UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉTUDE COMPARATIVE DE L'INFLUENCE DU TYPE DE PERTURBATION (FEU VS. COUPE) SUR LA RÉGÉNÉRATION INITIALE DE LA VÉGÉTATION BORÉALE

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

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AVANT-PROPOS

Ce mémoire expose sous forme de deux articles les résultats obtenus dans le cadre d'une étude comparative sur l'influence du type de perturbation sur la régénération initiale en forêt boréale. Cette étude est incluse dans un projet plus large Conseil de recherche en sciences naturelles et en génie du Canada (CRSNG) portant sur le maintien de la productivité suite à différents types de perturbation. Ce projet stratégique CRSNG est sous la coordination de David Paré du Centre de foresterie des Laurentides (Service canadien des forêts) et il regroupe les efforts de recherche de membres de plusieurs établissements universitaires. Le premier volet de ce projet consistait en une approche descriptive de la végétation et de la fertilité du sol observée durant les stades initiaux de régénération suite à des feux de forêts et des activités de coupes forestières. Mon projet de maîtrise était basé sur la composante végétale de ce volet et il était effectué sous la direction de Yves Bergeron de l'Université du Québec à Montréal. La composante des sols correspondait à un projet de maîtrise entrepris par Dan Simard au Collège Macdonald de l'Université McGill sous la direction de Jim Fyles.

Ces deux études ont été élaborées à travers l'effort concerté de toutes ces personnes. La récolte des échantillons de sol et des données de végétation a été menée par les deux étudiants durant une campagne d'échantillonnage commune. J'ai effectué le traitement et l'analyse des données de végétation. Les résultats de ces analyses sont inclus dans le premier article du présent mémoire. L'analyse des sols ainsi que le traitement et l'analyse des données du sol ont été effectués par Dan Simard. Les résultats de ces analyses sont exposés dans le premier chapitre de son mémoire de maîtrise. Le regroupement, le traitement et l'analyse des jeux communs de données ont été effectués par les deux étudiants. Ainsi, j'ai rédigé le premier article du présent mémoire sous la direction d'Yves Bergeron. La rédaction du deuxième article a été effectuée d'un commun effort avec Dan Simard sous la direction d'Yves Bergeron, de Jim Fyles et de David Paré. La liste des auteurs du premier article est donc : Thuy Nguyen-Xuan, Yves Bergeron, Dan Simard, Jim Fyles et Davis Paré. La liste des auteurs du deuxième article est : Thuy Nguyen-Xuan, Dan Simard, Yves Bergeron, Jim Fyles et David Paré. Les deux articles seront soumis au Journal canadien de recherche forestière.

Ce projet a été financé par le Conseil de recherche en sciences naturelles et en génie. Je tiens également à mentionner les contributions financières des compagnies forestières Cartons St-Laurent, Donohue et Tembec et les remercie pour leur support technique et logistique. Je remercie David Paré, Jim Fyles et Yves Bergeron pour leurs conseils, leur appui et leurs appréciations. Je remercie tout particulièrement Yves Bergeron pour la grande confiance qu'il a démontré à mon égard ainsi que pour sa disponibilité et sa sincérité. Je voudrais aussi remercier tous les gens de mon labo et des labos voisins pour ces deux années agréablement passées à l'UQAM où j'étais un nouveau venu. Merci tout particulièrement à Don, Alain et Danielle pour leur aide et conseils, à Patrick, Victor, Tech et Jean-François pour leur camaraderie, à Dan K., Yong, Louis, Jacques et France pour leur sagesse et leur spontanéité, et finalement un grand merci à Catherine et Christelle pour leur solidarité et leur amitié. Je souhaite bonne chance aux nouveaux venus Martin, Olivier, Hervé et Mark et leur souhaite une expérience aussi enrichissante que celle que j'ai vécue. J'aimerais dédier ce mémoire à Mercy Peterson, Alexandre Kadijevic et Christian Lefebvre qui ont partagé avec moi et Dan Simard la partie la plus éprouvante mais aussi la plus merveilleuse de ce projet de recherche. Je les remercie pour leur patience, leur persévérance et leur émerveillement. Je voudrais terminer en remerciant Dan Simard pour avoir su me supporter, m'encourager, m'écouter, m'aider, me comprendre, m'accepter et me surprendre tout au long de ces deux ans.

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RÉSUMÉ

Les perturbations jouent un rôle important dans la dynamique de la régénération de la forêt boréale. Les feux de forêt et les coupes forestières initient la régénération des peuplements forestiers en améliorant les conditions d'établissement et de croissance de la végétation, tout particulièrement en ce qui concerne les espèces de début de succession. Ces améliorations découlent des changements observés suite à la perturbation tant dans l'environnement physique que chimique du sol forestier. Plusieurs études ont démontré qu'il existait des différences importantes dans la composition de la régénération observée après feu et après coupe. L'étude présente vise à expliquer ces différences en évaluant premièrement l'influence de la perturbation physique du sol et deuxièmement celle de la fertilité du sol sur la composition de la régénération végétale initiale de 73 peuplements brûlés ou coupés de la pessière noire à mousses de l'ouest et du centre du Québec.

L'examen séparé de la composition de la régénération de chacun des secteurs en fonction de variables caractérisant l'environnement physique au niveau du sol suite au feu et à la coupe a permis d'illustrer que la sévérité de la perturbation du sol avait une très forte influence sur les patrons de régénération observés. Les analyses des correspondances détendancées effectuées sur l'ensemble des espèces et les comparaisons de recouvrement moyen des espèces prédominantes présentes suite au feu et à la coupe ont démontré que de façon générale le feu favorisait le maintien d'espèces pionnières ou de lichens. Ces différences étaient fortement liées à des différences de sévérité de perturbation du sol.

L'examen de l'ensemble des peuplements perturbés en fonction de variables caractérisant les sols forestiers a permis d'illustrer que la nature des relations entre le sol et la régénération végétale évoluait avec le temps écoulé depuis la perturbation. Une analyse canonique partielle des correspondances a démontré qu'immédiatement après le passage d'un feu la croissance de plusieurs espèces pionnières serait favorisée par une forte augmentation de la fertilité du sol et que durant les stades subséquents de début de succession les espèces pionnières auraient une influence bénéfique sur les dynamiques nutritionnelles des sols forestiers.

Les résultats de cette étude indiquent donc qu'en forêt boréale la sévérité de la perturbation du sol aurait une influence indirecte sur la fertilité du sol et de la productivité d'un peuplement forestier durant sa régénération à travers l'influence directe qu'elle exerce sur la composition initiale de sa régénération végétale. Ceci comporte certaines implications en terme d'aménagement durable de la forêt boréale. Ainsi, les pratiques sylvicoles qui occasionnent une perturbation de l'humus, tels la scarification et le brûlage dirigé, mèneraient à la préservation de la diversité biologique de l'écosystème boréal étant donné que l'établissement d'une majorité d'espèces pionnières est facilité par une perturbation importante du sol forestier. De plus, un aménagement qui vise au maintien et à l'amélioration de la productivité des écosystèmes forestiers se doit de favoriser la croissance d'espèces pionnières suite aux activités de coupe vu l'influence qu'elles semblent avoir sur la dynamique nutritionnelle du sol en début de succession.

INTRODUCTION GÉNÉRALE

L’industrie forestière est un secteur économique important qui emploie directement ou indirectement près d’un Canadien sur dix-sept (Service canadien des forêts, 1998). Afin de protéger l’avenir de ce secteur, les gouvernements canadien et provinciaux ont adopté des politiques d’aménagement durable des ressources forestières. La conservation de la diversité biologique ainsi que le maintien et l’amélioration de l’état et de la productivité des écosystèmes forestiers sont deux des critères et indicateurs écologiques utilisés pour définir une gestion durable des forêts (Conseil canadien des ministres des forêts, 1995). Il est de plus en plus reconnu que les perturbations naturelles peuvent servir de cadre de référence au développement de pratiques d’aménagement durable permettant le respect de plusieurs de ces indicateurs (Attiwill, 1994).

1.1 Rôle des perturbations dans les dynamiques de régénération en forêt boréale

La forêt boréale est la région forestière prédominante au Canada (Service canadien des forêts, 1996). Au Québec, elle couvre près du trois-quarts du territoire forestier et elle se compose à 78,7% de pessière (Parent, 1994). Un des types forestiers les plus communs en forêt boréale est la pessière noire à mousse dont les peuplements matures se caractérisent par un couvert forestier dense dominé par l’épinette noire (*Picea mariana* (Mill.) BSP.) ainsi que par un recouvrement continu de mousses et/ou sphaignes au sol (Larsen, 1980). Cette structure de peuplement résulte en de faibles taux d’ensoleillement en sous-bois menant à des conditions environnementales plutôt fraîche et humide au niveau du sol forestier. L’activité biologique du sol est fortement limitée par ces conditions environnementales, et par conséquent les taux de décomposition des sols forestiers sont souvent moins important que les taux d’accumulation de matière organique (MacLean *et al.*, 1983; Bonan, 1992). On y observe donc souvent avec le temps une augmentation de l’épaisseur de l’humus et une diminution de la productivité du peuplement (Van Cleve et Viereck, 1981). Ainsi, les perturbations naturelles et anthropiques qui modifient à divers degrés cette structure et ces conditions environnementales jouent un rôle important dans les dynamiques de ces peuplements initiant souvent leur régénération.

L’occurrence périodique de feux de forêt est l’un des principaux facteurs régissant les dynamiques de régénération de l’écosystème boréal (Payette, 1992). Les feux caractéristiques à ce système sont généralement des feux de couronne très intenses qui couvrent de grandes surfaces (Johnson, 1992). Leur passage entraîne souvent l'élimination de la canopée et des strates de végétation arbustive, herbacée et muscinale ainsi que la diminution de l'épaisseur de l'humus. De plus, il effectue un relargage des éléments nutritifs contenus dans cette biomasse (Van Cleve et Viereck, 1981; MacLean *et al.*, 1983). Ces modifications causent plusieurs changements en terme de la luminosité et des régimes thermique, hydrique et nutritionnel du sol, et de façon générale favorisent l'établissement et la croissance de la végétation ainsi que l'activité biologique du sol (Ahlgren et Ahlgren, 1960; Viereck, 1983; Bonan, 1992).

Les modifications similaires observées dans la structure des peuplements forestiers suite à des activités de coupe font en sorte que celles-ci initient également la régénération des écosystèmes forestiers. Ainsi, les coupes à blanc éliminent complètement la canopée et partiellement les autres strates de végétation des peuplements récoltés. De plus, les activités de coupes perturbent et modifient à divers degrés les caractéristiques physiques et chimiques des sols forestiers selon la texture et le drainage du sol, la saison et la méthode de récolte, le type de machinerie utilisé ainsi que les activités sylvicoles effectuées suite à la récolte (Plamondon *et al.*, 1980; Keenan et Kimmins, 1993; Brais *et al.*, 1995; Harvey *et al.*, 1995). Par exemple, suite aux activités de coupe à blanc le remaniement de l'humus et du sol minéral ainsi que la hausse des températures au sol entraînent une augmentation de l'activité biologique du sol, et conséquemment une hausse des taux de décomposition de la matière organique et du cyclage des éléments nutritifs (Keenan et Kimmins, 1993).

Suite à une perturbation, les dynamiques de régénération en forêt boréale résultent donc des changements apportés tant en terme de l'environnement physique (lumière, température, humidité) que de l'environnement chimique (pH, éléments nutritifs) au niveau du sol des peuplements. Cependant, la composition et la croissance de la végétation suite à une perturbation peuvent être grandement influencées par deux autres éléments : les sources de propagules et les facteurs stables du milieu. Ainsi il est reconnu qu'en forêt boréale la composition de la régénération est fortement influencée par les sources de propagules présentes suite à une perturbation (Rowe, 1983). La nature et la disponibilité de celles-ci sont grandement déterminées par la composition de la végétation présente avant la perturbation ainsi que par des facteurs historiques tel le temps écoulé depuis la perturbation précédente

(Taylor *et al.*, 1987; De Grandpré *et al.*, 1993; Brulisauer, 1996). Par ailleurs, les facteurs stables du milieu, tels la situation topographique (exposition, localisation dans la pente, degré de pente) ainsi que l'origine, la texture et le drainage du dépôt de surface, affectent les régimes lumineux, thermique, hydrique et/ou nutritionnel d'un site et exercent donc la plus forte influence sur la composition et la croissance de la végétation d'un peuplement forestier (Carleton et Maycock, 1980; Carleton et Maycock, 1981; Carleton *et al.*, 1985).

1.2 Influence du type de perturbation sur les dynamiques de régénération

Quelques études comparatives examinant la composition de la végétation présente après feu et après coupe ont déjà été effectuées en forêt boréale. Noble *et al*. (1977) ont examiné la végétation observée 5 et 15 ans après coupe à blanc, coupe et brûlage dirigé, coupe et scarifiage et feu de forêt dans des peuplements dominés par le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire du nord-est du Minnesota. Au Michigan, Abrams et Dickmann (1982) ont effectué le suivi de la végétation présente durant les cinq premières années suite à des activités de coupe, de brûlage dirigé et au passage d'un feu de forêt dans des peuplements de pin gris. Quant à eux, Johnston et Elliott (1996) ont étudié la végétation présente quelques années après coupe à blanc, coupe et brûlage et feu de forêt dans des peuplements dominés par l'épinette noire du nord-ouest de l'Ontario. Finalement, Ehnes (1998) a comparé la végétation observée 13 et 37 ans après coupe et feu dans des forêts conifériennes du Manitoba. De façon générale, ces différentes études ont démontré qu'il existait des différences dans la composition de la régénération suite à ces différents type de perturbation. Ces différences s'illustraient surtout par une plus forte présence et abondance de plantes pionnières suite au feu. Cependant, certaines de ces études ont aussi illustré que la nature du site (type de dépôt de surface et type de régime hydrique) ainsi que la composition de la végétation avant la perturbation pouvaient exercer une plus forte influence sur la composition de la régénération que le type de perturbation (Noble *et al.*, 1977; Ehnes, 1998). De plus, Carleton et MacLellan (1994) ont examiné des peuplements d'âges différents établis suite à des activités de coupe et au passage de plusieurs feux dans le nord-est de l'Ontario et ils ont noté que l'intensité de la perturbation avait aussi une forte influence sur la composition de la régénération arbustive et arborescente suite à ces perturbations.

Les études mentionnées précédemment ont toutes démontré qu'il existait des différences dans la composition de la régénération de la végétation boréale suite aux différents types de perturbation que sont le feu et la coupe. Cependant très peu d'entre elles ont examiné les mécanismes qui engendraient les différences en ce qui concerne les dynamiques de régénération suite à ces deux types de perturbation. Tel que mentionné auparavant, la dynamique de la régénération après perturbation en forêt boréale reflète surtout les changements amenés en terme l'environnement physique et nutritionnel au niveau du sol de la forêt. Les effets de ces changements sur la dynamique de la régénération végétale sont surtout évidents durant les stades initiaux de succession, avant la fermeture de la canopée arborescente (Heinselman, 1981; Van Cleve et Viereck, 1981). La compréhension des mécanismes et de la dynamique de régénération ainsi que leurs implications dans la différentiation de la végétation observée suite à ces deux types de perturbation est essentielle à l'élaboration d'un aménagement forestier qui soit considéré comme étant durable.

L'objectif principal de cette étude est d'évaluer l'influence du type de perturbation sur la régénération initiale de la végétation boréale. L'étude se restreint à la régénération de début de succession de peuplements forestiers sur till à dominance d'épinette noire au moment de la perturbation. Ce type de peuplement forestier est celui qui est le plus intensément exploité au Québec présentement. Les hypothèses de travail se basent sur le fait que la dynamique de la régénération suite à une perturbation en forêt boréale reflète principalement les changements environnementaux observés au niveau du sol forestier en terme de : 1) milieu physique et 2) milieu nutritionnel. Ainsi le chapitre 2 vise à vérifier que les différences de composition de végétation observées suite au feu et à la coupe peuvent être attribuées à des différences dans les modifications physiques du sol forestier apportées par chacun des types de perturbation. Le Chapitre 3 vise quant à lui à examiner l'influence des différences nutritionnelles des sols sur la composition de la végétation présente suite à ces deux types de perturbation.

