping via differential growth rates

All of the species in both forest types showed a remarkable capacity for growth, increasing their mass by 40-80% over two growing season. This is in concordance with the results of Wang *et al.* (2003) and Bisbee *et al.* (2001) among others who have documented the important role of bryophytes in the net primary production (NPP) of boreal coniferous forests.

Interestingly, contrary to the prediction that late successional species would grow bigger than early successional species and that species growth would be reduced in sub-optimal habitats, growth in length varied little among habitats for any species in both forest types, and almost all species grew at nearly the same rate, between 3-4 cm over the two growing seasons. In contrast, growth in mass varied significantly among habitat types for most species, and varied among species. Etiolation, the increase of length and not mass, has been documented in a number of bryophyte species when they are exposed to habitat conditions outside where they had been found (Hobbie *et al.,* 1999; Sonesson *et al.,* 2002; Dorrepaal *et al.,* 2003). The apparent lack of plasticity in growth in length may reflect the need of an individual bryophyte shoot to continue vertical growth at all costs, or the individual shoot becomes buried in the continually rising carpet, is shaded out and ultimately dies. In such a scenario increase in mass is sacrificed in order to maintain the upward rise.

While growth in length varied little among species, mass varied widely among species, and late successional species (*S. russowii, S. magellanicum*) were considerably heavier than the early successional species (*S. capillifolium, P. schreberi*), supporting our second hypothesis. This greater mass (and in many cases density; data not shown) may allow them to either retain space or to overtake space already occupied by a less heavy early successional species, in a phalanx model as defined by Herben and Hara (1997). As sphagna grow they increase not only in height but also in density via branching (Rydin, 1995). Using *S. russowii* and *P. schreberi* as an example, high density in the heavier *S. russowii* colony could create a pressure force against the adjacent patch of *P. schreberi*, and this pressure could ultimately permit *S. russowii* to occupy the space of *P. schreberi*. A similar situation was demonstrated with grasses, where species with a higher bulk density better resisted invasion by another species (Barthram *et al.,* 2005).

Several of the species were capable of growing (in both length and mass) in the habitats of the other species within the community. Within the young forest, *P. schreberi* and *S. capillifolium* grew as well in each others habitat as in their own; however there was also little difference in the two habitats, in terms of light availability and humidity. The space currently being occupied by *S. capillifolium* may have been occupied by *P. schreberi* in the past, but due to the similarity of the habitats, this does not represent a restriction of the realised niche of *P. schreberi*. Furthermore, due to the comparable growths in length, and even mass (*S. capillifolium* was only twice as heavy as *P. schreberi* compared to *S. magellanicum* which was ten times as heavy) it is doubtful whether the growth rates documented here can explain the ultimately explosive growth and overtopping that takes place in these communities as documented by monolith studies (Foster, 1984; Lecomte *et al.,* 2006; N. Fenton unpublished data) and current expansions were observed in the form of a wave of *S. capillifolium* that was “crashing” over the *P. schreberi*. A similar phenomenon was observed in Labrador by Foster (1985), where *S. girgensohnii* expanded over the feather mosses in a wave-like pattern. Two non-exclusive theories may explain this apparent contradiction. Punctual climatic conditions have been shown to play an important role in altering the balance between near competitive equivalents (Rydin, 1990), for example, annual variations in climate have been demonstrated to play a role in the relative dominance of terrestrial lichens and bryophytes within a community (Sulyma and Coxson, 2001; Sedia and Ehrenfield, 2003). A similar process may be in play here and the expansion of *S. capillifolium* may be dependant on years with a particular set of climatic conditions. An additional explanation may be that while the patches used in this study were in the median of the patches present in the forest (~ $5m^2$), we have documented that the truly large (>$25m^2$) patches tended to occur in canopy gaps created by fallen or snapped trees (unpubl. data). Therefore, the definitive overtopping of the feather mosses by *S. capillifolium* may depend on a dramatic increase in light availability (i.e. creation of a large canopy opening), which would allow the sphagna to increase its photosynthetic rate (Williams and Flanagan, 1998), and therefore growth rate.

Interestingly the ability of *S. capillifolium* to grow in all of the habitat conditions available in the young forest indicates that some other factor must have been limiting its abundance in the past. As S*phagnum* spores are relatively abundant (Fenton and Bergeron, 2006b) establishment substrates may be the limiting factor, as *P. schreberi* is probably not a good germination substrate for the spores. Coarse woody debris, which provides a substrate of constant humidity and may provide nutrients to the germinating spores (Sundberg and Rydin, 2002; Ganjegunte *et al.,* 2004), is the most frequent establishment substrate for *S. capillifolium* colonies in young forests (Fenton et al. submitted), and varies temporally and spatially within stands (Hély *et al.,* 2000; Harper *et al.,* 2005). This may limit the capacity of *S. capillifolium* to establish in young stands and explain its apparent limitation on the forest floor.

Within the old forest, all species showed some capacity to grow (in length and mass) outside of their own habitat, but no species was able to grow in all of the available habitats. There was a stratification of the habitats with species growing in the wettest (*S. magellanicum*) and driest (*P. schreberi*, and *S. fuscum*) sites able to grow in the intermediate habitat (*S. russowii*), but not the other extreme. *S. russowii* grew in almost all habitats except that of *S. fuscum.* This supports the ultimate end of this successional sequence (Fenton and Bergeron, 2006a) where *S. fuscum* is the dominant sphagna in an open forested peatland where the peat has risen high above the water table. A similar pattern is seen in succession post frost-mound collapse in permafrost landscapes, where *S. fuscum* is present in the driest habitats (Camill, 1999). The restriction of *P. schreberi* and *S. fuscum* to the extreme dry end of the gradient when they are capable of growing in the intermediate represents a case of competitive exclusion from the habitat, and the greater mass of the other species is probably the mechanism by which this is achieved.

4.5.3 Conclusions

The successional sequence documented here is a case of facilitative succession, to our knowledge the first such sequence documented empirically and experimentally. A similar, but opposite sequence has been documented via observational studies by Camill (1999) where succession after permafrost mound collapse is driven by the gradual increase in peat depth, towards a drier community. The end of the successional sequence in paludifying forests (Fenton and Bergeron, 2006a), not examined in detail here, may closely resemble this sequence.

Despite the role of competitive overtopping in determining the successional sequence, it was not the only process controlling community composition. Establishment factors and habitat limitation were also important. Establishment factors may explain the current pattern in the young forest, where the apparent competitive dominant was spatially restricted, and all species were at least partially habitat limited in the old forest. Furthermore, *P. schreberi* occupied significant portions of the habitat in the old forest, despite its competitive inferiority. The continued presence of this species over the long term supports the observation that while competitive overtopping exists, it rarely results in the complete elimination of a species from the community (Rydin, 1993). This may be due to fluctuations in the local environment due to either continued changes in the forest floor thickness and canopy closure, or to landscape level fluctuations in climate between years (Mulder *et al.,* 2001, Sulyma and Coxson, 2001; Sedia and Ehrenfield, 2003). Therefore the balanced approach of integrating several models to explain community composition and change across gradients is supported. The importance of climate fluctuations in maintaining species diversity and determining relative abundances within the community suggested by this and other studies implies that current and future fluctuations in the climate will have dramatic effects on community level interactions.

4.6 ACKNOWLEDGEMENTS

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CHAPITRE V

SPHAGNUM SPORE AVAILABILITY IN BOREAL FORESTS

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5.1 ABSTRACT

The role of propagule availability in determining community composition is poorly understood, and is infrequently investigated for bryophytes. In addition the extent to which spore availability is limited by dispersal is unknown. If spore availability is not dispersal-limited, local and regional spore dispersal and wind availability may affect spore availability at any point. In this study, the abundance of *Sphagnum* spores was investigated within the context of a successional sequence where *Sphagnum* spp. invade a feather moss community in black spruce boreal forests of northwestern Québec, Canada. Spores were trapped and grown in a greenhouse to protonemal stage to estimate the abundance of spores within three sites that varied in *Sphagnum* abundance, and stand density (a surrogate for wind intensity). Sporophyte production was also investigated in one site where individual *Sphagnum* colonies could be distinguished. Spores were less abundant in sites with less ground cover of *Sphagnum* present in the community, although spores were trapped in all sites. Spore abundance was inversely correlated with local stand density, indicating that wind intensity may play a role in limiting dispersal. Sporophytes were produced in colonies that were larger and had greater access to light. These results suggest that *Sphagnum* invasion into young dense forests may be partially limited by spore dispersal, although the availability of germination substrates may also play an important role.

Le rôle que joue la disponibilité des propagules dans la composition des communautés est peu connu et peu investigué dans les bryophytes. De plus, le où le moment où la disponibilité des propagules est limitée par la dispersion est également inconnu. Si la disponibilité des spores est limitée par la dispersion, la présence du vent pourrait influencer la disponibilité de spores. Dans cette étude, l'abondance des spores des sphaignes est investiguée dans le contexte d'une séquence successionelle où les sphaignes envahissent la communauté de mousse hypnacée dans les pessières boréales du nord-ouest du Québec, Canada. Pour estimer l'abondance des spores, ces derniers sont trappées dans trois sites qui varient dans l'abondance de sphaignes présentes et la densité du peuplement (un substitut pour l'intensité du vent) et par la suite elles sont incubées dans une serre jusqu'au stade du protonéma. La production de sporophytes a aussi été investiguée dans un site où les colonies de sphaignes sont distinctes. Les spores sont moins disponibles dans les sites avec moins de recouvrement de sphaignes mais elles sont présentes dans tous les sites. L'abondance des spores est corrélée négativement avec la densité du peuplement à l'échelle locale, ce qui indique que l'intensité pourrait limiter la dispersion des spores. Les sporophytes sont produits par les colonies qui sont les plus grandes et qui ont plus d'accès à la lumière. Les résultats de cette étude suggèrent que l'invasion des sphaignes dans les jeunes forêts denses pourrait être partiellement limitée par la dispersion des spores malgré que la disponibilité des substrats de germination puisse aussi y jouer un rôle important.

5.2 INTRODUCTION

Habitat characteristics are often invoked to account for the presence or absence of a species within a community. However, the absence of a species in a community may also be due to an absence of reproductive propagules or the conditions necessary for their germination, i.e. aspects of the regeneration niche (Grubb, 1977). While theories concerning the mechanics and establishment of bryophytes in a community are as of yet widely untested, asexual propagules are believed to play important roles in the maintenance and expansion of colonies (Laaka-Lindberg et al., 2003), while establishment of new colonies is believed to be dominated by spores. In the specific case of *Sphagnum*, evidence of sexual reproduction by spores has been historically rare (e.g. Clymo and Duckett, 1986) and it has been demonstrated that *Sphagnum* can regenerate from stem fragments (Clymo and Duckett, 1986). Therefore, it is possible that spores play little role in establishing colonies in new habitats, as fragments may be dispersed by animals or birds. However, there is growing evidence that sexual reproduction and establishment of new colonies by spores play an important role. Many genets have been found in close proximity and hybrid individuals have been identified (Cronberg, 1996), many species not present before disturbance recruit after disturbance (Soro et al., 1999), and spores have been shown to germinate in field conditions (Sundberg and Rydin, 2002).

Many factors influence spore availability at a given site, including the number of spores produced per individual, the number of individuals present locally and regionally, and the dispersal capacity of the spores. As sphagna are widely distributed in the boreal zone and produce numerous spores [18,000–200,000 per capsule (Sundberg, 2005)], dispersal may be the most important factor affecting spore availability. Whether or not sphagna are actually dispersal limited is as yet unclear. Spore dispersal is believed to be strongly leptokurtic to approximately 2 m (Cronberg, 1991; Miles and Longton, 1992), however over 50% of spores produced are unaccounted for in these studies, suggesting that many spores are dispersed outside the immediate area (Miles and Longton, 1992; Söderstrom and Jonsson, 1989; Sundberg, 2005). Studies examining the diaspore rain have supported this assertion, as they have found species that are absent from the surrounding community (Marshall and Convey, 1997; Ross-Davis and Frego, 2004). Sundberg (2005) suggested that a point isolated from spore-producing colonies will receive spores from sources at a variety of distances, and that local sources will only dominate if the distance isolating the point from the closest source is relatively short (i.e., <1 km). Therefore the relative importance of local and regional spore sources, and thus the potential dispersal limitation of any individual species is yet unclear.

Dispersal agent availability is a factor that has not been explicitly addressed in previous studies. Wind is the main dispersal agent of terrestrial bryophyte spores (Cronberg, 1991), and is likely to be unlimited in open environments, such as peatlands. However within forested environments, or other habitats that are protected from the wind, the very local intensity of wind may limit spore dispersal and result in variable spore abundance across the landscape.

Local sporophyte and spore production will strongly influence spore abundance, if it is dispersal-limited. Sporophyte production within a colony may be limited by spermatozoid dispersal, which is believed to be limited to tens of centimeters (Bisang et al., 2004); therefore, a colony must contain both male and female gametangia in order to produce sporophytes. Spatial clumping of colonies may favor the development of both sexes within a colony by the establishment of spores from neighboring colonies. In addition to limitations on fertilization, biotic (individual size) and abiotic (light, water) factors have been shown to influence sporophyte production in individual ramets (Rydgren and Økland, 2002; Stark et al., 2000).

Within the boreal forest, several forest communities see a gradual establishment and expansion of *Sphagnum* spp. into the feather moss (*Pleurozium schreberi, Ptilium crista-castrensis, Hylocomium splendens, Ptilidium ciliare*) dominated community (Fenton et al., 2005; Viereck et al., 1993). *Sphagnum capillifolium* is the first sphagnum to establish in the feather moss carpet (Fenton and Bergeron, 2006) and is generally considered to be a dioicous or polyoicous species, but its sexual reproductive potential in these habitats is unknown. The dramatic expansion of *Sphagnum* spp. observed in stands over 100 years old, and the eventual invasion of *S. russowii, S. magellanicum,* and *S. fallax* (Fenton and Bergeron, 2006) is believed to be due to a change in the environment that favors the growth of *Sphagnum*. It may also be that dispersal limitation caused by a lack of local spores, and reduced wind in dense young stands lengthens establishment time of *Sphagnum* spp. in these forests

The broad objective of this study was to determine the effect of local vs. regional spore dispersal and wind availability on spore abundance in black spruce stands. Specifically, we address three hypotheses: (1) there are fewer spores available in young stands with little *Sphagnum* compared to older stands with more *Sphagnum*; (2) because spore dispersal is predominantly local, spore abundance at a given point is correlated with *Sphagnum* cover and distance to reproductive colony, and is not correlated with wind intensity; and (3) sporophyte production is correlated with distance between colonies and with colony size and light availability.

The phenology of *Sphagnum* spore release has only been sporadically studied, and never in our region. However, based on Scandinavian studies, it can be expected that spore release would be later in shaded habitats such as forests where section Acutifolia dominates than in open peatlands where sections Acutifolia and Cuspidata are common (Sundberg, 2002; Cronberg, 1991). Because the phenology of spore release of the species present within the communities was unknown for this habitat and region, variation in the date of spore release within a forest habitat was also examined.

5.3 METHODS

5.3.1 Study site

The study was conducted in the western boreal forest of Québec, Canada, within the black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin, 1996). Specifically, the study took place within the Clay Belt of Québec and Ontario, a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsonian glaciation (Vincent and Hardy, 1977). Average annual temperature is 0.8°C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Québec (Environment Canada, 2004). On the Clay Belt stands on fine textured soils with light slopes tend to paludify over time, and dips are permanent peatlands. As a result, the regional cover of *Sphagnum* is high. Three sites (spread over 50 km) were chosen to represent a gradient in stand density and *Sphagnum* abundance. All three sites had only a light slope and a similar fine soil texture.

Annual spore production has been shown to vary with the climate of the preceding summer (Sundberg, 2002). Climate variables were collated from the data made available by the Meteorological Service of Environment Canada (2004). The weather station at Matagami (49°46’N, 77°48’W) was chosen, as it was the nearest station with a complete set of data available. Total volume of precipitation and number of degree-days (18°C) were determined for the last 30 years (mean 1971–2000), 2002, 2003, and 2004. Precipitation and degree-days varied widely between 2002 and 2004 (Figure 5.1). In 2002, there was very little precipitation in August, while there was nearly double the number of degree-days. In contrast, 2003 had near normal precipitation, but very few degree-days in July. In 2004, July and August were wet and cold, while September was dry and warm.

