UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

INFLUENCE DU PEUPLIER FAUX-TREMBLE SUR LE CYCLE DES ÉLÉMENTS NUTRITIFS, LA STRATE DU SOUS-BOIS ET LA PRODUCTIVITÉ DES PEUPLEMENTS FORESTIERS DOMINÉS PAR L'ÉPINETTE NOIRE DANS LA FORÊT BORÉALE DE L'OUEST DU QUÉBEC

THÈSE PRÉSENTÉE COMME EXIGENCE PARTIELLE DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

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SONIA LÉGARÉ

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RESUME DE LA THESE

La productivité des pessières voisinant le 49e parallèle à l'ouest du Québec est généralement inférieure à un mètre cube par hectare par année alors que la productivité des peuplements mixtes dans la même région oscille entre deux et trois mètres cube par hectare par année. Plusieurs facteurs peuvent expliquer cet écart, en particulier le sol mais aussi l'effet de la végétation sur la fertilité du sol. Pour des conditions de sols semblables, certaines études ont montré le potentiel des conifères à favoriser un couvert de mousses et d'éricacées qui peut réduire la température du sol, occasionner une remontée de la nappe phréatique et produire une litière de faible qualité favorisant ainsi une baisse de la fertilité du sol. D'autre part, la litière feuillue, notamment de peuplier faux-tremble, semble empêcher la croissance de mousses et accélérer le cycle des éléments nutritifs. Dans la forêt boréale du sud-ouest du Canada, la présence de peuplements mixtes d'épinette noire et de peuplier faux-tremble évoluant sur des conditions abiotiques similaires a offert l'opportunité d'étudier l'influence du peuplier faux-tremble sur le cycle des éléments nutritifs et la croissance de l'épinette noire. Un échantillonnage du sol minéral suivi par des analyses en laboratoire a permis de vérifier l'homogénéité des propriétés du sol minéral le long du gradient de surface terrière de peuplier faux-tremble. Bien qu'il y ait absence de corrélation entre la présence de tremble et les propriétés physiques et chimiques du sol minéral, la présence croissante du peuplier faux-tremble dans des peuplements dominés par l'épinette noire est associée avec une augmentation de la disponibilité des éléments nutritifs (Ca, Mg, K), du pH, du taux de décomposition et de la concentration en azote totale dans le sol organique, ce qui suggère que la présence de tremble pourrait augmenter la fertilité du site. De plus, la composition de la strate de sous-bois change en fonction de la présence de peuplier faux-tremble. Notamment, le recouvrement de mousses et de sphaignes diminue le long du gradient croissant de tremble suggérant que la présence de peuplier faux-tremble pourrait ralentir le processus de paludification rencontré dans les peuplements dominés par l'épinette noire sur la ceinture d'argile de l'Abitibi-Témiscamingue.

Un inventaire de la végétation arborescente ainsi que des analyses de tige révèlent qu'il y a une relation significative entre la surface terrière en peuplier et le volume marchand total du peuplement. Cependant, la relation entre la surface terrière en peuplier faux-tremble et le volume marchand en épinette noire n'est pas significative, suggérant un gain net en fibre de peuplier. L'effet positif du peuplier faux-tremble sur le dhp et la hauteur de l'épinette noire est présent seulement lorsque le peuplier faux-tremble couvre de 0 à 40 % de la surface terrière du peuplement. Ces résultats suggèrent que les deux espèces utilisent une niche écologique relativement différente et que la proportion de tremble influence l'intensité de la compétition interspécifique. De plus, l'augmentation significative de la hauteur de l'épinette noire le long du gradient de peuplier faux-tremble suggère que la présence du peuplier augmente la fertilité du sol par son influence sur la disponibilité des nutriments. L'aménagement de peuplements mixtes, qui sont abondamment représentés dans le paysage forestier, pourrait offrir une situation où l'utilisation économique la forêt pourrait être en accord avec l'aménagement écosystémique.

INTRODUCTION GENERALE

0.1 Dynamique naturelle et processus de paludification

La pessière noire est principalement structurée par les incendies forestiers (Heinselman, 1981; Payette, 1992) qui remettent en circulation les éléments nutritifs par la combustion de la litière et de la couche fibre-humus (FH) (MacLean et al., 1983). Le faible potentiel d'évapotranspiration de l'épinette et sa litière récalcitrante à la décomposition microbienne permet, en l'absence de feux de forêt, le développement d'une épaisse couche de matière organique composée principalement de sphaigne qui mène à une diminution de la profondeur de la nappe phréatique et au refroidissement du sol et, conséquemment, au ralentissement des cycles d'éléments nutritifs (Forster, 1985; Oechel et Van Cleve, 1986; Weber et Van Cleve, 1981). Ces conditions intensifient le processus d'appauvrissement du sol et peuvent mener à la convergence des peuplements matures vers une structure ouverte peu productive (1 m^3/ha/an; Foster, 1983; Oechel et Van Cleve, 1986; Van Cleve et Viereck, 1981; Viereck et Dyrness, 1979). Cependant, des peuplements de feuillus intolérants tel que le peuplier faux-tremble peuvent aussi dominer après feu (Gauthier et al., 2000). Ces peuplements évoluent vers des peuplements mixtes relativement productifs (2 - 3 m^3/ha/an). Contrairement à l'épinette noire, le peuplier faux-tremble, par ses exigences en terme d'éléments nutritifs, augmente la disponibilité des éléments nutritifs (Longpré et al., 1994; Paré et Bergeron, 1996; Van Cleve et Noonan, 1975). Le taux de décomposition supérieur de la litière dans les peuplements de peuplier faux-tremble que dans les peuplements résineux (Alban et Pastor, 1993; Bockheim et al., 1991) pourrait s'expliquer par la litière alcaline du peuplier faux-tremble, relativement facile à décomposer (Flanagan et Van Cleve, 1983; McClaugherty et al., 1985), qui est de plus négativement corrélée à la présence de bryophytes et de sphaignes. Dans un contexte d'aménagement forestier, le peuplier faux-tremble envahit les parterres de coupe de certains territoires autrefois occupés uniquement par l'épinette noire (Carleton et MacLellan, 1994; Fortin, 2000). La présence de peuplier faux-tremble dans les coupes nécessite des opérations de dégagement des jeunes plants dans les peuplements à vocation résineuse. Le peuplier faux-tremble, étant une espèce extrêmement bien adaptée aux conditions après perturbation (Peterson et

Peterson, 1992), peut être considéré comme une espèce compétitrice malgré son statut d'essence commerciale.

0.2 Aménagement écosystémique et aménagement mixte

L'aménagement écosystémique est une approche basée sur la dynamique naturelle de la forêt. Une approche d'aménagement écosystémique proposée par Bergeron et collaborateurs (Bergeron et Harvey, 1997; Bergeron et al., 1999) prône le maintien de la structure forestière à l'échelle du paysage en conservant trois cohortes de structure différente en proportion observée dans le paysage. Ainsi, l'aménagement de peuplements mixtes (feuillues et conifères) pourrait être perçu comme une composante, une cohorte, de l'aménagement écosystémique. Selon une théorie élaborée par Vandermeer (1989), l'aménagement de peuplements mixtes pourrait augmenter la productivité forestière sur une surface donnée due au principe d'exclusion compétitive et/ou aux mécanismes de facilitation de la productivité. L'exclusion compétitive est basée sur la séparation des niches écologiques des espèces combinées qui permet une utilisation complémentaire des ressources. La facilitation est décrite comme l'effet d'une espèce sur l'environnement qui affecte positivement les autres espèces. Selon Kelty (1992), des espèces forestières ayant une bonne différenciation de leur niche écologique et une utilisation efficiente de ressources limitées devrait fournir un rendement supérieur lorsque combiné en peuplement mixte. Ainsi, l'épinette noire, une espèce persistante tolérante à l'ombre ayant un réseau de racines fines localisé dans la couche superficielle du sol pourrait exploiter une dimension spatiale et temporelle différente du peuplier, une espèce décidue intolérante à l'ombre ayant un réseau de racines en profondeur (Strong et LaRoi, 1983). De plus, l'influence du peuplier faux tremble sur le cycle des éléments nutritifs pourrait contrecarrer le phénomène de paludification associé à la présence de l'épinette noire. L'aménagement mixte pourrait représenter dans certain cas une situation où les objectifs commerciaux de la forêt sont en accord avec l'aménagement écosystémique. En plus d'un souci croissant pour le maintien de la biodiversité et de gain possible en productivité, d'autres avantages pourraient stimuler l'aménagement mixte, tel que la diminution des risques associés aux chablis et aux épidémies d'insectes ou de maladies

(Kelty, 1992; Su, MacLean et Needham, 1996). De plus, le développement d'un marché croissant pour la fibre d'essences feuillues, comme le peuplier faux-tremble, rend plus réalisable l'aménagement de peuplements mixtes.

0.3 Influence de la composition forestière : l'œuf ou la poule?

Due à une multitude de combinaisons possibles d'espèces et à leurs différentes interactions sur le sol et la productivité, il n'y a pas de tendance générale dans la littérature scientifique pour guider concrètement l'aménagement mixte. En effet, le rendement des peuplements mixtes est controversé puisque selon les conditions environnementales, l'âge, les espèces et leurs proportions respectives, on observe des pertes ou des gains (Brown, 1992; Chen et Klinka, 2003; Frivold et Mielikäinen, 1990; MacPherson, Lieffers et Blenis, 2001). Tout comme pour l'observation de l'influence du couvert forestier sur la disponibilité des éléments nutritifs, l'observation d'une réelle augmentation du rendement est confrontée à un problème majeur lié à la stratégie d'échantillonnage. Est-ce que la combinaison de plusieurs espèces permet une augmentation du rendement ou est-ce seulement le reflet de la fertilité du site? Effectivement, dans plusieurs études, la présence d'une corrélation entre la fertilité du sol et la composition forestière ne permet pas de déterminer si l'augmentation du rendement est liée à la fertilité du sol ou à l'occurrence de mécanisme de facilitation et/ou d'exclusion compétitive.

0.4 Relations entre le couvert forestier et la strate de sous-bois

La strate de sous-bois est une composante importante de la biodiversité en forêt boréale. Elle reflète les conditions environnementales locales et est parfois considérée comme un indicateur de la productivité potentielle du site. De plus, les relations de compétition pour la lumière, l'eau et des éléments nutritifs disponibles dans cette strate affecte le succès initial des espèces arborescentes en régénération (Abrams et Dickmann, 1982; Brumelis et Carleton, 1989; George et Bazzaz, 1999; Kabzems et Lousier, 1992; Lieffers et MacDonald, 1993; Oechel et Van Cleve, 1986). La relation entre la strate de sous-bois et le couvert forestier est l'objet de plusieurs études qui concluent à un effet direct de la composition forestière, par son influence sur les processus écologiques tel que les cycles des éléments nutritifs et la disponibilité de l'eau et la lumière, sur la strate de sous-bois (Légaré et al., 2001; Légaré, Bergeron et Paré, 2002; Qian et al., 2003; Saetre et al., 1997; Whitney et Foster, 1988). Ces mécanismes sont souvent différents entre les peuplements feuillus intolérants et résineux (Anderson, Loucks et Swain, 1969; Brais et al., 1995; Constabel et Lieffers, 1996; Corns, 1989; Longpré et al., 1994; Messier, Parent et Bergeron, 1998; Paré et Bergeron, 1996; Van Cleve et Noonan, 1975). Cependant, nombres d'études expliquent la relation observée par une réponse similaire de la strate de sous-bois et de la composition forestière face aux variations des conditions environnementales (Carleton et Maycock, 1981; Gagnon et Bradfield, 1986; Gilliam et Roberts, 2003; Gilliam, Turrill et Adams, 1995; Host et Pregitzer, 1992). L'existence même de la relation entre les strates est aussi remise en question par certains auteurs (McCune et Antos, 1981).

0.5 Objectifs

Dans cette thèse, nous traiterons dans un premier chapitre de l'influence du peuplier faux-tremble sur les cycles des éléments nutritifs dans des peuplements dominés par l'épinette noire. Ensuite, l'influence du peuplier faux-tremble sur la croissance de l'épinette noire sera abordée sous deux angles différents : un chapitre utilisant une stratégie d'échantillonnage permettant d'avoir un maximum d'observations et un autre chapitre utilisant une approche qui permet de contourner la problématique de facteur confondant exposée ci-dessus. Finalement, un dernier chapitre sera consacré à la relation entre le couvert forestier et la strate de sous-bois. L'influence du peuplier faux-tremble dans les peuplements dominés par l'épinette noire sera discutée en fonction des processus écosystémiques, tels les cycles des éléments nutritifs et la transmission lumineuse, qui sont eux-mêmes affectés par le couvert forestier.

CHAPITRE I

THE RESPONSE OF BLACK SPRUCE GROWTH TO AN INCREASED PROPORTION OF ASPEN IN MIXED STANDS

Sonia Légaré, David Paré and Yves Bergeron

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1.1 Abstract

In the southeastern boreal forest of Canada, the presence of mixed stands of black spruce and aspen growing in similar abiotic conditions offers the opportunity to study the influence of aspen on stand volume and spruce growth. A regression analysis performed on field data from the ministère des Ressources naturelles du Québec revealed that there was a significant relationship between the relative basal area of aspen (aspen relative basal area was determined by the ratio of aspen basal area on total basal area of the stand) and the total stand merchantable volume after accounting for stand density. However, the relationship between total black spruce volume and relative basal area of aspen was not significant, implying that the volume gain was aspen fibre. The positive effects of aspen on black spruce dbh and height were only present when aspen proportion in the stand ranged between 0 and 41% of the total stand basal area. These results suggest that aspen uses a different niche than black spruce. Furthermore, the significant increase in black spruce dominant height along the aspen gradient suggests that aspen enhances soil fertility by its influence on nutrient availability. The management of mixed stands, which make up an important proportion of the landscape, offers an example as to how commercial management of the forest can be in agreement with ecosystem management.

1.2 Résumé

Dans la forêt boréale du sud-ouest du Canada, la présence de peuplements mixtes d'épinette noire et de peuplier faux-tremble évoluant sur des conditions abiotiques similaires a offert l'opportunité d'étudier l'influence du peuplier faux-tremble sur la croissance de l'épinette noire. Une analyse de régression effectuée sur des données d'inventaire du ministère des Ressources naturelles du Québec révèle qu'il y a une relation significative entre la surface terrière en peuplier et le volume marchand total du peuplement. Cependant, la relation entre la surface terrière en peuplier faux-tremble et le volume marchand en épinette noire n'est pas significative, suggérant un gain net en fibre de peuplier. L'effet positif du peuplier faux-tremble sur le dhp et la hauteur de l'épinette noire est présent seulement lorsque le peuplier faux-tremble couvre de 0 à 41 % de la surface terrière du peuplement. Ces résultats suggèrent que les deux espèces utilisent une niche écologique différente. De plus, l'augmentation significative de la hauteur de l'épinette noire le long du gradient de peuplier faux-tremble suggère que la présence du peuplier augmente la fertilité du sol par son influence sur la disponibilité des éléments nutritifs. L'aménagement de peuplements mixtes, qui sont abondamment représentés dans le paysage forestier, pourrait offrir une situation où les objectifs commerciaux de la forêt sont en accord avec l'aménagement écosystémique.

1.3 Introduction

The management of mixed stands, which make up an important proportion of the boreal forest landscape in Canada, is favoured by ecosystem management, which focuses on the conservation of all seral stages (Bergeron and Harvey, 1997; Bergeron et al., 1999). This coarse filter approach advocates that the conservation of the forest structure at the landscape level could allow the maintenance of biodiversity. In addition to maintaining biodiversity, mixed management could enhanced stand resistance to wind damage, diseases and insect outbreaks, and may represent a way to reduce economical risk by compensatory growth (Frivold and Mielikaïnen, 1990; Kelty, 1992). However, due to the large array of species combination and different structure possibilities, little is known about the dynamics of mixed stands (Assmann, 1961 in Frivold and Kolstrom, 1999) and mixed management is often associated with a lower yield. The outcome of mixed stand management in terms of forest productivity, which depends particularly on site conditions and species combinations, has been ambiguous, due in part to contrasting results and inappropriate study designs (Binkley, 1983; Binkley, 1992; Frivold and Mielikaïnen, 1990; Kelty, 1992; Perry, Choquette and Schroeder, 1987; Tarrant, 1961; Tarrant and Trappe, 1971)

There are two main mechanisms that may explain the improvement of stand growth in mixed stands: 1) the use of different ecological niches by each species, maximizing the use of site resources, and 2) the positive influence of deciduous species on nutrient cycling (Kelty, 1992). However, interspecific competition for resources such as light, water and nutrients may also negatively affect stand growth. In the southeastern boreal forest of Canada, the productivity of black spruce (*Picea mariana* (Mill.) BSP) stands is very low, averaging 1 to 2 m^3/(ha-yr). The influence of black spruce on nutrient cycling has been suggested as an explanation for the low productivity of these forests (Flanagan and Van Cleve, 1983). The poor quality of black spruce litter decreases decomposition rate, lowering nutrient availability as well as soil temperature. These conditions lead to an unproductive stand with a thick organic layer that inhibits the processes of nutrient mineralisation thus reducing nutrient uptake by plants (Foster, 1983; Van Cleve and

Viereck, 1981; Viereck, 1973). On the other hand, aspen (*Populus tremuloides* Michx.) increases nutrient cycling because of the chemical quality of its litter (Paré and Bergeron, 1996; Van Cleve and Noonan, 1975). The presence of aspen in a stand dominated by black spruce could influence positively the decomposition processes, nutrient availability and microclimatic conditions, which could allow for better growth of black spruce. In this paper, we hypothesized that the presence of aspen in mixed stands positively influences 1) the growth of black spruce, and 2) the total merchantable volume of the stand. The objectives of this study were to estimate the volume of black spruce stems and the total merchantable stand volume along a gradient of stands with increasing proportion of aspen and to test whether a certain proportion of aspen is conducive to a significant increase in the volume of black spruce stems and black spruce stands. The present study used the forest inventory data of the ministère des Ressources naturelles du Québec which provided observations of the volume of black spruce along a gradient of stands with various proportions of aspen. However, observational approaches like this one do not allow for a full control over environmental variables. Nevertheless, precautions were taken to avoid, as much as possible, the correlation between site characteristics and species composition.

1.4 Study area

The study area was located in the region of Abitibi-Témiscamingue, in the southeastern boreal forest of Canada. The latitude of the plots varied from 47°77′N to 50°10′N and the longitude from 76°47′W to 79°45′W. Selected plots are either part of the western balsam fir-paper birch (*Abies balsamea* (L.) Mill.–*Betula papyrifera* Marsh.) bioclimatic domain or part of the black spruce (*Picea mariana* (Mill.) BSP)-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.)) forest of western Quebec (Grondin, 1996). These domains extend over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the Wisconsinian stage (Vincent and Hardy, 1977). The nearest weather stations are located in Val d'Or, Amos and La Sarre, where the average annual precipitation is 927.2 mm, 920.0 mm and 856.8 mm, respectively, and average annual temperature is 1.2 ºC, 1.1 ºC and 0.8 ºC , respectively, according to Environment Canada (1993).