THE IMPORTANCE OF FOREST FLOOR DISTURBANCE IN THE EARLY REGENERATION PATTERNS OF THE BOREAL FOREST OF WESTERN AND CENTRAL QUEBEC : A WILDFIRE VS. LOGGING COMPARISON

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2.1 Abstract / Résumé

The invascular and vascular plant composition of the early regenerating vegetation present following wildfires and clear-cut logging has been compared separately in three areas of the black spruce-feathermoss forest of western and central Quebec. In each area, a detrended correspondence analysis (DCA) successful differentiated the burned and logged stands along the first ordination axis. This separation mainly resulted from the greater abundance of pioneer species or lichens after fire and the greater abundance of residual species after clear-cutting. A passive detrended canonical correspondence analysis (DCCA) was used to relate the post-disturbance compositional differences to variables characterizing physical disturbance of forest floor and general site conditions. Variables characterizing forest floor disturbance severity were strongly associated to the first ordination axis in two of the study areas but not in the third one. The interpretation of compositional differences in the light of plant reproductive strategies led to the identification of regeneration patterns that illustrated the influence of disturbance type and severity on post-disturbance vegetation composition. These results suggest that certain forestry practices such as careful logging with the protection of regeneration and soil (CPRS), scarification, and prescribed burning may differ in their capability to address sustainable forest management issues.

La composition invasculaire et vasculaire de la régénération initiale présente suite à des feux et des coupes à blanc a été comparée séparément pour trois secteurs d’étude situés dans la pessière noire à mousses de l’ouest et du centre du Québec. Dans chacun des secteurs d’étude, une analyse détendancée des correspondances (ADC) a distingué les stations brûlées des stations coupées le long du premier axe d’ordination. L’abondance d’espèces pionnières et de lichens suite au feu et l’abondance d’espèces résiduelles après coupe sont grandement responsables de la différentiation des stations. Une analyse canonique détendancée passive des correspondances (ACDC) a mis en évidence les liens qui existent entre la composition végétale de la régénération et plusieurs variables caractérisant la perturbation physique du sol forestier ainsi que des conditions de croissance. Les variables caractérisant la sévérité de la perturbation du sol ont été associées au premier axe dans deux des secteurs d’études. L’interprétation des différences de composition végétale en terme de stratégies de reproduction a également permis d’illustrer l’influence du type et de la sévérité des perturbations sur les patrons de régénération en forêt boréale. Ces résultats suggèrent que des pratiques forestières telles la coupe avec protection de la régénération et des sols (CPRS), la scarification et le brûlage dirigé comportent des différences importantes pouvant avoir des répercussions sur la pertinence de leur utilisation dans un contexte d’aménagement durable de la forêt boréale.

2.2 Introduction

Today's forest management policies aim at a sustainable use of the forest resource. This implies that the integrity of ecological processes of the forest ecosystems must be maintained. The boreal forest is an ecosystem in which natural disturbances play an essential role in stand dynamics, and extensive wildfires are one of the principal processes that initiate stand replacement (Payette, 1992). If logging activities are to be viewed as a different type of disturbance that can be integrated into sustainable forest management, it is then necessary to verify that these activities be able to maintain essential disturbance-related processes and dynamics in the ecosystem.

Initiation of stand replacement following major disturbances such as wildfires or clear-cut logging results from the important changes these disturbances bring forth in the forest stand dynamics. Their occurrence often leads to the complete removal of the overstorey canopy, complete or partial removal of the understorey and ground vegetation, and elimination and/or disturbance of the forest floor, creating favourable environmental conditions for the establishment and growth of a new forest stand (Johnson, 1992; Keenan and Kimmins, 1993). Although it has been recognized that both disturbance types initiate stand replacement, comparative studies previously conducted in the boreal forest have reported important compositional differences in the vegetation observed following logging and burning (Noble *et al.*, 1977; Abrams and Dickmann, 1982; Carleton and MacLellan, 1994; Johnston and Elliott, 1996; Ehnes, 1998). These compositional differences often reflected the increased presence and/or abundance of many pioneer species following wildfires or highly disruptive logging activities.

Rowe (1983) put in evidence the existence of five different reproductive strategies in boreal plants. These reflect different post-fire establishment strategies and illustrate the variety of adaptations boreal species have adopted in order to maintain their presence in the boreal landscape given the recurrent nature of fire. Three strategies are disseminule-based while two other are based on vegetative reproduction. Invaders are typically shade-intolerant pioneer species with short-lived but highly dispersive propagules (e.g. *Epilobium angustifolium* L.) while evaders are species that rely on seed banks in the soil or in the canopy for post-disturbance regeneration (e.g. *Geranium bicknellii* Britton). Avoiders are plant species, which often exhibit establishment requirements reflecting environmental conditions found only in late successional forest (e.g. *Goodyera repens* [L.] R.Br.). Resisters are species whose aboveground parts are able to withstand surface fires (e.g. *Pinus resinosa* Ait.). Finally, endurers are species who can vegetatively resprout from underground organs that survived the fire (*Equisetum sylvaticum* L.). These reproductive strategies are not exclusive and many boreal species exhibit more than one strategy.

In Quebec, black spruce-feathermoss forests represent a predominant portion of the boreal forest. Mature stands are characterized by a closed coniferous overstorey canopy, a sparse understorey, and a continuous feathermoss carpet covering a thick forest floor (Larsen, 1980). Given this stand structure, it is suggested that the physical structural changes brought about by major disturbances such as wildfires and clear-cut logging, especially at the level of the forest floor, are the principle factors which will influence post-disturbance vegetation regeneration patterns. Although most of the previously mentioned comparative studies have recognized the influence of the severity of forest floor disturbance on regeneration patterns, few have examined the importance of the direct relationship that exists between the level of forest floor disturbance and post-disturbance vegetation composition. In order to properly understand, and eventually correct, the factors that generate post-disturbance compositional differences following these two types of disturbance, it is necessary to clearly establish that these differences directly result from differences in the severity of forest floor disturbance. The objective of this study is then to relate the early vegetation development observed following wildfires and clear-cut logging to the level of removal and/or physical disturbance of the forest floor. It is believed that the examination of vegetation differences in terms of Rowe's reproductive strategies rather than species composition is as a more appropriate approach to illustrate the relationship that exists between vegetation composition and forest floor disturbance.

2.3 Materials and methods

2.3.1 *Study Areas*

In order to be able to observe a variety of disturbance levels in both wildfires and clear-cut logging, separate comparative studies were conducted from June to August 1997 in three different areas of the black spruce-feathermoss boreal forest of western and central

Quebec (Fig. 2.1). In all three areas, the studies focused on recently disturbed black-spruce dominated upland stands on glacial till deposits.

Dieppe area

The area is located more than 50 km north of Villebois (about 85 km north of Lasarre). It covers about 1700 km^2 and is situated between 49^o 17' and 49^o 52' north of latitude and 79^o 00' and 79^o 20' west of longitude. The annual mean temperature is 0.6^{o}C, the mean annual precipitation is 822 mm, and the mean annual number of frost-free days is 64 (Anon., 1982a and 1982b). The area belongs to the northern Clay Belt forest region (Rowe, 1972) which is characterized by forest stands generally dominated by black spruce (*Picea mariana* [Mill.] BSP) and jack pine (*Pinus banksiana* Lamb.) with mixed stands of trembling aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), white spruce *(Picea glauca* [Moench.] Voss), and balsam fir (*Abies balsamea* [L.] Miller) on coarser tills and alluvial deposits along rivers and lakes.

A 31 054 ha crown-fire burned across the area in June 1976. Twenty-four sites were sampled in this study area. They consist of 10 stands that burned in 1976, 10 stands that were clear-cut between 1975 and 1980 (with no additional silvicultural treatments), and 4 undisturbed stands.

St-Père area

The area is located about 40 km southeast of Lebel-sur-Quévillon. It covers about 1000 km^2 and is situated between 48^o 43' and 48^o 59' north of latitude and 76^o 08' and 76^o 38' west of longitude. The annual mean temperature is 1.2^{o}C, the mean annual precipitation is 840 mm, and the mean annual number of frost-free days is 87 (Anon., 1982a and 1982b). The area belongs to the Gouin forest region (Rowe, 1972). General tree species composition is similar to that of the Clay Belt forest region except that mixed stands now occur on elevated tills rather than on coarser tills.

A 47 709 ha crown-fire burned across the area in August 1995. Logging operations in the area consist of clear-cuts with protection of regeneration and soils (CPRS) (Canuel, 1989). Due to insufficient regeneration densities, site scarification and tree planting activities have been carried out in many of the logged areas. Twenty-eight stands were sampled in this

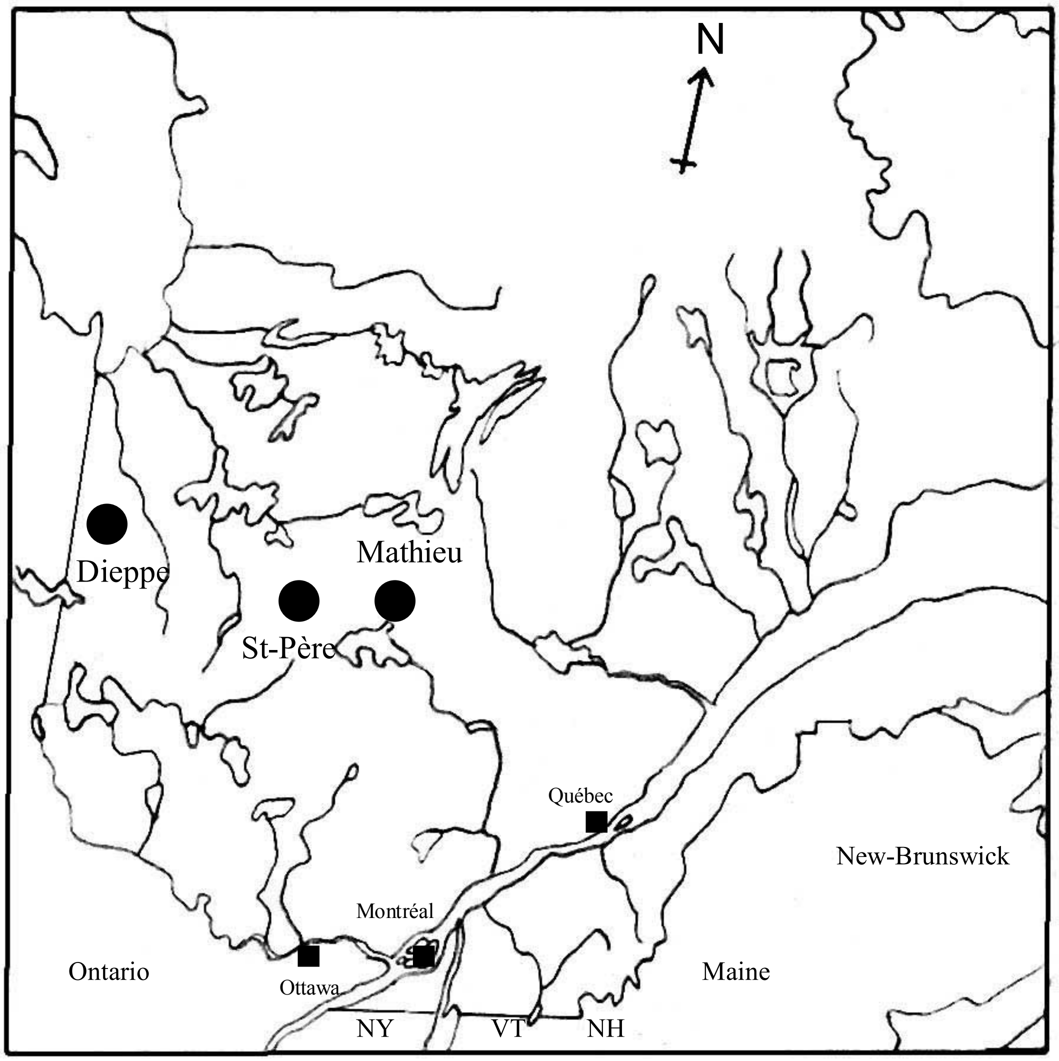

Fig. 2.1. Location of study areas.

study area. They consist of 10 stands that burned in 1995, 10 stands that were logged (CPRS), scarified and planted between 1992 and 1996, and 8 undisturbed stands.

Mathieu area

The area is located north of the Gouin Reservoir about 15 km north of Obedjiwan (about 100 km north of Parent). It covers about 675 km^2 and is situated between 48^o 45’ and 49^o 00’ north of latitude and 74^o 27’ and 75^o 00’ west of longitude. The annual mean temperature is 0.8^oC, the mean annual precipitation is 948.4 mm, and the mean annual number of frost-free days is 93 (Anon., 1982a and 1982b). The area belongs to the previously described Gouin forest region (Rowe, 1972).

A 14 535 ha crown-fire burned across the area in June 1983. Twenty-one sites were sampled in this study area. They consist of 8 stands which burned in 1983, 8 stands which were clear-cut logged between 1981 and 1986 (with no additional silvicultural activities), and 5 undisturbed stands.

2.3.2 *Sampling*

Prior to sampling, a first selection of disturbed and undisturbed stands was performed using the information available from a variety of maps (surficial deposit, forest inventory, history of logging and silvicultural activities). A stand was considered suitable for the study if it was found on a glacial till deposit, was previously dominated by black spruce, and had an upland stand structure and density prior to disturbance. Final stand selection was performed in the field following the confirmation of these stand attributes. The same sampling procedure was followed in all three study areas. In each selected stand, a 25m x 25m square plot was set up within which 15 sampling points were randomly located. The percent coverage of lichen, bryophyte, and vascular plant species below a height of 1m was estimated within a 1 m x 1m quadrat centered on each sampling point. Percent coverage of the vegetation between 1 to 3 m tall was separately recorded for each 1 m^2 quadrat. A stem count of tree/sapling individuals with a minimum height of 1.4 m and minimum dbh of 1 cm was performed within a 1.5 m radius around each sampling point (for a total area of 106.5 m^2 for the square plot). At 8 of the 15 sampling points, depth of the duff (FH layer) was measured and samples of the duff and mineral soil layers (upper 10 cm) were taken (Simard, 1998). These duff and mineral soil samples were used for density and granulometric analyses.

Aspect, slope, slope position, and moisture regime were recorded in each stand to characterize its site type. Finally, the age of the stand at the time of disturbance was estimated by sampling 5 trees (burned snags or logging stumps) at each site.

2.3.3 *Data analysis*

The data available for the analysis of compositional differences and their relationship to environmental variables consist of the average cover estimate of each species at each stand, the average forest floor characteristics for each stand, as well as other stand based variables. The data can be divided into two main sets: a vegetation data set and an environmental data set. In addition, two subsets can be derived from the vegetation data set. The first vegetation subset includes the average cover estimates of the 31 predominant taxa (species or genus) encountered in the different study areas. A species or genus was considered predominant if it occurred in at least one third of all sampled 1 m^2 quadrats and possessed an average cover greater than or equal to 1% for any disturbance type. The second vegetation data subset consists of all the species encountered in at least 1% of all the 1 m^2 quadrats in a given study area. Thus, it describes the overall species composition of stands sampled in that area and excludes the very infrequent species. The species retained for this second subset are listed in Appendix A. Finally, the environmental data set includes ten variables that either characterize forest floor disturbance (average duff depth, standard deviation of average duff depth, duff density, bulk density of upper mineral soil) or are related to additional site environmental characteristics, such as pre-disturbance composition, light and temperature regimes, and drainage, that also influence post-disturbance vegetation composition (stand age at time of disturbance, aspect, slope, slope position, % sand content of mineral soil, soil moisture regime).

Although a first correspondence analysis (Jongman *et al.*, 1987) was performed with all 73 stands to evaluate the overall compositional differences observed in the vegetation present after disturbance, the subsequent analyses were performed separately for each study area in order to focus on compositional differences between disturbance types rather than between study areas. Thus for each area, differences in the average cover of predominant species following fire and clear-cut logging were identified with the Mann-Whitney non-parametric means comparison test (Conover, 1980) while differences in the overall composition of burned and logged stands were explored with detrended correspondence analyses (DCA) (Jongman *et al.*, 1987). The use DCA was preferred to that of CA because the first ordination axis corresponded to the differentiating gradient of main interest and in some instances a slight arch effect could be observed on the second ordination axis. The degree of association of both sets of environmental variables with the main differentiating axes was examined through passive analyses of environmental variables in respect to the first DCA ordination axes (Jongman *et al.*, 1987). STATISTICA (StatSoft Inc., 1995) was used to perform the Mann-Whitney non-parametric means comparison tests while PCORD (McCune, 1993) and CANOCO (ter Braak, 1990) were used to perform the CA and DCA analyses.

As previously mentioned, Rowe's reproductive strategies were also used to illustrate the relationship that exists between vegetation composition and forest floor disturbance. In the context of the present study, it was thought that Rowe's concepts of invader and avoider species needed to be broadened to include pioneering lichens (as invaders of xeric environments) as well as lichens of later successional stages (avoiders) in the light of the cryptogram species establishment sequences often observed following fire (Scotter, 1964; Clayden and Bouchard, 1983; Foster, 1985; Morneau and Payette, 1989).