5.3.2 Study design and data collection.

In 2003, five 100 m^2 square plots were established in each of three forest sites, as part of a larger study (Table 5.1). Basal area, a measure of stand density, is used as a surrogate for potential wind intensity, as there is less wind in denser stands. The dbh of all trees over 8 cm were measured and the basal area per hectare was calculated. In all three stands the cover of *Sphagnum* spp. was visually assessed, and the distances from the plot center to the three nearest colonies of *Sphagnum* of any species were measured in site 1, where there is little *Sphagnum* present in the bryophyte community.

Table 5.1 Description of the three sites where studies were undertaken.

Variable	Site 1	Site 2	Site 3
Basal area (m^2/ha)	44.08±0.031	21.31±0.028	30.0±1.14
Open canopy (%)	43.67±2.48	67.40±2.51	62.72±2.60
Sphagnum cover (%)	10.14±1.49	62.6±4344	67.64±1.37

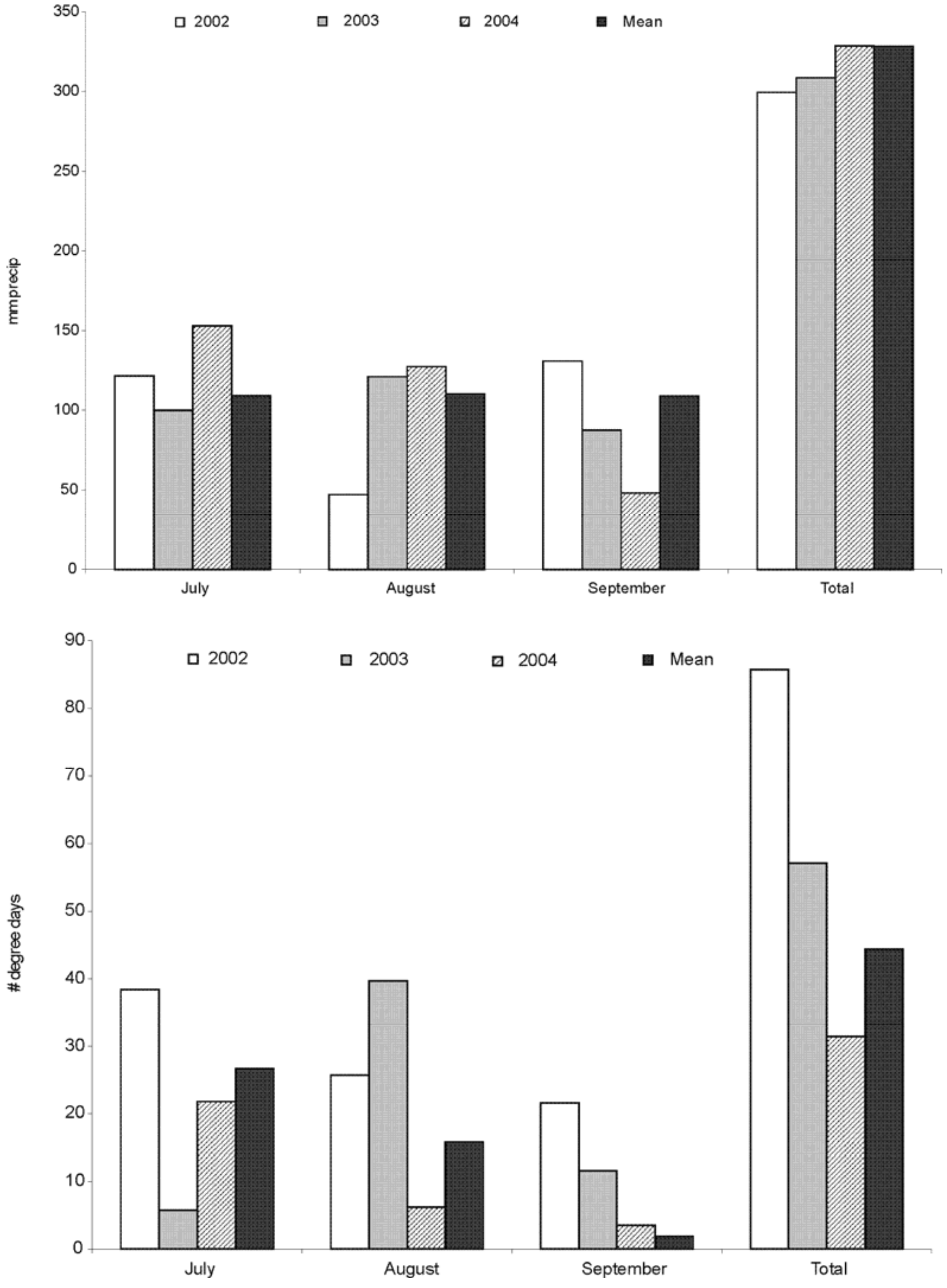

Figure 5.1 Precipitation (top) and degree-days (bottom) for Matagami, Québec for 2002, 2003, 2004 and the mean of 1971-2000. Precipitation is the total for year in millimetres, and degree-days are the sum of the temperature of all days over 18^0C. Data is compiled from the Environment Canada database.

In order to determine the phenology of spore abundance, 20 spore traps (see below) were exposed together in one plot at each site at approximately seven day intervals from July 24 to September 12, in 2003. In 2004, the experiment was repeated; however as results from 2003 indicated that spores were released in late August to early September, trapping began August 25 and ended on September 23. In addition, in order to correlate within-site variation in spore abundance with stand density and *Sphagnum* abundance, the 20 traps were spread out within each site with four spore traps exposed together in each of the five plots. In both 2003 and 2004, a total of 60 spore traps placed in the same position were exposed in each site on the same day, per week.

5.3.3 Spore trapping and germination.

The emergence method was used to determine the abundance of spores. Spores were trapped on 10 cm diameter petri plates filled with nutrient agar solution (modified from Parker Thompson's basal nutrient medium), which has previously been used with success in the germination of spores (Ross-Davis and Frego, 2004). Plates were placed on the forest floor for approximately six hours on dry, sunny or variably cloudy days, in order to ensure that plates were not flooded by precipitation, and that there was a potential for dispersal. Once plates were collected, they were placed in a greenhouse under ambient conditions for 3–5 weeks and surveyed for the development of protonemata under a dissecting microscope. Only *Sphagnum* protonemata were counted, which were easily distinguished from other developing protonemata by their thalloid form. They were not identified to species, as we were interested in total *Sphagnum* spore abundance, and also because *Sphagnum* spp. grown in petri plates frequently develop unusual traits that prevent positive identification (Fenton pers. obs.). A limitation of the emergence method is that only spores that successfully germinate are counted; therefore spores whose germination requirements were not met will not be included in the census. However, as very high numbers of spores germinated we feel confident that this margin of error is relatively small.

5.3.4 Sporophytes

The abundance of sporophytes was assessed in site 1, where *Sphagnum* was not the dominant ground cover and individual colonies could be determined. Each colony of

Sphagnum within the five 100 m^2 quadrats was examined and the species present identified; the canopy cover above the colony was determined with a densiometer, and the distance to the three nearest neighbor colonies was measured. Where sporophytes were found, they were counted within three randomly placed 10 × 10 cm squares per 1 m^2 of *Sphagnum*.

5.3.4 Analyses

Spore abundance for each plate was determined and placed into one of four classes: 0, 1–10, 11–50, >50, and the median value of each category was used in subsequent analyses, i.e., 0 (class 0), 5 (class 1–10), 30 (class 11–50), 80 (class >50). Mean spore abundance (the number of spores trapped) and standard error were calculated for each site, each week in 2003 and each plot in 2004. The data were checked for normality and heteroscedascity, and differences in means among weeks within a site were established with analysis of variance (ANOVA) followed by Bonferroni's post-hoc tests.

Peasrson's correlations were calculated between 2004 spore abundance (abundance) and local *Sphagnum* abundance, *Sphagnum* proximity (site 1 only) and stand density during high and low abundance weeks (September 1 and 23, respectively) at landscape (all sites) and local (each site separately) scales. In order to separate the effects of correlated explanatory variables (e.g., *Sphagnum* abundance and total basal area are negatively correlated), partial-correlations were calculated between spore abundance and total basal area, *Sphagnum* cover, mean distance to neighboring colony, and minimum distance to neighboring colony. This approach allows the separation of the effects of total basal area (wind) from amount of *Sphagnum* (local dispersal) despite their correlation.

The characteristics of colonies with and without sporophytes and their habitat conditions were compared with t-tests. Pearson's correlation was used to calculate the relationship between sporophyte density in colonies that were reproductive and internal resource availability (colony area and height) and external resource availability (light and mean and minimum distances to neighboring colonies). The critical level of p was 0.05 in all tests.

5.4 RESULTS

5.4.1 Spore abundance

Spore abundance was low in August 2003, and peaked in all sites in September 2003 and 2004 (Figures 5.2A and B). In addition to the temporal variation, spore abundance also varied spatially across the landscape. Fewer spores were trapped in site 1 compared to sites 2 or 3; spore abundance also varied within sites and within plots.

In 2004, spore abundance on September 9 (high abundance) in all sites was correlated with *Sphagnum* abundance (Table 5.2). In contrast spore abundance on September 23 (low abundance) was correlated with basal area. At a smaller spatial scale within individual sites, spore abundance was not correlated with *Sphagnum* cover or basal area in sites 1 or 2. However, spore abundance on September 23 was correlated to the minimum distance to a reproductive *Sphagnum* patch in site 1. In site 3, the pattern was similar to the pattern observed in all sites combined.

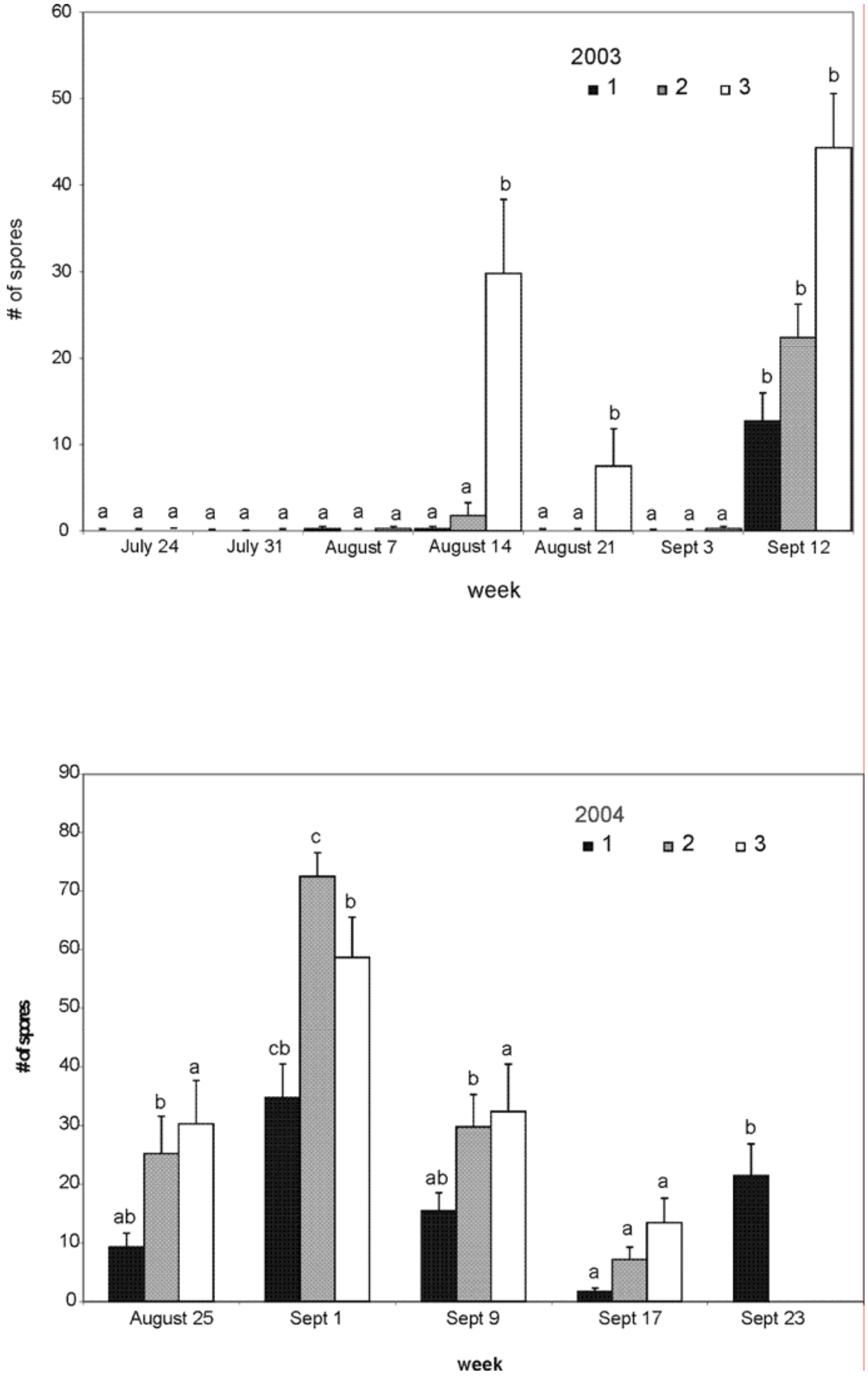

Figure 5.2 Mean and standard error of spore availability in three sites for each sampling date in 2003 (top) and 2004 (bottom). Within a site, dates with a different letter are significantly different a<b<c.

Table 5.2 Partial correlation (R^2, p value) between spore abundance and habitat characteristics for high (9 September) and low (23 September) abundance weeks in 2004. Distances between colonies were only measured at site 1, where discreet colonies were visible. Partial correlations are between spore abundance and the listed variable, while the other variables are held constant.

Site	Variable	Spore abundance	
		High	Low
1	Mean distance to *Sphagnum* colony	0.0491(0.842)	-0.417 (0.076)
	Minimum distance to *Sphagnum* colony	0.247(0.307)	**-0.471(0.042)**
	Mean basal area	0.0810(0.742)	0.213(0.383)
	Mean *Sphagnum* cover	0.0918(0.709)	0.346(0.147)
2	Mean basal area	-0.119(0.639)	**-0.432(0.05)**
	Mean *Sphagnum* cover	**-0.479(0.044)**	-0.154(0.506)
3	Mean basal area	0.323(0.177)	-0.293(0.210)
	Mean *Sphagnum* cover	-0.103(0.674)	-0.296(0.205)
All sites	Mean basal area	0.045(0.737)	**-0.248(0.052)**
	Mean *Sphagnum* cover	**0.286(0.029)**	0.0535(0.680)

5.4.2 Sporophytes

Of the 49 *Sphagnum* colonies found within the 500 m^2 surveyed in site 1, 43 were *S. capillifolium*, including all 17 (39.5%) of the colonies with sporophytes. The remaining patches were *S. wulfianum* (3) and *S. girgensohnii* (3). Compared to the *S. capillifolium* colonies without sporophytes, reproductive colonies were significantly larger and taller (Table 5.3). In contrast, sporophyte density on an individual patch was not correlated with colony size (not shown). Reproductive colonies were also associated with significantly more open canopy (Table 5.4). Reproductive and non-reproductive colonies did not differ in their proximity to neighboring *S. capillifolium* colonies; however the correlation between sporophyte density and mean and minimum distance to a neighboring colony was close to significant (R^2 0.290 p=0.073; R^2 0.306 p=0.058, respectively).

Table 5.3 Characteristics of patches with and without sporophytes in site 1. Values are means and standard errors, and values followed by different letters are significantly different, a<b.

	No sporophytes	Sporophytes
Sphagnum colony area (m^2)	0.388±0.008 a	2.83±1.2 b
Sphagnum colony height (m)	0.122±0.0015 a	0.202±0.0022 b

Table 5.4 Habitat conditions of colonies with and without sporophytes in site 1. Values are means and standard errors. Values followed by different letters are statistically different.