1.5 Sampling design

For this study, we used a part of the forest inventory database of the ministère des Ressources naturelles du Québec that covers two administrative regions (Abitibi-Témiscamingue and Nord du Québec). The sampling units of the forest inventory database was a circular plots of 0.04 ha, distributed every 150 m along transects of at least 1.5 km. Transects were first randomly determined and selected for composition by the Direction des inventaires forestiers of the ministère des Ressources naturelles du Québec (Forêt Québec, 2000). Starting with more than 8000 plots located over 40 000 km^2, we selected all plots (N=43) that were on lacustrine clay deposit, had moderate to imperfect drainage and contained aspen and black spruce (Figure 1.1). Plots having more than 10% of their total basal area occupied by species other than aspen or black spruce were also rejected of the forest inventory database. To ensure that drainage conditions were not associated with the abundance of aspen and that the two factors were not mixed up, we performed a t test to compare the relative basal area of aspen between plots with moderate drainage and ones with imperfect drainage. This test revealed no statistically significant difference (t value: 0.14; p = 0.8905). The average aspen relative basal area was 27% for imperfectly drained sites and 26% for moderately well-drained sites (aspen relative basal area was determined by the ratio of aspen basal area on total basal area of the stand). For the 43 plots selected, the mean density was 4475 stems/ha varying from 1200 stems/ha to 12 425 stems/ha and, the mean age of dominant black spruce trees was 55 years varying from 23 to 75 years (Table 1.1). In general, selected plots are relatively young mixed stands of black spruce and aspen on well-drained soil.

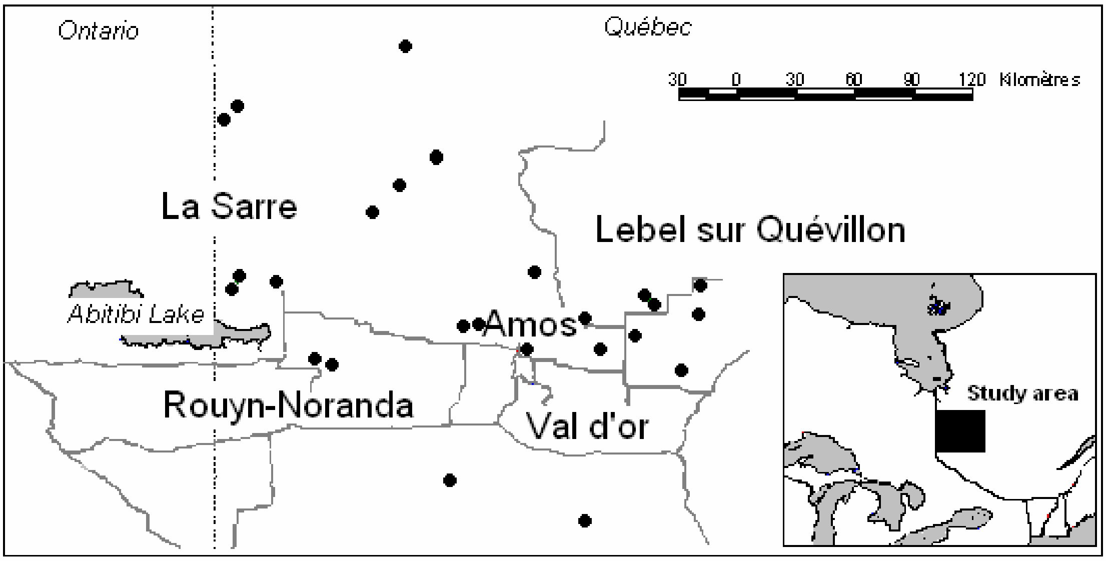


Figure 1.1 Plot locations in Abitibi-Témiscamingue, northwestern Quebec. Each black dot represents one or more plots.

Diameter at breast height (dbh) was measured for every stem in each plot. In each plot, the height of three dominant stems of black spruce was measured with a clinometer and the age was assessed by coring. Tree merchantable volume was calculated with equations using dbh and an estimated height to calculate the volume of each stem of > 10 cm dbh (Perron, 1985). These equations are inadequate for small stems under 10 cm of dbh and the information required to calculate the volume of these stems was not available in the forest inventory database thus total gross volume could not be calculated.

1.6 Forest dynamics

In the western balsam fir–paper birch bioclimatic domain and the black spruce–feathermoss forest of western Quebec the disturbance regime is dominated by large crown forest fires (Bergeron, 1991; Heinselman, 1981; Payette, 1992). In the southern part of the study area, after fires, the stands generally follow a successional path that is initiated with intolerant deciduous species that are gradually replaced by tolerant coniferous species (Bergeron and Dubuc, 1989). In the northern part of the study area, the black spruce−feathermoss domain, the first cohort of black spruce following fire is even-aged. Progressively, in the absence of fire, there is an accumulation of organic matter that is resistant to rapid decomposition and the stands evolve to open, irregular and unproductive black spruce forests (Foster, 1983; Van Cleve and Viereck, 1981). In mixed stands, aspen and black spruce establish themselves at the same time after the disturbance and either aspen or black spruce dominate, or co-dominate the stand depending on site conditions, time since last disturbance and pre-disturbance composition (Chen and Popadiouk, 2002). In the northern part of our study area, aspen currently invades logged or burned areas which had been dominated by black spruce for many years. In the Gaspésie region, in the eastern part of Quebec, this phenomenon was observed and the main vector for the spread of aspen was identified as the development of logging road networks (Fortin, 2000).

Table 1.1 Description of the 43 plots selected from the forest inventory database of the ministère des Ressources naturelles du Québec with 0 to 87 % of aspen basal area

	Mean	Standard deviation	Range
Basal area (m^2/ha)	31.4	8.6	15.3 – 49.5
Stand density (stems/ha)	4 475	2 741	1 200 - 12 425
Merchantable volume (m^3/ha)	152.3	86.2	33.6 – 462.0
Dominant black spruce age (years)	55	13	23 - 75
Dominant black spruce height (m)	13.9	2.9	8.2 – 21.5
Dominant black spruce dbh (cm)	14.6	2.3	10.5 – 20.6

1.7 Statistical analysis

1.7.1 Individual species scale

In order to explore the relationships between aspen relative basal area and black spruce average dbh without the influence of stem density, a polynomial regression analysis was performed between the relative basal area of aspen and the residuals of a regression analysis between black spruce average dbh and stem density. Polynomial regression was performed as a multiple regression with the relative basal area of aspen and the square of relative basal area of aspen as independent variables. Despite the common assumption that dominant tree height is not influenced by stand density, we used a polynomial regression analysis for investigating effects of aspen on black spruce average dominant height with density as a covariable. With a proportion of aspen basal area greater than approximately 45%, a negative influence of aspen was observed on the residuals of both regression analyses between dbh and height of black spruce and stem density. A piecewise regression was performed to test the significance of the model with two segments and to identify a breakpoint. The following equations were fit to the data:

$$\text{if } x < \tau \text{ then } y = b_0 + b_1 x$$
$$\text{if } x \geq \tau \text{ then } y = b_0 + (b_1 + b_2)x - b_2\tau$$

where x is relative basal area of aspen, τ is the breakpoint, b_0 is the y-intercept, b_1 is the slope for the first segment and b_1+b_2 is the slope for the second segment (Seber and Wild, 1989). The two piece regression was non-linear and involved parameter estimation (nlin procedure, Version 8, SAS Institute Inc. 1999-2001). Since the final parameter values were dependent on initial parameters, data were first assessed visually to estimate parameters. Regressions were considered significant when the 95% confidence intervals of one or more consecutive slopes did not contain zero ($p < 0.05$).

According to the breakpoint identified by the piecewise regression, it was then decided to test the influence of aspen on the residuals of black spruce average dbh and dominant height on a restricted gradient of aspen basal area (from 1% to 41% of the total stand basal area). A linear regression analysis was performed between the relative basal area of aspen and the residuals of a regression analysis between black spruce average dbh and stem density on a restricted gradient of aspen basal area (from 1% to 41% of the total stand basal area). The same method was followed to test the relationship between the relative basal area of aspen and mean dominant height of black spruce to control for the influence of stand density on a restricted gradient of aspen basal area (from 1% to 41% of the total stand basal area).

Finally, an analysis of covariance, with stem density as a covariable, was used to test the influence of aspen on black spruce stem volume. This analysis was performed on two types of sites with different proportions of aspen: 0-5% of total basal area, which were considered as control sites, and 5-15% of total basal area, which were considered as sites with a slight presence of aspen. Because the assumptions of the covariance analysis were not met, a nonparametric covariance analysis was performed on four ranges of aspen relative basal area (0-5%, 5-15%, 15-45%, 45-100% of basal area), and another nonparametric covariance analysis was performed on three ranges (0-5%, 5-15%, 15-45%) but there was no significant difference between these categories.

1.7.2 Stand scale

Because preliminary results suggested a negative impact of aspen on black spruce growth when it occupies more than 41% of the stand basal area, we tested the influence of the presence of aspen on stand volume along the restricted gradient (1-41%) of aspen used in the preceeding analysis. In order to control the influence of density on stand volume, we performed a regression analysis between the relative basal area of aspen and the residuals of the regression between total merchantable volume (all species) and stem density. And the same method was used to test the relationship between the relative basal area of aspen and the merchantable volume of black spruce on a restricted range of aspen importance (1 to 41% of basal area). All statistical analyses were performed using SAS (SAS Institute Inc. 1999-2001) and the statistical significance threshold was fixed at 5%.

1.7.3 Stand age

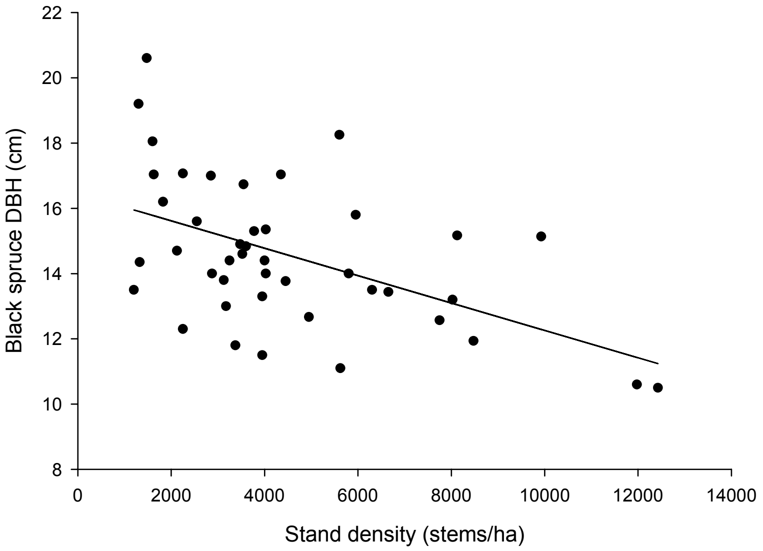
Despite the great variability among plots in the mean age of dominant black spruce trees, we did not include this variable in the analyses because, contrary to stand density, age since last disturbance was not correlated with the relative basal area of aspen (Spearman correlation tests (All data ($N = 43$): $r = -0.0978$, $p = 0.5325$; 1 to 41% of aspen basal area ($N = 33$): $r = 0.0449$, $p = 0.8041$)).

1.8 Results

1.8.1 Individual species scale

The relationship between dbh and stem density was significant and the residuals from the regression analysis were affected by the relative basal area of aspen ($p=0.0789$; Figure 1.2), and the relationship between black spruce dominant height and stem density was significant and the residuals from the regression analysis were significantly affected by the relative basal area of aspen ($p=0.0272$; Figure 1.3). Relative basal area was positively related to dbh and dominant height of black spruce when aspen comprised less than 40% of the basal stand area, but was negatively related when aspen proportion was greater than 40% of the total stand basal area (Table 1.2). Considering only the 0-41% part of the gradient, we observed that the relationship between black spruce dbh and stem density was significant and that the residuals from the regression analysis were, again, affected by the relative basal area of aspen ($p=0.0657$; Figure 1.4). The relationship between black spruce height and stem density was significant and the residuals from the regression analysis were significantly affected by the relative basal area of aspen from 0 to 41% ($p=0.0235$; Figure 1.5). Black spruce stem volume in a stand with 0-5% of aspen basal area was significantly lower than that in a stand with 5-15% of aspen basal area, according to the covariance analysis with stem density as the covariable (Table 1.3; Figure 1.6).

a)



b)

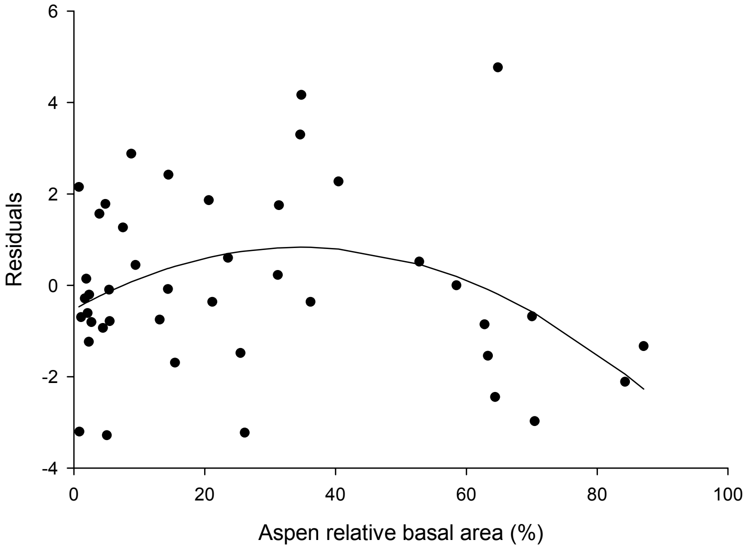
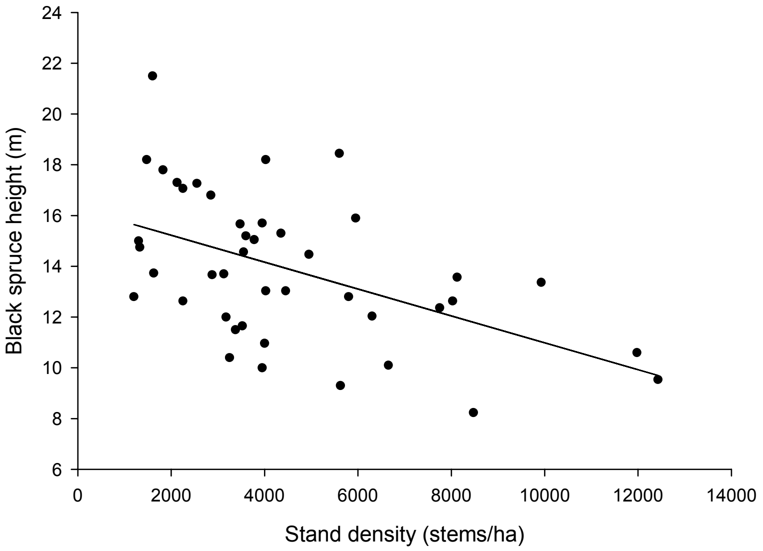


Figure 1.2 a) Regression analysis of black spruce average dbh against stem density, $Y = -0.0004X + 16.456$ ($R^2 = 0.2657$, $p = 0.0004$, N=43), and b) polynomial regression analysis of residuals from the precedent regression against full gradient of relative basal area of aspen, $Y = -0.0011X^2 + 0.0784X - 0.5284$ ($R^2 = 0.1193$, $p = 0.0789$, N=43).

a)



b)

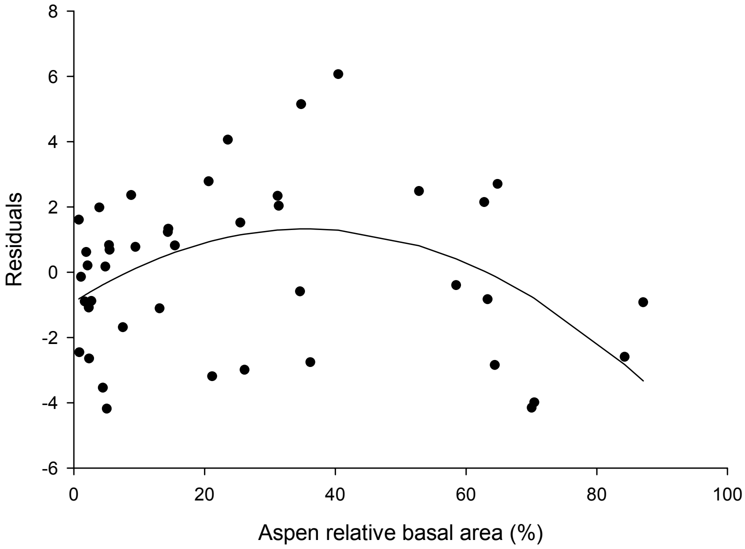


Figure 1.3 a) Regression analysis of black spruce average dominant height against stem density, $Y = -0.0005X + 16.283$ ($R^2 = 0.2537$, $p = 0.0006$, N=43), and b) polynomial regression analysis of residuals from the precedent regression against full gradient of relative basal area of aspen, $Y = -0.0018X^2 + 0.1256X - 0.9181$ ($R^2 = 0.1650, p = 0.0272$, N=43).