2.4 Results

Figure 2.2 shows the ordination of all 73 stands along the 3 first axes of the correspondence analysis that used the combined vegetation cover data of all 3 study areas. The eigenvalues of the 3 first axes are 0.696, 0.492, and 0.463 corresponding respectively to 20%, 14%, and 13% of the total variance observed in the vegetation data. Together, the 3 first axes can thus account for 47% of the observed variation in the vegetation of all 3 study areas. From this ordination, it can be seen that the burned stands of each study area are the most compositionally different out of all 73 stands as they are separated from undisturbed and logged stands along all 3 ordination axes. The burned stands of the St-Père study area are separated along the first axis while axis 2 separates the burned stands of the Dieppe study area and the third axis separates many of the burned stands of the Mathieu study area. The logged and undisturbed stands cluster around the origin of the ordination space. Thus each axis seems to correspond to a separate gradient that differentiates the burned and logged stands of the different study areas. Further analysis on a regional basis seems as the most

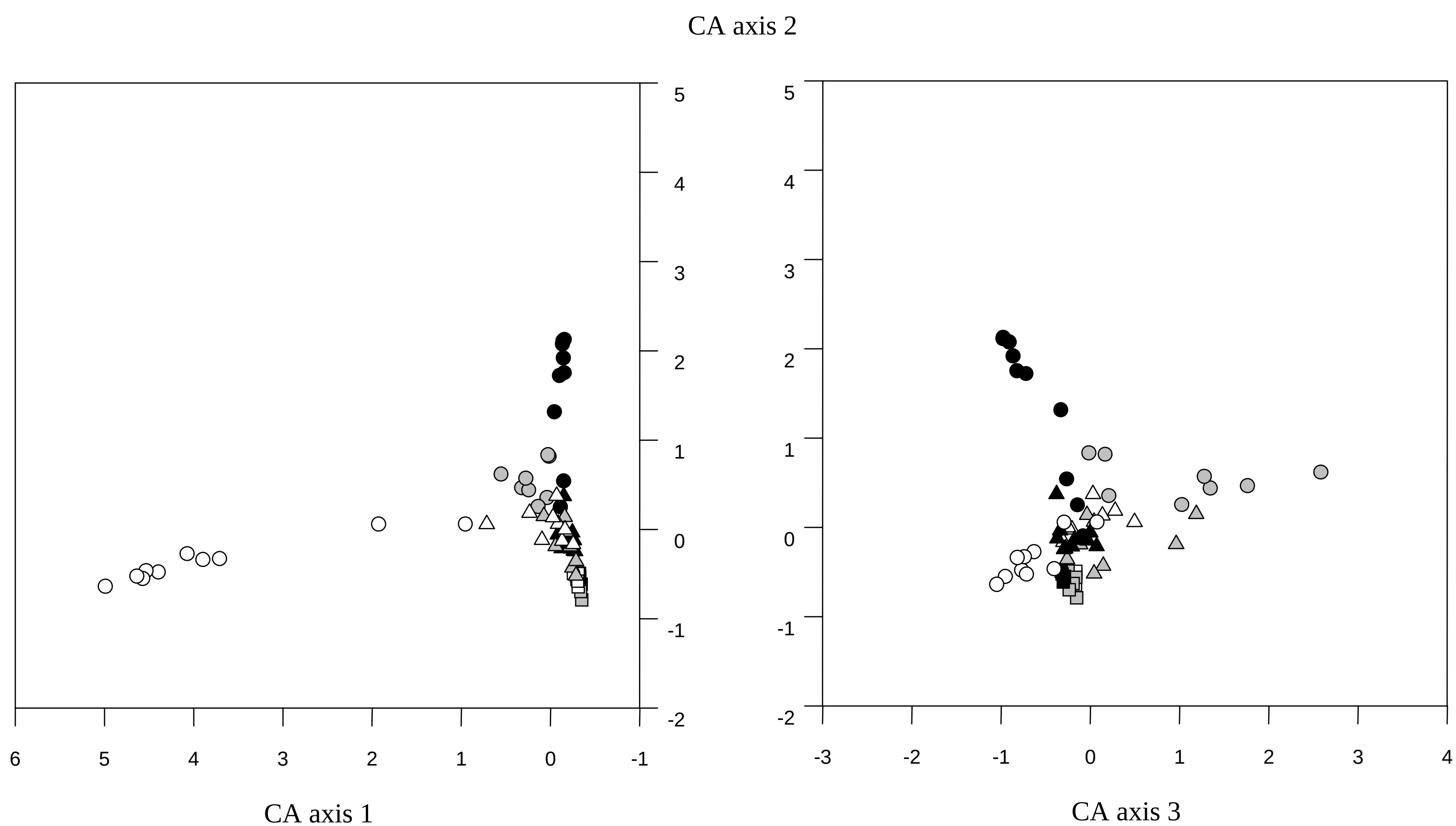

Fig. 2.2. CA ordination of all stands from the 3 study areas. Undisturbed (□), burned (○), and logged (△) stands of the St-Père area. Undisturbed (■), burned (●), and logged (▲) stands of the Dieppe area. Undisturbed (grey □), burned (grey ○), and logged (grey △) stands of the Mathieu area.

appropriate approach to adequately relate post-disturbance compositional differences following wildfires and clear-cut logging to forest floor disturbance. Moreover, given the very close proximity of the logged and undisturbed sites it also seems preferable to remove the undisturbed stands from the subsequent analyses in order to strictly focus on the compositional differences of burned and logged stands and avoid any possible confounding influence from the undisturbed stands when relating these compositional differences to the variables characterizing forest floor disturbance.

2.4.1 *Forest floor disturbance and post-disturbance composition in the Dieppe area*

Although the Dieppe study area is the oldest of the three study areas, the relatively low cover of vascular plants observed in the upper vegetation stratum seems to suggest that the revegetation following disturbance (of either type) in this area has not been very successful (Table 2.1). Nonetheless, the ordination of the disturbed stands of the Dieppe study area successfully differentiates a majority off burned and logged stands along the first DCA axis which accounts for 37% of the variation (Fig. 2.3). Following the passive analysis of the environmental variables with the ordination space derived from the detrended correspondence analysis, it appears that only four environmental variables possess a relatively high correlation coefficient (Pearson r with an absolute value greater than 0.50) with either of the two first DCA axis (Table 2.2). Out of these four variables, only average duff depth characterizes forest floor disturbance. Thus, even if burned and logged stands are successfully differentiated by the first DCA axis, this differentiation cannot be definitely attributed to differences in duff depth between the two disturbance types. None of the forest floor disturbance or site type variables are strongly associated to the second DCA axis (Table 2.2).

In the Dieppe study area, almost all of the vegetation cover occurs at the ground and below 1 m levels (48 to 51% and 36 to 50% respectively) (Table 2.1). Low stem densities of tree species in disturbed stands produce a sparse vegetation cover in the 1-3 m stratum (4 and 9%). An important part of the ground cover of burned stands is attributed to the crustose lichen *Trapeliopsis granulosa* while in logged stands it is attributed to the feathermoss *Pleurozium shreberi* (Table 2.3). Other predominant species that tend to have greater cover after fire include the cup lichens (*Cladonia cenotea*, *C. cornuta*, *C. crispata*, *C. cristatella*,

Table 2.1. General description of stands according to disturbance type in the 3 study areas. Types of disturbances : undisturbed (U), wildfire (WF), clear-cut (CC), scarification (S), tree planting (P).

	Dieppe			St-Père			Mathieu		
Type of disturbance	U	WF	CC	U	WF	CC, S, P	U	WF	CC
Number of stands	4	10	10	8	10	10	5	10	10
Time since most recent disturb. (yrs)	-	21	17-22	-	2	1-5	-	14	11-16
- *Tree stems*									
Average total stem density (stems/ha)	4856	340	1141	2393	0	189	2999	4974	6259
Average total basal area (m^2/ha)	36.1	0.3	1.4	42.6	0.0	0.1	29.6	4.8	6.5
- *Average total vegetation cover (%)*									
1 to 3 m	12	4	9	10	0	0	8	28	22
0 to 1 m	23	36	50	33	14	15	26	70	69
Ground	87	48	51	82	12	8	85	28	66
- *Average non-vegetation cover (%)*									
Exposed mineral soil	0	0	0	0	41	13	0	0	0
Exposed duff	0	0	0	0	37	59	0	0	0
Average duff thickness (cm)	18	12	16	21	6	14	20	10	14
Standard dev. of duff thickness (cm)	7	6	8	7	7	8	6	4	5

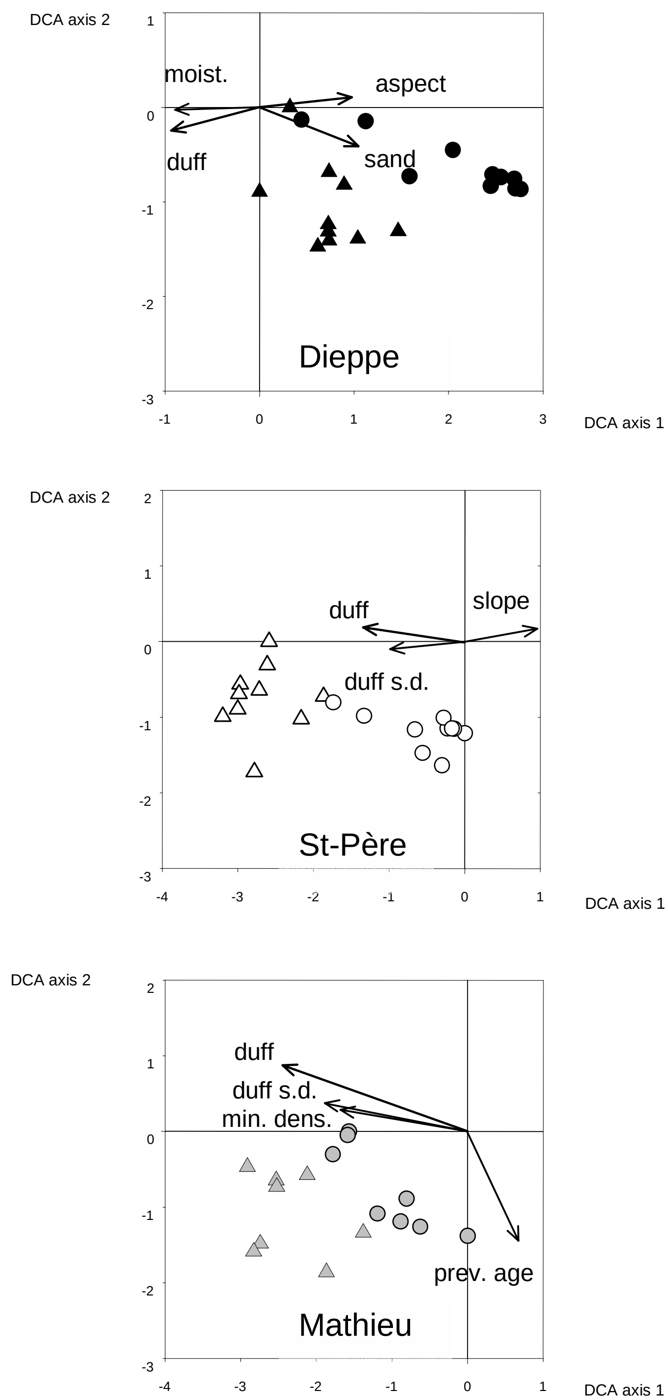

Fig. 2.3. DCA ordination of the disturbed stands and biplot of passive analysis of environmental variables in each study area. Variables represented possess interset correlation coefficients with an absolute value greater than 0.50 on either of the two first DCA axes. Symbols are the same as in previous area.

Table 2.2. Interset correlation coefficients of environmental variables with first and second axes of the DCA ordination of the disturbed stands in each study area. Correlation coefficients are from the passive analysis of the environmental variables in respect to the DCA axes.

	Dieppe		St-Père		Mathieu	
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
-*Variables characterizing physical disturbance of forest floor*						
Average duff depth	-0.56	-0.24	-0.81	0.53	-0.78	0.41
Standard dev. of avg. duff depth	-0.36	0.10	-0.58	0.24	-0.60	0.20
Duff density	0.13	0.09	0.12	-0.25	0.19	0.42
Bulk density of upper mineral soil	-0.46	0.40	-0.34	-0.02	-0.53	0.17
-*Variables characterizing site type*						
Percent sand	0.61	-0.28	-0.18	0.04	0.26	-0.32
Aspect	0.58	0.13	0.41	-0.08	0.13	-0.00
Slope	-0.16	-0.25	0.57	-0.17	0.39	-0.38
Slope position	0.36	-0.27	0.43	-0.49	0.28	-0.14
Soil moisture regime	-0.52	-0.07	0.31	0.45	-0.25	0.19
Stand age prior to disturbance	-0.25	0.04	-0.23	0.17	0.24	-0.55

Table 2.3. Average percent cover of predominant species in the different vegetation strata for the different disturbance types in each study area. Probabilities associated with the Mann-Whitney U test statistic are indicated for average cover comparisons between burned and logged stands. Disturbance types : undisturbed (U), burned (WF), and logged (CC) stands.

		Dieppe				St-Père				Mathieu			
	reprod. strategy	U	WF	CC	prob.	U	WF	CC	prob.	U	WF	CC	prob.
- ground													
Ceratodon purpureus	invader	-	-	-		-	9	0	0.0001	-	-	-	
Cladina spp.	avoider	3	3	4	0.5454	-	-	-		0	1	2	0.5635
Cladonia spp.	invader (xeric)	0	3	1	0.0028	-	-	-		0	1	1	0.9164
Dicranum spp.	avoider	1	0	2	0.0008	3	-	2	0.0001	4	0	2	0.0033
Gaultheria hispidula	avoider	1	1	1	0.0343	1	-	0	0.0006	1	1	1	0.7527
Marchantia polymorpha	invader	-	-	-		-	4	-	0.0001	-	-	-	
Pleurozium shreberi	avoider	70	2	29	0.0003	57	-	5	0.0001	55	6	49	0.0011
Polytrichum spp.	invader	0	6	3	0.0697	0	1	0	0.0529	0	14	0	0.0008
Ptilidium ciliare	avoider	3	0	1	0.0012	1	-	0	0.0002	1	0	2	0.0087
Ptilium cristacastrense	avoider	3	0	0	0.9699	14	-	0	0.0052	18	0	3	0.0181
Sphagnum spp.	avoider	7	5	8	0.3075	-	-	-		5	1	3	0.8748
Trapeliosis granulosa	invader (xeric)	-	27	2	0.0019	-	-	-		-	-	-	
- 0 to 1 m													
Abies balsamea	avoider	-	-	-		-	-	-		1	-	8	0.0357
Amelanchier spp.	endurer	-	-	-		-	-	-		0	1	1	0.5995
Aralia nudicaulis	endurer	-	-	-		-	-	-		-	2	1	0.0742
Betula papyrifera	invader / endurer	-	-	-		-	-	-		0	2	1	0.4008
Cornus canadensis	endurer	-	-	-		2	1	1	0.9396	2	7	4	0.0929
Deschampsia flexuosa	endurer	-	-	3	0.0001	-	-	-		-	-	-	
Diervilla lonicera	endurer	-	-	-		-	-	-		-	3	1	0.2480
Epilobium angustifolium	invader	-	-	-		-	4	-	0.0001	-	2	0	0.0011
Kalmia angustifolia	endurer	4	9	7	0.4497	6	1	3	0.0538	4	5	11	0.2702
Ledum groenlandicum	endurer	6	5	14	0.0041	5	1	2	0.0740	7	2	5	0.0929
Maianthemum canadense	endurer	-	-	-		-	-	-		-	6	3	0.1415

Table 2.3. (continued)

	reprod. strategy	St-Père U	WF	CC	prob.	Dieppe U	WF	CC	prob.	Mathieu U	WF	CC	prob.
- 0 to 1 m (continued)													
Picea mariana	invader / endurer	9	6	9	0.1306	11	0	1	0.0122	4	5	10	0.2076
Pinus banksiana	evader	-	-	-		-	1	0	0.0082	-	-	-	
Populus tremuloides	invader / endurer	-	-	-		-	2	0	0.0014	-	-	-	
Prunus pensylvanica	evader	-	-	-		-	-	-		-	1	0	0.0460
Pteridium aquilinum	endurer	-	-	-		-	-	-		-	6	3	0.2936
Solidago macrophylla	invader	-	-	-		-	-	-		-	1	0	0.0406
Vaccinium angustifolium	endurer	3	11	8	0.1306	2	1	4	0.0041	2	12	11	0.5995
Vaccinium myrtilloides	endurer	1	2	3	0.5708	4	1	2	0.2114	2	7	7	0.9164
- 1 to 3 m													
Abies balsamea	avoider	-	-	-		-	-	-		3	-	7	0.0001
Betula papyrifera	invader / endurer	-	-	-		-	-	-		-	8	4	0.2936
Picea mariana	invader / endurer	12	1	4	0.0041	9	-	0	0.0001	5	2	8	0.0831
Pinus banksiana	evader	-	-	-		-	-	-		-	7	0	0.0256
Prunus pensylvanica	evader	-	-	-		-	-	-		-	5	1	0.0520

C. deformis, *C. gracilis*) and *Polytrichum* spp. while *Dicranum* spp., *Ptilidium ciliare*, *Deschampsia flexuosa*, and *Ledum groenlandicum* tend to be more abundant following logging. *Sphagnum* spp., many low shrubs (*Kalmia angustifolia*, *Vaccinium angustifolium*, *Vaccinium myrtilloides*), and black spruce are common in sites of both disturbance types. Thus, it would seem that in this study area invaders of xeric environments (ix) are generally highly associated to burned stands (Fig. 2.4). Many avoiders appear to be more closely associated to logged stands while a certain number of endurers can be found following either wildfire or clear-cut logging (Table 2.3).