	No sporophytes	Sporophytes
Mean distance to *Sphagnum* colony (m)	1.71 ± 0.261 a	2.54 ± 0.614 a
Minimum distance to *Sphagnum* colony (m)	0.948 ± 0.210 a	1.78 ± 0.579 a
Open canopy (%)	21.88 ± 1.12 a	27.80 ± 1.74 b

5.5 DISCUSSION

5.5.1 Spores

The lower spore abundance in site 1 compared to sites 2 and 3, and the correlation between *Sphagnum* abundance and spore abundance indicate that local dispersal influences spore abundance during peak periods (Figure 5.2 and Table 5.2). Within site 1, spore abundance was also strongly influenced by local dispersal as the spore abundance was negatively correlated with the minimum distance to other *Sphagnum* colonies. The lack of a correlation with basal area during the peak period of spore abundance may suggest that most spores are produced locally and that when local production is high, reduced wind capacity (because of closed tree canopies) does not detectably limit spore abundance. However, the negative correlation with basal area at low overall spore abundance suggests that when local spore production is low, reduced wind capacity yields a detectable reduction in total spore rain. The difference in dispersal timing of local and regional spores may be related to either differences in dispersal phenology among species (Sundberg, 2002) or in environmental variables (Rydgren and Økland, 2002) within forest stands and across the region. These results support the hypothesis that abundance is relatively limited in young stands with little *Sphagnum* present due to the predominantly local dispersal of spores.

In site 1, the negative correlation between spore abundance and distance to a *Sphagnum* colony during the low density week suggests that the spores trapped on September 9 may not have been locally produced, but rather dispersed from the surrounding region, and that local dispersal occurred on September 17 and 23. This is supported by the observation that the sporophytes in site 1 were only slightly dehisced on September 1 (Fenton pers. obs). The lack of any correlation between spore density and *Sphagnum* abundance or stand density within site 2 is interesting. Other factors must be determining local dispersal of spores.

Overall, fewer spores were trapped in 2003 than in 2004 (Figure 5.2). Sundberg (2002) found that the production of sporophytes and spores was positively correlated with the amount and distribution of precipitation the summer before, due to gametangial production that takes place at that time. August 2003 was considerably wetter and warmer than August 2002, which may have resulted in the production of more gametangia, and therefore more spores the following fall (Figure 5.1).

Sphagnum spores were released in late summer and early fall (Figure 5.2) approximately one month later than what has been previously recorded for these species (Cronberg, 1991; Sundberg, 2002). This may be due to lower levels of light in forests compared to open peatlands, which would increase sporophyte development time during the summer or, later snow melt, which would result in a later fertilization period.

5.5.2 Sporophytes

Reproduction (sporophyte and spore production) is energetically expensive for the parent gametophyte plant (Ehrlèn et al., 2000), and may be limited to individuals with the internal resources (i.e., ramet size) and access to external resources (e.g., available light) to undertake reproduction (Rydgren and Økland, 2002). *Sphagnum capillifolium* colonies with sporophytes were larger, taller, and received more sunlight because of more open tree canopies than colonies without sporophytes (Table 5.4), suggesting that the limitations observed at the individual level in *Dicranum polysetum* (Ehrlèn et al., 2000) and *Hylocomium splendens* (Rydgren and Økland, 2002) also apply at the colony level in *S. capillifolium* in this environment. As a consequence, the relatively limited spore abundance in site 1 may not only be limited by lack of *Sphagnum* within the community, but also by reduced sporophyte production by the colonies present due to a lack of resources.

Despite the relatively limited spore abundance within site 1, nearly 40% of colonies contained sporophytes. The high number of sporophytes present within an environment where each colony is isolated from each other by approximately 1 m is surprising as *S. capillifolium* is generally listed as dioicous, and dioicous bryophytes are generally believed to be mate-limited (Bisang et al., 2004). The ability of these colonies to be fertilized suggests that *S. capillifolium* is polyoicous in this environment, as suggested by Cronberg (1991) and Pujos (1993). An alternative explanation is that each colony or colony is established by several spores. *Sphagnum capillifolium* may show a pattern of multiple spore establishment followed by genet exclusion as the colony grows (Cronberg, 1996), which would permit both male and female individuals to temporally co-exist within a single colony. However, determining which of these possibilities is correct is beyond the scope of this study.

5.5.3 Conclusions

Spore abundance was at least partially determined by local production of spores, however spores were also available via regional dispersal. Therefore, the long interval observed in the establishment of *Sphagnum* spp. into the feather moss carpet that is observed on the Clay Belt of Québec and Ontario may be partially due to dispersal limitation. Sites with no or very few *Sphagnum* colonies will depend on the relatively low number of spores that are dispersed regionally. A second limit to spore abundance in these sites may be a size and resource limitation on sporophyte production on the colonies that do establish within the closed forest. Therefore, the rapid expansion of *Sphagnum* documented in these stands approximately 150 years after fire may be partially related to the gradual opening of the forest stand during this period, allowing greater local sporophyte and spore production, and increased regional dispersal. However, gametangia production was not observed in this study, nor was spore germination and establishment assessed, and these processes should be further investigated to determine the relative roles of gametangia production, spore availability and germination site availability in *Sphagnum* establishment within the feather moss carpet.

5.6 ACKNOWLEDGEMENTS

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CHAPITRE VI

SPHAGNUM ESTABLISHMENT AND EXPANSION IN BLACK SPRUCE (*PICEA MARIANA*) BOREAL FORESTS

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6.1 ABSTRACT

Boreal forest bryophyte communities are made up of distinct patches of feather mosses that cover the forest floor. In some black spruce boreal forests, *Sphagnum* spp. establish colonies on the forest floor 30-40 years after the feather mosses, and ultimately expand to dominate the community. The mechanisms that permit the *Sphagnum* spp. to establish and expand are unknown. The objectives of this study were to examine the establishment and expansion substrates of *Sphagnum* spp., and the conditions correlated with colony expansion. Forty colonies, in six sites, of *Sphagnum capillifolium* were dissected to determine their substrates, and the environmental conditions in which all colonies present were measured. Coarse woody debris was the dominant establishment and early expansion substrate for *Sphagnum capillifolium* colonies. Colony size was negatively correlated with tree basal area, and there were fewer individuals per cm^3 in large compared to small colonies. These results suggest that *Sphagnum* establishment in these communities is dependant on the presence of coarse woody debris, and expansion is linked to stand break-up, which would allow greater light intensity, and rainfall to reach the colony. Consequently the community change is initially governed by a stochastic process (establishment) and ultimately by habitat availability and species competition.

Dans les forêts boréales, les communautés de bryophytes sont composées d'agglomérations de mousses hypnacées qui couvrent le sol. Dans les pessières, les sphaignes établissent des colonies sur le sol 30 à 40 ans après les mousses hypnacées et réussissent ultimement à dominer la communauté. Les mécanismes qui permettent cet établissement et étalement ne sont pas encore compris. Les objectifs de cette étude sont d'examiner les substrats d'établissement et d'expansion des sphaignes ainsi que les conditions environnementales qui permettent leur étalement. Pour ce faire, 40 colonies de *Sphagnum capillifolium* réparties sur six sites ont été disséquées pour déterminer leurs substrats d'établissement et les conditions environnementales présentes autour de toutes les colonies ont été mesurées. Le bois mort était le substrat dominant pour l'établissement et l'étalement des colonies. La taille des colonies était négativement corrélée avec la surface terrière des arbres et il y avait moins d'individus par cm^3 dans les grandes colonies versus les petites colonies. Ces résultats suggèrent que l'établissement des sphaignes dépend de la présence de bois mort et que l'étalement est corrélé avec l'ouverture du peuplement, phénomène qui permettrait à plus de lumière et de pluie d'atteindre les colonies. Par conséquent, les changements dans la communauté seraient gouvernés initialement par des processus stochastiques et ultimement par la disponibilité d'habitat et la compétition.

6.2 INTRODUCTION

Bryophytes play many roles in boreal forest ecosystems influencing, among others, total net primary production (Gower et al., 1997; Bisbee et al., 2001) and soil respiration (O'Connell et al., 2003). They are also associated with paludification, where a coniferous forest on mineral soil is transformed into a treed peatland, through tree diebacks caused mainly by the accumulation of a thick forest floor and water-logging (Glebov and Korzukhin, 1992; Fenton et al., 2005). Paludification is associated with a change in the bryophyte community, as *Sphagnum* spp. colonies establish and gradually overtop the previously dominant feather mosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*; Reiners et al., 1971; Foster, 1985; Boudreault et al., 2002).

Despite this important link with boreal forest dynamics, few studies have focused on *Sphagnum* spp. in forests, and most of the genus' known ecology is related to peatlands. However, in paludifying forests, *Sphagnum* spp. colonies are first documented 80-90 years after fire, while the feather mosses establish shortly after canopy cover is re-established around 50 years after fire (Noble et al., 1984; Foster, 1985; Taylor et al., 1987). The absence of *Sphagnum* spp. in these sites may be a function of propagule availability (in the case of *Sphagnum*, spores and unspecialized asexual propagules such as stem and branch fragments; Cronberg, 1991; Sundberg and Rydin, 2002), habitat tolerances, and inter-specific interactions of juvenile and adult stages. In parallel studies (Fenton and Bergeron, 2006a, b), we have demonstrated that adult colonies of *S. capillifolium* are capable of tolerating a wide variety of habitat conditions on the forest floor, and that spores are available at least in limited quantities even in areas where there are no or few *Sphagnum* spp. colonies. This suggests that habitat requirements during colony establishment may be the rate limiting step.

The regeneration niche (Grubb, 1977) or the establishment conditions required for *Sphagnum* spp. colony establishment are generally unknown; however in peatlands, sphagna have shown higher germination rates on substrates with constant hydration and supplies of phosphorous and nitrogen (Sundberg and Rydin, 2002). Within forests, Noble et al. (1984) documented that *S. girgensohnii* established in tree tip ups, and Lawrence (1958) speculated on the role of animal urine in creating holes in the feather moss carpet that allow *Sphagnum* spp. establishment.

The conditions that permit or encourage the expansion of these colonies at the expense of the feather moss carpet are also unclear. At the community level, *Sphagnum* spp. expansion was correlated with canopy openness in early successional stages (Fenton and Bergeron, 2006a), and similarly Hayward and Clymo (1983) found that *S. capillifolium* growth was dependent on an optimum shade level, yet was independent of water-table depth. Competition from already established bryophytes has also been suggested as an important factor influencing *Sphagnum* spp. colony establishment and expansion, and some authors have suggested colony density (i.e. number of individuals per cubic area) as a way for bryophyte colonies to respond to inter-specific competition (Rydin, 1995; Frego, 1996). Moreover, Rydin (1995) found that *Sphagnum* spp. horizontal colony expansion was positively related to colony density, and found increasing colony density with increasing height above the water-table, suggesting high density as a way to counter desiccation.

This article therefore addresses three objectives: (1) to describe establishment substrate preferences for pioneer *Sphagnum* spp. in young black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) stands; and to examine colony expansion, specifically (2) to define the habitat requirements for *Sphagnum* spp. colony expansion in young stands, in terms of canopy opening and stand basal area, as proxies for microclimate; and (3) to assess the role of *Sphagnum* colony density in expansion, by examining its relationship with colony surface area, and habitat requirements.

6.3 MATERIALS AND METHODS

6.3.1 Study Area

The study was conducted in the western boreal forest of Québec (Canada) in the black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin, 1996). The study took place within the Clay Belt of Québec and Ontario, a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsinian glaciation (Vincent and Hardy, 1977). Average annual temperature is 0.8°C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Québec (Environment Canada, 2004). On the Clay Belt, forest stands on fine textured soils with light slopes tend to paludify over time, and dips are permanent peatlands. The main disturbances are large, severe fires that kill all above ground vegetation. The fire cycle has been consistently increasing, from ca 83 years prior to 1850 to ca 325 years for the period 1920-1999 (Bergeron et al., 2001). Three *Sphagnum* species are pioneers in the process of paludification and are commonly found in young black spruce (*Picea mariana* (Mill.) BSP)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) stands of the Clay Belt of Québec and Ontario: *S. capillifolium* (Ehrh.) Hedw., *S. girgensohnii* Warnst., and *S. russowii* Russ. (Fenton and Bergeron, 2006a). These species form dense or loose colonies on the predominantly feather moss covered forest floor, and are capable of tolerating desiccating and shady conditions (Hayward and Clymo, 1983; Gignac, 1992). Nomenclature of sphagna follows Anderson (1990).

6.3.2 Sampling

Six sites, ranging from 50 to 182 years post-fire, were chosen within the study area (Table 6.1). All six sites had a canopy dominated by black spruce (*Picea mariana*), and an understory of scattered *Vaccinium angustifolium*, *V. myrtilloides* and *Rhododendron groenlandicum*. The bryophyte layer was a continuous carpet of feather mosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*), with isolated and scattered *Sphagnum* spp. colonies. Stand age (time since stand replacing fire) was established by verification of stand initiation map dates by dating basal cross-sections of a few dominant trees (for more details see Lecomte et al., 2006). At each of the sites, a 100 m transect was randomly established with the beginning at least 50 m from the nearest road, along which were delimited five 100 m^2 square plots, at least 10m between plots. Each 100 m^2 plot was subdivided into four 25 m^2 nested quadrats. Within these plots three data sets were gathered.

In order to study the establishment substrate preferences for *Sphagnum* colonies, a minimum of five colonies of *Sphagnum capillifolium* were sampled per site (one per 100 m^2 plot), chosen to represent a range of colony surface areas. *Sphagnum capillifolium* was chosen as it was the most common species in these forests. At each colony, the canopy openness was measured above the colony centre, using a densiometer (a scored concave mirror). The colony was then cut into a grid (10x10 cm for small colonies, and 20x20 cm for large colonies), with a coordinate system over each colony, including in the grid the area of feather mosses immediately adjacent to the colony; length of colony was arbitrarily assigned

Table 6.1 Description of survey sites. Time since fire is an estimation of the age of the forest; basal area bS is the basal area of black spruce per hectare; basal area secondary species is the basal area of the second most prominent species per hectare, where bF = balsam fir, La = larch, jP = jack pine, tA = trembling aspen; %CWD is the sum of the average coarse woody debris cover for all four decay classes within each $25m^2$ quadrat; organic matter thickness as measured for each $25m^2$ quadrat; % exposed mineral soil for each $25m^2$ quadrat; % sphagnum cover is the cover of all *Sphagnum* species within each $25m^2$ quadrat. All values are means and standard errors.

Site	Time since fire (yrs)	BA bS (m^2/ha)	BA secondary species (m^2/ha)	% CWD	Organic matter depth (cm)	%Exposed mineral soil	%*Sphagnum* cover
D2	50	44.4 ±1.67	bF;1.73 ±0.584	14.17 ±1.39	19.9±1.4	0.83 ±0.35	9.5±2.4
N23	85	32.3 ±1.90	jP;11.8 ±2.99	17.31 ±2.39	16.6±1.3	0.6 ±0.20	9.7±4.9
S1	90	39.9 ±3.86	tA;4.98 ±4.45	5.73 ±1.80	19.7±1.5	2.97 ±1.14	21.8±4.4
N18	128	26.6 ±4.45	La;1.53 ±0.05	13.58 ±2.15	33.6±3.0	1.81 ±0.54	15.4±5.2
W1	130	42.5 ±5.54	tA;5.94 ±0.0	5.73 ±2.49	29.9±2.4	0.56 ±0.34	11.0±3.2
D1	182	19.1 ±0.797	tA;2.35 ±0.0	31.1 ±2.82	31.0±2.0	1.86 ±0.74	23.7±5.9

as the longest axis. At each coordinate, the bryophyte species on the surface, the height and depth of the colony, and the substrate on which the bryophytes were growing was recorded. When there was no clearly dominant substrate, all identifiable substrates present under the coordinate were noted. The percent cover of coarse woody debris (CWD), deciduous leaf cover, and exposed mineral soil were assessed in order to compare their availability on the forest floor and their frequency as establishment substrates.

In order to examine the role of habitat factors in determining *Sphagnum* spp. colony size, a detailed habitat survey was carried out. Within each 25 m^2 quadrat, open canopy (with a densiometer), and tree basal area (by species) of all trees over 9 cm dbh were measured. In order to increase the sample size, *Sphagnum* spp. colony size, tree basal area, and canopy openness data from two additional sites initially sampled for a separate study were included.