Table 1.2 Piecewise regressions performed between aspen relative basal area and the residuals of both regression analyses on dbh and height of black spruce against stem density

Covariate	dbh	Height
Breakpoint (% aspen basal area)	40.4700	40.6335
Standard error (% aspen basal area)	10.5037	9.2312
Slope first segment	0.8976	1.3074
Slope second segment	-0.8561	-1.2907
R^2 (model with 2 segments)	0.2310	0.2950
p-value	<0.0001	<0.0001

$R^2 = SS_{regression}/SS_{corrected\ total}$, Slope second segment = b_1+b_2

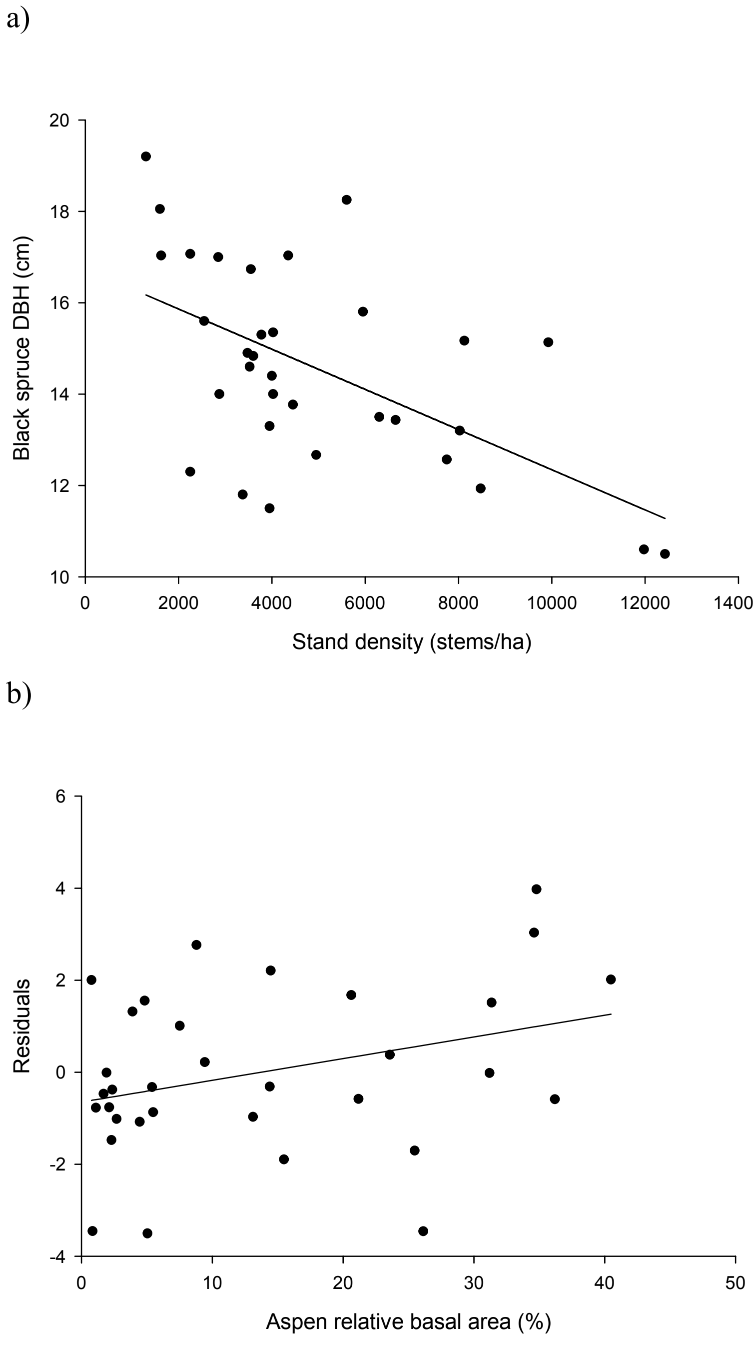
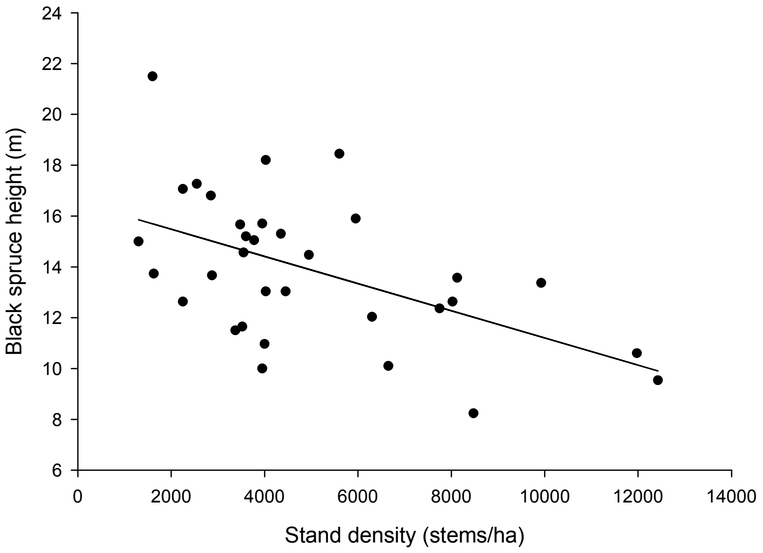


Figure 1.4 a) Regression analysis of black spruce average dbh against stem density, $Y = -0.0004X + 16.742$ ($R^2 = 0.3180$, $p = 0.0006$, N=33), and b) regression analysis of residuals from the precedent regression against restricted gradient of relative basal area of aspen (0-41%), $Y = 0.0472X - 0.648$ ($R^2 = 0.1051$, p = 0.0657, N=33).

a)



b)

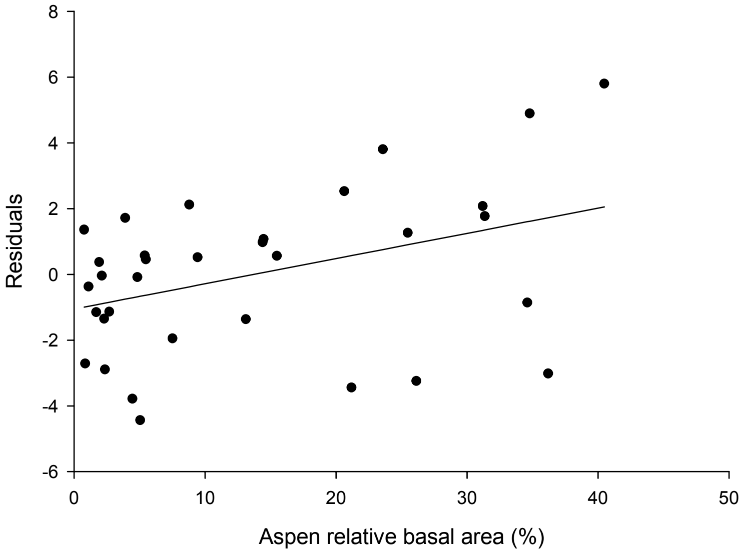


Figure 1.5 a) Regression analysis of black spruce average dominant height against stem density, $Y = -0.0005X + 16.553$ ($R^2 = 0.2769$, $p = 0.0017$, N=33), and b) regression analysis of residuals from the precedent regression against restricted gradient of relative basal area of aspen (0-41%), $Y = 0.7674X - 1.055$ ($R^2 = 0.1549$, p = 0.0235, N=33).

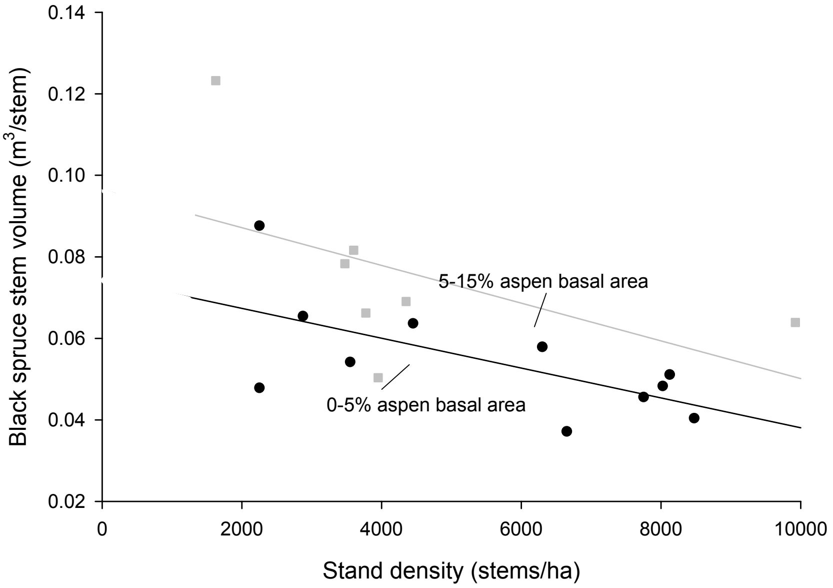


Figure 1.6 Covariance analysis comparing the relative importance of stem density and the relative basal area on the variation of black spruce average stem volume (m^3/stem). Grey line = relationship between density and black spruce volume in stands with 5 to 15% of aspen basal area (■), black line = relationship between density and black spruce volume in stands with 0 to 5% of aspen basal area (●).

Table 1.3 Covariance analysis comparing the relative importance of stem density and relative basal area of aspen on the variation of volume by stem of black spruce (m^3/stem)

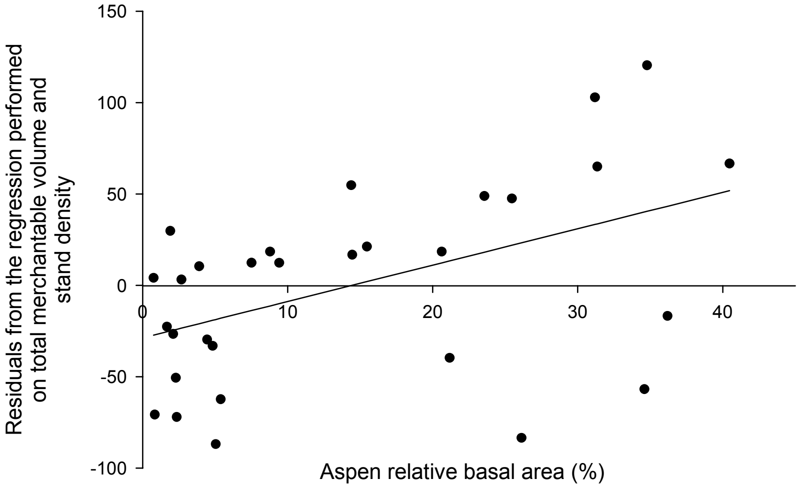
Source of variation		DF	SS	*F*-ratio
Full model: testing for slope homogeneity				
R^2: 0.51	Model	3	0.0037	4.92*
	Error	14	0.0035	
Stem density		1	0.0017	6.72*
Relative basal area		1	0.0039	1.56
Stem density X relative basal area		1	0.0000	0.09
Model testing for homogeneity of ordinate at the beginning				
R^2: 0.51	Model	2	0.0037	7.81**
	Error	15	0.0035	
Stem density		1	0.0017	7.12*
Relative basal area of aspen		1	0.0012	5.01*

* = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$.

1.8.2 Stand scale

Residuals from the significant regression analysis performed on total (all species) merchantable volume and stem density were significantly affected by aspen basal area when aspen proportion varied between 0 and 41% of the total stand basal area. However, the residuals from the significant regression analysis of black spruce merchantable volume and stem density were not significantly affected by aspen (0-41%; Figure 1.7).

a)



b)

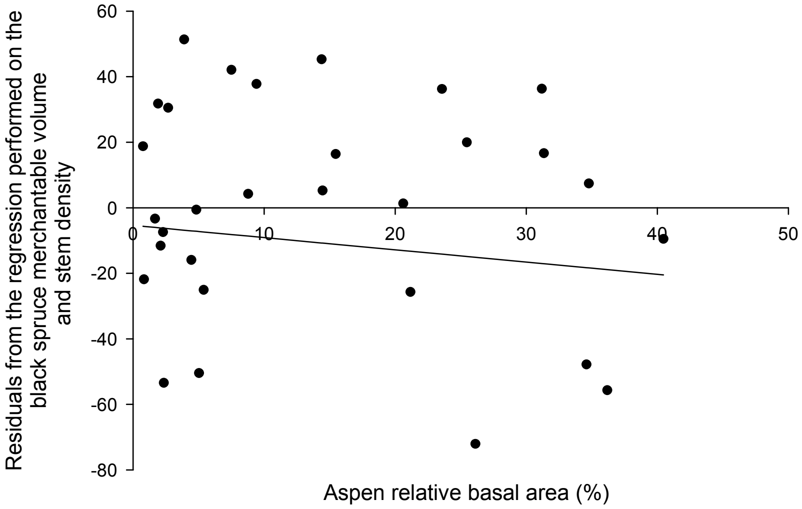


Figure 1.7 a) Regression analysis on residuals, from the regression performed on total merchantable volume against stem density Y = -0.0105X + 188.776 (R^2 = 0.1619, p = 0.0275, N=30), and relative basal area of aspen (0-41%) Y = 1.9912X – 28.792 (R^2 = 0.2284, p = 0.0076, N=30), and b) regression analysis on residuals, from the regression performed on merchantable volume of black spruce against stem density Y = -0.0047X + 125.824 (R^2 = 0.0920, p = 0.1032, N=30), and restricted gradient of relative basal area of aspen (0-41%), Y = -0.3731X + 5.3957 (R^2 = 0.0209, p = 0.4464, N=30).

1.9 Discussion

Despite the presence of similar abiotic conditions, black spruce growth differed with the proportion of aspen in the stand and the nature of the influence of aspen also changed with the proportion of aspen in the stand. The apparent absence in the literature (see review by Rothe and Binkley, 2001) of a clear trend regarding the effect of mixed stand management on stand productivity could be explained in part by the variability in the influence of the companion species with respect to its abundance in a stand. In this study, the presence of aspen in proportions lower than 41% of total basal area of the stand increased black spruce dbh and height. According to the piecewise analysis models, we estimated an increase in dbh of approximately 13 to 17 cm, and an increase in height of 12 to 17 m with aspen varying from more than 0 to 41% of relative basal area, which suggests that facilitative production mechanisms could be present between aspen and black spruce. Reported site indices for black spruce in Quebec's commercial forest vary from 9 to 18 meters (Pothier and Savard, 1998). Observed gains are therefore highly significant from a growth and yield perspective. For example, the commercial volume of a 90-year-old medium density black spruce with a site index of 12 m is 80 m^3/ha compared to 240 m^3/ha for a similar stand with a site index of 18 m (Pothier and Savard, 1998).

In addition to a positive influence of aspen on diameter growth of black spruce, which could increase the economic value per hectare, the presence of 5 to 15% of aspen basal area in a stand is sufficient to obtain a higher volume of black spruce per stem, which could also benefit commercial users of the forest. However, the presence of aspen seemed to negatively influence black spruce dbh (12 cm at 85% of aspen basal area) and height (13 m at 85% of aspen basal area) when the proportion of aspen reached values greater than 41% of the total stand basal area. Over this threshold, the decrease in black spruce growth could be explained by higher interspecific competition. However, the estimation of the difference of dbh (1 cm) and height (1 m) between both extremes of the gradient of aspen (more than 0 vs 85%) could be negligible. The relative proportion of aspen in the stand is a major parameter in mixed management and more studies are needed to understand the dynamics of these stands and to fix a range or a threshold of aspen proportion for successful management. Despite the attention given to selecting plots with similar abiotic conditions, there is still a possibility that the positive influence of aspen on height and dbh was confused with differences in soil properties that were correlated with stand composition and productivity. The influence of stem density on black spruce dominant height was not expected, but this relationship has been observed before in black spruce stands of high density (Grondin et al., 2000).

At the stand scale, the presence of aspen in proportions lower than 41% of total stand basal area increased the total merchantable volume of the stand. The absence of a significant relationship between the merchantable volume of black spruce and the relative basal area of aspen implies that volume gain in the stand is essentially aspen fibre. This suggests that aspen uses a different ecological niche than black spruce, thus reducing the competition between the species. In additional to providing an "extra cubic meter" of aspen fibre, the presence of aspen appears to provide similar merchantable volume of black spruce that is distributed in fewer stems of greater height and dbh.

Man and Lieffers (1999) discussed two main mechanisms by which mixed stands of aspen and white spruce could be more productive than a single species stand: competitive reduction and facilitative production. Our results can also be interpreted as competitive reduction, which arises from ecological niche differentiation between species, and facilitative production, which is a positive influence of one species on another (Vandermeer, 1989). Similar to the aspen-white spruce case, aspen and black spruce differ in their shade tolerance. Moreover, the timing of foliage production of these species is different (phenological separation). Black spruce keeps its foliage all year long and could benefit from the absence of aspen foliage in spring and fall to achieve better growth or resource allocation without, or with less, competition for water and nutrients (Constabel and Lieffers, 1996). However, aspen shade could likely limits the growth of black spruce in summer. Parallel to a reduction in crown competition, there may also be reduced root competition between aspen and black spruce due to niche separation. In fact, some studies have observed that early successional species have deeper root systems than late successional ones (Gale and Grigal, 1987; Grier et al., 1981), and this root stratification could be a competition avoidance strategy (Kabzems and Lousier, 1992; Perry, Bell and Amaranthus, 1992; Strong and La Roi, 1983). A study conducted in the southern part of our study area indicated that stratification of fine roots changed with the age of the stand (Finér, Messier and De Grandpré, 1997).

Our results suggest that the presence of aspen could enhance the productivity of black spruce in mixed stands. Previous studies conducted in the southern part of our study area indicated that aspen positively influences nutrient cycling (Brais et al., 1995; Longpré et al., 1994; Paré and Bergeron, 1996). Moreover, forest composition, by its effects on nutrient cycling, influences understory composition (Légaré et al., 2001). By influencing the composition of the understory layer, and especially the presence of sphagnum that deteriorate the conditions of the decomposition process, aspen could ameliorate the negative effects of black spruce on nutrient cycling and consequently on stand productivity. The dominance of aspen in a stand may change growth conditions such as the availability of light, nutrients and water. Some of these conditions may become unfavourable to black spruce over a certain threshold.

The presence of more than one tree species may allow a more efficient use of resources (Vandermeer, 1989) and increase the total biomass of a stand even though the biomass of each species in the stand may decrease relative to the biomass of single species stands (Lehman and Tilman, 2000). In this study, black spruce total volume was stable along a gradient of aspen proportion in the stand. However, there was a positive influence of aspen on stand biomass and black spruce volume within a specific range of aspen abundance. By using a different ecological niche than black spruce and by improving the conditions for the decomposition process, the presence of aspen could improve the growth of the stand and the growth of black spruce.

1.10 Management Implications

For the forest industry, which uses mainly softwood species, the presence of aspen requires an additional silvicultural treatment that is conducted to release black spruce saplings. Despite the commercial value of aspen, the invasive character of the species in the managed landscape, which has been observed by Fortin (2000), is a concern for industrial foresters who ask themselves: “How can we fight this well-adapted species?” In the light of our results, this question could be changed to: “What proportion of aspen do we need to keep in the stand to reduce the negative impact of black spruce on nutrient cycling and stand productivity?”. At different temporal and spatial scales, the presence of aspen could be important for the maintenance of forest productivity. Moreover, the management of mixed stands, which make up an important proportion of the landscape, could offer an example as to how the commercial objectives for the forest can be harmonized with ecosystem management.

1.11 Acknowledgments

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CHAPITRE II

INFLUENCE OF ASPEN ON FOREST FLOOR PROPERTIES IN BLACK SPRUCE-DOMINATED STANDS

Sonia Légaré, David Paré & Yves Bergeron

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2.1 Abstract

In the claybelt of northwestern Quebec, in the absence of fire, black spruce-feathermoss stands are characterized by a thick forest floor layer formed by an accumulation of bryophytes and sphagnum. This layer is associated with wet, cool and nutrient-poor soil conditions conducive to the paludification process and development of an unproductive open black spruce forests. The presence of aspen (*Populus tremuloides)* in these stands may halt or slow this process because aspen has a high nutrient cycling rate and a litter that represses moss cover. The main hypothesis of this study is that, within similar abiotic conditions (slope and drainage), the presence of aspen in stands dominated by black spruce (*Picea mariana)* affects surface soil nutrient availability, total N, pH, and decomposition. The abundance of aspen trees was associated with higher exchangeable cations, cation exchange capacity and pH of the forest floor layer on all sites. A decrease in organic matter thickness with increasing aspen presence was also found on all sites, suggesting that this species affects the decomposition process by the quality of its litter as well as by a general improvement of soil physical and chemical properties. The decomposition rate of a standard substrate as well as in vitro potential net nitrogen mineralization were positively related to aspen on only one of the three sites, and non-significant on the other sites. Strong immobilization of added nitrogen during incubation was observed on all sites and was not related to aspen, which suggests that in these stands, the soil microbial community is uniformly and strongly nitrogen limited. The zone of influence of aspen was evaluated in areas around the soil sampling plot ranging from 3 to 7 m of radius. The results revealed that this zone varies with soil properties. The results suggest that the presence of aspen accelerates nutrients cycling, which could have an effect on stand productivity.