2.4.2 *Forest floor disturbance and post-disturbance composition in the St-Père area*

The St-Père area is the most recently and highly disturbed study area (Table 2.1). The high severity of the wildfire on the forest floor can be seen by the important average cover of exposed mineral soil in burned stands (41%) while the high degree of forest floor disturbance by the logging and planting activities can be seen by the important average cover of exposed duff (59%). The detrended correspondence analysis ordination of the disturbed stands of this area shows a clear differentiation of disturbance type along the first axis (Fig. 2.3). This axis accounts for 36% of the total variation observed in the vegetation data. From the biplot obtained with the passive analysis of the environmental variables, it appears that the vector representing duff depth is the strongest vector associated to the first DCA axis (Fig. 2.3). This is also the variable which possesses the greatest correlation coefficient with that axis (Table 2.2). No environmental variables seem to be strongly associated to the second CA axis.

In the disturbed stands of the St-Père study area, the average ground vegetation cover does not exceed 12% and the average cover of the vascular vegetation below 1 m is no greater than 15% (Table 2.1). No vegetation taller than 1 m is observed. In Table 2.3, it can be seen that *Epilobium angustifolium* and the bryophytes *Ceratodon purpureus* and *Marchantia polymorpha* are some of the predominant plant species frequently observed after fire while *Pleurozium shreberi* and *Dicranum* spp. are frequently observed after logging. *Vaccinium angustifolium*, *Vaccinium myrtilloides*, *Kalmia angustifolia*, *Ledum groenlandicum*, *Cornus canadense*, and *Polytrichum* spp. are frequently observed after both fires and cuts. Tree species regeneration mostly consists of trembling aspen and jack pine seedlings in burned stands, and of black spruce advanced regeneration or planted seedlings

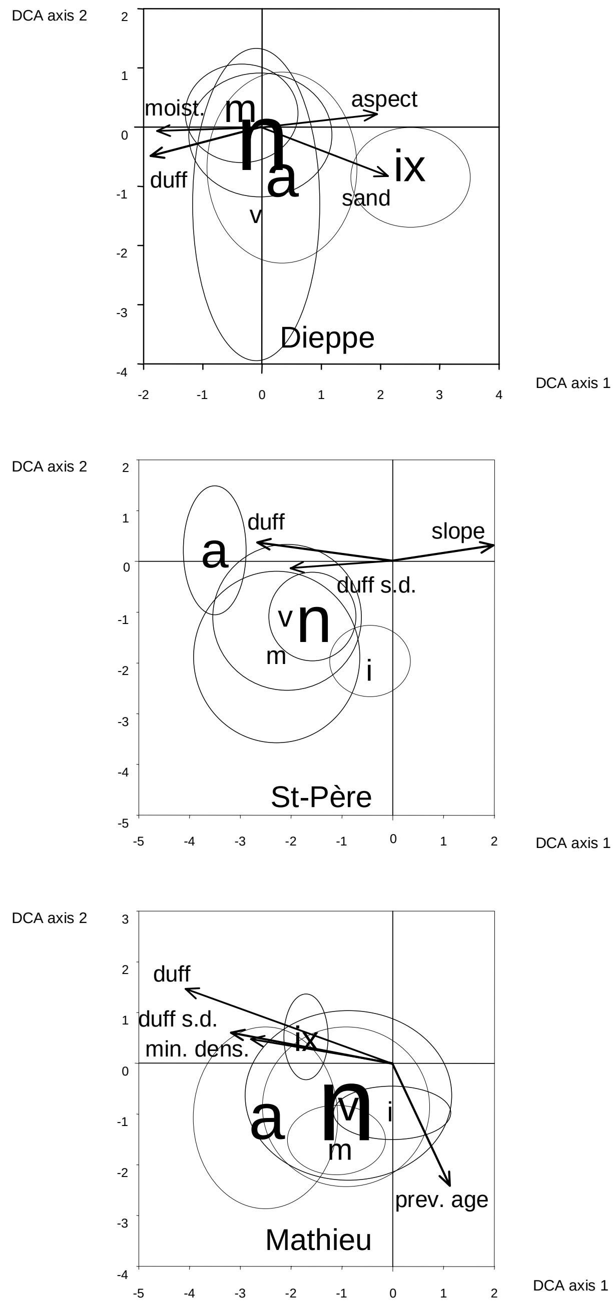

Fig. 2.4. DCA ordination of species and biplot of passive environmental variables of the disturbed stands in each study area. General location of reproductive strategies determined by averaging the species scores of all the species belonging to a given reproductive strategy. Size of symbol proportional to the number of species used to determine the average location. Height and width of ellipse determined from the standard deviation of the species scores for each reproductive strategies. Reproductive strategies: a (avoiders), v (evaders), i (invaders), ix (invaders of xeric environments), n (endurers), m (multiple strategists). Same environmental variables as in previous figure.

in logged stands. Hence, in this study area a clear differentiation of reproductive strategies can be observed along the average duff depth vector (Fig. 2.4). Most invading species (i) are located towards the right end of the ordination space, the direction associated with the burned stands and lower duff depths. In contrast, most avoiding species (a) are located towards the left end of the ordination space and thus seem to be associated with logged stands and greater duff depths. Endurers (n), evaders (v) and multiple strategists (m) tend to be more widely and centrally distributed, commonly occurring after both disturbances.

2.4.3 *Forest floor disturbance and post-disturbance composition in the Mathieu area*

As in the two previous areas, the burned and logged stands of the Mathieu study area are successfully differentiated by the DCA ordination (Fig. 2.3). However, two aspects of the ordination suggest that this differentiation is slightly more elaborate than in the Dieppe and St-Père areas. Firstly, the differentiating gradient that separates the burned and logged stands runs more along a diagonal running from the lower left corner to the upper right corner of the ordination space rather than strictly along the first DCA axis. Secondly, there seems to be a distinct separation of stands belonging to the same disturbance type on either side of this line. It would seem that the first DCA axis, which represents 32% of the variation, mostly contributes to the differentiation of stands belonging to different disturbance types while the second axis (11% of the variance) separates stands belonging to the same disturbance type. The passive analysis of the environmental variables in respect to the ordination space reveals that average duff depth is the variables that shows the greatest degree of association with the first DCA axis ($r = -0.78$) (Table 2.2). Out of the four environmental variables that possess correlation coefficients with an absolute value greater than 0,50 on either of the two first axes, three characterize forest floor disturbance (Fig. 2.3). A t-test comparison, indicates that the average duff depths observed in the stands of the upper left portion of the ordination space (3 burns, 6 clear-cuts) are significantly greater than those of the stands in the lower right portion (5 burns, 26 clear-cuts) ($p < 0.001$).

In contrast to the previous study areas, the Mathieu study area shows a dense revegetation following disturbance (Table 2.1). Tree species stem densities are high resulting in a vegetation cover of 28% and 22% in the 1-3 m stratum for the burned and logged stands respectively. The most common tree and tall shrub species that have regenerated following disturbance are balsam fir, white birch, black spruce, jack pine and pin cherry (*Prunus pensylvanica*) (Table 2.3). Burned stands are often mixed (*Pinus banksiana*, *Picea mariana*, *Betula papyrifera*, *Prunus pensylvanica*) while logged stands are predominantly coniferous (*Abies balsamea*, *Picea mariana*). Vascular plants are abundant after disturbance as shown by the important vegetation cover observed in the 0 to 1 m stratum of Table 1 (70 and 69% in burned and logged stands respectively). *Vaccinium angustifolium*, *Vaccinium myrtilloides*, *Kalmia angustifolia*, *Ledum groenlandicum*, *Cornus canadensis*, *Maianthemum canadense*, and *Pteridium aquilinum* are predominant species of most burned and logged stands (Table 2.3). *Polytrichum* spp. are an important ground cover of burned stands while *Pleurozium shreberi* is the predominant ground cover of most logged stands. Thus, in the ordination of the species observed in the Mathieu area following wildfire and clear-cut logging (Fig. 2.4), it can be seen that the lower duff depth of many fires favours invader species (i) while the greater duff depth of many clear-cuts favours avoiders (a). Furthermore, the greater duff depth of certain fires seems to favour the invaders of xeric environments (ix) rather than the "classical" invaders while the lower duff depth of certain cuts favours multiple strategists (m). Finally, endurers (n) and evaders (v) are centrally and widely distributed throughout the ordination space.

2.5 Discussion

2.5.1 *Disturbance of the forest floor*

In previous comparative studies, factors such as pre-disturbance stand composition, stand moisture and nutrient regime, and time since the last disturbance have all been recognized as exerting a greater influence on post-disturbance stand composition than disturbance type itself (Noble *et al.*, 1977; Carleton and MacLellan, 1994; Ehnes, 1998). Given that the three areas examined in the present study cover a broad geographic range with possibly varying topography and disturbance history, to perform a single analysis encompassing all 73 sites is to the least disputable. So much the more given that important compositional changes occur during early post-fire succession (Shafi and Yarranton, 1973) and considering that the time since disturbance differs greatly between the three areas. The strong influence of time since the last fire on vegetation composition is put in evidence by the CA ordination of all 73 sites from the three study areas. However, treating each study area separately in the subsequent analysis limits the factors affecting post-disturbance regeneration to disturbance type alone and it allows for the identification of similar differentiation patterns for all three areas. Hence, in all three areas burned and logged stands are most strongly differentiated along the first detrended correspondence analysis axis.

The main postulate of the present study is that the differences in the composition of the vegetation observed following wildfires and clear-cuts reflect differences in the impacts of each disturbance type on the structure of the forest floor. In the St-Père and Mathieu study areas, pioneer species such as *Marchantia polymorpha*, *Polytrichum juniperinum*, *Polytrichum piliferum*, *Carex aenea*, *Epilobium angustifolium*, and *Pinus banksiana* greatly contribute to the differentiation of burned and logged stands. These species are also reported to be more abundant after fire by other comparative studies (Noble *et al.*, 1977; Abrams and Dickmann, 1982; Johnston and Elliott, 1996; Ehnes, 1998). However, many pioneer species are also commonly observed on logged stands that have been subjected to a high degree of forest floor disturbance (Noble *et al.*, 1977; Outcalt and White, 1981; Carleton and MacLellan, 1994). In general, a large number of these pioneer species show a more successful establishment on a thin humus layer or on exposed mineral soil (Ahlgren, 1960). This suggests that in the St-Père and Mathieu study areas wildfires have brought about a greater disturbance of the forest floor than has clear-cut logging. In effect, in these two areas the passive analysis of the environmental variables shows that average duff depth is the variable most consistently associated to the main differentiating axis. Moreover, out of the four variables related to forest floor disturbance, it is the one that possesses the highest correlation coefficient with the first DCA axis. Thus, in these study areas the differences in vegetation composition observed between burned and logged stands does appear to mainly reflect differences in the amount of forest floor removed by each disturbance type.

Interestingly, the burned and logged stands of the Dieppe study area are also successfully differentiated along the first ordination axis, but in this area the main differentiating axis does not seem to be most highly associated to the residual depth of the forest floor. Furthermore, the pioneer species that contributed to the differentiation of burned and logged stands in the two previous study areas are not the ones that contribute to the differentiation of the burned stands of this study area. Thus even if the detrended correspondence analyses successfully differentiate stands originating from different disturbance types on the basis of their vegetation composition in all three study areas, this differentiation does not always directly reflect differences in residual forest floor depths and it is not always caused by the same type of compositional differences. The use of Rowe's reproductive strategies for the examination of the differentiation patterns of burned and logged stands more clearly illustrates the similarities that exist in the relationships observed between post-disturbance composition and forest floor disturbance in the three study areas.

2.5.2 *Reproductive strategies*

The incomplete combustion of the forest floor during a forest fire leaves a substrate consisting of charred duff. The blackened and porous nature of this substrate results in highly fluctuating temperature and moisture regimes at its surface (Kershaw, 1977). These environmental conditions are highly inhospitable for the majority of the vascular pioneer species discussed previously. Lichens, however, are plants that are better suited for the successful colonization of such substrates (Ahti, 1977; Kershaw, 1985). Thus, many lichens can also be viewed as early invaders of exposed duff (Scotter, 1964; Foster, 1985; Morneau and Payette, 1989). When early successional lichens are included in Rowe's invader strategy (1983), similar general patterns of post-disturbance regeneration are then observed across all three study areas: invaders are favoured by fire, avoiders are favoured by logging, and endurers are not favoured by any particular disturbance type. The same patterns are put in evidence by counting the occurrences of greater abundance for the different predominant species in respect to their reproductive strategy (Table 2.4). Therefore, these repeated patterns are the basis for the successful differentiation of burned and logged stands in all three study areas.

However, in the St-Père and Dieppe study areas the two differentiation patterns observed result from two distinct forest floor disturbance events. The wildfire of the St-Père area occurred in late summer and a considerable surface of mineral soil surface was exposed. Thus, the stand differentiation observed in the St-Père area reflects differences in the residual duff depth observed after each disturbance type as was shown by the passive analysis of the environmental variables. The regeneration pattern of this area is similar to those observed in other studies that related post-disturbance compositional differences within the same

Table 2.4. Occurrences of each possible outcome for the comparisons between the average cover of the predominant species of the different disturbance types. Includes comparisons of all study areas. Outcome significant at $p < 0.05$.

Strategy	Possible outcome		
	WF > CC	CC > WF	WF = CC
Invaders	9	0	3
Evaders	3	0	1
Avoiders	0	15	6
Endurers	0	3	17
Invaders/Endurers	1	3	5

disturbance type to differences in the severity of the disturbance of the forest floor (Flinn and Wein, 1977; Brumelis and Carleton, 1988; Brumelis and Carleton, 1989; Harvey and Bergeron, 1995; Schimmel and Granstrom, 1996). Such compositional differences have often been associated to differences in species reproductive strategies as well as differences in the distribution of their regenerative propagules throughout the forest floor (McLean, 1969; Johnson, 1975; Flinn and Wein, 1977; Moore and Wein, 1977; Schimmel and Granstrom, 1996; Rydgren and Hestmark, 1997; Qi and Scarrett, 1998).

In contrast, the wildfire of the Dieppe area occurred in late spring at a time where the forest floor had not completely thawed, leaving the partially burned duff as the predominant ground surface. Thus, in this case the stand differentiation observed in the area reflects differences in the forest floor temperature and hydric regimes encountered after each disturbance type rather than differences in residual duff depths. Interestingly, both differentiation patterns are observed in the Mathieu area as shown by the site and species ordinations. Some of the Mathieu burned stands are differentiated from the logged stands by a greater presence of "classical" invaders as in the St-Père area while others are differentiated by "xeric" invaders as in Dieppe. The stand and species ordinations obtained in this study area illustrate that differences in the severity of forest floor disturbance lead to compositional differences between disturbance types, but also within the same disturbance type.

2.6 Conclusion

In the boreal forest, the forest floor of mature stands exerts a significant influence on ecosystem dynamics at the ground and below ground levels (Van Cleve and Viereck, 1981; MacLean *et al.*, 1983; Bonan, 1992). The results obtained in the present study support the idea that forest floor disturbance is an important element in the dynamics of boreal forest regeneration. However, the forest floor environment generated by the forestry practices examined in this study has not led to the development of regeneration patterns similar to those observed following fire. Thus certain concerns need to be expressed in regards to the types of harvesting methods that can be associated to sustainable forestry. For example, clear-cut logging with protection of natural regeneration and protection of soils (CPRS) aims for the maintenance of a sustainable yield by improving natural tree regeneration and minimizing soil disturbance. However, it also promotes the subsistence of a significant expanse of undisturbed feathermoss cover on the forest floor which does not correspond to the environmental conditions usually found following a fire. The exclusion of many pioneer species and the promotion of the residual species that result may have profound implications for the conservation of diversity in the boreal forest and the maintenance of natural regeneration dynamics at the stand level or any other successional processes occurring under a natural disturbance regime.