Within each quadrat two colonies of each *Sphagnum* spp. (*girgensohnii, russowii* or *capillifolium*) and *Pleurozium schreberi* (the dominant feather moss) were randomly chosen, from which $10cm^3$ samples were taken for density measurements. The surface area of the sampled bryophyte colonies was also measured. The volume of each wet *Sphagnum* spp. and *P. schreberi* sample was measured, the samples were oven-dried over 24 hours the dry weight for each sample was recorded, and the density as grams (dry-weight) per centimetre cubed was calculated.

6.3.3 Data analysis

The percent frequency of establishment substrates was calculated, using the deepest point of each *S. capillifolium* colony as its presumed establishment point. Chi-square tests comparing observed and expected establishment substrate frequencies were performed. Expected substrate frequencies were determined by the percent cover of each substrate type measured in each plot (coarse woody debris, basal area, feather moss cover, and exposed mineral soil).

Colony expansion was analysed in terms of substrate (dissected colony data set) and habitat conditions (colony and quadrat data). Expansion substrates were determined to be all substrates above the deepest point (the establishment substrate). They were expressed as a percent frequency. Linear regression was used to analyse the relationship between colony area and colony depth. Correlation coefficients (Pearson's Rho; SPSS v. 12.0) were calculated between colony area, depth and tree basal area and canopy openness. Similarly, correlation coefficients were calculated between colony density and explanatory variables (colony size, feather moss density, tree basal area, canopy openness). Finally a t-test was performed to compare the density of large and small colonies. The critical value of p in all tests was 0.05.

Even though the measured conditions vary with stand age (Fenton et al., 2005), age was not included as a separate variable, as the target variables were the habitat conditions.

6.4 RESULTS

6.4.1 *Sphagnum* colonies

Surface area varied among the 40 sampled colonies in the 6 sites, from 0.05 to 3.34 m^2 with an average of 0.56 m^2. Average maximum colony depth was 30.1cm (range 14 to 55 cm), average length and width for the colonies were respectively 0.76 m and 0.53 m, and the average height of the colony above the surrounding forest floor, based on the highest point for each colony, was 20.22 cm, ranging from 0 to 47 cm.

6.4.2 *Sphagnum capillifolium* colony establishment

The frequency of establishment substrates [coarse woody debris (CWD), mineral soil and feather moss] differed significantly from the expected distribution ($\chi^2 = 82.09$, $P<0.0001$). The most frequently observed establishment substrate was CWD (Figure 6.1), present in 30% of colonies and when the combined substrates are included, 72.5% of colonies had at least some CWD as their establishment substrate. CWD was the most frequent substrate at all establishment depths, except in the shallowest colonies (11-16cm) where feather mosses were the most frequent substrate. Mineral soil ($\chi^2 = 10.13$) and live wood ($\chi^2 = 12.26$) were also more frequently observed than would be predicted by their availability on the forest floor, while feather mosses ($\chi^2 = 48.28$) were underrepresented.

Very small colonies (0-0.56 m^2, mean establish. depth 26.85±9.51 cm) and larger colonies (>0.56 m^2, n = 14, mean establish. depth 36.14±9.47cm) show the same establishment substrate distribution as the larger colonies, with pure CWD representing the establishment substrate for approximately 30% of the colonies (data not shown).

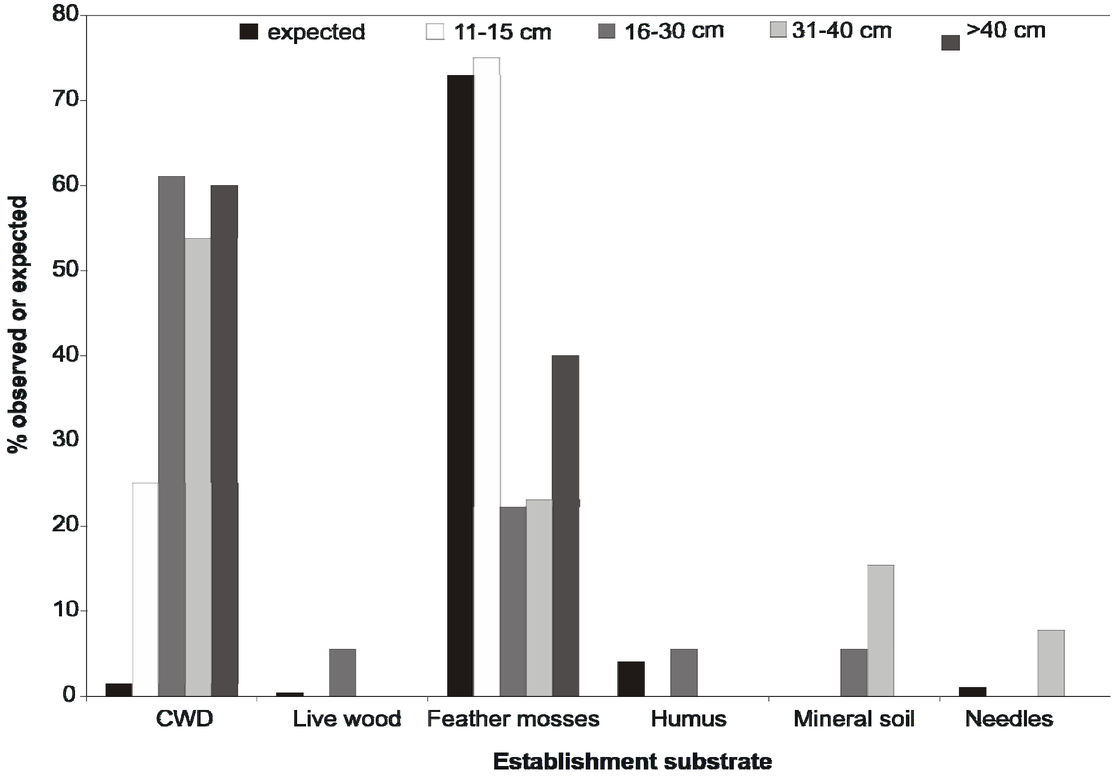

Figure 6.1 Observed and expected % frequencies of establishment substrates for *S. capillifolium* colonies at different depths (cm). Expected values were calculated based on percent cover of the substrate types observed on the forest floor.

6.4.3 *Sphagnum* colony expansion

Feather mosses and coarse woody debris were the two dominant expansion substrates beneath *S. capillifolium* colonies with 42.1 and 37% of recorded values respectively (Table 6.2). Humus (9.3%), mineral soil (7.1%), and charcoal (3.8%) were the other substrates. In three cases *S. capillifolium* was found to be expanding over an older *Sphagnum* colony. Interestingly, the importance of these substrates varied between shallow and deep colonies or portions of colonies, as the mean depth for the feather moss substrate was 15.3 cm, while the mean depth for the other substrates were all over 20 cm. There was a linear relationship between colony area and colony depth (F = 10.783; P<0.002; Figure 6.2a).

The influence of microclimate (as estimated by canopy openness and tree basal area) on colony size, and therefore expansion, was weak, the combined data for *S. capillifolium, S. russowii,* and *S. girgensohnii* colonies showing a slight negative correlation between colony surface area and tree basal area (Pearson's Rho -0.175, P<0.012; Figure 6.2b). Interestingly, there was no significant correlation (Pearson's Rho = -0.240, P<0.136) between colony surface area and canopy opening above the colony. However, there was an apparent light threshold at 20% canopy opening, as no colonies were found in areas where the canopy opening is less than 20%. There was no threshold effect in terms of canopy opening for colony expansion, either vertically (increased colony depth) or horizontally (increased colony surface area).

Table 6.2 *S. capillifolium* expansion substrate frequency (%) and mean depth. Differences in mean depths, as determined by ANOVA (F 10.13, p<0.0001), are indicated by letters a<b. Due to the small number of samples, *Sphagnum* was not included in the ANOVA.

Substrate	Overall frequency	Mean depth± SE
CWD	37%	21.39±0.75 b
Charcoal	3.8%	20.00±1.93 ab
Humus	9.3%	20.54±1.66 b
Feather mosses	42.1%	15.39±0.62 a
Mineral soil	7.1%	22.88±1.13 b
Sphagnum	0.6%	11.00±3.79

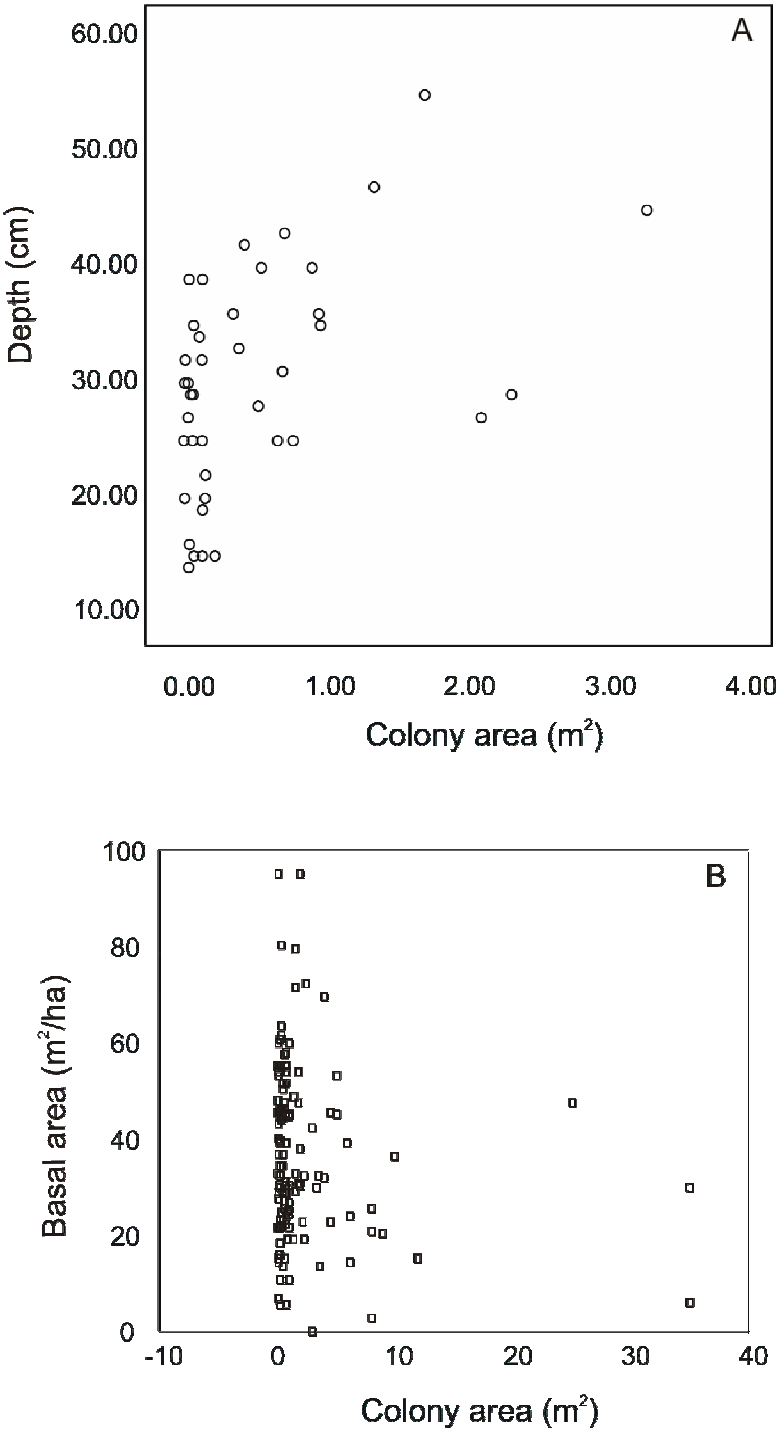

Figure 6.2 Relationships between colony area and (a) colony depth and (b) tree basal area.

6.4.4 *Sphagnum* colony density

Sphagnum spp. colony surface area and colony density were not correlated (Pearson's Rho =-0.094, P = 0.231; Figure 6.3a), however when size classes are introduced, there was a significant difference in density between small colonies (<4 m^2) and large colonies (>4 m^2; t = -2.12 p = 0.036). This suggests a threshold effect, with larger *Sphagnum* colonies generally exhibiting lower densities than smaller colonies.

Sphagnum spp. colony density was correlated with environmental conditions, with a significant positive correlation between *Sphagnum* colony density and quadrat basal area (Pearson's Rho = 0.253, P<0.001; Figure 6.3b). Consequently there was also a significant negative correlation between colony density and canopy opening (Pearson's Rho = -0.277, P<0.0001). Interestingly, there was a significant positive correlation between *Sphagnum* colony density and feather moss density (Pearson's Rho = 0.527, P<0.0001; Figure 6.3c).

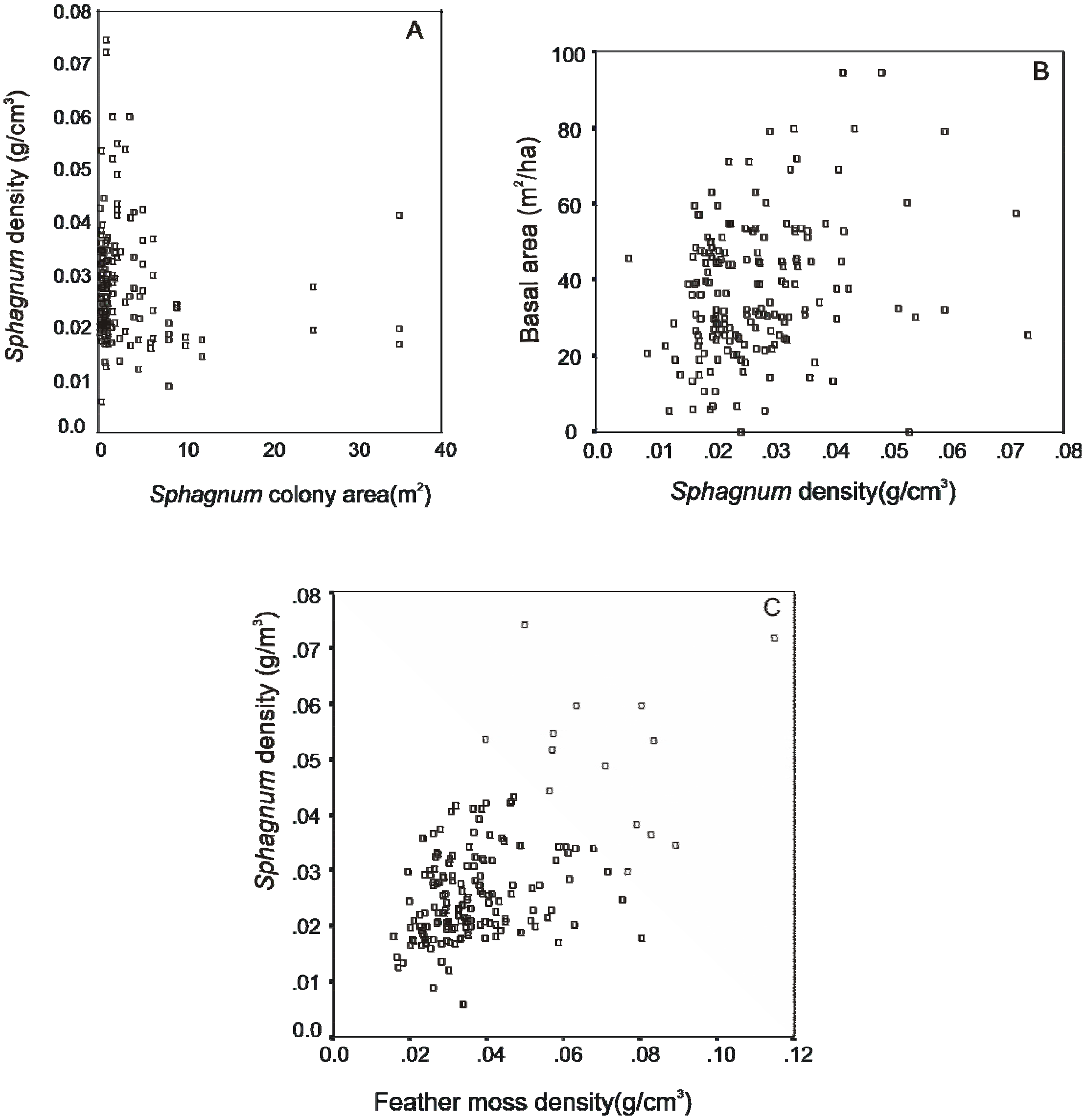

Figure 6.3 Relationships between *Sphagnum* colony density (g/cm^3) and (a) *Sphagnum* colony area (m^2), (b) tree basal area (m^2/ha), and (c) feather moss density (g/cm^3).