Key words: Mixed stand, nitrogen, nutrient cycle, *Picea mariana*, *Populus tremuloides*

2.2 Introduction

In the absence of fire, black spruce-feathermoss stands are prone to paludification (i.e. organic matter accumulation with time since fire; MacLean et al., 1983). The low evapotranspiration rate of black spruce, its recalcitrant litter and the development of a sphagnum layer are all conducive to organic matter accumulation, cooler soil temperatures, a rise of the water table and, consequently, reduced nutrient cycling (Foster, 1985; Oechel and Van Cleve, 1986; Weber and Van Cleve, 1981) and reduced forest productivity (Foster, 1983; Oechel and Van Cleve, 1986; Van Cleve and Viereck, 1981; Viereck and Dyrness, 1979). Aspen, which sometimes grows in association with black spruce, is known as a highly nutrient-demanding species, which could accelerate nutrient cycling and thus increase nutrient availability (Longpré et al., 1994; Paré and Bergeron, 1996; Van Cleve and Noonan, 1975). According to Alban and Pastor (1993) and Bockheim, Jepsen and Heisey (1991), soil organic matter decomposition rates are higher in aspen stands than in coniferous stands because of a relatively easily decomposable litter (Flanagan and Van Cleve, 1983; McClaugherty et al., 1985), a more alkaline humus, and because deciduous litter is detrimental to moss and sphagnum growth. The impact of forest composition on soil could lead to a different understory composition and influence the productivity of coniferous species (Légaré et al., 2001; Légaré, Paré and Bergeron, 2004; Longpré et al., 1994). Using forest inventory databases, Légaré, Paré and Bergeron (2004) found a positive effect of the presence of aspen on total stand merchantable volume. We thus hypothesized that in the humus layer, the chemical properties (total nitrogen, pH, exchangeable Ca, Mg and K) and organic matter depth could be affected by the presence of aspen in stands dominated by black spruce. Moreover, we hypothesized that the presence of aspen could influence decomposition rates, mineralization and nitrification rates in the humus layer as well as the nitrogen limitation of the microbial community.

The first objective of this study was to ensure that the presence of aspen was not correlated with abiotic properties such as soil type, slope and drainage. This objective was fundamental to properly testing our hypotheses. The second objective was to determine the zone of influence of aspen on soil properties and to investigate the relationships between soil properties and the basal area of aspen by fitting a linear model at the proper scale. The third objective was to explore the relationship between the presence of aspen and the mineralization and nitrification processes at different levels of nitrogen limitation of the microbial community.

2.3 Material and methods

2.3.1 Study area

The study area was located in northwestwern Quebec (49° 03′ N to 49° 11′ N and 78° 50′ W to 79° 09′ W). This area is part of the black spruce (*Picea mariana* (Mill.) BSP) – feathermoss (*Pleurozium schreberi* (Brid.) Mitt.)) forest domain of western Quebec (Grondin, 1996). This domain extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the Wisconsinian glacial stage (Vincent and Hardy, 1977). Sites are located on lacustrine clay deposits, and mesics fine textured soils are generally classified as Grey Luvisols (Soil Classification Working Group, 1998). The closest weather station was located at La Sarre. Average annual precipitation totals 856.8 mm and average annual temperature is 0.8 °C (Environment Canada, 1993). Forest dynamics in this ecosystem are dominated by large stand-replacing fires that kill most of the trees and aboveground vegetation. Mean stand age is 139 years and fire cycle length has increased from 141 years, between 1850 and 1920, to 326 years since 1920 (Bergeron et al., 2001).

2.3.2 Sampling design

Three sites were chosen according to the following criterias: gentle slope, moderate drainage, soil type and stand composition dominated by *Picea mariana* with heterogeneous presence of *Populus tremuloides*. All stands originate from fires that took place around 1920 according to the fire map producted by Bergeron et al. (2004). More precisely, sites 1, 2 and 3 originate from 1926, 1916 and 1916 fires, respectively, according to local data obtained from cross-sectional tree-discs of 10 *Populus* *tremuloides* trees taken at ground level (0 m) at each site. The sampling unit of this study was a circular plot of 14 m in diameter, distributed at every 20 m along a transect of at least 180 m. The number and length of transect lines depended on the size and form of the *Picea mariana*-*Populus tremuloides* stands. Each sampling unit was considered independent because tree species composition influences soil properties at a small spatial scale (Boettcher and Kalisz, 1991; Rhoades, 1997; Turner and Franz, 1985). Sites 1, 2 and 3 had respectively 28, 33 and 34 plots. Sites were different on the basis of stand density and soil texture (Table 2.1). Site 1 had higher mean stand stem density, with 3220 stems/ha, and sites 2 and 3 had mean stem densities of 2014 and 1993 stems/ha, respectively. On each site, black spruce basal area decreases as aspen basal area increases. Fine roots were mostly located at the interface between the A mineral horizon and the humus layer. Humus layer thickness was lower in site 1 and higher in site 3 (Table 2.2). To ensure that mineral soil properties were not correlated with *Populus tremuloides* presence, we selected five plots in each site corresponding to of the three following categories for further analyses (total of 45 selected plots): 1) plots dominated by *Picea mariana* with less than 15 % of relative basal area of *Populus tremuloides*, 2) plots with 15 to 50 % relative *Populus tremuloides* basal area, and 3) plots with 50 to 75 % relative *Populus tremuloides* basal area.

Table 2.1 Mineral soil properties and stand characteristics on sites 1, 2 and 3

	Means ± standard deviations		
	Site 1	Site 2	Site 3
Mineral soil properties (N=15 for each site)			
pH (water)	4.58 ± 0.30	4.69 ± 0.50	4.56 ± 0.38
Exchangeable K (mmol(+)/kg)	22.04 ± 22.73	6.30 ± 1.75	6.61 ± 1.53
Exchangeable Mg (mmol(+)/kg)	30. 01 ± 11.69	30.39 ± 28.24	25.64 ± 20.50
Exchangeable Ca (mmol(+)/kg)	82.26 ± 34.39	104.98 ± 94.48	76.57 ± 58.53
CEC (mmol(+)/kg)	164.01 ± 48.91	170.42 ± 113.62	134.06 ± 69.07
Total N (mg/g of soil)	1.79 ± 1.27	2.03 ± 1.09	2.68 ± 1.65
Clay %	50.4 ± 6.3	39.5 ± 14.9	24.5 ± 9.2
Stand characteristics (N=12 for each site)			
Aspen DBH (cm)	12.97 ± 6.41	21.06 ± 9.07	24.04 ± 13.85
Aspen height (m)	13.25 ± 6.38	20.33 ± 7.49	21.06 ± 11.12
Stand density (stem/ha)	3 220 ± 698	2 014 ± 603	1 993 ± 708

Table 2.2 FH layer properties on sites 1, 2 and 3

FH layer properties	Means ± standard deviations		
	Site 1 N=31	Site 2 N=35	Site 3 N=43
FH layer thickness (cm)	9.34 ± 3.19	8.75 ± 3.37	11.40 ± 4.19
Decomposition rate (g/yr)	1.61 ± 0.69	2.29 ± 0.76	1.81 ± 0.79
pH (water)	3.96 ± 0.28	4.30 ± 0.36	3.86 ± 0.34
Exchangeable K (mmol(+)/kg)	52.80 ± 14.81	41.59 ± 11.80	46.90 ± 16.24
Exchangeable Mg (mmol(+)/kg)	62.85 ± 25.27	85.56 ± 28.47	55.49 ± 19.13
Exchangeable Ca (mmol(+)/kg)	251.96 ± 152.01	483.85 ± 175.40	287.44 ± 109.76
CEC (mmol(+)/kg)	452.46 ± 143.77	651.29 ± 187.61	544.36 ± 176.85
N total (mg/g soil)	11.74 ± 2.43	14.82 ± 0.27	11.08 ± 5.40
C:N ratio	43.42 ± 10.41	33.93 ± 9.17	44.45 ± 13.82

2.3.3 Methods

Between the third week of July and the third week of August 2001, we measured the diameter at breast height (DBH) and the distance from the sampling point (centre of the circular plot) of every tree in each plot to determine the basal area of each species. Three samples of FH layer (0.01 m^2) were taken in three different directions at 1 m from the centre of each plot and, similarly, three samples of the first 0.1 m of mineral soil (Ae horizon and the top of the B horizon) were taken in the 45 selected plots (15/site). For each plot, soil samples were pooled by horizon, air dried, and ground. Forest floor and mineral soil pH were analyzed in distilled water (McKeague, 1976). Exchangeable cations in the forest floor and mineral soil were extracted with 0.1 M $BaCl_2$ and determined by atomic absorption, while cation exchange capacity (CEC) was determined by the sum of exchangeable cations (Hendershot, Lalande and Duquette, 1993). Total N was determined colorimetrically following a H_2SO_4/H_2O_2 digestion (Keeney and Nelson, 1982) and total C was measured by loss on ignition (Carter, 1993). Soil texture was determined by granulometric analyses (McKeague, 1976). In each plot, decomposition rate was determined by measuring the dry mass loss of wooden coffee sticks (made of white birch wood) enclosed in three screen bags buried in the humus layer from August 2001 to August 2002.

FH layer samples were collected from the 45 selected plots, ground, and stored at 4 °C. Net N mineralization and nitrification were determined in laboratory incubations using fresh humid samples. Three doses of N were added to the soil (control, single dose, double dose) to evaluate the potential of microbial communities to immobilize incoming sources of N. For each sample, we prepared four plastic goblets with 15-40 g of fresh soil (5.00 g dry weight equivalent). The first goblet was set aside for immediate extraction and analysis of NH_4-N and NO_3-N following a 2 M KCl extraction. The other goblets were incubated. One glass received only deionized water (control C), another received a single dose of the nitrogen treatment (D, 1300 $\mu g\ N\ g^{-1}$ dry soil added), and the last one received a double dose (DD, 2600 $\mu g\ N\ g^{-1}$ dry soil added). All treatments received the same amount of water. Glasses were covered with a polyethylene film during incubation in order to limit evaporation. Samples were still humid at the end of incubation. Net N mineralization and net N nitrification were estimated as the difference between the amounts of NH_4-N and NO_3-N extracted with a 2M KCl solution and analyzed by spectrophotometry before and after a 65 days incubation at 10 °C (which is the average soil temperature during the growing season for all 95 plots of the sampling design).

2.3.4 Statistical analyses

To ensure that mineral soil properties were not positively correlated with *Populus tremuloides* presence, Spearman correlations between *Populus tremuloides* basal area in areas of 3 m, 5 m and 7 m of radius around each sampling point and the following soil properties: clay percentage, pH, exchangeable potassium (K), magnesium (Mg) and calcium (Ca), cationic exchange capacity (CEC) and total nitrogen. Correlations were performed for each site separately because soil texture changed among sites. The null hypothesis means that the relationships between aspen basal area and these mineral soil properties are significant and positive unless we have strong evidence that they are not significant. Thus, a p-value over 0.40 or a negative coefficient of correlation was considered to be evidence of an absence of a significant positive relationship.

To describe the zone of influence of *Populus tremuloides* trees, we calculated the basal area of *Populus tremuloides* in a circle with a 3 m radius around each sampling point (centre of 14 m of diameter plot), in a ring with a radius ranging from 3 to 5 m, and finally in a ring with a radius ranging from 5 to 7 m. We then performed a type 1 covariance analysis (ANCOVA) to test the contribution of *Populus tremuloides* at each range of distance from the sampling point on FH layer soil properties including: total nitrogen, pH, exchangeable K, Mg and Ca, CEC, organic matter thickness and decomposition rate. This analysis allowed us to evaluate statistically the contribution of the *Populus tremuloides* basal area located in the incremental rings around the sampling points. We included site as a classification variable in the model. Interaction between site and *Populus tremuloides* basal area in each area around the sampling point was also considered for the following distances: 0-3 m, 3-5 m and 5-7 m from the sampling point. When interactions were not significant, they were removed from the model. When interaction terms that included sites were significant, we performed a regression analysis for each site separately. When a regression model was not significant the regression was performed on the next smaller circle of *Populus tremuloides* basal area. To simplify the results and visualize the relationships between *Populus tremuloides* basal area and soil properties when more than one range of distance was significant (e.g. 3 m and 5 m), we performed a simple linear regression analysis including basal area of *Populus tremuloides* in a circle of the largest significant range of distance (e.g. 5 m) radius around the sampling point. All soil properties except forest floor pH were $\log_{10}$ transformed for normal distribution.

Covariance analyses were also used to evaluate the influence of *Populus tremuloides* on net N mineralization/immobilization and net N nitrification. *Populus tremuloides* basal area within 7 m was used to test the influence of *Populus tremuloides* because total N was significantly affected by *Populus tremuloides* at 7 m. In addition, sites and amounts of N added were considered. The analysis was performed on ranks of net N mineralization and nitrification because no simple transformation allowed a normal distribution of the residuals. Tukey's multiple comparison tests were performed on the ranks to test the influence of treatments. For each site, Spearman correlations were performed between the C:N ratio and the net N mineralization and nitrification in the control treatment. Statistical analyses were performed using SAS software (SAS Institute Inc., Cary, N.C.) and the significance threshold was fixed at 0.05.

2.4 Results

2.4.1 Mineral soil properties along aspen basal area gradient

On site 1, mineral soil pH and clay percentage were positively correlated with aspen basal area at less than 3, 5 and 7 m around the sampling point, and exchangeable potassium (K) was positively correlated with aspen basal area at less than 5 and 7 m around the sampling point (Table 2.3). On sites 2 and 3, significant relationships (i.e. with a p-value under 0.40) were all negative. Exchangeable magnesium (Mg) and calcium (Ca), and cation exchange capacity (CEC) were negatively correlated with aspen basal area at less than 7 m around the sampling point. Total nitrogen was negatively correlated with aspen basal area at less than 3, 5 and 7 m around the sampling point in site 2. Clay percentage was also negatively correlated with aspen basal area at less than 3 m around the sampling point on site 2. On site 3, exchangeable magnesium (Mg) and calcium (Ca), cation exchange capacity (CEC) and total nitrogen were negatively correlated with aspen basal area at less than 3, 5 and 7 m around the sampling point. Clay percentage of mineral soil was significantly correlated with aspen basal area at 5 m of the sampling point on site 3.

Table 2.3 Spearman correlation coefficients between variables related to mineral soil and aspen absolute basal area within 3 m, 5 m and 7 m

	Variables	Rho (p > |r|) AABA3	Rho (p > |r|) AABA5	Rho (p > |r|) AABA7
Site 1	pH (water)	**0.39 (0.169)**	**0.31 (0.288)**	**0.33 (0.246)**
	Exchangeable K (mmol(+)/kg)	0.24 (0.413)	**0.40 (0.159)**	**0.35 (0.215)**
	Exchangeable Mg (mmol(+)/kg)	0.11 (0.711)	0.04 (0.905)	0.05 (0.887)
	Exchangeable Ca (mmol(+)/kg)	0.06 (0.839)	-0.03 (0.917)	-0.02 (0.935)
	CEC (mmol(+)/kg)	0.21 (0.469)	0.24 (0.400)	0.24 (0.409)
	N total (mg/g of soil)	-0.07 (0.821)	-0.13 (0.669)	-0.11 (0.714)
	% Clay	**0.35 (0.225)**	**0.38 (0.182)**	**0.45 (0.106)**
Site 2	pH (water)	0.21 (0.459)	0.07 (0.808)	-0.19 (0.498)
	Exchangeable K (mmol(+)/kg)	-0.03 (0.905)	0.08 (0.789)	-0.03 (0.919)
	Exchangeable Mg (mmol(+)/kg)	0.06 (0.821)	-0.14 (0.622)	-0.33 (0.225)
	Exchangeable Ca (mmol(+)/kg)	0.07 (0.790)	-0.14 (0.613)	-0.34 (0.220)
	CEC (mmol(+)/kg)	0.05 (0.852)	-0.18 (0.521)	-0.36 (0.185)
	N total (mg/g of soil)	-0.42 (0.121)	-0.55 (0.035)	-0.55 (0.031)
	% Clay	-0.34 (0.211)	-0.17 (0.546)	-0.22 (0.434)
Site 3	pH (water)	-0.04 (0.882)	-0.13 (0.657)	-0.05 (0.856)
	Exchangeable K (mmol(+)/kg)	-0.05 (0.855)	-0.19 (0.521)	-0.08 (0.797)
	Exchangeable Mg (mmol(+)/kg)	-0.29 (0.307)	-0.30 (0.302)	-0.32 (0.258
	Exchangeable Ca (mmol(+)/kg)	-0.26 (0.362)	-0.29 (0.310)	-0.33 (0.248)
	CEC (mmol(+)/kg)	-0.39 (0.172)	-0.39 (0.169)	-0.30 (0.297)
	N total (mg/g of soil)	-0.43 (0.127)	-0.51 (0.065)	-0.48 (0.084)
	% Clay	-0.06 (0.848)	-0.26 (0.378)	0.02 (0.952)

2.4.2 Humus layer chemical properties and aspen basal area relationships

On all sites, forest floor pH increased significantly with basal area of aspen within 7 m (Figure 2.1). CEC, exchangeable K and Ca were significantly related to aspen basal area within 5 m of the sampling point while exchangeable Mg was only affected by aspen located within 3 m. The influence of aspen located within 3 m of the sampling point on exchangeable K is considered significant ($p = 0.0537$) and will be discussed later in this paper. The slopes of the relationships between aspen and exchangeable cations were not different between sites. Exchangeable K was lower in site 2 than in sites 1 and 3, exchangeable Mg was higher in site 2, and exchangeable Ca and CEC were significantly higher in site 2 and significantly lower in site 1 (Figure 2.2). Total nitrogen and C:N ratio were affected by aspen basal area within a distance of 7 m from the sampling point. Slopes were similar and intercept points of both FH properties were higher in site 2 than in the other sites according to the type I ANCOVA (Table 2.4). Total nitrogen increased while C:N ratio decreased along the gradient of aspen basal area within 7 m of the sampling point (Figure 2.3).