On the other hand, silvicultural practices that create favourable forest floor conditions for the establishment of pioneer species, many of which are commercial tree species, have a greater chance of preserving the integrity of ecological dynamics and processes of the boreal forest ecosystem. Scarification following logging has been reported to significantly increase the area of favourable seedbed surfaces and to improve certain growth conditions for pioneer tree species of the boreal forest (Prévost, 1996; Prévost, 1997). However, a decrease in available soil nutrients has also been observed following scarification (Prévost, 1996). Prescribed burning is another post-harvest site preparation method which has been reported to improve the regeneration of many pioneer boreal species (Johnston and Elliott, 1996; Whittle *et al*., 1997). Improvement of seedbed and growth conditions as well as control of competing species are two silvicultural objectives that can be attained with the use of this method (Tellier *et al*., 1995a). As with wildfires, patterns of revegetation following prescribed burning are dependent upon its severity (Tellier *et al*., 1995b; Whittle *et al*.).

The regeneration of boreal forest stands following major disturbances does not only depend on the modification in the stand's physical structure, but also on changes brought about by the disturbances in the soil nutritional dynamics (Viereck, 1983). Simard *et al*. (1999) has observed differences between the soil nutrient status of the burned and logged stands examined in this study. Given that the maintenance of forest soil productivity is also a defining element of sustainable forestry, the next step in the evaluation of intensive logging activities as a sustainable forestry practices should include an examination of the relationships that exist between soil nutrient dynamics and the composition of the regenerating vegetation following wildfire and logging.

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2.8 Appendix A

List of species used in correspondence analyses with attributed reproductive strategy.

Species	strategy	source
- Lichens		
Cladina mitis (Sandst.) Hale and Culb.	avoider	1, 2, 3
Cladina rangiferina (L.) Harm	avoider	1, 2, 3
Cladina stellaris (Opiz) Brodo	avoider	1, 2, 3
Cladonia botrytes (Hag.) Willd.	invader (xeric)	1, 2, 3
Cladonia cenotea (Ach.) Schaer.	invader (xeric)	1, 2, 3
Cladonia cornuta (L.) Hoffm.	invader (xeric)	1, 2, 3
Cladonia crispata ((Ach.) Flot.	invader (xeric)	1, 2, 3
Cladonia cristatella Tuck./*coccifera* (L.) Willd.	invader (xeric)	1, 2, 3
Cladonia deformis (L.) Hoffm.	invader (xeric)	1, 2, 3
Cladonia gracilis ((L.) Willd.	invader (xeric)	1, 2, 3
Cladonia spp.	invader (xeric)	1, 2, 3
Trapeliopsis granulosa	invader (xeric)	1, 2, 3
- Mosses and liverworts		
Brachythecium sp.	avoider	
Ceratodon purpureus	invader	4
Dicranum spp.	avoider	
Hylocomnium splendens (Hedw.) BSG	avoider	4, 5
Marchantia polymorpha	invader	1,4, 6
Pleurozium shreberi (BSG) Mitt.	avoider	5
Pohlia sp.	invader	7
Polytrichum spp.	invader	4
Ptilidium ciliare	avoider	5
Ptilium crista-castrensis (Hedw.) De Not	avoider	5
Sphagnum spp.	avoider	
- Herbs, grasses and sedges, and low shrubs		
Aralia hispidula Vent.	evader	4
Aralia nudicaulis L.	endurer	4, 6
Calamagrostis canadensis (Michx) Nutt.	invader / endurer	1, 4, 6
Carex aenea Fern.	invader	1, 4
Carex brunnescens(Pers) Poir.	invader	1
Carex deflexa Hornem.	invader	1

Species	strategy	source
- Herbs, grasses and sedges, and low shrubs (continued)		
Carex tonsa (Fern.) Bickn		
Carex spp.	invader / endurer	6
Cassandra caliculata (L.) D. Don.	endurer	8
Clintonia borealis (Ait.) Raf.	endurer	6
Comandra livida Richards	evader	4
Coptis groenlandicus (Oeder) Fern.	avoider	8
Cornus canadensis L.	endurer	4, 6, 9
Deschampsia flexuosa (L.) Trin	endurer	
Diervilla lonicera Mill.	endurer	6
Dryopteris spinulosa (O. F. Muell.) Watt.	endurer	6
Epigaea repens L.	evader	10
Epilobium angustifolium L.	invader	4
Equisetum silvaticum L.	endurer	4, 11
Gaultheria hispidula (L.) Muhl.	evader	6
Kalmia angustifolia L.	endurer	8
Ledum groenlandicum Retzius	endurer	4, 8
Linnaea borealis L.	avoider	4, 8, 9
Listera cordata (L .) R. Br.	avoider	
Lycopodium annotinum L.	avoider	8
Lycopodium clavatum L.	avoider	8
Lycopodium obscurum L.	endurer	6, 8
Maianthemum canadense Desf.	endurer	4, 6
Melampyrum lineare Desr.	evader	
Monotropa uniflora L.	avoider	4
Poaceae		
Pteridium aquilinum (L.) Kuhn.	endurer	4, 8
Pyrola secunda L.	avoider	9
Ribes glandulosum Grauer	evader	4, 6
Rubus chamaemorus L.	endurer	
Rubus idaeus L.	evader / endurer	1, 6, 12
Solidago macrophylla Pursh.	invader	
Trientalis borealis Raf.	endurer	6, 13
Vaccinium angustifolium Ait.	endurer	6
Vaccinium cespitosum Michx	endurer	
Vaccinium myrtilloides Michx	endurer	4, 8
Vaccinium oxycoccos L.	endurer	8
Viola sp.	evader	6
- Tall shrubs and trees		
Abies balsamea (L.) Mill.	avoider	4

Species	strategy	source
- Tall shrubs and trees (continued)		
Acer spicatum Lam.	endurer	
Alnus rugosa (Du Roi) Sprang	endurer	6
Amelanchier spp.	endurer	6
Betula papyrifera Marsh.	invader / endurer	4
Corylus cornuta Marsh.	endurer	6, 12
Nemopanthus mucronatus (L.) Trel.	endurer	
Picea mariana (Mill.) BSP	evader / endurer	10
Pinus banksiana Lamb.	evader	4, 10
Populus tremuloides Michx.	invader / endurer	4, 10
Prunus pensylvanica L.	evader	4, 13
Salix spp.	endurer	
Sorbus americana Marsh.	endurer	
Viburnum cassinoides L.	evader	4
Viburnum edule L.	evader	4

Sources : [1]Scotter, 1964; [2]Foster, 1984; [3]Morneau and Payette, 1989; [4]Rowe, 1983; [5]Rydgren and Hestmark, 1997; [6]Ahlgren, 1960; [7]Ahlgren and Ahlgren, 1960; [8]Flinn and Wein, 1977; [9]McLean, 1969; [10]Sirois, 1995; [11]Beasleigh and Yarranton; [12]Ahlgren, 1974; [13]Anderson and Loucks, 1973; [13]Marks, 1974;

SOIL AND PLANT INTERACTIONS FOLLOWING CLEARCUT HARVESTING AND WILDFIRE IN THE QUEBEC BLACK SPRUCE-FEATHERMOSS FOREST

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3.1 Abstract / Résumé

Relationships between early regenerating vegetation and soil fertility were examined for 73 clear-cut and burned stands of the black spruce-feathermoss forest of central and western Quebec. Partitioning of the variance of the vegetation data between soil fertility and general site characteristic variables was carried out to evaluate the direct influence of post-disturbance soil fertility on the composition of the regeneration. 54% of the variance was explained by all the measured environmental variables, of which 23% was exclusively attributed to soil fertility variables. A partial CCA performed with soil fertility as constraining variables and site characteristics as covariables identified two general patterns of soil-plant interactions during early regeneration. The first gradient of stand differentiation illustrated the important influence of the nutrient pulse often observed in the initial years following disturbance by fire. The second gradient of stand differentiation illustrated the increasing influence of the regenerating vegetation on soil nutritional dynamics in the following stages of early succession. These results indicate that disturbance severity, which directly affects the initial composition of the regenerating vegetation, may indirectly affect soil fertility and stand productivity in the later stages of regeneration.

Les relations existant entre la végétation de début de succession et la fertilité du sol ont été examinées à l'aide de 73 peuplements coupés ou brûlés dans la pessière noire à mousses du centre et de l'ouest du Québec. Afin d'évaluer l'influence directe de la fertilité du sol sur la composition de la régénération végétale, la variance observée dans les données de végétation a été partitionnée entre des variables reflétant la fertilité du sol et les caractéristiques générales des sites. Cinquante-quatre pourcent de la variance a pu être expliquée par l'ensemble des variables environnementales mesurées, dont 23% exclusivement attribués à la fertilité des sols. Une ACC partielle a été effectuée en utilisant les variables de fertilité de sol comme contrainte et les variables de caractéristiques générales des sites comme covariables. L'ordination obtenue a permis d'identifier 2 patrons généraux d'interaction sol-plantes durant les stades initiaux de succession. Le premier gradient de différentiation des peuplements illustre l'influence de la forte augmentation initiale de la fertilité des sols durant les premières années suite au feu. Le deuxième gradient de différentiation illustre l'influence croissante de la régénération végétale sur les dynamiques nutritionnelles des sols durant les stades subséquents de début de succession. Ces résultats indiquent que la sévérité de la perturbation affecterait indirectement la fertilité du sol et la productivité d'un peuplement forestier durant sa régénération à travers son influence directe sur la composition initiale de la régénération végétale.

3.2 Introduction

Mature black spruce-feathermoss stands are characterized by a closed coniferous canopy, sparse understory vegetation and a continuous mat of feathermoss (Larsen, 1980). As crown closure increases, light and temperature at the forest floor decreases, slowing decomposition and increasing productivity of the feathermoss layer (Larsen, 1980; Van Cleve and Viereck, 1981; Bonan, 1992). Weber and Van Cleve (1984) observed the primary productivity of feathermoss to exceed that of the tree species present in late boreal succession. The build-up of organic matter in the forest floor represents an increasing nutrient sink whereby large amounts of nutrients are removed from circulation and nutrient supply may limit plant growth (MacLean *et al*., 1983).

In Canada, clear-cut harvesting annually affects an area of productive forest proportional to that of wildfire (Canadian Council of Forest Ministers, 1996). Both these disturbances are major agents of stand initiation in the boreal forest as they generate favorable establishment conditions for pioneer species by removing the forest canopy and modifying forest floor structure (Kelsall *et al*.; 1977, Payette, 1992; Keenan and Kimmins, 1993). In addition, growth of regenerating vegetation is facilitated by the release of nutrients immobilized in the forest floor during wildfire (Viereck, 1983). Similarly, improved environmental conditions at the level of the forest floor following clear-cutting increase nutrient mineralization (Keenan and Kimmins, 1993). However, many comparative studies have found differences in the composition of regenerating vegetation following wildfire and clear-cutting in the boreal forest (Noble *et al*., 1977; Abrams and Dickmann, 1982; Carleton and MacLellan, 1994; Johnston and Elliott, 1996; Ehnes, 1998; Nguyen-Xuan *et al*., 1999). This suggests that these two disturbance types may exert different influences on the dynamics of stand regeneration.

Ecosystem processes such as the bioregulation and feedback mechanisms between soil and plants are an important part of successional dynamics in the boreal forest. Brumelis and Carleton (1988, 1989) observed that differences in post-disturbance vegetation composition could be associated to different soil nutritional dynamics. Chapin (1995) demonstrated that different colonizing species exhibited differences in their capacity to exploit soil nutrients following a major disturbance. Rintoul (1997) showed that differences in disturbance severity affected the plant tissue nutrient content of the regenerating vegetation. Differences in plant-soil relationships observed following different disturbance types and severity levels may have profound implications in the maintenance of soil processes (Perry, 1994).

Many studies have focused on the nutritional dynamics and/or vegetation composition following clear-cutting (Brumelis and Carleton, 1988; Brumelis and Carleton, 1989; Keenan and Kimmins, 1993; Brais et al., 1995a) or following wildfire (Alhgren and Alhgren 1960; Kelsall *et al.* 1977; Paré *et al.*, 1993; Brais *et al.*, 1995b). However there exists few comparative studies that have examined the possible influence of disturbance type and severity on the interaction between soil fertility and regenerating vegetation in the boreal forest (Johnston and Elliott, 1998). The objective of this study is then to examine the interactions between soil fertility and early regenerating vegetation after clear-cut harvesting and wildfire in the Quebec boreal forest. Previous parts of this study have shown that: 1) differences in the severity of forest floor disturbance can explain some of the compositional differences observed in early post-fire and post-logging vegetation (Nguyen-Xuan *et al.*, 1999), and 2) important differences in soil fertility exist following these two disturbance types (Simard *et al.*, 1999). The present part aims at showing that these differences in soil fertility following wildfire and clear-cut harvesting are also reflected in the post-disturbance vegetation composition.

3.3 Materials and methods

3.3.1 *Study Areas*

During the summer of 1997, forest stands disturbed within the last 21 years by extensive wildfires and clear-cut harvesting were compared in three separate study areas (Dieppe, St-Père, and Mathieu) located in the black spruce-feathermoss zone of the Quebec boreal forest. At the time of disturbance, all stands were mature, dominated by black spruce (*Picea mariana* [Mill.] BSP), and underlain by glacial till. The Dieppe study area was located in the northern clay belt and its surficial deposit consisted of till from glacial-lacustrine origin that was much finer than the glacial tills found in the other two study areas located on the boreal shield.

Timber was harvested by conventional clear-cut harvesting in the Dieppe and Mathieu study areas and by clear-cut harvesting with protection of regeneration and soils (CPRS) in the St-Père study area. CPRS resembles conventional clear-cutting with emphasis put on protecting natural tree regeneration and limiting the impact of mechanical harvesting on soils (Chevalier, 1993). However, due to insufficient densities of natural regeneration, scarification (disk) and tree planting were performed following harvesting in the St-Père study area. Main study area characteristics are provided in Table 3.1.

3.3.2 *Sampling*

In each stand a 25m x 25m plot was set up, within which the vegetation was sampled in 15 randomly located 1m x 1m quadrats. An estimation of the percent coverage of invascular and vascular plant species was performed for the vegetation on the ground, below 1m, and from 1-3m. The forest floor and mineral horizon were sampled at 8 of the 15 sampling points. Forest floor depth was measured, and a volumetric sample of both the forest floor (FH), and the mineral soil (0-10 cm) were taken at each sampling point. Forest floor samples were passed through a 1.5 cm sieve to remove coarse fragments and homogenize the sample (Paré et al. 1993). Samples were bulked to produce a composite sample of the forest floor and mineral soil in each plot. All samples were air dried prior to analysis. Aspect, slope, slope position, and moisture regime were recorded and the age of each stand at the time of disturbance was estimated by a count of the annual growth rings of five trees killed during the disturbance (burned snags or logging stumps).

3.3.3 *Lab Analysis*

Ahlgren and Ahlgren (1960) and Keenan and Kimmins (1993) provide reviews of the effects of wildfire and clear-cut harvesting on soil fertility. In general, significant effects can be observed in soil following these disturbances in terms of organic matter content, total and available nitrogen, available phosphorus, base cations, and pH. Forest floor and mineral soil samples were analyzed for organic carbon content using a modification of the Mebius procedure (Yeomans & Bemner, 1988), pH in 0.01M $CaCl_2$ (Hendershot *et al.* 1993), extractable base cations using 0.1N $BaCl_2$ (Hendershot & Duquette 1986) and Mehlich

Table 3.1. Site characteristics.

Study Area	Location	Replic.	Fire yr.	Fire Area (ha)	Cut yrs.	Forestry Region[a]	Avg. Soil Text. (0-10cm)	Avg. Annual Temp. (°C)[b]	Avg. Annual Precip. (mm)[b]
Dieppe	49°17'-51' 00 N 79°00'-19' 00 W	10 Fire 10 Cut	1976	31 054	1975-80	Northern Clay	Sandy Clay Loam	0.6	822
St-Père	48°44'-59' 00 N 76°08'-38' 00 W	10 Fire 10 Cut	1995	47 709	1992-94	Gouin	Loamy Sand	1.2	840
Mathieu	48°44'-57' 00 N 74°31'-54' 00 W	8 Fire 8 Cut	1983	14 535	1981-86	Gouin	Loamy Sand	0.8	948.4

[a]Forestry regions as proposed by Rowe (1972).
[b]Meteorological data provided by the nearest weather station (Anon,1982).

III available P (Tran & Simard 1993). Particle size analysis was performed on mineral samples pretreated for organic matter using the hydrometer method (McKeague 1976). Organic matter content of the forest floor was determined by loss on ignition using 2g of sample brought up to 550°C for two hours in a muffle furnace (Kalra and Maynard 1991). Forest floor samples were digested for measurements of total N, P, K, Ca and Mg (Parkinson & Allen, 1975). Concentrations of extractable and total Ca, K and Mg were measured using a Perkin-Elmer atomic absorption spectrometer. Total P and N and Mehlich III P, were determined colormetrically using a Lachat Quickchem automated chemical analysis system.