6.5 DISCUSSION

6.5.1 Colony establishment

Coarse woody debris (CWD) was the dominant establishment substrate within the colonies examined in this study. CWD may be the most suitable habitat for *Sphagnum capillifolium* spores as once it has reached a minimal level of decomposition, it provides a habitat with constant humidity and nutrients (Ganjegunte et al., 2004), two of the potential limiting factors to spore establishment (Sundberg and Rydin, 2002). CWD might also permit the newly developing colony to temporarily escape inter-specific competition from the dominant feather mosses. The under-representation of mineral soil as a substrate suggests that the mechanism of establishment in this study from that described by Noble et al. (1984) where *S. girgensohnii* established in the pits created by treefall. This may in part be due to the shallow roots of black spruce (Greene et al., 2004) that expose less mineral soil when they fall, compared to the deeper rooted white spruce.

The near restriction of establishing colonies to CWD suggests that substrate availability, at least during the early stages of stand development, may be the limiting factor for establishment of *Sphagnum* spp. in these forests, as spores are available (Fenton and Bergeron, 2006b). Coarse woody debris is high immediately after stand replacing disturbance, and then decreases, until the self thinning stage, where it begins to increase again (Hély et al., 2000; Harper et al., 2005). In the very early stages of stand initiation *Sphagnum* spp. establishment may be limited by microclimate, as the open canopy creates a very hot and dry environment not favourable to spore germination. Then, once the canopy is closed, it may be a lack of coarse woody debris that limits *Sphagnum* establishment, until the self-thinning stage (70-80 years post-fire; Taylor et al., 1987) when coarse woody debris once again becomes available. This may partly explain why sphagna are rarely found in relatively young (i.e. less than 60 years post fire) black spruce stands (Foster, 1985; Taylor et al., 1987; Boudreault et al., 2002). A similar mechanism is reported in the late post-fire establishment of eastern white cedar (*Thuja occidentalis*; Simard et al., 2003). These hypotheses need to be tested experimentally.

Feather mosses were rarely an establishment substrate for *S. capillifolium*. This may have been due to the poikilohydric nature of these species, as they would not provide constant humidity for germinating spores. Similarly, Sundberg (2000) found that *Sphagnum* spores were generally unable to germinate within established colonies.

6.5.2 Colony expansion

The expansion of *S. capillifolium* colonies at deeper points over CWD supports the hypothesis that CWD provides a competition free habitat for the initial small colony.

However, *S. capillifolium* is ultimately able to expand over the feather mosses potentially in part due to the elevated position of the *Sphagnum*, which would allow them to smother the feather mosses. The lower growth rates of feather mosses (Williams and Flanagan, 1998; Bisbee et al., 2001) may explain why they were rarely found to have overtopped *S. capillifolium*. The cases where the feather mosses were able to overtop the *Sphagnum* may represent habitats that were too dark even for the shade tolerant *S. capillifolium* (Hayward and Clymo, 1984; Gignac, 1992).

Overall, *Sphagnum* (*capillifolium, russowii, girgensohnii*) colonies were found in sites where canopy opening was at least 20%, which appears to constitute a threshold for colony establishment and subsequent expansion. This is consistent with these species' shade tolerance and the broad range of light conditions under which *Sphagnum* was found to grow (20 to 80% canopy opening) suggests that above this threshold, light is not a limiting factor.

Empirical observations (Foster, 1985; Taylor et al., 1987; Boudreault et al., 2002) have generally shown a positive relationship between canopy openness and *Sphagnum* spp. cover. The relative photosynthetic capacities of *Sphagnum* spp. and *Pleurozium schreberi* (Williams and Flanagan, 1998) suggest that *Sphagnum* spp. are able to increase their photosynthetic rates at higher incident light levels, while *P. schreberi* reaches its maximum photosynthetic rate at low light levels. However, in our study *Sphagnum* spp. colonies did not show a positive growth response to increased light availability through a more open canopy. Despite the fact that our data did not reflect this, most very large colonies were found in canopy gaps. The lack of relationship in our data may be due to an under-representation of the larger colonies, or the influence of the shape of canopy opening, rather than total canopy openness, in influencing growth. However, there was a negative correlation between patch surface area and quadrat basal area. This effect could be due to either increased light availability, or increased moisture due to more rain throughfall, both of which would favour *Sphagnum* spp. growth.

6.5.3 Colony density

There was no significant relationship between *Sphagnum* spp. patch density and patch surface area, possibly due to the low number of large colonies. However, smaller (<4m^2) colonies had high density, while larger (>4m^2) colonies had low density, suggesting density decreases with increasing colony surface area. High density in small colonies may be an adaptation to tolerate adverse growth conditions such as low humidity or competitive pressure from surrounding species (Rydin, 1985, 1995). High density colonies have branches and capitula packed tighter together, which would maximise water retention within the colony, and reduce colony roughness (Hayward and Clymo, 1984). Similarly, a more tightly packed *Sphagnum* spp. colony may better resist invasion by surrounding species (Rydin, 1995). Larger colonies may have lower densities either because they are able to grow faster, because they are growing over more favourable substrates, under more favourable light or moisture conditions, or because they have grown large enough that competition is no longer a threat to colony survival. Lower densities would be an advantage for a colony as it would result in more stem and leaf area exposed to incoming radiation, and therefore a larger photosynthetically active surface.

Sphagnum colony density and canopy opening were highly negatively correlated suggesting that colonies were able to expand faster when more light is available. *Sphagnum* density was also positively correlated with tree basal area, which would suggest that the larger, less dense colonies would be in environments where the tree basal area would be lower, allowing more light and precipitation to reach the forest floor.

6.5.4 Conclusion

In previous studies we have shown that the factor limiting the presence of *S. capillifolium* in black spruce stands on the Clay Belt of Québec and Ontario, is not habitat limitation of adult plants (Fenton and Bergeron in review), and is not predominantly due to spore availability (Fenton and Bergeron, 2006b). The importance of coarse woody debris as an establishment substrate as demonstrated by this study, suggests that the regeneration niche (Grubb, 1977) as well as stochastic establishment factors may be the driving forces. Several other bryophyte communities in coniferous forests, such as the feather moss patterns, have been shown to be at least partially controlled by the regeneration niche and stochastic establishment factors (Lloret, 1994; Frego and Carelton, 1995a, b; Frego, 1996). Subsequent to establishment, the apparent control of colony expansion by environmental factors suggests that once *Sphagnum* are established in the community, successional changes in the forest environment switch the control of the community pattern from establishment to habitat and competitive factors. This supports the hypothesis of Rydin (1997) that early successional communities are dominated by stochastic and establishment factors as lower community richness reduces the chance of inter-specific interactions, while richer, late successional communities are controlled by habitat and competitive interactions due to the greater chance of inter-specific interactions.

6.6 ACKNOWLEDGEMENTS

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CHAPITRE VII

SPHAGNUM COMMUNITY CHANGE AFTER PARTIAL HARVEST IN BLACK SPRUCE BOREAL FOREST

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7.1 ABSTRACT

In eastern Canada, boreal forests develop structural diversity in association with time since stand replacing fire. In some regions, this is associated with significant changes in the bryophyte community (*Sphagnum* moss invasion) and paludification (thick waterlogged forest floor development). The bryophyte community responds to opening of the canopy, and increasing moisture by replacement of slow growing species by faster growing *Sphagnum* spp. (e.g. *magellanicum*, *fallax*) that are dependent on constant hydration. Within a forest management context, partial harvest systems have been proposed as a strategy to maintain structural diversity, which is currently not accomplished with low retention systems. However it is unknown whether these interventions will effectively accelerate community succession. The questions addressed in this study were (1) is the composition of *Sphagnum* colonies in partially cut stands more similar to old-growth communities than in control stands, and low retention cut stands, (2) what aspects of harvest disturbance drive these changes, and (3) is the growth rate of *Sphagnum capillifolium* (an early successional shade tolerant species) different in partial vs. low retention harvest systems? After harvest, *Sphagnum* patch size was reduced by -19.8% and -11.7% after low retention and partial harvest respectively. While trends were not constant across three separate partial cut trials, the proportion of *Sphagnum magellanicum*, *fallax* and *fuscum* increased compared to controls and low retention one to two years after harvest. Models of % *Sphagnum* cover indicated track cover, % cover of vascular plants and patch depth were positive factors, while the influence of open canopy varied among species. Despite the inclusion of individual disturbance variables, the summary variable treatment was significant in all models. Growth of *S. capillifolium* in partial cuts was intermediate to growth rates in control and low-retention cuts. Growth was positively influenced by slash cover, and contrary to the patch level negatively influenced by track cover. These results indicate that partial harvest does represent an intermediate level of disturbance, as direct and indirect harvest effects were reduced, as was *Sphagnum* death. Change in composition one and two years after harvest indicates that partial harvests may effectively shift the bryophyte community towards an older community type and may be used preserve to landscape diversity. Long term trends and entire community compositions need to be assessed before this can be stated definitively. However, as paludified stands are less productive, the capacity of these partially harvested sites to produce merchantable timber is questioned.

Dans l’est du Canada, les forêts boréales développent une diversité de structures avec le passage du temps depuis le dernier feu. Dans quelques régions, cette diversité structurale est associée avec des changements significatifs dans la communauté de bryophytes (l’invasion des sphaignes) et l’entourbement, soit le développement d’une couche épaisse de matière organique saturée d’eau. Avec l’ouverture de la couronne et l’augmentation du taux d’humidité de la forêt, la communauté de bryophyte change, les espèces à faible croissance y étant remplacées par des espèces à croissance rapide (e.g. *Sphagnum magellanicum, fallax*) qui sont dépendantes d’un taux d’humidité constant. Dans un contexte d’aménagement écosystèmique des forêts, les coupes partielles ont été proposées comme technique pour maintenir la diversité structurale des forêts, ce qui n’est pas accompli avec l’utilisation courante des coupes totales. Par contre, l’impact de ce type d’intervention sur la succession dans la communauté des bryophytes est inconnu. Les questions abordées dans cette étude sont (1) est-ce que la composition des colonies de sphaignes dans les coupes partielles est

plus similaire à la composition des vieilles forêts que celles des témoins et des coupes totales, (2) quelles caractéristiques de la récolte dirigent ces changements et (3) est-ce que le taux de croissance de *Sphagnum capillifolium* (une espèce de début de succession tolérante à l'ombre et à la dessiccation) est différent dans les coupes partielles comparé aux coupes totales ? La taille moyenne des colonies des sphaignes est réduite de -19,8% et -11,7% par les coupes partielles et totales respectivement. Bien que les tendances ne soient pas constantes dans tous les sites d'échantillonnages, les proportions de *Sphagnum magellanicum*, *fallax*, et *fuscum* augmentent dans les coupes partielles comparées aux coupes totales et les témoins. Des modèles de pourcentage de recouvrement des sphaignes indiquent que le recouvrement des chemins, le recouvrement des plantes vasculaires et la profondeur des colonies sont des facteurs positifs, et que l'influence de la canopée varie entre les espèces. Malgré l'inclusion des variables décrivant la perturbation, la variable sommaire traitement est significative dans tous les modèles. Le taux de croissance de *S. capillifolium* dans les coupes partielles est intérmédiaire au taux dans les coupes totales ou les témoins. Le recouvrement de slash est un facteur positif sur la croissance tant que le recouvrement des sentiers est un facteur négatif. Ces résultats indiquent que les coupes partielles représentent une perturbation intermédiaire étant donné que les effets directs et indirects de la récolte ainsi que la mort des sphaignes sont réduits comparé aux coupes totales. Les changements dans la composition de la communauté un et deux ans après la récolte indiquent que les coupes partielles peuvent forcer la communauté des bryophytes vers une composition typique des vieilles forêts. Des résultats à long terme sont nécessaires avant que cela puisse être constaté définitivement. Cependant, étant donné que les forêts entourbées sont moins productives, la capacité des coupes partielles à produire des volumes de bois significatifs est remisse en question.

7.2 INTRODUCTION

Black spruce (*Picea mariana*) forests develop structural diversity in association with time since stand replacing fire (Lecomte et al. in press; Lussier et al., 2002) and in the eastern boreal forest, where fire cycles are longer (Bergeron et al., 2001; Foster, 1985) these forests can dominate the landscape. With death of the initial post-fire tree cohort, the canopy opens, and new individuals are regenerated by layering (asexual reproduction of black spruce; Groot, 2002) and seed. In some regions, including the Clay Belt of Québec and Ontario, this is associated with significant changes in the bryophyte community (i.e. *Sphagnum* moss invasion) and paludification (thick waterlogged forest floor development; Fenton et al., 2005; Foster, 1985). This multi-layer, paludified forest structure represents a diverse habitat that supports rich bird (Drapeau et al., 2003), and bryophyte communities (Harper et al., 2003). Within the bryophyte community the gradient in canopy openness and paludification associated with time since fire results in a replacement series of sphagna, with *S. capillifolium* that dominates in young forests gradually being replaced by *S. magellanicum, S. fallax* and eventually *S. fuscum* (Fenton and Bergeron 2006). These changes are a result of the increase in light and moisture availability at the forest floor both of which are limiting growth factors (Gignac, 1992; Vitt, 1990) for the late successional *Sphagnum*, which are typically found in open bogs.

The complex structure of older forests is not maintained by low retention systems, which regenerate even-age stands, and are harvested before they reach this stage (Bergeron et al., 1999). Total cut and low retention systems alter existing vegetation via substrate damage and slash deposition (direct disturbance) and microclimatic change due to canopy removal (indirect disturbance; Nelson and Halpern, 2005; Fenton et al., 2003). While they partially mimic stand replacing disturbance, such as fire, they do not always result in a community similar to early successional communities (McRae et al., 2001).

Partial harvest systems have been proposed (e.g. Halpern et al. 2005; Bergeron et al., 1999) as a complementary strategy to low retention harvest that maintain some tree cover and have a less severe impact on the existing vegetation. Furthermore, they encourage the rapid development of old-growth features such as structural diversity, and a more open canopy (Carey, 2003; Deal, 2001; Deans et al., 2003). In the specific case of black spruce forests on the Clay Belt, partial cuts have the possibility of recreating habitat associated with old forests by opening up the canopy (via stem removal) and raising the water table (via reduced precipitation interception and evapotranspiration; Roy et al., 2000). However, the efficacy of these modified sylvicultural treatments in creating habitat conditions similar to older forests is unknown, as is the extent and rate at which the biological communities respond to these "new" old forest conditions.

This study takes part of a larger partial harvest trial where the effects of low retention and partial harvest on a variety of forest community components are compared. The long-term goal is to determine whether the partial cut techniques applied (variable retention and diameter limit harvest) successfully recreate the habitat of old forests, and whether this habitat is used by a variety of forest species (e.g. birds, insects, lichens and bryophytes). As such it differs from most studies that examine the effect of forest harvest as compared to the pre-harvest condition (e.g. Fenton et al., 2003; Frisvoll and Prestø, 1997), rather than in comparison to a desired habitat type (cf. Halpern et al., 2005; Carey, 2003).

Specifically this article examines the efficacy of partial (63-68% harvest of commercial stems) compared to low retention (100% harvest commercial stems) harvest by using the bryophyte community as an early indicator of compositional change towards an old growth state. In addition to community composition, growth of *S. capillifolium* was measured. While compositional changes may be less evident soon after harvest, effects on the growth of individuals are immediately measurable. *S. capillifolium* was chosen, as it was common in all sites and treatments.