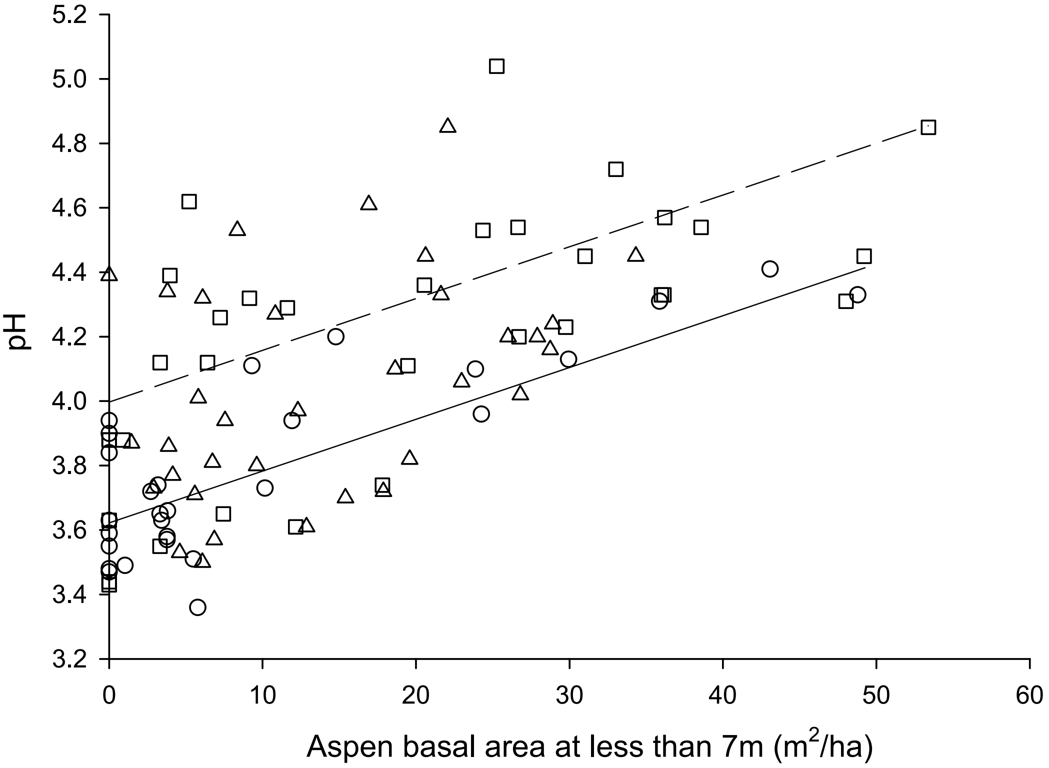

Figure 2.1 Relationship between pH and aspen basal area within 7 m (ABA7) of the sampling point; pH = 3.6241 + 0.0160 ABA7 + 0.3767 dummy2, R^2:0.5972, p=<0.0001, N=95, Δ = site 1 (solid line), ☐ = site 2 (long dash line), o = site 3 (solid line).

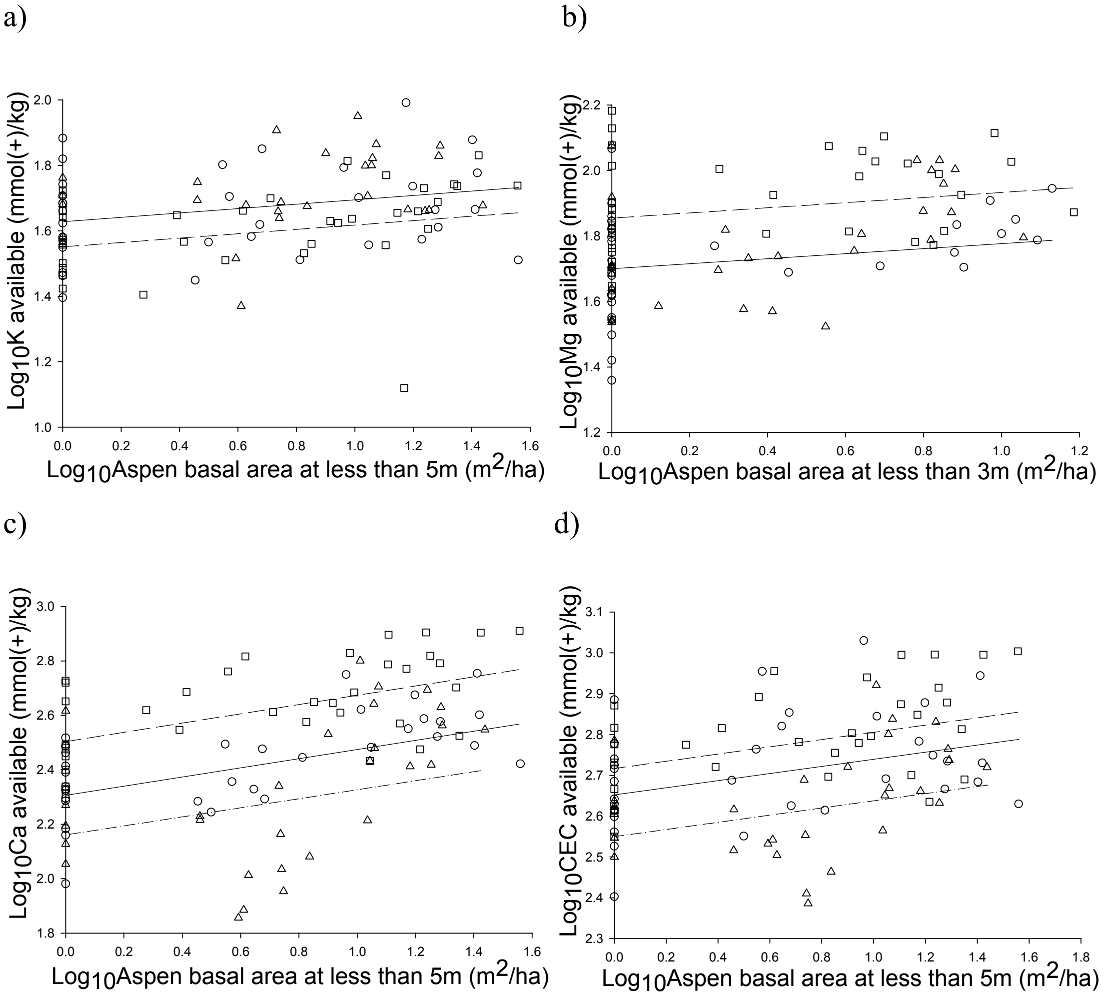

Figure 2.2 (a) Relationship between K and aspen basal area within 5 m (ABA5) of the sampling point; $Log_{10}K = 1.6267 + 0.0672\ log_{10}ABA5 - 0.0772\ dummy2$, R^2:0.1564, p=0.0004, N=95, Δ = site 1 (solid line), ☐ = site 2 (long dash line), o = site 3 (solid line). (b) Relationship between Mg and aspen basal area within 3 m (ABA3) of the sampling point; $Log_{10}Mg = 1.6988 + 0.0771\ log_{10}ABA3 + 0.1578\ dummy2$, R^2:0.3146, $p<0.0001$, N=95. (c) Relationship between Ca and aspen basal area within 5 m (ABA5) of the sampling point; $Log_{10}Ca = 2.3045 + 0.1695\ log_{10}ABA5 - 0.1455\ dummy1 + 0.1986\ dummy2$, R^2:0.5133, $p<0.0001$, N=95, site 1 (dash dotted line). (d) Relationship between CEC and aspen basal area within 5 m (ABA5) of the sampling point; $Log_{10}CEC = 2.6514 + 0.0881\ log_{10}ABA5 - 0.1013\ dummy1 + 0.0659\ dummy2$, R^2:0.3451, $p<0.0001$, N=95.

Table 2.4 Type 1 covariance analysis (ANCOVA) to test the influence of aspen at each range of distance of the sampling point on FH layer soil properties (total nitrogen (TN), C:N ratio, pH, exchangeable K, Mg and Ca, CEC, organic matter (OM) thickness and decomposition rate (DECAY))

	Total N (R^2:0.4169)		C:N (R^2: 0.5197)		OM thickness (R^2: 0.4758)	
	SS1	F value	SS1	F value	SS1	F value
Model	0.4204	12.73***	0.7271	19.26***	0.9685	16.16***
Error	0.5880		0.6720		1.0670	
Site	0.1465	11.09***	0.2506	16.59***	0.1809	7.55***
ABA3	0.1404	21.26***	0.2282	30.23***	0.5330	44.46***
ABA35	0.0664	10.05**	0.1250	16.55***	0.1577	13.15***
ABA57	0.0671	10.16**	0.1233	16.33***	0.0969	8.08**

	pH (R^2: 0.6089)		DECAY (R^2: 0.3429)		K (R^2: 0.1742)	
	SS1	F value	SS1	F value	SS1	F value
Model	8.4368	27.71***	0.4130	7.65***	0.3192	4.74**
Error	5.4189		0.7914		1.5135	
Site	3.8000	31.21***	0.1551	8.62***	0.1642	4.88**
ABA3	3.0155	49.53***	0.1194	13.28***	0.0583	3.46^{+}
ABA35	1.0424	17.12***	0.0202	2.25	0.0967	5.75*
ABA35 *site			0.1183	6.58**		
ABA57	0.5790	9.51**				

Table 2.4 (continued)

	Mg (R^2:0.3169)		Ca (R^2: 0. 5217		CEC (R^2: 0.3320)	
	SS1	F value	SS1	F value	SS1	F value
Model	0.8856	14.07***	2.8969	24.54***	0.6536	11.18***
Error	1.9091		2.6560		1.3148	
Site	0.6257	14.91***	1.7875	30.29***	0.3923	13.43***
ABA3	0.2600	12.39***	0.9253	31.36***	0.1721	11.78***
ABA35			0.1841	6.24*	0.0891	6.10*

* = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$, + p=0.0660, all soil properties are $\log_{10}$ transformed except forest floor pH.

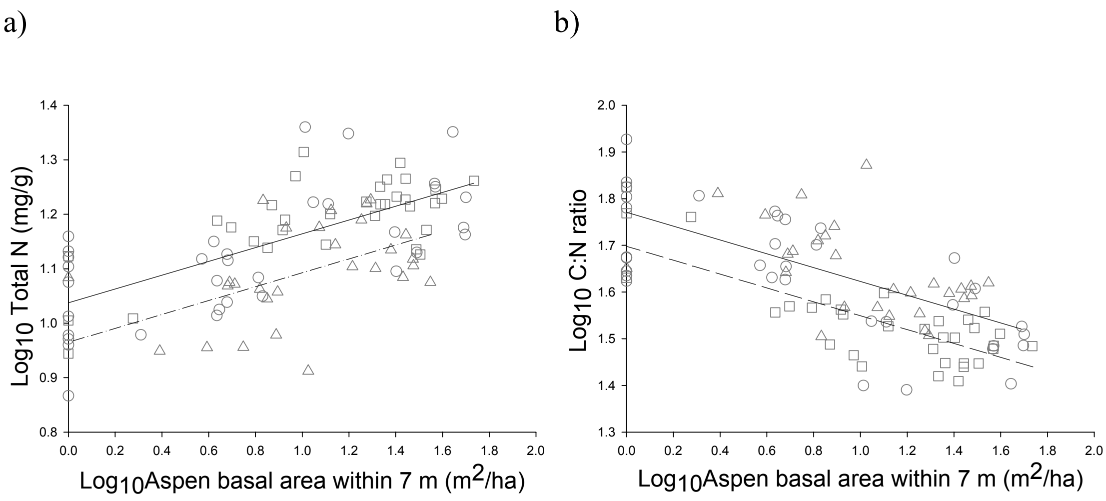

Figure 2.3 (a) Relationship between total nitrogen and aspen basal area within 7 m (ABA7) of the sampling point; Log$_{10}$TN = 1.0379 + 0.1262 log$_{10}$ABA7 – 0.0713 dummy1, R^2:0.4764, $p<0.0001$, N=95, Δ = site 1 (dash dotted line), □ = site 2 (solid line), o = site 3 (solid line). (b) Relationship between CN ratio and aspen basal area within 7 m (ABA7) of the sampling point; Log$_{10}$CN = 0.3708 + 0.0574 log$_{10}$ABA7 – 0.0775 dummy2, R^2:0.2205, $p<0.0001$, N=95, sites 1 and 3 (solid line), site 2 (long dash line).

2.4.3 Relationships between aspen basal area and organic matter depth and the decomposition rates of a standard substrate

Organic matter thickness was influenced by presence of aspen trees located within 7 m of the sampling point while decay rates were significantly affected by aspen basal area within 5 m of the sampling point. Slopes of the relationships between aspen and FH layer organic matter thickness was not different between sites (Table 2.4). The effect of aspen on decay rates was different across sites. The decay rate increased along the gradient of aspen in site 3 while it was not significantly affected by aspen basal area in sites 1 and 2 according to the regression analysis (Figure 2.4). Organic matter thickness decreased along the gradient of aspen basal area within 7 m of the sampling point (Figure 2.4).

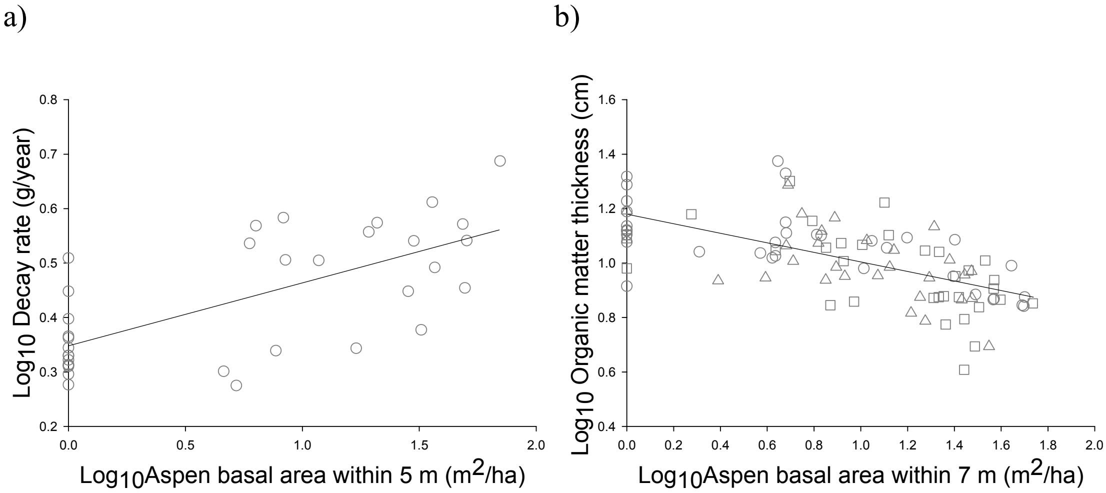

Figure 2.4 (a) Relationship between decay rate and aspen basal area within 5 m (ABA5) of the sampling point; Log$_{10}$DECAY = 0.3483 + 0.1151 log$_{10}$ABA5, R^2:0.4638, $p<0.0001$, N=34, o = site 3. (b) Relationship between organic matter thickness (OM) and aspen basal area within 7 m (ABA7) of the sampling point; Log$_{10}$OM = 1.1771 - 0.1750 log$_{10}$ABA7, R^2:0.3905, $p<0.0001$, sites 1, 2 and 3.

2.4.4 Net N mineralization and nitrification

On site 1, net N mineralization rates in all treatments were significantly and positively related to aspen basal area within 7 m of the sampling point, with similar slopes across treatments (Table 2. 5, Figure 2.5). On sites 2 and 3, there were no significant relationships between net N mineralization and aspen basal area. On site 1, there were no significant relationships between net N nitrification. On site 2, only net N nitrification in the double-dose treatment decreased significantly with aspen (Figure 2.5), and on site 3, net N nitrification increased with aspen basal area within 7 m of the sampling point for all treatments. Net N mineralization and nitrification were lower for the double-dose treatment than for the single-dose treatment, and significantly lower for the single-dose treatment than for the control treatment (Table 2.6). Spearman correlation between C:N ratio and net N mineralization was not significant on site 1 (Rho = -0.33, p = 0.2713) and site 2 (Rho = -0.41, p = 0.1491), while the correlation was significant on site 3 (Rho = -0.76, p = 0.0111). Spearman correlation between C:N ratio and net N nitrification was not significant on site 1 (Rho = -0.51, p = 0.0725) and site 2 (Rho = -0.29, p = 0.3162), while the correlation was significant on site 3 (Rho = -0.81, p = 0.0047).

Table 2.5 Non-parametric variance analyses and covariance analyses performed on the ranks of net N mineralization and net N nitrification in the humus layer to test the influence of aspen basal area and the fertilization treatment

Variable	Source	DF	SS	F-values[4]
Site 1 (ANCOVA)				
Ranks of net N mineralization	Model	3	6871.90	130.78***
R^2: 0.9054	Error	41	718.10	
	Treatment	2	6750.00	192.70***
	ABA7	1	121.90	6.96*
Site 2 (ANOVA)				
Rank of net N mineralization	Model	2	6720.13	162.23***
R^2: 0.8854	Error	42	869.87	
	Treatment	2	6720.13	162.23***
Site 3 (ANOVA)				
Ranks of net N mineralization	Model	2	5544.13	56.91***
R^2: 0.7305	Error	42	2045.87	
	Treatment	2	5544.13	56.91***
Site 1 (ANOVA)				
Ranks of net N nitrification	Model	2	6603.33	141.26***
R^2: 0.8706	Error	42	981.67	
	Treatment	2	6603.33	141.26***

Table 2.5 (continued)

Site 2 (ANCOVA)				
Ranks of net N nitrification	Model	5	6823.18	81.03***
R^2: 0.9122	Error	39	656.82	
	Treatment	2	702.85	20.87***
	ABA7	1	50.39	2.99
	ABA7 *Treatment	2	226.25	6.72**
Site 3 (ANCOVA)				
Ranks of net N nitrification	Model	3	6615.33	96.94***
R^2: 0.8764	Error	41	932.67	
	Treatment	2	6436.13	141.47***
	ABA7	1	179.20	7.88**

* = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

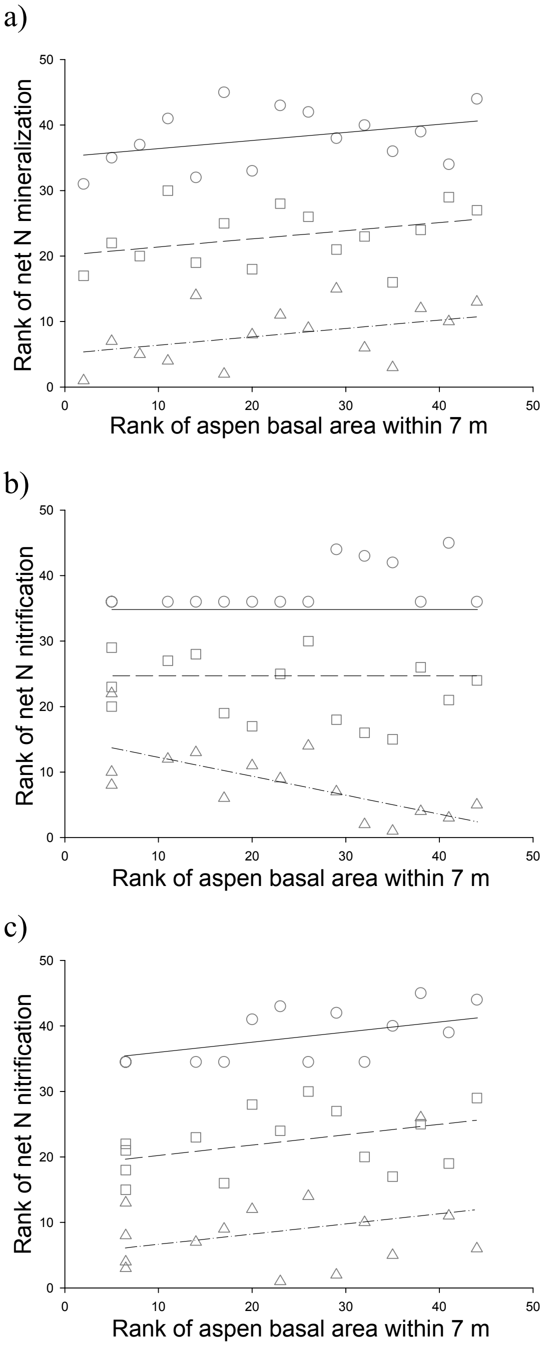

Figure 2.5 (a) Relationship between rank of net N mineralization and rank of aspen basal area within 7 m (ABA7) of the sampling point in site 1. Relationship between rank of net N nitrification and rank of aspen basal area within 7 m (ABA7) of the sampling point in (b) site 2 and (c) site 3. o = Control treatment (solid line), □ = single dose treatment (long dash line), Δ= double dose treatment (dash dotted line), see details in Table 2.5.