Net nitrogen mineralization (available N) and nitrification was measured on 5g of forest floor and 10g of mineral soil, brought up and regulated to 60% of field capacity during a 45 day aerobic incubation period in the dark at 24°C. Samples were then extracted with 1N KCl for available N and determined colormetrically as for total N above. Available N was determined as the concentration of NH_4^+ and NO_3^- in the incubated samples minus the concentration of NH_4^+ and NO_3^- in non-incubated samples. Net nitrification was calculated as the concentration of NO_3^- in the incubated samples minus the concentration of NO_3^- in non-incubated samples.

Microbial basal respiration was measured on 7g of forest floor and 15g of mineral soil, brought up to 60% of field capacity and incubated for 10 days at room temperature in 30 ml plastic jars. Prior to sampling the jars were flushed with ambient air and sealed for 1 hour. The accumulation of CO_2 in the plastic jars during the incubation period was determined using gas chromatography.

3.3.4 *Data Analysis*

Only species occurring in more than 10% and less than 90% of disturbed stands were selected for data analysis and the average cover of each of these species was determined for each sampled stand. A species list with the species codes used in graphical representations is provided in Appendix B. Canonical correspondence analysis (CCA) (ter Braak, 1986) was used to see if differences in species composition following wildfire and clear-cutting could be related to differences in soil fertility following these two disturbance types. CCA allows the simultaneous analysis of the overall species composition in relation to numerous environmental variables (ter Braak, 1987). In addition to, and in interaction with soil fertility, many other site-related factors can influence post-disturbance vegetation composition. These include light, temperature, and moisture regimes, and disturbance history. Thus the environmental variables used in the CCA included soil fertility variables as well as site characteristics variables. Since CCA is a multivariate method closely related to multiple linear regression (ter Braak, 1986), the number of environmental variables used and the amount of collinearity between them had to be minimized. Thus, subsets of soil fertility and site characteristic variables were separately chosen through forward selection at a level of significance of 0.1. The final soil fertility subset consisted of the following variables: concentrations of extractable Ca, organic C, and mineralized N, pH, and basal respiration in the mineral soil, and concentrations of extractable Ca, P, and total N, mass of organic matter and mineralized N in the forest floor. The description and abbreviation of each soil variable is provided in Table 3.2. The final site characteristics subset consisted of: average duff depth, percent sand (0-10cm), aspect, moisture regime, stand age at the time of disturbance, time since most recent disturbance, and longitude.

The relationships between early post-disturbance vegetation composition and soil fertility were examined using three different CCAs. The first CCA (Global) included both explanatory subsets as environmental variables. The second CCA (Soil Fertility) only included the soil fertility subset as environmental variables, while the third CCA (Partial Soil Fertility) used the soil fertility subset as environmental variables and the site characteristics subset as covariables. These different CCAs enabled a better evaluation of the effects of soil fertility on post-disturbance vegetation with and without the consideration of the influence of site characteristics. The importance of this influence was evaluated through the partitioning of the variance (Borcard *et al.*, 1992) observed in the vegetation between the subsets of soil fertility and site characteristic variables. Levels of correlation (Spearman) between fertility variables and descriptive vegetation variables were also examined. Except for Spearman's and Pearson's correlation performed using the SPSS analytical software package (SPSS, 1997), statistical analysis were performed using the CANOCO statistical package (ter Braak, 1987-1992).

Table 3.2. Environmental variables used in the variance partitioning and canonical correspondence analysis.

Subset	Environmental Variable	Description
Site Characteristics	Duff	Average duff depth in each site
	Sand	Percent sand of the first 10cm
	Aspect	Aspect of site - between 0 (N) and 180 (S)
	Moist.	Moisture regime
	Time	Time since most recent disturbance
	Age	Stand age at time of disturbance
	Long.	Longitude of each site
Soil Fertility	MCExtCa	Concentration of extractable Ca in the mineral soil
	MCOrgC	Concentration of organic C in the mineral soil
	MCMin	Concentration of mineralized N (available N) in the mineral soil
	MpH	Mineral soil pH
	Mbasal	Basal respiration in the mineral soil
	FCExtCa	Concentration of extractable Ca in the forest floor
	FCExtP	Concentration of Mehlich III extractable P in the forest floor
	FCTotN	Concentration of total N in the forest floor
	FMIgn	Mass of organic matter in the forest floor determined by loss on ignition
	FMMin	Mass of N mineralization (available N) in the forest floor

3.4 Results

3.4.1 *Variance Partitioning and the Global Perspective*

All explanatory variables (Global CCA) accounted for 63.6% of the variance in the vegetation data set (Figure 3.1). Soil fertility and site characteristics exclusively accounted for 23.2% and 14.7%, respectively, of the variance in the vegetation data set with the remaining 25.7% of the variance explained by the confounded effect of both sets of explanatory variables. The first axis in the Global CCA accounted for nearly 17% of the total variance in the vegetation data set and separated out the St-Père burned stands from the other disturbed stands (Figure 3.2). Associated with the St-Père burned stands was a nutrient pulse represented by extractable P (FCExtP). The environmental variables with the highest level of association to the first axis were: extractable P, time since most recent disturbance, and duff depth (Table 3.3). The second axis represented about 14% of the total variance and separated out the Mathieu and Dieppe burned stands from the cluster of cut stands around the origin (Figure 3.2). Longitude and total N in the forest floor were the environmental variables that showed the greatest association to this axis ($r > 0.50$), and mineralized N in the mineral soil, percent sand, mineralized N in the forest floor, and pH of the mineral soil also showed some degree of association to it (Table 3.3).

The Soil Fertility CCA (not shown) was very similar to the Global CCA. For the first three axes of the two ordinations, correlation coefficients (Pearson's r) between the site scores of the two ordinations were 1.00, 0.93 and 0.92. The correlation coefficients were 0.97, 0.94 and 0.89 between species scores. Both ordinations were therefore very similar, having similar patterns of stand differentiation. Furthermore, even though the soil fertility variables were the only variables used to constrain the ordination axes of the Soil Fertility CCA, little change was seen in the correlation coefficients of most environmental variables in comparison to the ones obtained in the Global CCA (Table 3.3). Thus, the Soil Fertility CCA represented the influence of soil fertility with the confounded influence of site characteristics. The Soil Fertility CCA explained 48.9% of the total variance in the vegetation data set (Figure 3.1).

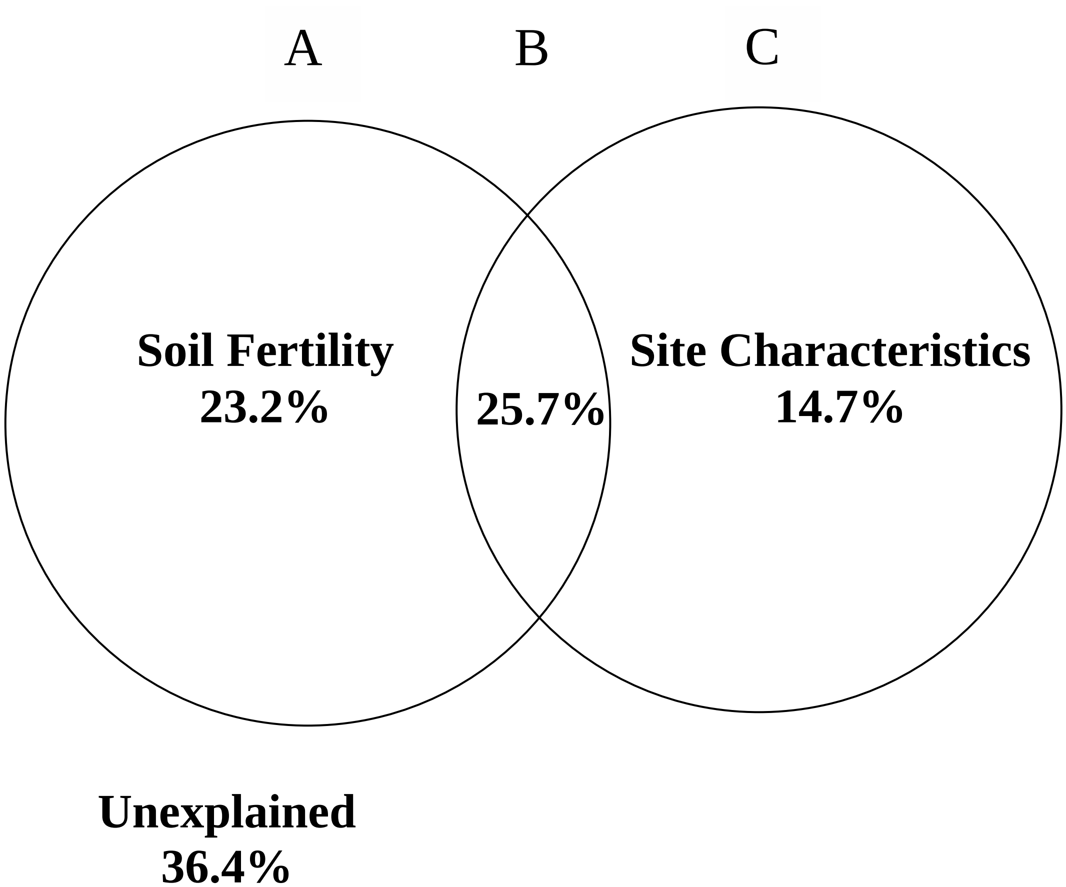

Figure 3.1. Partitioning of the vegetation data set variance using soil fertility and site characteristics as subsets of explanatory variables. Global CCA = A + B + C. Soil Fertility CCA = A + B. Partial Soil Fertility = A.

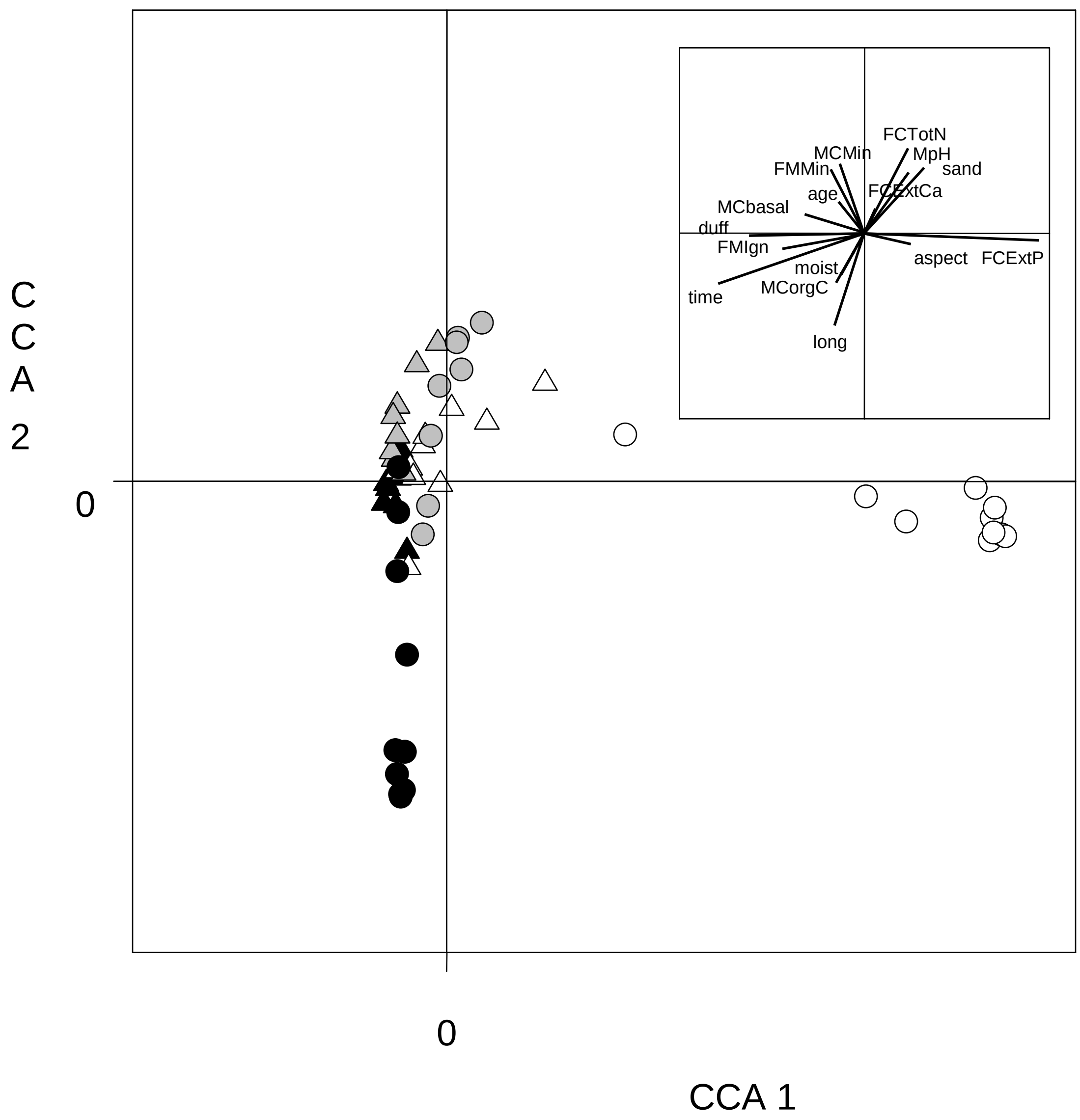

Fig. 3.2. Global CCA ordination of disturbed sites along two first CCA axes. Fire (○) and clear-cut (△) sites of the St-Père area. Fire (●) and clear-cut (▲) sites of the Dieppe area. Fire (◯) and clear-cut (△) sites of the Mathieu area.

Table 3.3. Interset correlation coefficients of environmental variables with the first and second axes of the Global CCA, Soil CCA, and Partial Soil CCA. Passive analysis of site characteristics variables was used to determine their interset correlation coefficients for the Soil CCA. There are no interset correlation coefficients given for the site characteristics variables in the Partial Soil CCA since these variables are used as covariables in this analysis.

	Global CCA		Soil CCA		Partial Soil CCA	
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
-Soil fertility variables						
MCExtCa	-0.07	-0.03	-0.08	-0.08	0.23	0.25
MCOrgC	-0.13	-0.34	-0.15	-0.43	0.05	0.02
MCMin	-0.12	0.49	-0.10	0.41	0.26	0.15
MpH	0.21	0.43	0.23	0.53	0.37	0.09
Mbasal	-0.28	0.14	-0.27	0.16	0.23	-0.09
FCExtCa	0.05	0.18	0.06	0.34	0.63	0.38
FCExtP	0.82	-0.04	0.84	-0.12	-0.38	0.69
FCTotN	0.21	0.59	0.25	0.73	0.49	0.48
FMIgn	-0.38	-0.11	-0.41	-0.21	0.05	0.03
FMMin	-0.16	0.45	-0.14	0.36	0.33	-0.05
-Site characteristics variables						
Duff depth	-0.54	-0.01	-0.56	-0.17	-	-
Percent sand	0.28	0.46	0.32	0.54	-	-
Aspect	0.22	-0.07	0.23	0.03	-	-
Moisture regime	-0.11	-0.28	-0.12	-0.40	-	-
Time since most recent disturbance	-0.69	-0.35	-0.69	-0.29	-	-
Stand age at time of disturbance	-0.12	0.22	-0.09	0.29	-	-
Longitude	-0.14	-0.63	-0.19	-0.69	-	-

3.4.2 *The Soil Fertility Perspective*

About 52% of the variation explained by the Partial Soil Fertility CCA can be represented on the first two ordination axes. Two main directions of stand differentiation could be observed in the ordination space of the two first CCA axes (Figure 3.3). The cut and burned stands of the St-Père study area were separated from disturbed sites of the two other study areas along the first direction of differentiation. Associated with the fire sites of the St-Père area is a pulse of available nutrients represented by extractable P in the forest floor (FCExtP). The average concentration of extractable P in the cluster of fire sites of this area is 2.5 times greater than any site outside the association. This first gradient was more strongly associated with the second ordination axis (Table 3.3). Also associated with the early fire and nutrient pulse was a high presence and abundance of *Marchantia polymorpha* (bmp), *Ceratodon purpureus* (bcp), and *Epilobium angustifolium* (cea) (Figure 3.4). The cut sites of the St-Père area were located at the opposite end of the first differentiating gradient in respect to the fire sites of the same area, and were characterized by a high presence and abundance of *Aralia hispida* (cah), *Carex deflexa* (ccxd), and *Betula papyrifera* (cbp).