Overall, this study addresses three main questions: (1) do partial harvests result in less damage and death to *Sphagnum* colonies than low retention harvest; (2) do partial harvests push community composition toward an older community composition compared to low retention harvest and which, if any, aspects of disturbance are these changes related to; (3) is the growth rate of *Sphagnum capillifolium* (an early successional shade tolerant species) different in partial versus low retention harvest systems, and to what aspects of the disturbance altered habitat is growth rate related?

7.3 STUDY AREA

The Clay Belt of Ontario and Quebec is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent and Hardy, 1977). In its northern portion, it is dominated by black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin, 1996), and is particularly prone to paludification between fires due to its poorly drained clay dominated soil, low topographic relief, and moderately humid and cold climate [889.9 mm of precipitation annually; annual mean temperature 0.7^0C (Environment Canada, 2004)]. The dominant disturbance types are large fires that kill all above ground vegetation. Between 1850 and 1920 the fire cycle was ca 135 years, and it has since increased to ca 398 years (Bergeron et al., 2004), as a result the average age of the forests is in excess of 100 years. It lies just south of the Hudson Bay-James Bay Lowlands, the second largest peatland complex on the globe.

7.4 METHODS

7.4.1 Sampling

This study takes part of a larger project to compare the effects of partial harvest and low retention-cut systems on ecosystem function, diversity and merchantable timber. Each site in the network consists of 1 block (each >50 ha) of each of three treatments: low retention-cut (cut with protection of regeneration and soils), partial harvest with variable retention, and control. Three sites were chosen for this study that were comparable in terms of clay dominated soil texture and light slope from the network of 12 sites. All three sites were dominated by black spruce approximately 120 years after stand replacing fire. Within this matrix, patches of different forest types were found, due to the large size of the sites (>150 ha each). The understory was dominated by bryophytes, with *Pleurozium schreberi, Dicranum polysetum, Hylocomium splendens, Ptilium crista-castrensis, Sphagnum capillifolium, S. girgensohnii, S. russowii, S. fallax* and *S. fuscun. S. wulfianum* was occasionally found. Lichens *Cladina rangifera* and *C. stellaris* were also common. The herb layer was dominated by *Vaccinium* spp., *Trientalis borealis, Cornus canadensis, Gaultheria* *hispidula, Rhododendron groenlandicum,* and saplings of black spruce and balsam fir. Two of these sites, Fénelon and Puiseaux were harvested in the winter of 2003-2004, while the third, Gaudet, was harvested in the winter of 2002. The level of extraction varied among the three sites, from 63 to 69% of the stems in the partial harvest. A range of stem sizes were retained. All low retention harvest removed all commercial stems (>9.9 cm DBH).

In the summer of 2004, three 20x20 m (400 m^2) plots were established per treatment in each site (i.e. a total of 9 plots per site, and 27 in total). An effort was made to capture the variability in forest structure within the 50ha blocks of each treatment type, by widely spacing the three plots (generally >100m), which were all located >50m from an edge. Each 20x20m plot was surveyed for *Sphagnum* spp. patches, and at each patch that was found, the following measures were taken to describe the patch: species composition (% cover of patch); size of patch (in m^2 calculated as the area occupied by a contiguous colony of *Sphagnum* spp.); depth of patch (in cm). Depth was measured in the center of each patch. In particularly large patches more than one measurement was taken, and they were averaged. The following direct or indirect disturbance variables were also measured at each patch : % of patch buried under slash; % crushed by machinery trails; and canopy openness (measured with a densiometer, a concave scored mirror). The % cover of vascular species (including tree saplings) growing within the patch was also measured as Malmer et al. (2003) indicated that they can accelerate *Sphagnum* growth by serving as a ladder or scaffolding. Every other patch that crossed the plot line was included. The area (m^2) by species per patch was calculated by multiplying the % cover of an individual species in a specific patch and the area of the entire patch. *Sphagnum* spp. species were determined in the field, except for difficult specimens, which were sampled and determined in the laboratory. Sphagna taxonomy follows Anderson (1990). *Sphagnum fallax* is treated in the large sense to include the different species of the *recurvum* complex.

Growth of *Sphagnum capillifolium* was measured in all three sites in the three treatment types. *S capillifolium* was chosen for this study as it was consistently found in all sites, and is easily identifiable in the field. In a total of 5 patches per treatment per site, three cranked wires were installed in August 2004. Cranked wires are a widely used technique to measure *Sphagnum* growth (Clymo, 1970). The distance from the patch surface to the end of the wire is measured when they are installed, and again after a growth period, in this case 13 months. The difference in the length is the height of new biomass produced during the growth period. A cross bar is used to limit wire movement within the colony. *Sphagnum* growth was measured in September 2005.

7.4.2 Analyses

The relative abundances of *S. capillifolium, S. magellanicum, S. fallax* and *S. fuscum* within patches were compared, as they differ in their microhabitat requirements (Table 7.1), from shade and desiccation tolerant to shade and desiccation intolerant, and shade intolerant and desiccation resistant (Mulligan and Gignac, 2001; Gignac, 1992). Comparisons in variable values were made among treatments within a site, as differences in sites 50-100km apart may have masked treatment differences. Differences in total *Sphagnum* cover, mean *Sphagnum* patch size, % of patch killed, depth of patch, mean % cover of species in a patch and mean cover of species in a patch, and in disturbance variables were tested with the non-parametric Kruskal-Wallis Test (SPSS v.10), as the data was not normally distributed, and could not be normalised with a transformation.

Table 7.1 Description of habitat tolerances of the species examined in detail in this study. Shade tolerance is inferred from the frequency at which the species was found in shaded and un-shaded habitats. Position relative to water table indicates is the habitat relative to the water table where the species are typically found. From Gignac, 1992; Mulligan and Gignac, 2001; Moore, 1989; Johnson and Dammam, 1991; Fenton unpubl. data.

Species	Shade	Position relative to water table	Growth form	Growth rate	Decomposition rate
S. capillifolium	Tolerant	High above	Hummock	Low	High
S. magellanicum	Intolerant	Low above	Low hummock-lawn	High	Moderate
S. fallax	Intolerant	Low above	Lawn	High	Moderate
S. fuscum	Intolerant	High above	High hummock	Low	Low

Path analysis was used to determine the potential structure (including direction) of the relationships among the % cover of *Sphagnum* (total and relative cover of *S. capillifolium, S. fallax* and *S. fuscum*) and potential explanatory variables (ln track cover, ln log slash cover, open canopy, ladder species cover, ln patch depth, treatment and site). Path analysis (and partial correlation) were used instead of multiple regression as many of the explanatory variables were correlated. The variables included in each path analysis were selected from the list of potential variables based on strong partial correlations, indicating that they were still significant when the other variables were held constant. All sites were analysed together as this method is better equipped to deal with site as a covariable. A d-sep test (Shipley, 2000) was used to determine the likelihood that an a-priori structure was correct. Partial correlation coefficients (or path coefficients) among the variables allowed the determination of the magnitude of direct and indirect effects. The percent of variation of the response variable explained by the selected explanatory variables was calculated using multiple regression (SPSS v.10).

Differences in growth (cm) were examined by general linear model (GLM) in SPSS v. 10, with natural log transformed (ln) growth, for normality. The interaction term between site and treatment was not significant. Regression was used to look at the effect of different habitat variables on growth, with ln live *Sphagnum* area, ln track cover, ln slash cover, and two dummy site and treatment variables respectively. The critical value of p was 0.05 in all tests.

7.5 RESULTS

7.5.1 Disturbance effect

Patch size varied greatly in all sites and treatments, but in the sites Gaudet and Fénelon total *Sphagnum* area, patch size and live patch size decreased from control, to partial cut, and to low retention (Table 7.2). While there was no significant difference, on average more *Sphagnum* was killed in low retention cuts than in partial cuts in Puiseaux and Gaudet, except in Fénelon where there was no difference between partial and low retention cuts and this may have been due to the smaller patch size at this site. In terms of the habitat (Table

7.3), the canopy was more open and in Puiseaux and Gaudet more slash was deposited on the *Sphagnum* patches in low retention cuts compared to partial cuts and controls.

Table 7.2 Total *Sphagnum* (*Spha.)* area and mean *Sphagnum* patch characteristics by site and treatment. The number in brackets indicates the number of patches found in each treatment per site. L.R. equals low retention. Values are means followed by standard error. Italics indicate significant differences within a site. The letters indicate statistical difference, a<b.

	Fénelon			Puiseaux			Gaudet		
Variable	Control (12)	Partial-cut (24)	L. R. cut (18)	Control (37)	Partial-cut (24)	L. R. cut (34)	Control (17)	Partial-cut (51)	L. R. cut (38)
Total *Spha.* area (m^2)	209.57 (115.81)	161.65 (71.39)	79.56 (47.97)	205.27 (20.82)	289.89 (31.56)	182.03 (21.80)	337.15 (54.82)	223.00 (50.26)	151.25 (17.44)
Patch size (m^2)	48.36 (30.10)	21.61 (9.62)	13.52 (6.39)	*16.64 (5.54) a*	*39.28 (7.85) b*	*20.31 (4.25) ab*	*59.50 (25.52) b*	*15.80 (2.71) a*	*14.08 (2.78) a*
Live patch size (m^2)	48.36 (30.10)	19.40 (8.37)	13.26 (6.41)	*16.64 (5.54) a*	*36.24 (6.99) b*	*15.60 (3.06) a*	*59.50 (25.52) b*	*13.12 (2.34) a*	*11.94 (2.49) a*
% *Spha.* patch killed	0.00	7.00 (4.26)	10.28 (5.92)	*0.00 a*	*3.75 (2.32) ab*	*24.86 (4.77) b*	*0.00 a*	*10.78 (3.48)ab*	*16.05 (3.75) b*
Mean depth of patch (cm)	38.79 (3.10)	31.74 (2.37)	31.26 (3.37)	48.53 (1.84)	46.26 (2.04)	47.22 (2.11)	*57.53 (2.51) b*	*46.72 (2.61) a*	*52.54 (2.08) ab*

Table 7.3 Patch size and habitat variables by site and treatment. L.R. equals low retention. Values are means of all patches per treatment per site followed by standard error. Italics indicate significant differences within a site. The letters indicate statistical difference, a<b.

	Fénelon			Puiseaux			Gaudet		
Variable	Control	Partial-cut	L.R. cut	Control	Partial-cut	L.R. cut	Control	Partial-cut	L.R. cut
% of patch on track	0.00	13.20 (5.99)	22.78 (8.82)	*0.00 a*	*23.75 (7.16) b*	*20.57 (5.98) b*	*0.00 a*	*28.33 (5.63) b*	*16.62 (5.31) a*
% of patch under slash	0.00	6.60 (3.90)	1.39 (1.39)	*0.00 a*	*2.92 (2.21)a*	*17.88 (4.46) b*	*0.00 a*	*0.20 (0.20) a*	*15.81 (3.83) b*
% open canopy above patch	*64.87 (2.39) a*	*90.10 (2.47) b*	*90.47 (3.58) b*	*66.37 (2.53) a*	*82.67 (3.07) b*	*97.49 (0.66) c*	*51.60 (4.90) a*	*84.46 (2.21) b*	*96.66 (1.56) c*
% ericaceous cover in patch	54.62 (8.59)	32.29 (5.52)	34.44 (7.55)	*50.27 (3.54) b*	*43.75 (5.91) ab*	*33.28 (5.62) a*	45.88 (5.53)	47.55 (4.59)	49.14 (3.96)

7.5.2 Species composition

The composition of the patches varied among sites and treatments (Figure 7.1). The relative abundance (percent cover) of *S. capillifolium, S. russowii, S. magellanicum, S. fallax,* and *S. fuscum* in each patch was examined. *S. capillifolium* dominated all sites and patches, but was significantly lower in the partial cuts in all sites. *S. russowii* and *S. magellanicum* had varied responses, while *S. fallax* and *S. fuscum* had a greater relative cover in partial cuts than in low retention cuts and controls in all three sites. When the actual area covered (in m^2) is examined, the decrease in *Sphagnum* cover in the partial cut and low retention cuts is apparent (Figure 7.2), as the cover of almost all species is lower in these treatments, if not statistically significant. The exception is Puiseaux, where the cover of all species was greater in partial cut compared to control and low retention cut treatments.

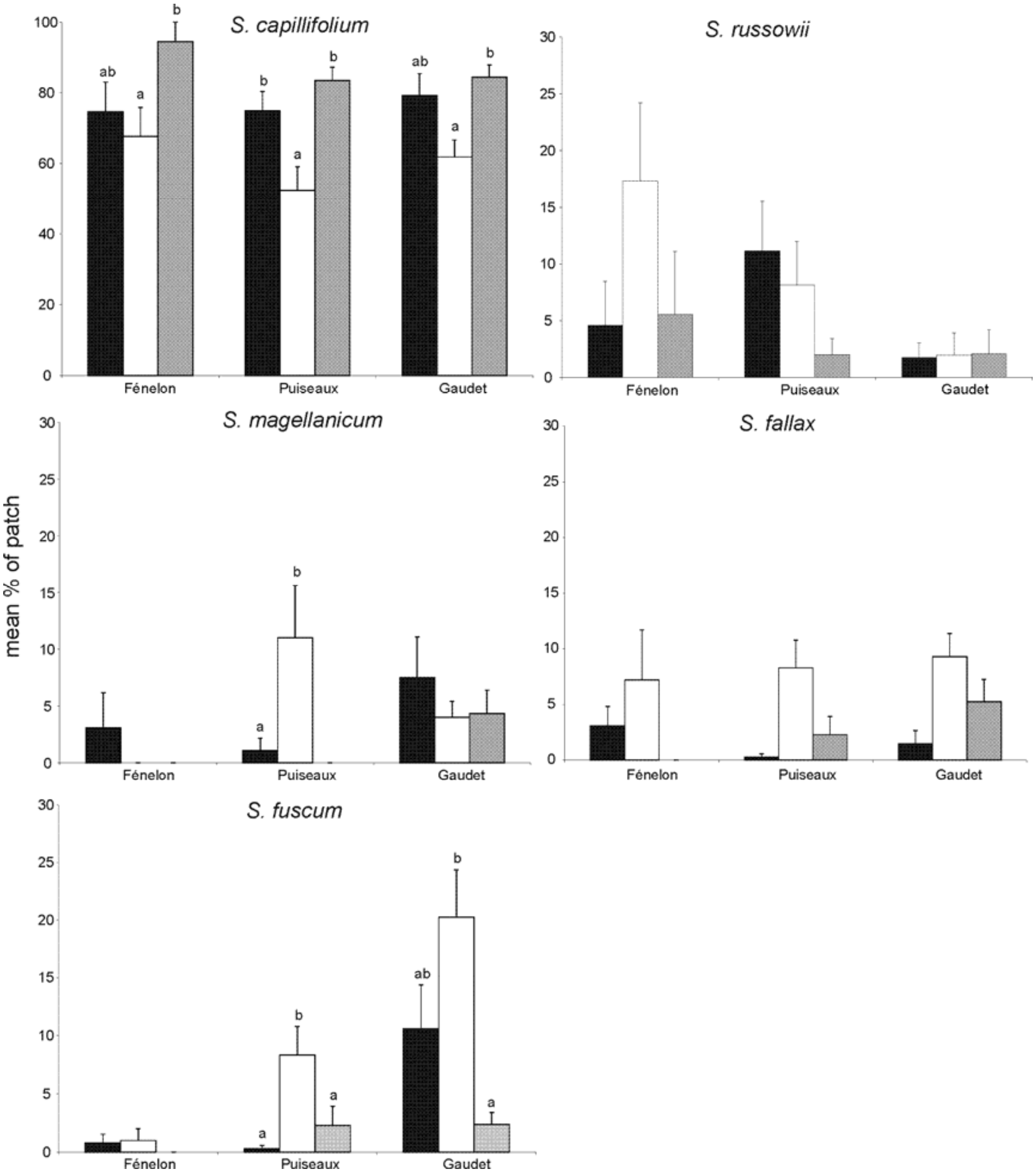

Figure 7.1 Percent of cover of species in each patch per site and treatment type. Values are means + standard error. Bars within a site with a different letter are significantly different. Black, control; white, partial harvest; grey, low retention cut.