Table 2.6 Means of net N mineralization and net N nitrification by treatment for each site

	Means ± standard deviations		
	C treatment	D treatment	DD treatment
Site 1			
Net N mineralization (μg N g^{-1} day^{-1})	9.87 ± 14.96 a	-9.83 ± 1.17 b	-22.81 ± 1.73 c
Net N nitrification (μg N g^{-1} day^{-1})	0.13 ± 0.16 a	-7.21 ± 0.76 b	-11.49 ± 1.74 c
Site 2			
Net N mineralization (μg N g^{-1} day^{-1})	1.51 ± 1.74 a	-8.50 ± 1.25 b	-23.12 ± 4.15 c
Net N nitrification (μg N g^{-1} day^{-1})	0.02 ± 0.04 a	-6.49 ± 1.01 b	-11.94 ± 2.27 c
Site 3			
Net N mineralization (μg N g^{-1} day^{-1})	5.81 ± 9.76 a	-10.29 ± 1.52 b	-21.06 ± 15.11 c
Net N nitrification (μg N g^{-1} day^{-1})	0.83 ± 1.91 a	-7.34 ± 0.71 b	-12.35 ± 2.31 c

**Columns with identical letters within a row are not significantly different according to Tukey's multiple comparisons test.

2.5 Discussion

2.5.1 Homogeneity of mineral soil properties along the gradient of aspen

The influence of forest composition on nutrient cycling is a controversial and long-lasting issue in the literature (Binkley, 1995; Rothe and Binkley, 2001). Does forest composition influence soil properties or does it just reflect original conditions? The effect of soil types, slope and drainage on forest composition is essentially accepted in the scientific community (Bergeron and Bouchard, 1984; Carleton and Maycock, 1978; Gauthier, De Grandpré and Bergeron, 2000). It is however possible to find different forest communities on sites sharing similar soil conditions (Gauthier, De Grandpré and Bergeron, 2000), which provides the possibility to properly test the influence of forest composition on soil properties. To ensure that the importance of aspen was not linked to mineral soil conditions, this study was conducted on three large sites which we presumed to be homogeneous in terms of mineral soil characteristics. Each site contained a gradient in aspen−black spruce composition. Only three mineral soil properties (percent clay, pH and exchangeable K) out of the seven investigated were positively correlated with the aspen gradient and that was the case exclusively on site 1 (p-value of 0.10). We therefore concluded that mineral soil properties were not responsible for the aspen gradient on sites 2 and 3. Given the fact that all forest floor properties were affected by aspen to the same amplitude on all three sites (except in the case of decay rate where the influence of aspen was significant only on site 3), we accepted that there could be a minor confusing influence of mineral soil on forest floor properties for site 1.

2.5.2 Soil chemistry properties along the gradient of aspen

Despite the convincing absence of correlations between mineral soil properties and stand composition on sites 2 and 3, the presence of aspen influenced several soil chemistry properties of the FH layer in all three sites. Our results are consistent with those in the literature that show that forest composition affects nutrient cycling (Alban, 1982; Finzi and Canham, 1998; Hobbie, 1992; Paré and Bergeron, 1996; van Breemen, Finzi and Canham, 1997) and that the influence of tree species depends on the soil properties explored (Rothe, Kreutzer and Küchenhoff, 2002). Aspen, a highly nutrient demanding species, is known to act as a cation pump by reallocating cations from the mineral soil to the humus layer soil through litterfall (Alban, 1982; Corns, 1989; Paré and Bergeron, 1996). Despite the presence of similar abiotic conditions (surface deposit, slope, drainage), the presence of aspen trees on the three sites was associated with higher exchangeable cations, CEC and pH of FH layer, suggesting that the potential fertility of soil increases with aspen basal area.

The influence of single trees on soil properties changes with distance from the trunk (Lodhi, 1977; Riha et al., 1986; Zinke, 1962). Lodhi (1977) and Zinke (1962) observed a decrease in pH in the first metre from the trunk, followed by an increase. Unfortunately, the design used in our study did not allow us to test the influence of aspen at this fine scale. However, our study suggests that the zone of influence of aspen depends on the soil properties considered. In fact, the zone of influence of aspen on pH and total nitrogen was 7 m while it was 5 m on CEC, exchangeable Ca and K and 3 m on exchangeable Mg. Potassium which, unlike other cations (Binkley, 1986), cycles rapidly in throughfall washed from the leaves, is the only soil property to be slightly ($p = 0.0660$) affected by aspen located at 3 m and significantly affected by aspen at 5 m. The richness of throughfall in K could explain the ring distribution of the aspen effect for this nutrient. The size of the crown area projection on the soil surface was identified as a major variable corresponding to the influence of individual trees on soil properties according to Zinke (1962). Moreover, aspen leaf dispersion could also be affected by wind and slopes steepness (Zinke, 1962). Aspen mean DBH, height and fine root network development can also affect litterfall distribution (Staelens et al., 2003). The 5 m zone of influence of aspen on CEC, exchangeable K and Ca, and the 3 m zone of influence of aspen on exchangeable Mg suggest that the influence of aspen on soil chemical properties is confined to a local zone.

2.5.3 Effect of aspen on the decomposition process

The decomposition rate of soil organic matter is related to the quality of the litter and to soil chemical and microenvironmental conditions (Moore et al., 1999; Trofymow et al., 2002). While a significant effect of aspen on the decay rate of wooden sticks was only found for site 3, suggesting that soil chemical and microenvironmental conditions could be affected by aspen, the decrease in organic matter thickness on all sites suggested a more general influence of aspen on the decomposition process, including a litter of higher quality as well as a general improvement of soil physical and chemical properties. In fact, C:N ratio of the FH layer decreased with aspen basal area and shared the same zone of influence as organic matter depth. Changes in total nitrogen, C:N ratio, organic matter depth, exchangeable cations, pH and CEC on all sites suggested that the presence of aspen accelerates nutrient cycling, which could affect stand productivity to some extent. However, physical conditions such as forest floor moisture and temperature were unfortunately not measured directly in this study. It is important to emphasize the fact that forest floor depth was comparable to estimates from other studies conducted in stands of similar age (80 years) in the Canadian boreal forest (Boudreault et al., 2002; Yu, Apps and Bhatti, 2002). Charcoal was found at the interface of mineral soil and humus layer all over the sites, both in black spruce- and aspen-dominated experimental units, suggesting that most of the forest floor is newly formed and that the possibility of a carry-over from the previous stand is minimal.

2.5.4 N availability

The effect of aspen was tested on several indices of N availability. The total C:N ratio of humus, which is an indicator of N mineralization rate (Côté et al., 2000; Flanagan and Van Cleve, 1983; Paré and Bergeron, 1996; Thomas and Prescott, 2000; Wedin and Tilman, 1990), indicated a straightforward effect of aspen on all sites as it decreased with increasing presence of aspen in a radius of 7 m.

Results from laboratory incubation were less straightforward as only one site showed a significant effect of aspen on net N mineralization. On site 1, aspen basal area was positively related to net N mineralization, irrespective of the amount of N added. It is noteworthy that the conditions for soil microbial activity, such as high pH, nutrient availability and litter quality (C:N ratio), were relatively more favourable on sites 2 and 3 than on site 1, which suggests that presence of aspen could have a greater potential influence on relatively poorer sites.

Laboratory incubation was conducted under standard conditions of temperature and water content for all samples. These conditions may differ from these in the field, which are more favourable to microbial activities; adequate water content and pH were generally observed with increasing presence of aspen. The best field conditions for the decomposition process in the presence of aspen were also revealed by humus thickness and by the increased decomposition of a standard substrate. The results from laboratory incubation should be interpreted with caution since the end results may depend on the temperature and length of the incubation period. A longer incubation conducted by Côté et al. (2000) indicated a greater N mineralization potential of aspen compared with white spruce. Côté et al. (2000) also observed a significant relationship between C:N and N mineralization. The lack of an observed relationship in the present study between total C:N and N mineralization, with the exception of site 3, suggests that the experiment was not conducted for a long enough time period to evaluate the true soil potential for N nutrition. It should be noted that the incubation temperature of 10 ^{o}C was under optimal conditions. In conclusion, the positive effects of aspen on soil C:N ratio, on humus depth, on the decomposition rates of a standard substrate, and the positive or non-significant effects on laboratory rates of N mineralization suggest that aspen accelerates the cycling of C and N in black spruce stands.

The high immobilization rates observed upon N additions revealed that the microbial communities of those mixed stands are strongly N limited. The varying results obtained for nitrification also suggest complex processes within the microbial communities that could be elucidated using methods to describe gross N fluxes.

2.6 Conclusion

Our results suggest that the presence of aspen at different temporal and spatial scales could accelerate nutrient cycling, which may improve or preserve the productivity of the stand. These results support the hypothesis that the presence of aspen could enhance black spruce productivity. However, our results are not sufficient to conclude about the potenital of mixed management for these types of stands. Management strategies will depend on site characteristics and on the species present and their proportions. It could also depend on ecological niche separation, which reduces competition between species. The different combinations of species and the property-specific responses studied could also explain the variety of responses reported in the litterature about the influence of forest composition on soil properties.

2.7 Acknowledgments

We are grateful to Annie Belleau and Alain Courcelles for their great assistance in the field and in the laboratory. This study was supported by the Fonds québécois de la recherche sur la nature et les technologies, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Tembec Inc., the Canadian Forest Service and the Natural Sciences and Engineering Research Council of Canada.

CHAPITRE III

EFFECT OF ASPEN (POPULUS TREMULOIDES) AS A COMPANION SPECIES ON THE GROWTH OF BLACK SPRUCE (PICEA MARIANA) IN THE SOUTHWESTERN BOREAL FOREST OF QUEBEC

Sonia Légaré, Yves Bergeron and David Paré

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3.1 Abstract

In the western boreal forest of Quebec, black spruce stand productivity is approximately 1 m^3 ha^{-1} yr^{-1}. The low productivity of these stands is often attributed to the paludification process, which is sustained by low quality black spruce litter and the influence of black spruce on soil moisture. In contrast, aspen increases nutrient cycling, suggesting that the presence of aspen in black spruce-dominated stands could offset the effect of black spruce on soil processes and positively affect stand productivity. We hypothesised that aspen in black spruce-dominated stands could: 1) increase black spruce DBH, height and volume per stem, 2) increase black spruce productivity without affecting black spruce volume in the stand, and 3) increase total stand volume. In 2001, twelve 14 m diameter plots were sampled for DBH and height of every stem on three black spruce-dominated sites containing various proportions of aspen. Using stem analysis, the time to grow from a height of 5 m to a height of 10 m was determined on three dominant black spruces in each plot. Statistical analyses revealed that DBH, height and volume per black spruce stem were not affected by aspen. However, total black spruce volume decreased with increasing aspen basal area in sites 2 and 3, suggesting that the presence of aspen reduced black spruce density. In site 1, black spruce volume was not affected by aspen, indicating, for total stand productivity, a net gain in aspen fibre. Along a gradient of increasing aspen basal area, the time to grow 5 m decreased in sites 1 and 3. These results suggest that the presence of aspen influences black spruce productivity, although this influence is site-specific and could be dependent on the proportion of aspen, its hierarchical position in the canopy, and the nutrient status of the site. To some extent, this could explain the absence of a general trend concerning mixed stand productivity.

Keywords: *Populus tremuloides*; *Picea mariana*; Merchantable volume; Productivity; Mixed-species stands

3.2 Introduction

A general theory to the effect that intercropping should allow higher yield due to the competitive exclusion principle and/or the facilitation mechanism was elaborated by Vandermeer (1989). The competitive exclusion principle is based on the ecological niche separation of combined species, which involves a more complete utilization of resources. Facilitation is described as the influence of a species on the environment, which positively affects other species. Forest mixed management based on this theory was explored by Kelty (1992), who suggested that species with a good ecological niche separation (Harper, 1977) and species that have a high efficiency in the use of a limiting resource should present higher yield in mixed stands than in monoculture stands. However, due to the multiple combinations of species and their different interactions on soil and stand productivity, there is no general trend in the scientific literature to guide mixed management choices. In fact, according to the age, species and proportion of each species in the stand, growth loss or gain may be observed (Brown, 1992; Frivold and Mielikäinen, 1990; Lieffers and Blenis, 2001; MacPherson, Chen and Klinka, 2003).

Since the 1990s, the Canadien forest industry has had a growing interest in the use of intolerant deciduous species of the boreal forest. This fact, together with an increasing concern for the maintenance of biodiversity, could promote mixed-species management as a component of ecosystem management (Bergeron and Harvey, 1997; Bergeron et al., 1999). Mixed stands that include more than one commercial species can be advantageous even if the yield of the mixture exceeds only the yield of the monoculture of the less productive species included in the mixture. Moreover, in addition to its role in the maintenance of biodiversity, mixed-stand management could have other advantages such as a decreasing risk of wind damage and pest or disease outbreaks (Kelty, 1992; Su, MacLean and Needham, 1996).

North of the 49th parallel in the western Quebec boreal forest, most sites are commonly colonized by black spruce following wildfire. These even-aged seed-origin stands progressively become uneven-aged (Groot and Horton, 1994). These stands generate litter that is relatively resistant to decomposition processes and which promotes the growth of mosses, including sphagnum (Flanagan and Van Cleve, 1983). In the absence of fire, the accumulation of organic matter forms a thick LFH layer dominated by feathermoss and sphagnum that immobilize nutrients (Foster, 1985; Oechel and Van Cleve, 1986; Weber and Van Cleve, 1981). It has been suggested that the paludification process could explain the low productivity of black spruce in these stands (1 m^3/ha/yr; Foster, 1983; Oechel and Van Cleve, 1986; Van Cleve and Viereck, 1981; Viereck and Dyrness, 1979). However, natural stands of shade-intolerant deciduous species, such as aspen, which hasten nutrient cycling (Corns, 1989; Longpré et al., 1994; Paré and Bergeron, 1996; Van Cleve and Noonan, 1975), can also dominate after fire (Gauthier, De Grandpré and Bergeron, 2000). These stands generally evolve into mixed-species stands that are relatively productive (2 to 3 m^3/ha/yr). Following forest harvesting, stands originally dominated by black spruce may be invaded by deciduous species such as willow and aspen (Carleton and MacLellan, 1994; Fortin, 2000). Despite the economic value of aspen, from the view point of the sawmill industry, the presence of aspen in black spruce stands is generally considered as a competitive species to be controlled. However, in addition to a potential distinct ecological niche between these species, the increased nutrient cycling rates of aspen could offset the effect of black spruce on soil processes and positively affect stand productivity in black spruce-dominated stands. Légaré, Paré and Bergeron (2004) observed in a landscape-scale study that an increasing proportion of aspen was related to an increase in black spruce DBH and height up to a threshold of 40% of aspen basal area. They also observed a stable black spruce volume with an increasing total volume along the gradient of aspen that suggested a natural additive pattern (Harper, 1977). However, the confounding effect of soil on black spruce growth was still a preoccupation in that previous study. Thus, the objectives of the present study were to test the following hypotheses in black spruce-dominated stands: 1) the presence of aspen increases mean DBH, height and volume per stem of black spruce, 2) the presence of aspen does not affect black spruce total stand volume and total stand merchantable volume but increases the volume and merchantable volume of the stand, and 3) the presence of aspen increases black spruce productivity. In order to test those hypotheses we sampled three black spruce stands and assessed the effects of aspen basal area on growth and yield of black spruce.

3.3 Material and methods

3.3.1 Study area

The study area is part of the black spruce (*Picea mariana* (Mill.) BSP) – feather moss (*Pleurozium schreberi* (Brid.) Mitt.)) forest of western Quebec (Grondin, 1996), located at the border of the Abitibi-Témiscamingue and Nord du Québec regions, in the south-western boreal forest of Quebec (49°03′N to 49°11′N, 78°50′W to 79°09′W). The study area extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the Wisconsinian glacial stage (Vincent and Hardy, 1977). The closest weather station is located at La Sarre, approximately 30 km south of the study area. Average annual precipitation totals 856.8 mm and average annual temperature is 0.8°C (Environment Canada, 1993). This ecosystem is dominated by large fires that kill most of the trees and aboveground vegetation (Viereck et al., 1983). Mean stand age is 139 years and fire cycle length has increased from 141 years, between 1850 and 1920, to 326 years since 1920 (Bergeron et al., 2001).

3.3.2 Sampling design

In a previous study (Légaré, Paré and Bergeron, 2004), the potential of aspen-spruce mixture to increase forest productivity could have been obscured by confounding factors relative to soil fertility. The presence of a correlation between soil fertility and forest composition inherent in the sampling design did not allow us to determine whether the highest total stand yield was a matter of soil fertility or a matter of the occurrence of competitive reduction or productive facilitation between species. The originality of the current study lies in the adoption of an approach through which the confounding factors issue are avoided by the examination of correlations between aspen basal area and mineral soil properties such as soil texture, total nitrogen concentration and cation exchange capacity, in addition to sampling stands with similar abiotic conditions (surface deposit, drainage).

Three sites were chosen according to the following criteria: gentle slope, moderate drainage, similar surface deposit and stand composition dominated by black spruce with heterogeneous presence of aspen. Stands at all three sites originated from wildfires that took place around 1920 according to the fire map producted by Bergeron et al. (2004). More precisely, stands 1, 2 and 3 originated from fires that occurred around 1926, 1916 and 1916, respectively, according to aspen base cross-sections (0 m) at each site. Sites were different in terms of stem density, soil texture, site index and mean aspen proportion (Table 3.1). The number and length of transect lines in a site depended on the size and form of the spruce—aspen stands. The sampling unit of this study was a circular plot of 14 m in diameter, distributed at every 20 m along a transect of at least 180 m. Sites 1, 2 and 3 had respectively 28, 34 and 38 plots.