The second differentiating direction corresponded to a soil fertility gradient represented by extractable Ca (FCExtCa) and total N (FCTotN) in the forest floor, extractable Ca (MCExtCa), mineralized N (MCMin), pH (MpH), and basal respiration (MCBasal) in the mineral soil, and finally mineralized N in the forest floor (FMMin) (Figure 3.3). The following vascular plants were associated with increasing fertility (Figure 3.4): *Aralia nudicaulis* (can), *Clintonia borealis* (ccb), *Deschampsia flexuosa* (cdf), *Pinus banksiana* (cpb, dpb), *Prunus pensylvanica* (cpp, dpp), *Pteridium aquilinum* (cpa), *Rubus idaeus* (cri), *Solidago macrophylla* (csm), *Sorbus americana* (csa, dsa), *Trientalis borealis* (ctb) *Viburnum cassinoides* (cvbc, dvbc). Associated with decreasing fertility were *Abies balsamea* (cab, dab) and many cryptograms: *Cladina mitis* (acm), *Cladonia cenotea* (accn), *Cladonia crispata* (accp), *Hylocomnium splendens* (bhs), *Pleurozium shreberi* (bps), *Ptilidium ciliare* (bpcl), *Ptilium crista-castrense* (bpcr), *Trapeliopsis granulosa* (atg). Associated with the fertility gradient was the differentiation of the majority of Mathieu burned and Dieppe cuts stands with increasing fertility, and the majority of Mathieu cut and Fig. 3.3.

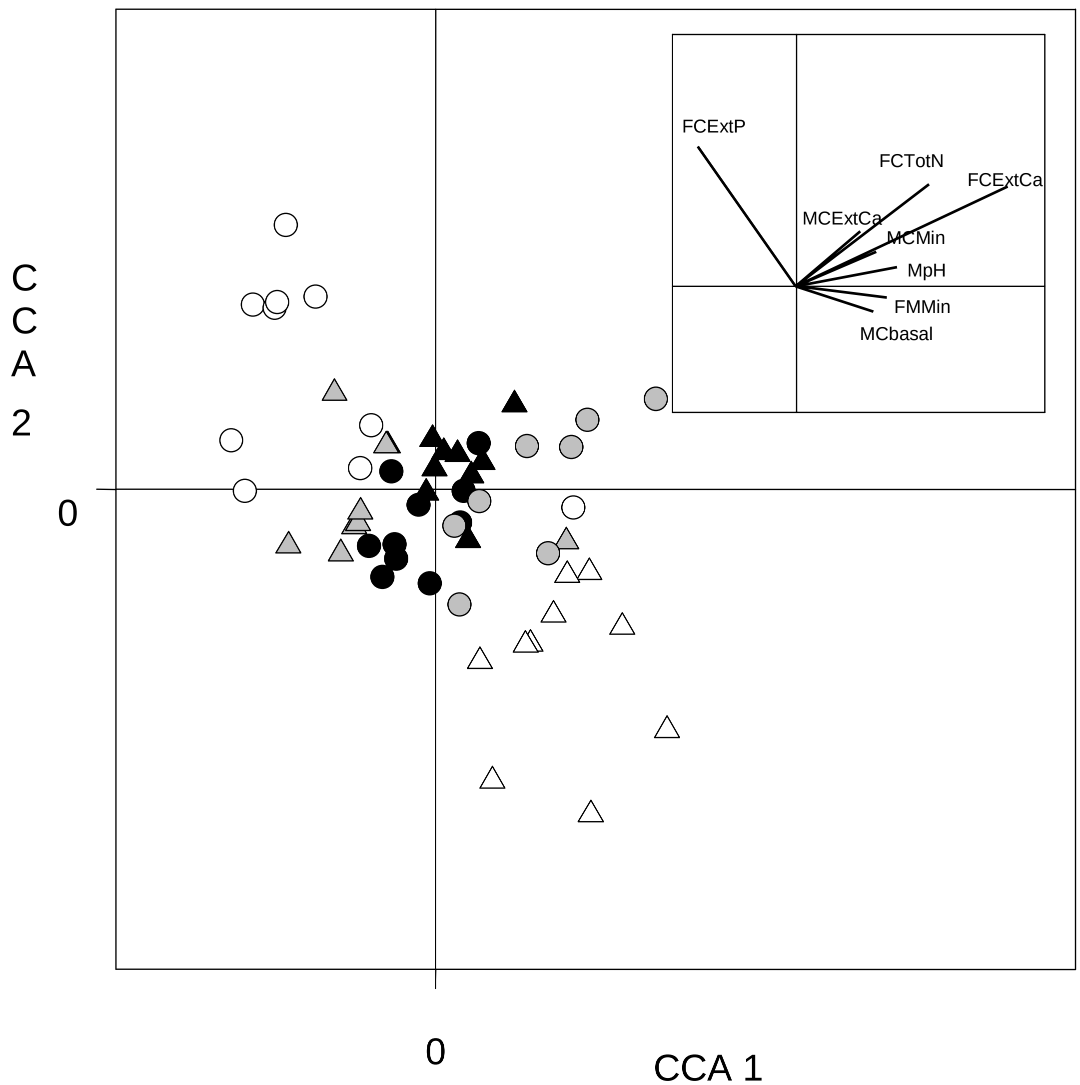

Fig. 3.3. Partial Soil Fertility CCA ordination of disturbed along two first CCA axes. Symbols are the same as in previous figure.

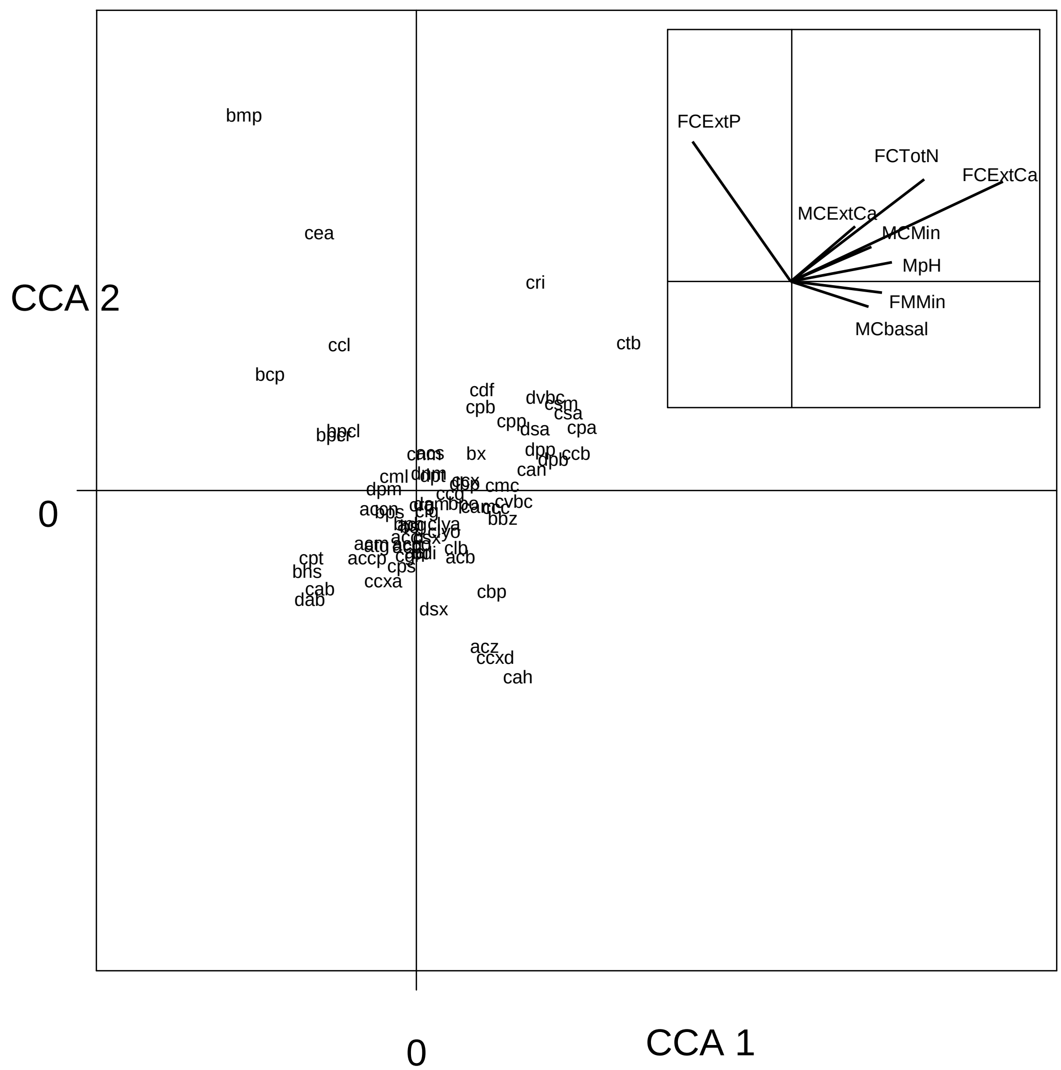

Fig. 3.4. Partial Soil Fertility CCA ordination of species along two first ordination axes. Species full name provided in appendix 1. Prefixes describe plant form : lichens (a), bryophytes (b), vascular plants below 1 m (c), vascular plants between 1 and 3 m (d).

Dieppe burned stands with decreasing fertility (Figure 3.3). This second differentiating gradient is generally more pronounced along the first ordination axis (Table 3.3). The position of the stands on the second and third CCA axes (not shown) indicated that increased extractable Ca (FCExtCa) and total N (FCTotN) in the forest floor greatly contributed to the differentiation of the Mathieu fires from the Mathieu cuts, while increased mineralized N in the forest floor and mineral soil (FCMin, MCMin) greatly contributed to the differentiation of the Dieppe cuts from the Dieppe fires.

The concentration of total N in the forest floor showed a significant positive correlation (Spearman's r, $p<0.01$) with the concentration of mineralized N in the forest floor (r = 0.38), the total cover of deciduous shrubs and trees (r = 0.38), and the total cover of herbaceous plants (r = 0.67). It showed a significant negative correlation with the C:N in the forest floor (r = -0.64) and total cover of lichens (r = -0.32, p = 0.015). Herbaceous vegetation was also significantly positively correlated with the concentration of mineralized N in the forest floor (r = 0.42) while lichens were negatively correlated to it (r = -0.43). Cover of deciduous shrubs and trees and total cover of vascular plants (herbs and deciduous) were positively correlated to extractable Ca in the forest floor (r = 0.44 and 0.47 respectively). Increasing humus depth was associated with decreasing herbaceous cover (r = -0.32, p = 0.016), decreasing total N in forest floor (r = -0.29, p = 0.029). The most important relationships are illustrated in Fig. 3.5.

3.5 Discussion

3.5.1 *Importance of the influence of soil fertility on post-disturbance vegetation composition*

The series of canonical correspondence analyses (CCA) using different sets of explanatory variables provides insight into the respective influence of physical site characteristics and site fertility variables on post-disturbance vegetation composition. Variance partitioning and the high correlation between the scores in the Global and Soil Fertility CCAs demonstrate the importance of the interaction between nutritional dynamics and the physical environment in describing the variation in the composition of vegetation in the boreal forest. It has long been recognized that physical environmental variables, such as moisture and temperature regimes affect nutrient dynamics in forest ecosystems (Perry,

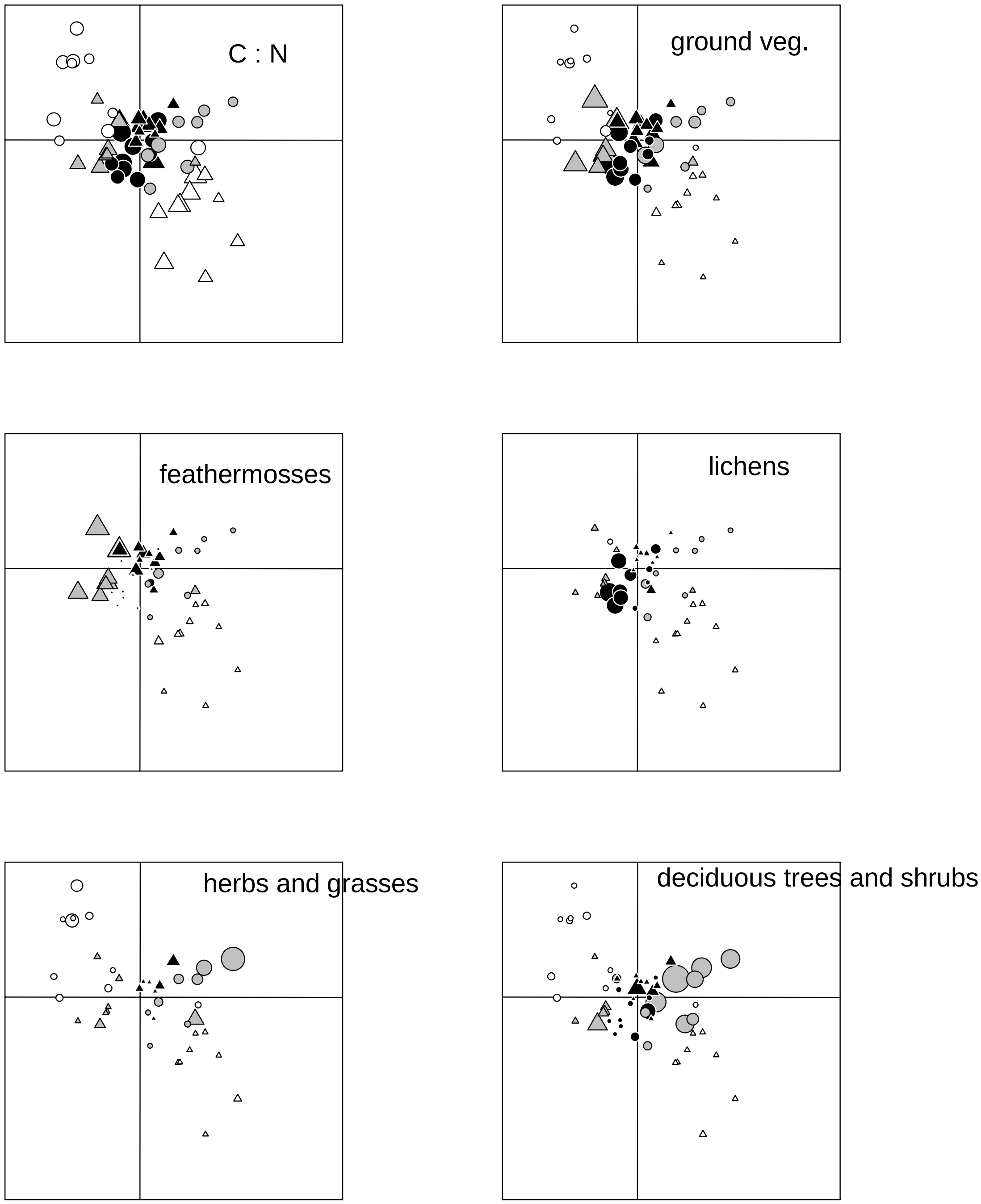

Fig. 3.5. Partial Soil Fertility CCA ordination of disturbed stands. Size of symbol is proportional to value of descriptor observed at a given site. Descriptors illustrated are : forest floor C : N, % cover of groung vegetation, % cover of feathermosses, % cover of lichens, % cover of herbs and grasses, % cover of deciduous shrubs and trees. Symbol legend same as in previous figures.

1994). However, although a large part of the changes observed in soil nutritional dynamics following wildfire and clear-cut harvesting indirectly result from changes in the physical properties of the forest floor (Woodmansee and Wallach 1981; Keenan and Kimmins 1993), an important portion of the nutrient changes can also be directly attributed to disturbance itself as illustrated by the significant amount of variance accounted for by the third CCA (Partial Soil Fertility). This is especially true for disturbances such as wildfire which are capable of generating a pulse of available nutrients through the oxidization of carbon, mineralizing nutrients in the forest floor and aboveground biomass (Simard *et al.*, 1999). Thus it becomes interesting to examine the relationship that exists strictly between soil nutrients and plants during early succession.

3.5.2 *Interactions between post-disturbance soil fertility and vegetation composition*

Soil-plant interactions are an integral part of the regeneration dynamics of forest ecosystems. Plant growth is directly linked to the availability of the of soil nutrients and the life histories of many boreal plant species greatly reflects their ability to exploit the available nutrient resources at different times during forest succession (Chapin and Van Cleve, 1981). Thus, in many instances the vegetation composition of boreal stands can be determined by soil fertility (Carleton *et al.*, 1985). However, plants can equally influence soil fertility as they play a major role in soil nutrient cycling during all stages of succession through nutrient absorption, storage and release in the different compartments of the boreal forest (Van Cleve and Viereck, 1981). Therefore, vegetation composition can have an important influence on soil fertility (Paré *et al.*, 1993; Brais *et al.*, 1995b). When examining post-disturbance soil plant interactions, it is often difficult to determine which element (the vegetation or the soil nutrients) exerts the most influence on the other. The 2 main stand differentiating directions observed in the Global and Partial Soil Fertility CCAs are almost orthogonal, suggesting that they represent two distinct dynamics in the regeneration of forest stands following disturbance. They may provide some insight on the nature of soil-plant interactions during the regeneration of burned and clear-cut stands and their possible evolution with time.