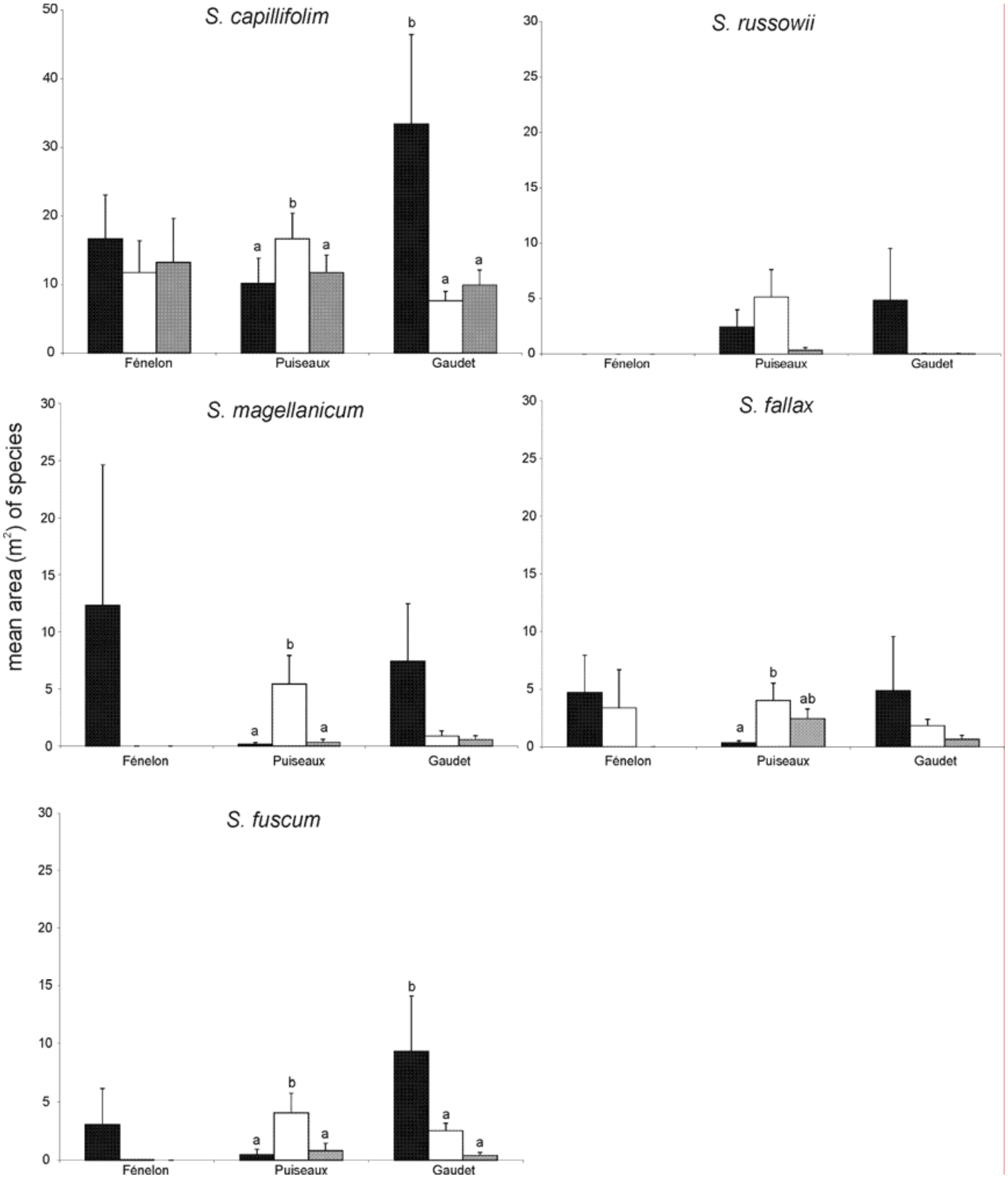

Figure 7.2 Area (m^2) of species per site and treatment type. Values are means + standard error. Bars within a site with a different letter are significantly different. Black, control; white, partial harvest; grey, low retention cut.

7.5.3 Relationship between *Sphagnum* cover, composition, disturbance, and habitat variables

The models between *Sphagnum* cover and the explanatory variable were only significant for total *Sphagnum* cover, *S. capillifolium, S. fallax* and *S. fuscum.* The relationship between *Sphagnum* cover, % cover of individual species and disturbance and habitat variables was relatively consistent (Table 7.4). The measured direct (only track cover, slash was not significant) and indirect effects (open canopy) of the harvest treatments were both significant in the majority of the models. Track cover tended to be connected with larger patches and higher cover of *S. capillifolium, S. fallax* and *S. fuscum*, while open canopy was positively correlated with *S. fallax* and negatively correlated with *S. capillifolium* and *S. fuscum*. In addition to the measured effects of harvest, the summary variable "treatment" was significantly partially correlated with the response variable in all the models, although the indirect effects were generally larger than the direct effects. Depth of patch was always correlated with bigger patches and higher percent cover of all the species, and % cover of ladder species had the largest direct effect in the *Sphagnum* area and *S. capillifolium* models. Site was the largest direct effect in the *S. fuscum* model.

7.5.3 Patch growth measurements

Overall, growth differed by site and treatment, with no interaction between the two terms. Growth was greatest in Fénelon and lowest in Puiseaux, with Gaudet intermediate, although there was no significant difference between Puiseaux and Gaudet (Figure 7.3). In terms of treatment, plants in control plots grew significantly more than those in the partial and low retention cuts, and while the difference was not significant, plants in partial cut plots grew at rates intermediate to control and low retention cut plots.

Multiple regression indicated that growth was influenced by cover of slash (0.243 β coefficient), and machinery tracks on the patch (-0.221 β coefficient), and treatment type (control 0.501 β coefficient, partial cut 0.250 β coefficient; $p<0.001$; R^2 0.272).

Table 7.4 Direct (due only to the factor) and indirect (due to interactions with other factors) coefficients (which indicate effect), error and total correlation for factors as determined by path analysis for Ln total *Sphagnum* area, % *S capillifolium*, % *S fallax*, and % *S fuscum.* All included factors are significant. The likelihood that the structure was correct is indicated by a *p* value for each model, and the % of the variability explained (as determined by multiple regression) by R^2.

Variable	Direct	Indirect	Error	Total
Ln total *Sphagnum* area *p 0.827* R^2 *0.340*				
Ln track cover	0.255	-0.0160	0.132	0.107
Ladder cover	0.488	0.0325	0.0605	0.541
Ln depth	0.204	0.0497	0.0923	0.346
Treatment	-0.077	0.163	0.0141	0.072
% Ln *S capillifolium p 0.998* R^2 *0.359*				
Ln track cover	0.171	-0.0504	0.0466	0.074
Open canopy	-0.100	-.0770	0.0120	-0.035
Ladder cover	0.442	0.0889	0	0.529
Ln depth	0.255	0.171	0.0353	0.391
Treatment	0.044	-0.0685	0.0105	-0.035
Site	0	0.180	0.0918	0.088
% Ln *S fallax p 0.779* R^2 *0.023*				
Ln track cover	0.015	0.0467	0.0327	0.029
Open canopy	0	0.055	0.0479	0.103
Ln depth	0.097	0.0295	0.00853	0.118
Treatment	0.063	0.00308	0.002	0.064
Site	0.064	0.0488	0.00681	0.106
% Ln *S fuscum p 0.996* R^2 *0.203*				
Ln track cover	0.097	-0.0865	0.0065	0.017
Open canopy	-0.155	0.00095	0.007	-0.163
Ladder cover	0.137	0.0885	0.0115	0.214
Ln depth	0.127	0.166	0.0359	0.257
Treatment	-0.034	-0.0587	0.0363	-0.129
Site	0.198	0.0757	0	0.273

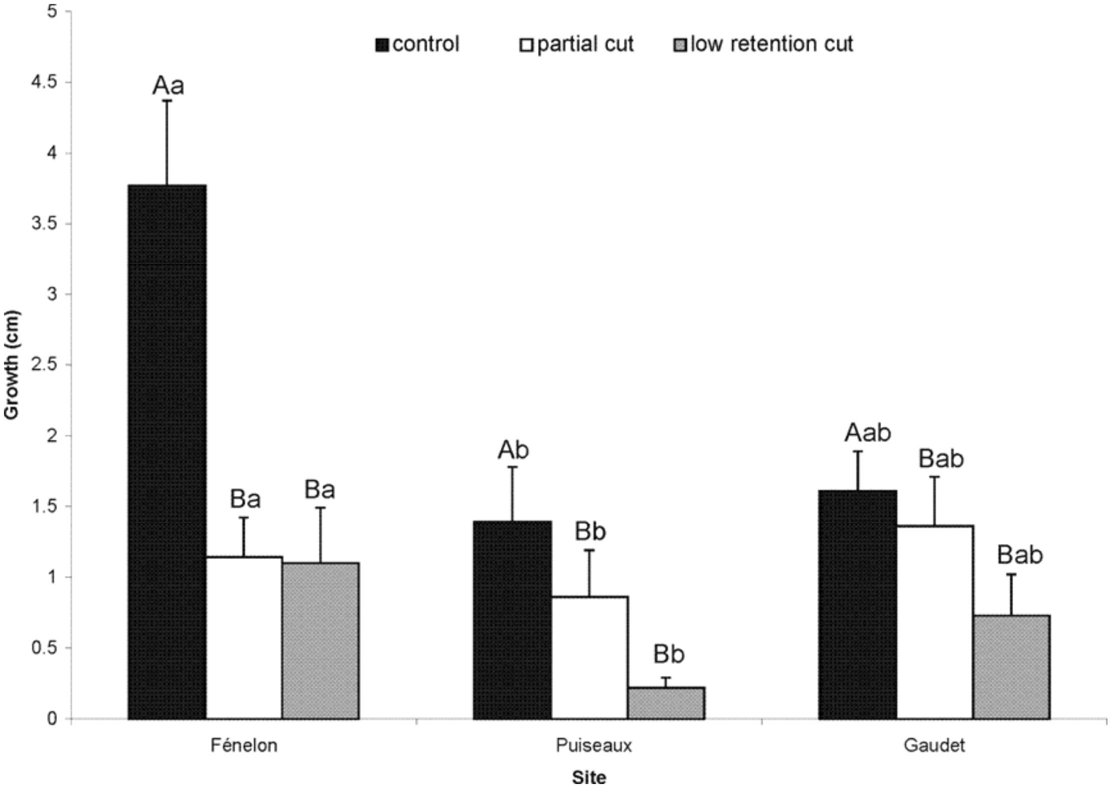

Figure 7.3 Growth (cm) of *Sphagnum capillifolium* among sites and treatments. Black, control; white, partial harvest; grey, low retention cut. Letters indicated differences in growth; capital letters indicated differences among treatments, and lower case letters indicated differences among sites.

7.6. DISCUSSION

7.6.1 Disturbance effect

As has been indicated in previous studies (Halpern et al., 2005; Carey, 2003; Deal, 2001), partial and low retention harvests created a gradient of disturbance severity, as perceived by the bryophyte community. Both direct substrate disturbance (cover of machinery track, slash deposition) and indirect disturbance via microclimatic change caused by canopy removal were lower in the partial cut compared to the low retention harvests for at least two of three sites for each variable. As a consequence, there was more *Sphagnum* death in the low retention cut than the partial cut harvests.

7.6.2 Patch composition and disturbance and habitat variables

Despite the fact that only one to two years had passed since harvest, in all sites the community had changed in response to treatment. Compared to the control the partial cut harvests had a community composition (relative abundance of species; Figure 7.1) that was closer to that which is found in older forests (Fenton and Bergeron 2006), i.e. reduced cover of *Sphagnum capillifolium* and increased cover of *S. fallax* and *S. fuscum*. Similar results for the vascular plant, fungi, and bird communities were found less than five years after variable retention thinning in the Pacific Northwest (Carey, 2003). The low retention harvests had a community that more closely resembled a community in a younger forest, as did the control. However, when actual surface area is examined, both the partial cut and low retention harvests had smaller surface areas of the late successional species, as defined in introduction and Table 7.1 (Figure 7.2), and the process is not yet advanced. Initial changes in relative cover suggest that partial cuts may in fact be efficient in pushing sites to an older community, however longer term studies should be completed to document that the actual rate of expansion is faster than what would have occurred naturally.

While the changes in relative abundance of the species appeared to match normal habitat requirements, correlations between species abundance and the disturbance altered habitat variables were less clear. Surprisingly direct disturbance (machinery track cover) had a positive influence on *Sphagnum* cover overall, and in *S. capillifolium* and *S. fuscum*. *S. capillifolium* and *S. fuscum*, which are both high hummock species that form tight colonies and are therefore able to tolerate dry conditions (Schipperges and Rydin, 1998; Hayward and Clymo, 1983), may have been able to develop new colonies, or expand existing colonies, onto the newly available dry surfaces of the machinery tracks.

Open canopy had a negative influence on the relative abundance of *S. capillifolium*, as would be expected of the shade tolerant species (Gignac, 1992), but the negative impact of open canopy on the late successional *S. fuscum,* which typically grows in well illuminated high hummocks in bogs (Gignac, 1992), is surprising. It may be due to the physiological shock of the colony being suddenly exposed to new conditions, and if so it may be only temporary, as the individuals develop new growth beneath the colony surface (e.g. Coates and Duckett 1986).

In addition to the measured effects of harvest (machinery track, slash deposition, and canopy opening), the variable “treatment” was also significant in all of the models. The fact that the summary variable treatment was significant, despite the fact that individual factors were taken into account suggests that there are aspects of the treatment effect that were not captured in these individual variables.

In addition to the factors associated with harvest, patch depth, cover of vascular plant ladder species and site were significant factors. While it is generally accepted that *Sphagnum* patches spread clonally by vertical and horizontal growth (Hayward and Clymo, 1983) the fact that depth positively influenced not only total *Sphagnum* area but also the relative cover of all three species suggests that their capacity to occupy space is augmented by the depth of the patch. This is potentially due to increased water retention volume, which would limit evaporation stress. Furthermore, the substantial indirect effect of patch depth (particularly via the cover of ladder species, not shown) results in depth being a dominant factor.

The cover of vascular plant species that may act as ladders for *Sphagnum* was the most important factor in the *Sphagnum* area, and the area of *S. capillifolium*. These vascular plants may be influencing the patches via both shading of the patch, and physical support of *Sphagnum* individuals. Light shading of bryophytes by slash in low retention cuts has been shown to be beneficial in a variety of forest habitats as it attenuates the increase in solar radiation (Fenton et al., 2003; Olsson and Staaf, 1995), and vascular plants growing in bogs are generally believed to not offer competition for light to *Sphagnum* under 60% cover (Heijmans et al., 2002). Therefore the vascular plants growing in the *Sphagnum* patches may be allowing individuals to tolerate the sudden change in light intensity, and indeed individuals shaded by ericaceous shrubs had a denser green pigmentation (Fenton pers. obs.). In addition to the shading effect, the vascular plants may be providing a physical support that allows the *Sphagnum* to grow at a faster rate. As cushion sphagna generally grow vertically, but lack any type of internal support mechanism, they depend on colony density to remain upright (Hayward and Clymo, 1983). With the presence of ladder species, they may be able to grow vertically at a lower density, limiting the need for energy expensive asexual budding to increase patch density.

7.6.3 Patch growth

The growth rate of *Sphagnum capillifolium* varied widely among sites and treatments from an average of over 3.7 cm (from August 2004 to September 2005) in the control of Fénelon to less than 0.5 cm in the clear cut at Puiseaux. This rate is similar to what has been documented for *S. capillifolium* in other studies that vary from 1.6 cm per year to 5.0 cm per year (Asada et al., 2003; Gunnarsson et al., 2002). While Roy et al. (2000) found no variation in *Sphagnum* growth rate among low retention cut and control plots (potentially due to confounding of species), the growth rates of the individuals in the partial cuts were intermediate to those of the control and low retention cuts, but varied among sites from nearly identical to the low retention cut at Fénelon to nearing the rate of control at Gaudet. As Gaudet is the site where two years have passed since treatment, this may suggest that the plants in the partial cut recover faster than those in the low retention cut. However, due to the lack of replicates at the site level, these observations will have to be confirmed in the future.