Table 3.1 Description of mineral soil properties, stand and tree characteristics in sites 1, 2 and 3

	Means ± standard deviations		
	Site 1	Site 2	Site 3
Site characteristics			
Total stem density (# of stems/ha)	3220.82 ± 698.40	2013. 80 ± 602.63	1992.65 ± 707.61
Proportion of aspen in terms of basal area (%)	28.24 ± 18.89	38.54 ± 24.84	24.99 ± 29.55
Site index at 50 years (9 trees per sites)	11.62 ± 0.83	12.18 ± 0.84	12.72 ± 1.37
Tree characteristic (in the 12 selected plots per site)			
Aspen DBH (cm)	12.88 ± 6.39	21.06 ± 9.07	25.70 ± 12.31
Black spruce DBH (cm)	11.60 ± 0.90	14.29 ± 1.21	15.04 ± 1.27
Aspen height (m)	13.20 ± 6.36	20.33 ± 7.49	22.63 ± 9.34
Black spruce height (m)	12.12 ± 1.30	15.13 ± 1.25	15.86 ± 1.01
Black spruce age (yr)	66.76 ± 2.58	74.95 ± 2.04	77.1 ± 0.91
Mineral soil properties (in the 12 selected plots per site)			
CEC (cmol(+)/kg)	16.18 ± 4.79	17.04 ± 11.36	15.04 ± 8.42
Total N (mg/g of soil)	1.79 ± 1.27	2.03 ± 1.09	2.68 ± 1.65
Clay (%)	50.4 ± 6.3	39.5 ± 14.9	24.5 ± 9.2
Sand (%)	14.3 ± 4.7	25.3 ± 17.1	19.1 ± 4.4
Silt (%)	35.3 ± 7.1	35.2 ± 7.0	56.5 ± 8.4
Oxygenated layer depth (cm)	21.49 ± 7.03	41.70 ± 18.80	34.53 ± 12.03

To test our hypotheses, only 12 plots in each site were selected on the basis of their composition in order to minimize the presence of species other than aspen or black spruce and to incorporate a gradient of aspen as wide as possible. Moreover, plots were selected in order to create an even distribution of plot number across the aspen gradient and also to reduce the possibility of autocorrelation between plots by selecting plots with a distance of at least 40 m between each other. However, in site 3, one plot was removed from the statistical analysis because of its particularly low basal area due to windthrow. In 2001, we measured the diameter at breast height (DBH) of every tree in each of the 35 plots (11 or 12 at each site) of the sampling plan to determine the basal area covered by each species. Heights were measured with a clinometer. The volume of each species was estimated with Honer's respective equation (Honer, Ker and Alemdag, 1983) and merchantable volume was calculated using stems with DBH over 9 cm only. In 2002, we conducted stem analyses on the three tallest black spruce trees in each plot. These black spruce trees were generally dominant or co-dominant, however, in a few plots, the tallest black spruce trees were suppressed. Cross-sections were taken at the base and at 0.40, 1.0, 1.30 m and then at every meter up to the top. Cross-sections were measured and cross-dated in the laboratory with a binocular microscope. We determined the time to grow from a height of 5 m to a height of 10 m (TTG510) by subtracting age at 10 m by age at 5 m of height. Nine clearly dominant black spruce stems in each site were also selected and cut at the base and at every meter to determine the site index which is the height of trees at 50 years.

Three samples of the first 10 cm of mineral soil (Ae horizon and the top of the B horizon) were taken in each plot (12/sites). For each plot, soil samples were pooled, air dried, ground and then analysed. CEC was determined by the sum of exchangeable cations (Hendershot et al., 1993). Total N was determined colorimetrically following a H_2SO_4/H_2O_2 digestion (Keeney and Nelson, 1982). Soil texture was determined by granulometric analyses (McKeague, 1976). Moreover, one steel rod per plot, approximately 120 cm long, was driven into the soil and left for a period of 4 weeks to measure the oxygenated layer depth. Steel rods were removed with locking pliers and immediately taped with different colours in order to identify zones with orange/brown and black rust. Distance from the soil surface to the bottom of the orange/brown and black rust zones were measured (Carnell and Anderson, 1986).

3.3.3 Statistical analyses

To test the homogeneity of mineral soil properties and water regime (percent clay, silt and sand, CEC, total nitrogen and oxygenated layer depth) along the gradient of increasing aspen basal area, Spearman correlations were performed for each site separately because soil texture differed between sites. According to the Bonferroni method (Sokal and Rohlf, 1995), a significant threshold was fixed at 0.0033 to keep an overall significant threshold of 0.05 for the 15 correlations performed. According to Kelty (1992), the spatial arrangement of trees of different species must be fine-grained (i.e. trees must be adjacent to trees of different species) to observe a reduction in competition. The structure proposed by Kelty (1992) is a widely spaced overstory of the most productive species with understory trees that are not completely suppressed. Thus, to test the spatial segregation of aspen in each site, we performed a Mantel test between the matrix of Euclidean distance between each circular plot and the matrix of Sorensen (Bray-Curtis) similarity coefficient based on basal area of each tree species in each circular plot. Randomization test (Monte Carlo) was used for calculating p-value (Douglas and Endler, 1982; Mantel, 1967). Then we performed a general linear model (GLM) analysis on black spruce mean DBH of all plots with site as a main effect and aspen basal area as a continuous nested effect. When the aspen basal area effect was significant, stand density was added to the model as a regression effect to ensure that the significant influence of aspen basal area was not induced by stand density. This procedure was repeated to test the influence of aspen basal area on mean height, mean volume per stem, total volume and merchantable volume of black spruce, as well as stand volume, stand merchantable volume and TTG510 for black spruce. Moreover, to ensure that there would be no autocorrelation, this procedure was followed by a multiple regression analysis on residuals from the GLM analysis against x and y coordinates as nested continuous effect. This procedure was also repeated for each variable tested.

Mantel tests were performed using PC-ORD software (MjM Software, Gleneden Beach, OR) and all other statistical analyses were performed using SAS software (SAS Institute Inc., Cary, N.C.). Statistical significance threshold was fixed at 0.05.

3.4 Results

3.4.1 Correlation between mineral soil conditions and the presence of aspen

In all sites, none of the correlations tested between aspen basal area and mineral soil properties and oxygenated layer depth were significant according to the Bonferroni method. Nevertheless, in site 2, total nitrogen was negatively correlated to aspen basal area at $p<0.05$ (Table 3.2).

Table 3.2 Spearman correlation coefficients between aspen basal area and variables related to mineral soil properties

Variables	Rho (p > |r|) between aspen basal area and variables		
	Site 1	Site 2	Site 3
CEC (cmol(+)/kg)	0.24 (0.409)	-0.36 (0.185)	-0.30 (0.297)
N total (mg/g of soil)	-0.11 (0.714)	-0.55 (0.031)	-0.48 (0.084)
% Clay	0.45 (0.106)	-0.22 (0.434)	0.02 (0.952)
% Sand	-0.19 (0.523)	0.13 (0.638)	-0.25 (0.395)
% Silt	-0.35 (0.227)	0.24 (0.381)	0.06 (0.839)
Oxygenated layer depth (cm)	0.44 (0.200)	0.35 (0.270)	-0.41 (0.181)

Bonferoni correction: α: 0.05/15 = 0.0033.

3.4.2 Individual tree scale

In contrast with the first hypothesis, general linear model analysis revealed that black spruce mean DBH, height and volume per stem were not significantly affected by aspen basal area (Table 3.3). The third hypothesis was also partially rejected. In sites 1 and 3, TTG510 of black spruce decreased with aspen basal area, but TTG510 of black spruce was not significantly affected by aspen in site 2 (Table 3.3; Figure 3.1).

Table 3.3 General linear model (GLM) analysis between aspen basal area as a continuous nested effect and each variable related to stand or black spruce growth, with stand density as a regression effect when the first model tested was significant (N=35)

Variables	Source	SS	F value	Parameters (b_0, b_1 and b_2)		
				Site 1	Site 2	Site 3
BS DBH (R^2: 0.6835)	Model	80.29	12.53 (<0.0001)			
	Error	37.17				
	Site	48.87	19.07 (<0.0001)	11.06 (<0.0001)	14.94 (<0.0001)	14.94 (<0.0001)
	ABA (site)	4.05	1.05 (0.3835)			
BS height (R^2: 0.7303)	Model	100.73	15.70 (<0.0001)			
	Error	37.21				
	Site	70.21	27.36 (<0.0001)	11.65 (<0.0001)	16.53 (<0.0001)	16.53 (<0.0001)
	ABA (site)	8.62	2.24 (0.1049)			
BS volume per stem (R^2: 0.6249)	Model	0.03	9.66 (0.0001)			
	Error	0.02				
	Site	0.02	14.22 (<0.0001)	0.07(<0.0001)	0.14(<0.0001)	0.14(<0.0001)
	ABA (site)	0.00	0.71 (0.5535)			
BS TTG510 (R^2: 0.474	Model	60.66	9.34 (0.0001)			
	Error	67.12				
	ABA (site)	60.66	9.34 (0.0001)	-0.19 (0.0007)	0.01 (0.1690)	-0.13 (0.0039)
BS volume (R^2: 0.6503)	Model	74110.27	8.68 (<0.0001)			
	Error	39850.23				
	Site	19408.92	6.82 (0.0039)	89.11(0.0039)	168.59 (0.0039)	184.55 (0.0039)
	Stand density	21017.55	14.77 (0.0006)	0.04 (0.0006)	0.04 (0.0006)	0.04 (0.0006)
	ABA (site)	33322.75	7.80 (0.0006)	-1.84 (0.2808)	-4.49 (0.0016)	-4.51 (0.00029)
BS merchantable volume (R^2: 0.6075)	Model	54217.60	7.22 (<0.0001)			
	Error	35022.47				
	Site	18462.52	7.38 (0.0027)	89.67 (0.0027)	168.39 (0.0027)	181.60 (0.0027)
	Stand density	9271.13	7.41 (0.0110)	0.03 (0.0110)	0.03 (0.0110)	0.03 (0.0110)
	ABA (site)	27786.47	7.40 (0.0008)	-1.36 (0.3939)	-4.17 (0.0017)	-4.10 (0.0036)
Stand volume (R^2: 0.7760)	Model	141588.66	16.22 (<0.0001)			
	Error	40728.24				
	Site	30133.24	10.36 (0.0004)	128.02 (0.0004)	240.60 (0.0004)	219.92 (0.0004)
	Stand density	9526.01	6.55 (0.0162)	0.03 (0.0162)	0.03 (0.0162)	0.03 (0.0162)
	ABA (site)	86644.50	19.86 (<0.0001)	6.25 (0.0009)	4.31 (0.0025)	8.49 (<0.0001)
Merchantable stand volume (R^2: 0.7840)	Model	141700.95	21.06 (<0.0001)			
	Error	39028.96				
	Site	26 067.34	9.68 (0.0006)	175.62 (0.0006)	269.72 (0.0006)	243.41 (0.0006)
	ABA (site)	75664.73	18.74 (<0.0001)	5.58 (0.0015)	3.68 (0.0053)	7.89 (<0.0001)

BS: black spruce; ABA: aspen basal area; SS: sum of square; *: $p < 0.01$, **: $0.01 <= p < 0.001$, ***: $p < 0.001$; $Y = b_0 + b_1$ (Stand density) $+ b_2$ (Aspen basal area(site)).

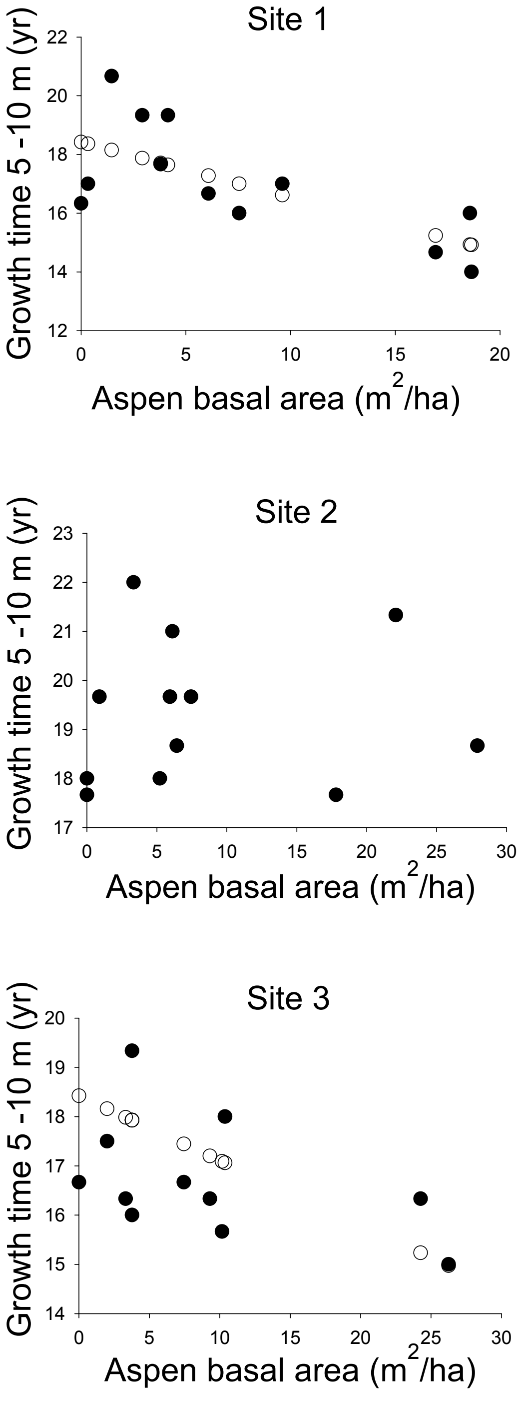

Figure 3.1 Relationships between aspen basal area and black spruce TTG510 in sites 1 (a), 2 (b) and 3 (c) (N=12, 12 and 11, respectively; ●: observed, o: predicted by the GLM procedure).

3.4.3 Stand scale

The second hypothesis was accepted for site 1 where volume and merchantable volume of black spruce were not affected by aspen basal area, and stand volume and merchantable stand volume increased significantly along the gradient of aspen basal area. However, the second hypothesis was partially rejected in sites 2 and 3 where a significant increase in stand volume and merchantable stand volume along the gradient of aspen basal area was observed while total and merchantable volume of black spruce decreased significantly (Table 3.3; Figures 3.2 and 3.3). Stand density positively influenced stand volume, black spruce volume and merchantable volume of black spruce. The presence of aspen, according to Mantel tests, was not correlated with the spatial distribution of circular plots in sites 1 ($r = 0.0129$; $p = 0.3760$) and 3 ($r = -0.0312$; $p = 0.2850$). However, the Mantel test shows a significant correlation between Euclidean distance between plots and their tree species composition in site 2 ($r = 0.1769$; $p = 0.0020$). Residuals from all GLM procedures were normally distributed, homoscedastic, and not significantly related to plot localization (results not shown).

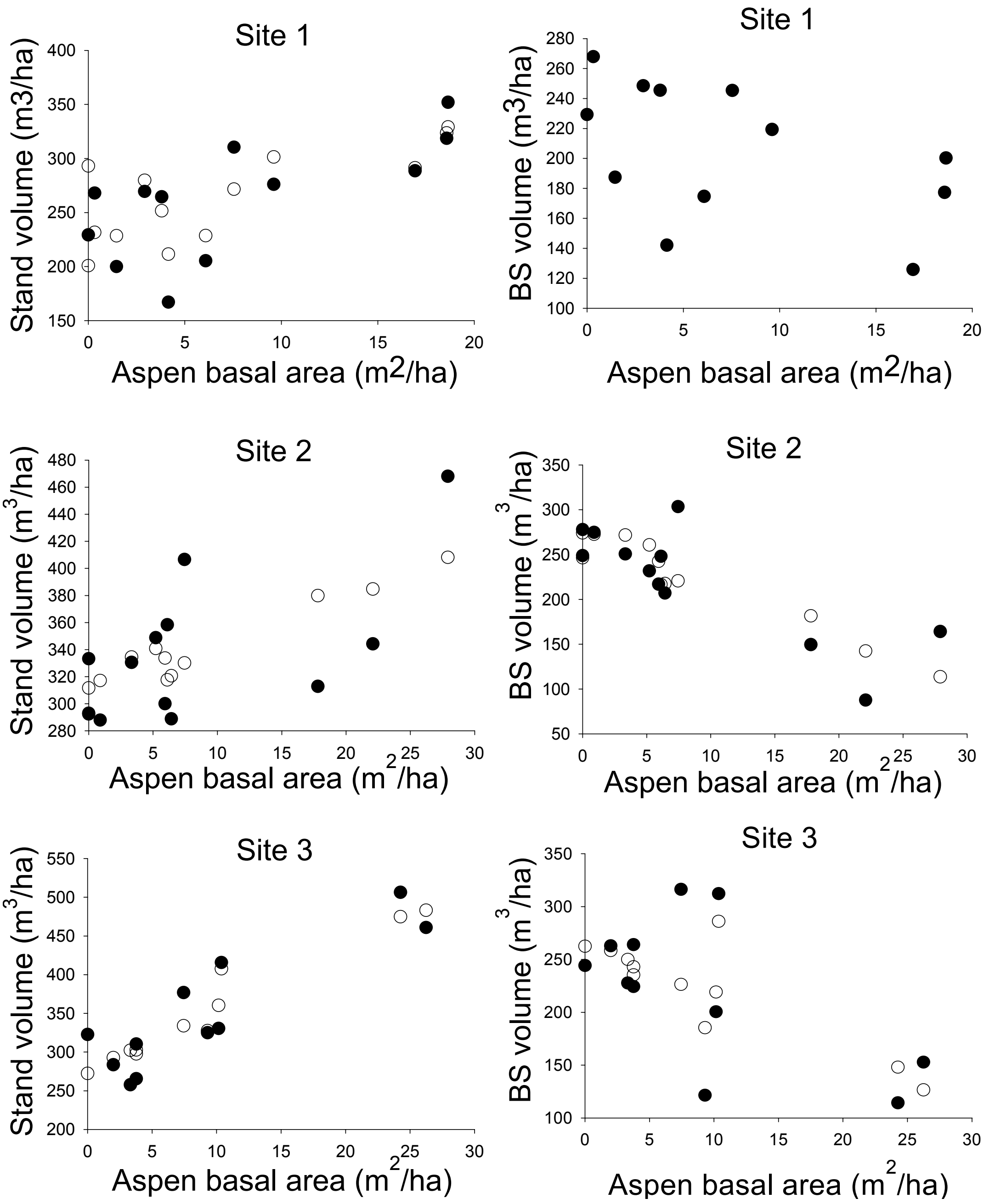

Figure 3.2 Relationships between aspen basal area and volume (black spruce (BS) and stand) in sites 1, 2 and 3 (N=12, 12 and 11, respectively; •: observed, o: predicted by the GLM procedure).