The differential direction involving the sites of the St-Père area illustrates some of the soil-plant interactions observed immediately after disturbance. Many of the species strongly associated with the clear-cut and burned sites of this area (*Betula papyrifera*, *Carex deflexa*, *Ceratodon purpureus*, *Epilobium angustifolium* and *Marchantia polymorpha*) have often been reported as successful colonizers of exposed mineral soil after disturbance (Rowe 1983; Oswald and Brown 1993; Prévost 1997). *Betula papyrifera*, *Carex spp*., and *Epilobium angustifolium* are often the predominant species in the seed rain shortly after wildfire and clear-cut harvesting (Johnson, 1975; Archibold, 1980; Qi and Scarrett, 1998), and their association with recently disturbed sites reflects the favourable establishment conditions often encountered following severe wildfires and scarified clear-cuts (Nguyen-Xuan *et al*., 1999). Given that the ground and understorey vegetation cover did not exceed 15% in either burned or clear-cut sites, the influence of plants on soil fertility in the St-Père area was probably minimal. However, significant differences were observed for many soil fertility variables between the fire and cut sites (Simard *et al*., 1999). Thus, the differential direction observed illustrates the influence of soil fertility differences on the vegetation composition of early regeneration following wildfire and clear-cutting. The positioning of the phosphorus vector in the direction of the St-Père burned stands illustrates the importance of the nutritional pulse generated during fire. Phosphorus is an element that is highly available following fire, but whose availability quickly decreases afterwards (Viereck 1983). This nutrient pulse greatly favors the growth of post-fire thrivers such as *Marchantia polymorpha* and *Epilobium angustifolium* and their abundance soon decreases as the pulse subsides (Ahlgren, 1960; Stark and Steele, 1977).

The differential gradient involving the sites of the Mathieu and Dieppe areas illustrates some of the soil-plant interactions observed once most of the regenerating vegetation has become established, before tree dominance is attained in the canopy. The species that are located at the opposing ends of this gradient define two contrasting compositional types. The species associated with increased soil fertility characterize a vegetation composition that is mostly dense, tall, and dominated by herbaceous vascular plants and deciduous shrubs and trees. Many of them are shade intolerant species whose establishment and/or germination has been facilitated by the disturbance of the forest floor (Nguyen-Xuan *et al*., 1999). The species that are associated with lower soil fertility represent a vegetation composition that is dominated by conifers and high bryophyte or lichen ground cover. This compositional type often reflects lower levels of forest floor disturbance (Nguyen-Xuan *et al*., 1999). Given the greater cover of ground and understorey vegetation (28 to 66% and 36 to 70% respectively) in the disturbed stands of these two areas, the influence of plant composition on soil fertility is certainly more important than in the St-Père area. The litter produced by deciduous shrubs and trees, broadleaf herbs, grasses, and ferns associated with the direction of greater N mineralization is easier to degrade and therefore has a higher turnover rate than coniferous or invascular litter (Moore 1984). Furthermore, the lower ground cover of invascular vegetation amongst sites associated with increased mineralization is beneficial to nutrient turnover. Reindeer lichens and feather mosses, such as *Pleurozium schreberi* and *Hylocomnium splendens*, contain low concentrations of nutrients (Moore 1981), decreasing litter quality (Larsen, 1980; Van Cleve 1974). However, cool soil temperatures due to the insulating effect of the feather moss layer is often the most severe effect of the dominance of invascular plants on nutrient cycling in the boreal forest (Moore, 1981; Weber and Van Cleve, 1984). The nutritional gradient observed in the second differentiating direction thus corresponds to increased litter quality and rates of nutrient cycling associated with increased dominance of vascular plants as suggested by the positive correlation between total N, cover of vascular plants and N mineralization in the forest floor. In the boreal forest, nutrient inputs from atmospheric deposition and N fixation from plants like alder (*Alnus* spp.) are relatively low, causing the ecosystem to have a high dependence on the internal cycling of nutrients (Perry 1994).

3.5.3 *Severity of forest floor disturbance and post-disturbance soil fertility*

This study suggests that there is a dichotomy between stands regenerating with greater cover of lichens and mosses and those predominantly regenerating with vascular plants. Feathermosses are considered effective competitors for nutritional resources, intercepting nutrients from precipitation, throughfall and decomposing litter, reducing the availability of nutrients for vascular plant growth (Weber and Van Cleve, 1984). If disturbance is not severe enough to disrupt the competitive ability of the feather moss community present in late boreal succession, their dominance is likely to continue during stand initiation, suppressing seedling establishment and slowing rates of nutrient turnover (Fisher 1979; Steijlen et al. 1995).

In the present study, clear-cut harvesting often left a large portion of the forest floor untouched, whereas wildfire consumed at least a portion of the forest floor, and the ground and aboveground vegetation. It would seem that wildfire has greater potential to improve stand fertility as it disrupts the competitive ability of the understory and ground plant communities, and favours the establishment of vascular species that generate more labile litter. For clear-cut harvesting to maintain the productivity of boreal ecosystems, it must sufficiently disturb the competitive advantage of the nonvascular ground community. However, the location of the Dieppe fires at the lower end of the soil fertility gradient suggests that wildfires that only partially burn the forest floor do not necessarily improve stand fertility. In this area revegetation of burnt humus is often dominated by lichen communities, while vascular plant regeneration occurred mainly from the resprouting of underground parts and was predominated by ericaceous shrubs (Nguyen-Xuan *et al*., 1999). The resistance to decomposition of such vegetation types was demonstrated by greater N cycling following logging than burning nearly 20 years after disturbance (Simard *et al*., 1999). Thus even though the fire event in the Dieppe area might have provided a nutrient pulse in the early post-fire years, as is suggested in the St-Père area, forest floor disturbance was not severe enough to permit a broad establishment of a herbaceous and/or deciduous vascular vegetation that would have produced a litter of higher quality and enabled a greater nutrient turnover in the following years as suggested by many burns of the Mathieu area.

3.6 Conclusion

Disturbance type and severity of forest floor disturbance can affect post-disturbance regeneration dynamics in two ways. First, disturbance type and severity determine the composition of the vegetation that will establish itself immediately following disturbance. Second, once the immediate and direct effects of disturbance on vegetation establishment and soil nutrients have subsided, the indirect effects of disturbance type and severity on the regenerating stand can be observed through the increasing influence exerted by the established vegetation on soil nutritional dynamics. This has implications for sustainable forestry in the following ways: 1) the choice of harvesting method and post-harvest silvicultural treatments has to be made in function of the regeneration dynamics desired, with an important consideration for their effects on soil fertility, 2) concerns for the composition of the regenerating vegetation should not be exclusively in terms of commercial tree species, but should include other pioneer species that have beneficial effects on soil fertility.

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3.8 Appendix B

List of species used in ordinations. Ordination codes and litter quality producing types. Lichens (L), feathermosses (F), herbaceous (H), deciduous (D).

- Lichens

Trapeliosis granulosa	atg	L
Cladonia botrytes (Hag.) Willd.	acb	L
Cladonia cenotea (Ach.) Schaer.	accn	L
Cladonia cornuta (L.) Hoffm.	acco	L
Cladonia crispata (Ach) Flot.	accp	L
Cladonia cristatella Tuck./*coccifera* (L.) Willd.	acct	L
Cladonia deformis (L.) Hoffm.	acd	L
Cladonia gracilis (L.) Willd	acg	L
Cladonia spp.	acz	L
Cladina mitis (Sandst.) Hale and Culb	acm	L
Cladina rangiferina (L.) Harm.	acr	L
Cladina stellaris (Opiz) Brodo	acs	L

- Bryophytes

Brachythecium spp.	bbz	
Ceratodon purpureus	bcp	
Dicranum spp.	bdi	F
Hylocomnium splendens (Hedw.) BSG	bhs	F
Marchantia polymorpha	bmp	
Pleurozium shreberi (BSG) Mitt.	bps	F
Pohlia spp.	bph	
Polytrichum spp.	bpo	
Ptilidium ciliare	bpcl	F
Ptilium crista-castrensis (Hedw.) De Not	bpcr	F
Sphagnum spp.	bs	F
Unknown moss	bx	

- vascular plants (below 1 m)

Abies balsamea (L.) Mill.	cab	
Aralia hispida Vent.	cah	H
Amelanchier spp.	cam	D
Aralia nudicaulis L.	can	H
Betula papyrifera Marsh.	cbp	D
Clintonia borealis (Ait.) Raf.	ccb	

Cornus canadensis L.	ccc	
Coptis groenlandicus (Oeder) Fern.	ccg	
Comandra livida Richards	ccl	
Carex spp.	ccx	H
Carex aenea Fern.	ccxa	H
Carex deflexa Hornem.	ccxd	H
Deschampsia flexuosa (L.) Trin.	cdf	H
Epilobium angustifolium L.	cea	H
Gaultheria hispidula (L.) Muhl.	cgh	
Linnaea borealis L.	clb	
Ledum groenlandicum Retzius	clg	
Lycopodium annotinum L.	clya	
Lycopodium obscurum L.	clyo	
Maianthemum canadense Desf.	cmc	
Melampyrum lineare desr.	cml	
Nemopanthus mucronatus (L.) Trel.	cnm	D
Pteridium aquilinum (L.) Kuhn.	cpa	H
Pinus banksiana Lamb.	cpb	
Prunus pensylvanica L.	cpp	D
Pyrola secunda L.	cps	
Populus tremuloides Michx.	cpt	D
Ribes glandulosum Grauer.	crg	H
Rubus idaeus L.	cri	H
Sorbus americana Marsh.	csa	D
Solidago macrophylla Pursh.	csm	H
Salix spp.	csx	D
Trientalis borealis Raf.	ctb	

- vascular plants (1 – 3 m)

Abies balsamea (L.) Mill.	dab	
Amelanchier spp.	dam	D
Betula papyrifera Marsh.	dbp	D
Kalmia angustifolium L.	dka	
Nemopanthus mucronatus(L.) Trel.	dnm	D
Picea mariana (Mill.) BSP	dpm	
Pinus banksiana Lamb.	dpb	
Populus tremuloides Michx.	dpt	D
Prunus pensylvanica L.	dpp	D
Sorbus americana Marsh.	dsa	D
Salix spp.	dsx	D
Viburnum cassinoides L.	dvbc	D

CONCLUSION GÉNÉRALE

L'objectif principal de cette étude est d'évaluer l'influence du type de perturbation sur la dynamique de la régénération initiale de la végétation boréale. L'existence de différences importantes dans la composition de la végétation suite à la coupe et au feu a déjà été confirmée par des études effectuées dans d'autres régions de la forêt boréale (Noble *et al.*, 1977; Abrams et Dickmann, 1982; Carleton et MacLellan, 1994; Johnston et Elliott, 1996; Ehnes, 1998). L'étude présente vise plutôt à examiner les mécanismes de régénération qui peuvent expliquer ces différences.

Le chapitre 2 vérifie l'hypothèse que les modifications amenées à la structure du sol forestier par les différents types de perturbation jouent un rôle important dans les dynamiques de régénération de la végétation boréale. Ainsi, il est démontré que la sévérité de la perturbation du sol a une très forte influence sur les patrons de régénération observés. Une sévérité plus élevée associée aux stations brûlées du secteur de St-Père mène à une plus forte abondance d'espèces pionnières sur ces sites que sur les sites de coupe. Dans le secteur de Dieppe, même si la sévérité plus faible du feu ne permet pas l'établissement d'espèces pionnières classiques, l'élimination de la végétation au sol mène quand même à l'établissement d'une communauté végétale au sol significativement différente de celle observée après coupe. L'utilisation de stratégies de reproduction permet de comparer les patrons de régénération des différents secteurs d'étude et met en évidence que les différents patrons observés dans les secteurs de St-Père et de Dieppe ont été reproduits dans le secteur de Mathieu. L'ensemble de ces résultats démontre donc que la perturbation physique du sol est une composante importante des mécanismes régissant la régénération en forêt boréale. Cet aspect des mécanismes de régénération a déjà été étudié pour le feu (Ahlgren, 1960; Flinn et Wein, 1977; Schimmel et Granstrom, 1996) ou pour la coupe (Durand, 1989, Harvey et Bergeron, 1995; Prévost, 1996; Prévost, 1997) mais rarement dans le cadre d'une étude comparative (Rintoul, 1997).

Le chapitre 3 a pour but d'examiner l'influence que peuvent avoir sur la composition de la végétation les différences de fertilité du sol observées suite à différents événements de perturbation. L'examen commun de la végétation des trois secteurs d'étude en fonction des diverses variables caractérisant la fertilité des sols des sites perturbés permet d'illustrer que la nature des interactions sol-plantes durant la régénération évolue avec le temps. Durant les premières années suivant la perturbation, ce sont les changements engendrés au niveau de la fertilité des sols qui exercent une forte influence sur la composition de la végétation. Cependant, à mesure que s'estompe l'effet de ces changements l'influence de la composition de la végétation devient de plus en plus importante. De plus, ce chapitre met en évidence l'existence d'un lien important entre les stratégies de reproduction des espèces boréales et leurs stratégies nutritionnelles, tel que suggéré par Chapin et Van Cleve (1981). Ainsi, un grand nombre d'espèces pionnières affichent des taux élevés d'absorption, d'utilisation et d'accumulation d'éléments nutritifs et sont donc favorisées par l'augmentation de la fertilité des sols observée suite à plusieurs perturbations. Leur abondance en début de succession permettrait de minimiser la perte d'éléments nutritifs du système, de faciliter le cyclage des éléments nutritifs et d'établir un équilibre dans les dynamiques nutritionnelles durant la régénération du peuplement forestier (Marks et Borman, 1972; Marks, 1974). Ce lien qui existe entre les stratégies de reproduction et les stratégies nutritionnelles des espèces boréales implique que la sévérité de la perturbation du sol forestier aurait une influence tant sur la composition de la végétation durant la régénération de la forêt que sur la fertilité de ses sols.

Les résultats obtenus dans le cadre de cette étude ont donc certaines implications en terme des politiques d'aménagement durable de la forêt. L'un des premiers critères et indicateurs d'un aménagement durable (Conseil canadien des ministres des forêts, 1995) est la conservation de la diversité biologique. Les espèces pionnières sont une partie intégrante de la diversité biologique de la forêt boréale. Le maintien de leur présence dans le paysage forestier est donc essentiel à la conservation de cette biodiversité et un aménagement durable de la forêt nécessite donc que les pratiques sylvicoles prônées permettent l'établissement des ces espèces de début de succession suite à la récolte du peuplement. Un deuxième critère d'aménagement durable est le maintien et l'amélioration de l'état de productivité des écosystèmes forestiers. Le rôle important que jouent les plantes pionnières dans les dynamiques nutritionnelles des sols durant la régénération de la forêt démontre l'importance qu'il faut apporter à cette composante de la régénération naturelle dans nos politiques d'aménagement forestier. Cependant, plusieurs de ces espèces sont encore considérées comme étant des espèces compétitrices en terme de régénération commerciale (Jobidon, 1995). Il est donc important que l'aménagement forestier intègre l'ensemble de la composition végétale dans sa définition de la régénération forestière adéquate afin de respecter les critères et indicateurs d'aménagement durable mentionnés plus haut.

La présente étude ainsi que celle effectuée par Simard *et al*. (1999) forment le premier volet d'un projet visant à examiner l'influence du type de perturbation sur la productivité à long terme de la forêt boréale. Les relations observées en terme de composition de la végétation, de la fertilité des sols et de l'interaction entre ces deux éléments proviennent de comparaisons effectuées pour des peuplements à dominance d'épinette noire sur dépôt de till. Cependant la sévérité d'un feu ou d'une coupe peut varier en fonction du dépôt de surface et de la composition de la canopée forestière (Harvey et Bergeron, 1989; Kafka, 1997). Il est donc important d'évaluer comment les relations observées varient en fonction de ces facteurs. Les volets subséquents du projet s'efforceront également à examiner en profondeur la nature des interactions qui existent entre la végétation et les dynamiques nutritionnelles du sol ainsi que les différents mécanismes de cyclage des éléments nutritifs impliqués. Tous ces éléments serviront à l'élaboration d'un modèle qui permettra d'évaluer l'influence de différents types et régimes de perturbation sur la productivité à long terme de la forêt boréale menant à l'élaboration de politiques d'aménagement durable des ressources forestières.

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