The growth rate of *S. capillifolium,* a shade tolerant species (Gignac, 1992) responded positively to slash cover, which confirms the positive role of moderate slash levels in attenuating extreme light levels after forest harvest (Peterson, 1999; Ohlsson and Staaf, 1995). The negative partial correlation of machinery tracks suggests that at the individual level damage by tracks has a negative effect, which contrasts with the patch level relative abundance. This undoubtedly reflects the impact of individuals that were actually damaged by the machinery compared to the space created by the machinery tracks. The positive influence of both control and partial cut treatments reflects that in two of the three sites (Puiseaux and Gaudet) the growth rate of individuals in partial cuts was intermediate to the control and low retention treatments. Again as in patch relative abundance treatment was a significant variable despite the inclusion of the measured effects.

The model of *S. capillifolium* growth explains, however, only a relatively small percentage of the variation in the data set. Two additional factors that influence *Sphagnum* growth may be responsible for part of the unexplained variance: night-time temperature and nutrient deposition via throughfall and stem flow. Low night-time temperatures retard *Sphagnum* growth (Gerdol et al., 1998) and the lack of forest cover may have resulted in lower temperatures in the low retention cuts compared to partial cuts. Similarly, *Sphagnum* are dependant on aerial deposition of nutrients, and are capable of extracting >90% (Malmer et al., 2003) of available nutrients present in water falling from above. The removal of the canopy undoubtedly reduced the nutrient input to the patches, and may have lowered their growth rate.

7.6.4 Conclusions

The *Sphagnum* communities in black spruce forests on fine textured soils in the Clay Belt of Québec and Ontario are good indicators of water table position and canopy openness, as they responded to the change in conditions created by forest harvest in 1-2 years after treatment. The composition of the bryophyte community in stands that have been harvested also indicates the effect of partial and low retention cuts not only on the bryophyte community but also on the level of paludification. These results indicate that at least in the initial post-harvest stage, partially harvested stands are developing a community typical of an old paludified stand. Therefore including partial harvests in management plans on this landscape may help preserve *Sphagnum* biodiversity, however, only widespread macroscopic species were examined here, and it is not yet clear whether created habitat will succeed in recruiting potential dispersal limited smaller species. Furthermore as paludified stands have reduced productivity, it also indicates that partial harvest of these stands may not create productive forests in the immediate future (Lecomte et al., 2005).

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CONCLUSION GÉNÉRALE

Cette thèse avait comme principaux objectifs la détermination des mécanismes d'entourbement et le rôle des bryophytes dans le processus d'entourbement des forêts d'épinettes noires situées sur les dépôts fins de la ceinture d'argile du Québec et de l'Ontario. Les études entreprises pour atteindre ces objectifs, ont démontré que l'accumulation avec le temps de matériel organique sur le sol minéral est causée par le climat régional, ainsi que la présence de sphaignes et de plantes éricacées. En plus, il a été démontré que la remontée de la nappe phréatique n'est pas une cause de l'accumulation de la matière organique, mais une conséquence de cette dernière. La nappe phréatique monte dans la couche organique quand il y a à peu près 40-50 cm de matière organique accumulée. Ce changement au niveau de la nappe phréatique a des conséquences importantes pour le fonctionnement de l'écosystème et aurait plus d'influence que les changements qui surviennent dans l'épaisseur de la couche oxydée. En plus l'épaisseur de la couche oxydée n'était pas corrélée avec l'âge du peuplement, mais était légèrement plus profonde dans les peuplements de moyenne âges. Malgré des hypothèses avancées il y a plus de 50 ans (e.g. Lawrence 1958), la sphaigne n'a pas joué de rôle direct dans la remontée de la nappe phréatique, mais plutôt un rôle indirect via sa contribution à l'accumulation de la matière organique.

Les études portant sur le phénomène de l'entourbement lui-même, ont illustré l'importance de la communauté des bryophytes dans le fonctionnement de l'écosystème. Grâce à cette deuxième série d'études les changements qui surviennent dans la communauté des bryophytes associée à l'entourbement ont pu être décrits. À mesure que le temps après feu s'écoule, la communauté de bryophytes passe d'une communauté dominée par les mousses hypnacées, à une communauté dominée par des sphaignes formant des buttes (hummocks), à une communauté dominée par les sphaignes de milieux humides. Finalement, les sphaignes qui forment des buttes de haute dimension vont dominer les communautés à la fin de la succession. À l'opposé des études précédentes qui considéraient l'invasion par les sphaignes en générale comme la fin de la succession, les différentes étapes de la succession incluant plusieurs espèces de sphaignes, ont été mises en lumière et détaillées. Les changements de la lumière et de l'humidité disponibles associés à l'entourbement, ont été identifiés comme étant les facteurs qui causent les changements dans les associations de bryophytes lors de la succession. La quantité de lumière disponible pour les bryophytes augmente avec l'âge du peuplement à cause de l'ouverture du couvert forestier suite à la sénescence par pied d'arbre. Le taux d'humidité disponible augmente quant à lui avec l'accumulation de la matière organique et la remontée éventuelle de la nappe phréatique. Puisque les mousses et les sphaignes sont en partie responsables de l'accumulation de la matière organique, ces résultats suggèrent que la succession dans la communauté des bryophytes appuie le modèle de facilitation proposé par Connell et Slayter (1977).

Une expérience a pu confirmer que la transition d'une communauté dominée par les mousses hypnacées et les sphaignes associées aux buttes à une communauté dominée par les sphaignes de milieux humides est un exemple de la succession facilitatrice. Cependant, l'expérience n'a pas pu expliquer l'absence des sphaignes de buttes dans les plus jeunes peuplements, ni leur confinement spatial dans les peuplements où elles sont présentes. Les sphaignes (*S. capillifolium*) poussaient à des taux similaires peu importe qu'elles croissent dans leur habitat ou dans l'habitat des mousses hypnacées. Deux études ont été complétées pour examiner cette question. La disponibilité des spores de sphaignes a été évaluée dans un jeune et deux vieux peuplements qui représentaient non pas seulement un gradient d'âge après feu, mais aussi de recouvrement en sphaigne et de la densité du peuplement arborescent. La disponibilité des spores est plus faible dans le jeune peuplement comparée aux vieux peuplements, mais il y avait quand même des spores présentes. De plus, en absence de production locale la pluie de spores régionale était abondante. Ces résultats suggèrent qu'un manque de spores n'est pas la cause du retard de colonisation par les sphaignes dans les peuplements. Puisque les conditions nécessaires (substrats, microclimat, etc.) pour la germination des sphaignes étaient inconnues, une deuxième étude a examinée les substrats d'établissements des sphaignes dans des peuplements dominés par les mousses hypnacées. Les colonies de sphaignes se sont établies à plus de 70% du temps sur le bois mort, ce qui potentiellement expliquerait une restriction dans le temps et l'espace de la colonisation. Le bois mort est un substrat dont la disponibilité est variable dans le temps et l'espace. Dans les forêts fermées qui n'ont pas encore atteint le stade d'auto-éclaircie la disponibilité est limitée et la colonisation par les sphaignes coïnciderait avec le début de ce stade d'auto-éclaircie qui produit du bois mort. Ensemble, ces résultats nous permettent de voir que les changements dans la communauté de sphaignes sont influencés plutôt par des processus stochastiques (la colonisation) au début de la succession, et par des processus de compétition à la fin de la succession.

Ces études mettent l'emphase sur deux lacunes dans l'aménagement forestier des peuplements d'épinettes noires susceptibles à l'entourbement de la ceinture d'argile. Les forêts entourbées contiennent des communautés de bryophyte riches et qui varient grandement en fonction de la topographie et de la sévérité des feux et du temps après feu. L'utilisation généralisée de la coupe avec la protection des sols et de la régénération (CPRS), qui est la norme dans la forêt boréale au Québec, ne recrée pas cette diversité et le manque de ce type d'habitat dans le futur pourrait mettre des espèces et des communautés en périls. Bien que la CPRS vise à produire des peuplements équiennes, on doute qu'une intervention de ce type dans des peuplements entourbées crée ce genre de structure. Le manque de perturbation au niveau de l'épaisse couche de matière organique présente dans ces peuplements entourbés, n'imite pas les feux de forêts sévères, qui sont l'agent de perturbation naturel responsable pour l'établissement de jeunes peuplements denses. L'absence de perturbation du sol, en maintenant ou en favorisant les espèces de sphaignes associées aux peuplements plus âgées, pourrait causer une décroissance importante de la productivité forestière.

Ces deux problématiques ont été touchées dans la thèse, mais plusieurs questions demeurent. Les coupes partielles ont le potentiel de recréer les communautés de bryophytes associées avec les vieilles forêts, mais à date uniquement les sphaignes ont été examinées, et cela à court-terme. Pour avoir un portrait plus complet, des études qui incluent le reste des bryophytes (les vrais mousses, les hépatiques) et des autres organismes et qui suivent les coupes partielles pour plusieurs années devraient être réalisées.

Les facteurs qui influencent l'entourbement incluent aussi la sévérité du feu. Après intervention dans un milieu entourbé, les CPRS ressemblent aux feux peu sévères qui tuent les arbres mais ne brûlent pas toute la matière organique. Les techniques de préparation de terrain pourraient mieux imiter les feux sévères parce qu'elles perturbent la couche de matière organique. Comme après un feu sévère, cette perturbation pourrait augmenter la température du sol qui pourrait alors stimuler la décomposition de la matière organique, et entrainer à son tour une réduction de l'épaisseur de la matière organique. De plus les traitements de préparation de terrain tuent les sphaignes et les plantes éricacées ou ralentissent leur croissance, et cela permettra aux arbres de prendre une avance de croissance en hauteur sur leur compétiteurs. La technique de préparation de terrain qui imite le mieux les feux sévères est le brûlage dirigé. Des études dans les années 1970 ont indiqué que cette technique est très efficace (e.g. Chrosciewicz, 1976). Les coupes totales d'été (où les machines passent sur tout le parterre de coupe) et les scarifiages devraient aussi avoir le même effet, mais cela n'a pas encore été vérifié.

En conclusion, une meilleure connaissance et compréhension de la communauté des bryophytes dans les forêts d'épinette noires sur les dépôts fin nous permettra de formuler une meilleure stratégie d'aménagement qui prend en compte la biodiversité et la productivité de ces forêts uniques au monde.

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APPENDICE A

DESCRIPTION OF HIGH AND LOW FIRE SEVERITY SITES USED IN ANALYSES. VALUES ARE MEANS AND STANDARD ERRORS

Appendix A: Description of high and low fire severity sites used in analyses. Values are means and standard errors.

Severity	Site	TSF*	Forest floor thickness (cm)	Basal area‡	PET basal area‡	Open canopy	*Sphagnum* cover	Ericaceous cover
High	D2	56	19.9±1.4	45.82±0.022	0.00±0.00	35.85±0.87	9.5±2.4	1.1±0.58
	N23	88	16.6±1.3	44.08±0.031	0.00±0.00	43.67±2.48	9.7±4.9	5.74±3.79
	S1	90	19.7±1.5	41.94±0.057	0.0050±0.0035	29.07±2.0	21.8±4.4	7.87±1.73
	N12	99	20.9±1.2	47.41±0.039	0.0073±0.0052	52.68±1.71	7.4±2.6	6.05±2.55
	N18	130	33.6±3.0	27.23±0.042	0.00±0.00	55.59±2.73	15.4±5.2	32.26±5.42
	W1	130	29.9±2.4	43.74±0.057	0.0030±0.0030	53.75±1.38	11.0±3.2	30.26±4.31
	D1	187	31.0±2.0	21.17±0.017	0.0012±0.0012	57.36±3.27	23.7±5.9	57.85±4.74
	S74	220	55.2±4.0	30.38±3.73	0.00±0.00	54.71±2.43	35.0±3.6	60.50±5.04
	N50	224	50.4±6.0	20.67±0.020	0.00±0.00	67.40±2.74	68.5±4.6	74.25±3.27
	L22	272	51.4±3.5	22.89±0.032	0.00±0.00	68.75±2.97	55.0±4.1	67.25±4.22
	N16	290	74.9±6.7	15.19±0.021	0.00±0.00	73.49±4.03	67.3±3.4	63.25±4.16
	N6	290	60.9±6.5	21.31±0.028	0.00±0.00	67.40±2.74	62.7±2.9	49.25±5.22
	N20	357	90.0±10.3	7.19±0.017	0.00±0.00	74.83±3.29	62.0±4.2	76.00±1.84

Low	D3	56	39.9±3.4	16.33±0.027	0.00±0.00	59.08±3.07	31.4±6.6	60.0±4.14
	N3	97	50.7±3.0	17.14±0.020	0.00±0.00	65.83±2.85	56.3±3.8	69.5±3.68
	N5	173	49±2.4	30.41±0.057	0.00±0.00	62.72±2.60	67.5±3.9	41.90±5.00
	L9724	262	65.8±5.5	20.14±0.027	0.00±0.00	69.11±2.60	31.8±3.3	71.75±4.33
	H1	350	150±0†	2.70±0.0027	0.00±0.00	78.32±3.87	51.5±3.3	79.25±2.95

* Time since fire

† Estimation only, no mineral soil was reached

‡ m^2/ ha

APPENDICE B

SPECIES CODES AND NAMES USED IN DETRENDED CORRESPONDENDCE ANALYSIS

Appendix B. Species names: Dicont *Dicranum ontariense,* Dicpol *Dicranum polysetum*, Dicsco *Dicranum scoparium*, Hylspl *Hylocomium splendens*, Plesch *Pleurozium schreberi*, Polcom *Polytrichum commune*, Pticri *Ptilium crista-castrensis*, Pticil *Ptilidium ciliare*, Sphang *Sphagnum angustifolium*, Sphcap *Sphagnum capillifolium*, Sphfal *Sphagnum fallax*, Sphfus *Sphagnum fuscum*, Sphgir *Sphagnum girgensohnii*, Sphmag *Sphagnum magellanicum*, Sphrub *Sphagnum rubellum*, Sphrus *Sphagnum russowii*, Sphsub *Sphagnum subtile*, Sphwar *Sphagnum warnstorfii*, Sphwul *Sphagnum wulfianum*, Claran *Cladonia rangiferina*, Claste *Cladonia stellaris.* Species included as an asterix : *Aulacomnium palustre, Brachythecium campestre, Brachythecium salebrosum, Brachythecium starkei, Brotherella recurvans, Callicladium haldanianum, Calligeron stramineum, Campylium hispidulum, Ceratodon purpureus, Dicranella heteromalla, Dicranum flagellare, Dicranum fragilifolium, Dicranum fuscescens, Dicranum montanum, Dicranum undulatum, Drepanocladus fluitans, Drepanocladus revolvens, Drepanocladus uncinatus (Sonionia uncinata), Eurhynchium pulchellum, Herzogiella turfacea, Hypnum imponens, Hypnum pallescens, Mnium spinulosum, Oncophorus virens, Oncophorus wahlenbergii, Plagiothecium cavifolium, Plagiothecium laetum, Platygyrium repens, Pohlia nutans, Polytrichum juniperinum, Polytrichum strictum, Tetraphis pellucida,Tomenthypnum nitens, Tomenthypnum falcifolium, Anastrophyllum hellerianum, Anastrophyllum michauxii, Bazzania denudata, Blepharostoma trichophyllum, Calypogeia integristipula, Calypogeia muellariana, Calypogeia neesiana, Calypogeia sphagnicola, Cephalozia bicuspidata, Cephalozia catenulata, Cephalozia connivens, Cephalozia lunulifolia, Cephalozia pleniceps, Cephaloziella divaricata, Cephaloziella rubella, Cladiopella fluitans, Geocalyx graveolens, Jamesionella autumnallis, Jungermannia lanceolatum, Lepidozia repens, Lophocolea heterophylla, Lophozia lycopodioides, Lophozia guttulata, Lophozia incisa, Lophozia kunzeana, Lophozia longidens, Lophozia marchica, Lophozia ventricosa, Mylia anomola, Nowellia curvifolium, Odontoschism denudatum, Ptillidium ciliare, Ptillidium pulcherrimum, Riccia latifrons, Scapania hyperborea, Scapania irrigua, Scapania mucronata, Trimotaria exsecta, Trimotaria exsectiformis*