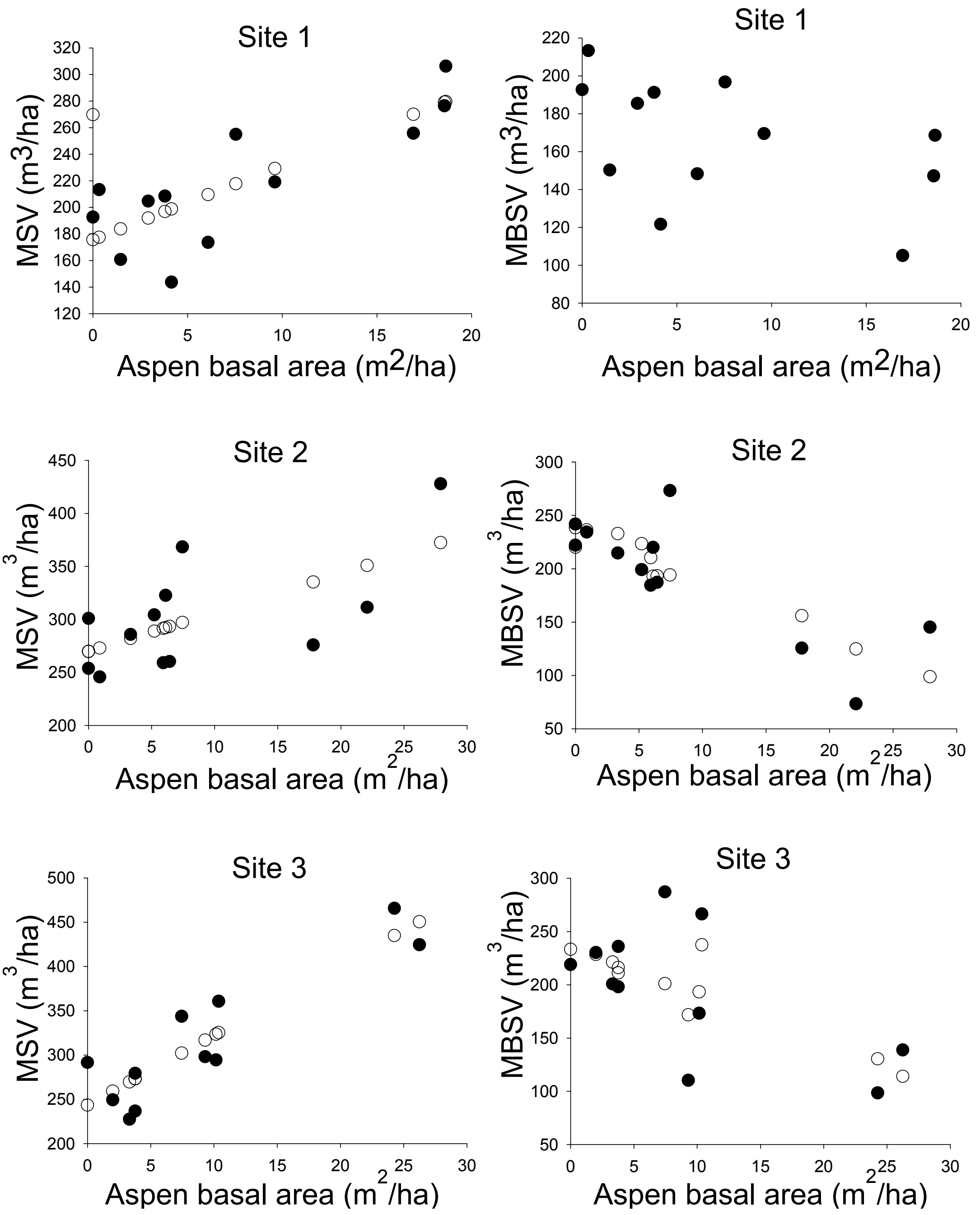

Figure 3.3 Relationships between aspen basal area and merchantable stand volume (MSV) and merchantable black spruce volume (MBSV) in sites 1, 2 and 3 (N=12, 12 and 11, respectively; ●: observed, o: predicted by the GLM procedure).

3.5 Discussion

3.5.1 Homogeneity of mineral soil properties along the gradient of aspen

In addition to the special attention given the selection of sites with homogenous drainage and slope conditions, the absence of a significant correlation between aspen basal area and oxygenated layer depth suggests that no hydrologic gradient was inherent to the aspen gradient. Decreased total nitrogen concentrations in the mineral soil with increasing relative basal area of aspen loosely suggests that forest composition could affect the mineral soil nutrient availability by reallocating nutrients from the mineral soil to the vegetation and the humus layer. This is also supported by a positive correlation between total nitrogen concentration percentage in the needles of balsam fir seedlings on site 2 and aspen basal area (Légaré, Paré and Begeron, unpublished data).

3.5.2 Competitive reduction principle

As observed by Légaré, Bergeron and Paré (2004) using forest inventory information, black spruce volume is stable despite the increase in aspen basal area in site 1, which suggests that black spruce uses, to some extent, a different ecological niche than aspen. Niche separation, by reducing the competition for light, water and nutrient, allows a more complete use of available resources (Vandermeer, 1989). Black spruce, which is a shade-tolerant evergreen species with a shallow root network, could exploit a spatially and temporally different dimension of the ecosystem than aspen, which is a shade-intolerant deciduous species with a deeper root network (Strong and La Roi, 1983; Viereck and Johnston, 1990). The absence of a significant influence of aspen on black spruce DBH, height and volume per stem in site 1 reveals a natural “additive” pattern in the aspen−black spruce mixed stand (Harper, 1977), which supports the possibility of competitive exclusion between both species. However, in sites 2 and 3, the absence of a significant influence of aspen on black spruce DBH, height and volume per stem while volume of black spruce decreases along the gradient of aspen suggests that aspen stems are replacing black spruce stems along this gradient. Thus, the natural pattern observed in these stands can be described as a “substitutive” pattern according to Harper (1977), which reflects a strong competition for resources between aspen and black spruce. This is not surprising considering the nutrient requirements of these species. Paré, Rochon and Brais (2002) estimated that the major nutrient requirements of aspen were, on an aerial basis, roughly two times higher than those of black spruce. Therefore, it is likely that the replacement of a black spruce tree by an aspen represents an increase in competition for both nutrients and light. Légaré, Bergeron and Paré (2004) reported that stands having an aspen relative basal of 40% had height of 5 m over pure black spruce stands. However, the gradient of variability is much shorter in the present study where only three sites of comparable age and density and a maximum distance of 22 km between sites were considered.

From an economic standpoint, the absence of a significant variation in black spruce merchantable volume along an increasing gradient of aspen indicates a net gain in aspen fibre considering the total stand volume. In practical terms, the total merchantable stand volume in site 1 varied from approximately 180 to 280 m^3/ha along the increasing gradient of aspen basal area (0 to 18.64 m^2/ha). This corresponds to an aspen proportion of 0 to 43.67% of total stand basal area, and represents a gain of approximately 100 m^3/ha while the black spruce volume component (180 m^3/ha) is maintained. In site 2 (estimated volumes of site 3 are relatively similar to those of site 2), for a range of relative basal area of aspen similar to that of site 1 (0 to 41.29%), there is still a net gain in total merchantable volume of approximately 75 m^3/ha, but it comes with a loss of approximately 100 m^3/ha of black spruce that is replaced by aspen (Figure 3.3).

3.5.3 Facilitation

In two of our sites (1 and 3), black spruce TTG510 was positively affected by the increasing presence of aspen. However, the absence of a significant influence of aspen on mean height of black spruce suggests that only dominant or co-dominant stems of black spruce in the stand are positively affected by aspen. From a more concrete perspective, the ANCOVA model for site 1 suggests that a dominant black spruce will take 3.5 additional years to grow 5 m in a stand without the presence of aspen compared with a dominant black spruce located in a stand with 18.64 m^2/ha of aspen (corresponding to

43.67% of aspen relative basal area in the stand). The effect of aspen on forest floor nutrient availability, pH and moisture content in pure and mixed stands, which is well documented (Brais et al., 1995; Corns, 1989; Longpré et al., 1994; Paré and Bergeron, 1996), could have a direct positive influence on black spruce productivity as proposed by the concept of productive facilitation (Vandermeer, 1989). The fact there were no significant correlations between mineral soil properties and increasing aspen basal area emphasizes that aspen could change site productivity by its effect on nutrient availability (Brais et al., 1995; Corns, 1989; Longpré et al., 1994; Paré and Bergeron, 1996). However, in site 2, TTG510 was not affected significantly by the presence of aspen, which suggests that the interspecific competition was strong on this site. In a previous study, it was observed that beyond a certain proportion of aspen (≈ 40% of basal area), black spruce growth decreased (Légaré, Bergeron and Paré, 2004). Mean relative aspen basal area, which was relatively higher in site 2 (38.54 ± 24.84%) than in sites 1 (28.24 ± 18.89%) and 3 (24.99 ± 29.55%), suggests stronger competition by aspen in site 2. Moreover, in site 2, aspen was spatially correlated, which could be interpreted as a coarse grain spatial arrangement, which is in contrast with the spatial arrangement suggested by Kelty (1992) to create a reduction in competition. Thus, the absence of the positive influence of aspen on the growth of black spruce in site 2 could possibly be explained by the horizontal stem distribution.

The presence of both patterns, substitutive and additive, suggests that the competitive relationship between species is site-specific and could not be explained exclusively by the respective proportions of the species in the stand. The relationship between species as a dominant, co-dominant or suppressed species in a mixed stand, which depends on site conditions, type and timing of disturbance, time since last disturbance and pre-disturbance composition, could explain part of the site-specific issue (Chen and Popadiouk, 2002). In site 1, mean height of aspen was similar to that of black spruce, but aspen mean height in sites 2 and 3 was superior to that of black spruce by more than 5 m, which possibly increased inter-specific competition for light. Therefore, not only should the proportion of aspen basal area in a black spruce stand be considered but its hierarchical position in the canopy should be considered as well. Moreover, the nutrient status of the site seemed to affect the influence of aspen on black spruce growth. With its low nutrient requirements (Chapin, 1980), black spruce could be a stronger competitor in relatively poor sites, such as site 1, compared with sites 2 and 3, building more biomass on a nutrient unit basis. According to a complementary study on the effect of aspen on nutrient cycling that was conducted on the same sites, N net mineralization, as determined in the laboratory, increased with increasing aspen basal area in site 1 but not in sites 2 and 3 (voir le chapitre 2). However, in site 3, N net nitrification increased with aspen basal area, which reflects a change in nutrient cycling suggesting that the presence of aspen in a relatively poor site could have a larger effect on growth than in a relatively rich site.

The influence of aspen on stand productivity could have been different if we had included a buffer zone around the 14 m of diameter plot in order to take into account edge effect. In site 2, in which aspen distribution is auto-correlated in space, the influence of aspen could have been over estimated. However, on sites 1 and 3, we hypothesised that the influence of aspen could have been either under- or over-estimated. Due to these potential uncertainties, estimate of increasing volumes along the gradient of aspen should be considered as guide-lines including a non negligible range of variation.

3.6 Implications for forest management

Because of the lack of a full gradient (0-100%) of aspen in the study design, it is impossible to know if the mixture of aspen and black spruce will exceed the yield of a monoculture of aspen or if it will be in between the yield of a monoculture of black spruce and a monoculture of aspen. However, mixtures that outyield the monoculture of the most productive component species are not common according to Kelty (1992). Nevertheless, a study conducted south of our study area reported a volume of 331 ± 121 m^3/ha for pure aspen stands on clay deposits of 50-year-old stands (Paré, Bergeron and Longpré, 2001), which is close to the mean stand volume calculated for sites 1, 2 and 3 (262.43 ± 53.75 m^3/ha; 339.33 ± 53.36 m^3/ha; 350.42 ± 80.75 m^3/ha, respectively). This suggests that the presence of aspen in black spruce-dominated stands could outyield pure stands of aspen (monoculture of the most productive component) in some conditions by way of facilitation and competitive exclusion. The results of this study suggest that the influence of aspen on black spruce growth depends on the respective proportions of species, on their vertical dominance and on site fertility, which could explain the absence of a general trend relative to yield or productivity of mixed management experimentations in the scientific literature (Rothe and Binkley, 2001).

Unfortunately, mixed management dynamics are not as simple as those of pure stands. Ecosystem simplification represents an advantage for productivity prediction but not for biodiversity and long-term productivity maintenance (O'Hara et al., 1994). To reach a suitable level of predictability, more studies are needed to understand mixed stand dynamics and their consequences on stand productivity. The results of this study suggest that, at least on specific sites and within certain limits in the proportion of aspen, management of mixed stands could be economically interesting. In addition to a spatial issue, management of alternating pure stands of aspen and black spruce could also affect stand diversity and productivity in time, thus representing another management option.

3.7 Acknowledgements

We are grateful to Annie Belleau, Benoît St-Vincent and Josée Chrétien for field assistance, and Alain Courcelles for laboratory work. This study was supported by the Fonds québécois de la recherche sur la nature et les technologies, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Tembec Inc., the Canadian Forest Service, the Natural Sciences and Engineering Research Council of Canada, and Canada Economic Development.

CHAPITRE IV

OVERSTORY – UNDERSTORY RELATIONSHIPS ALONG AN ASPEN GRADIENT IN BLACK SPRUCE DOMINATED STANDS OF WESTERN QUEBEC

Sonia Légaré, Yves Bergeron and David Paré

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4.1 Abstract

Most studies conducted on the understory layer of forests interprete the correlation between the understory and overstory strata as a similar response to an environmental gradient. A few other studies have concluded that dominant canopy trees have a direct effect on the understory vegetation through the modification of ecological processes. This paper tests the hypotheses that the presence of aspen in black spruce dominated stands has a direct effect on the composition, cover, richness, evenness, and diversity of understory communities in the boreal forest of western Quebec. Understory species were sampled in 98 14m-diameter plots located in three black spruce dominated stands with a heterogeneous component of aspen. The stands possessed homogeneous site conditions (mineral soil properties and drainage). In plots with a low component of aspen, the understory was mainly composed of ericaceous, bryophyte and sphagnum species. Along the gradient of increasing aspen basal area, the cover of mosses and sphagnum decreased but the cover of herb and shrub species was unaffected. Our results suggested that stands with a low component of aspen possess a bryophyte layer that is associated with cold and nutrient-deprived soil conditions. Moreover, despite the absence of a significant change in understory richness, evenness and diversity along the aspen gradient, the significant change in understory composition between overstory types suggests that, at a higher spatial scale, understory species richness and diversity is higher for mixed stands than for pure stands.

Keywords: Mixedwood composition, Understory cover, Diversity, Ecological processes, Evenness, Richness, Understory layer.

Abbreviations: CA = correspondence analysis; CEC = Cation exchange capacity; FH layer = Fibric-Humus layer; PPFD = photosynthetic photon flux density.

4.2 Introduction

A study by McCune and Antos (1981) failed to reveal the existence of significant relationships between the composition of forest strata. However, this is interpreted by Gilliam and Roberts (2003) as a scaling issue. Of the studies conducted on the herbaceous layer of forests in which a correlation between the understory and overstory strata was observed, most have attributed it to a similar response to an environmental gradient (Carleton and Maycock, 1981; Gagnon and Bradfield, 1986; Gilliam and Roberts, 2003; Gilliam, Turrill and Adams, 1995; Host and Pregitzer, 1992). Others have concluded that the dominant canopy trees have a direct influence on understory vegetation through their effect on ecological processes such as nutrient cycling and water and light availability (Légaré et al., 2001; Légaré et al., 2002; Qian et al., 2003; Saetre et al., 1997; Whitney and Foster, 1988). Such mechanisms of the overstory-understory relationships are affected by forest canopy composition and a contrast is often observed between deciduous and coniferous species.

In the boreal forest, understory composition is mainly affected by the time elapsed since the last fire (Ahlgren, 1960; Carleton and Maycock, 1978; De Grandpré, Gagnon and Bergeron, 1993) and by soil drainage and fertility (Bergeron and Bouchard, 1983; Carleton and Maycock, 1980). Nonetheless, forest composition has also been suggested by Légaré et al. (2001) as a controlling factor of understory composition through its influence on nutrient cycling. In their study, a gradient in soil nutrient availability was observed in concomitance with a gradient in the understory composition, all of this under a series of different stand types that ranged from aspen, white birch, mixed white spruce and fir to jack pine. Aspen is known to hasten nutrient cycling and to increase forest floor pH and nutrient availability in the boreal forest (Brais et al., 1995; Corns, 1989; Longpré et al., 1994; Paré and Bergeron, 1996; Van Cleve and Noonan, 1975). In contrast, black spruce is known to have a low evapotranspiration rate and recalcitrant litter, both of which support the development of a sphagnum layer and lead to accumulation of organic matter, cooler soil temperature, the rise of the water table and, consequently, reduced nutrient cycling (Foster 1985; Oechel and Van Cleve, 1986;

Weber and Van Cleve, 1981). Furthermore, forest composition affects understory light availability. Stands composed of shade intolerant species generally have higher understory light availability than stands composed of shade tolerant trees (Anderson, Loucks and Swain, 1969; Constabel and Lieffers 1996; Messier, Parent and Bergeron, 1998). Thus, in black spruce dominated stands, the composition of the understory layer, which reflects the environmental conditions of the site, should be affected by the presence of aspen as these mixed stands represent the northernmost extension of mixed forest types in the boreal forest of western Quebec.

Mixed stands generate patchy environmental conditions and a wider gradient of nutrient cycling rates (Crozier and Boerner, 1984; Simmons and Buckley, 1992) and of light availability (Beatty, 1984; Brewer, 1980). Through its influence on stand structure attributes, light availability, and nutrient cycling, overstory composition may affect differently several attributes of the understory layer, such as cover, richness, and diversity, in different ways (Klinka et al., 1996; Légaré, Bergeron and Paré, 2002; Whittaker and Likens, 1973; Zavitkovski, 1976). According to Saetre et al. (1997) and Simmons and Buckley (1992), low light conditions associated with the presence of spruce suppress the herb layer cover while the dominance of spruce increases the bryophyte cover. Thus the relative proportion of aspen in black spruce dominated stands should positively affect shrub and herb cover and negatively affect bryophyte cover. Berger and Puettmann (2000) showed that the diversity of herbaceous plants species was positively correlated to the relative basal area of aspen in aspen monocultures. Moreover, a higher species richness was observed in *Populus tremuloides* stands than in *Picea mariana* stands by Qian et al. (2003). However, Légaré et al. (2001) observed no significant difference in species richness, evenness and diversity of the understory layer between stand types. The multiplicity of responses recorded in the literature suggests therefore that overstory and understory relationships could be site-specific (Berger and Puettmann, 2000; Qian et al., 2003).

The presence of aspen in a black spruce dominated stand could accelerate nutrient cycling (voir le chapitre 2), which is believed to slow down the paludification process in the absence of disturbance, and thus affect the understory layers. We hypothesized that the proportion of aspen in a black spruce dominated stand 1) affects understory composition, 2) increases the cover of woody and herb species while decreasing the cover of bryophytes species, and 3) increases the richness, evenness, and diversity of understory species. The main objective of this study was to investigate the relationships between the composition of the overstory and understory layers and to assess the influence of overstory composition on ecological processes.

4.3 Study area

The study area was located in northwestwern Quebec at latitude 49° 03′ N to 49° 11′ N and longitude 78° 50′ W to 79° 09′ W. This area is part of the black spruce (*Picea mariana* (Mill.) BSP) - feathermoss (*Pleurozium schreberi* (Brid.) Mitt.)) forest of western Quebec (Grondin, 1996). This boreal zone extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum extent, during the Wisconsinian glacial stage (Vincent and Hardy, 1977). Sites are located on lacustrine clay deposits, and soils are generally classified as Grey Luvisols (Soil Classification Working Group, 1998). The closest weather station was located at La Sarre. Mean annual precipitation totals 856.8 mm and mean annual temperature is 0.8°C (Environment Canada, 1993). This ecosystem is dominated by large stand replacing fires that kill most of the trees and aboveground vegetation. Mean stand age is 139 years and fire cycle length has increased from 141 years, between 1850 and 1920, to 326 years since 1920 (Bergeron et al., 2001).

4.4 Methods

4.4.1 Sampling approach

The possible direct influence of overstory species on understory composition could be obscured by confounding factors related to environmental conditions. For example, the existence of a correlation between site conditions and forest composition inherent to forest landscapes could limit the interpretation of the cause of an observed association between the plant composition of the different forest layers. In such a case it would be difficult to determine if this association is related to an environmental gradient or to a direct species effect of the canopy trees. To circumvent this problem, the study was conducted on three large sites where abiotic conditions, such as drainage, slope, and deposit, were relatively homogeneous. This homogeneity has actually been verified in a previous study that found no significant relationship between mineral soil properties (specifically soil texture, total nitrogen concentration and cation exchange capacity) and the proportion of basal area of aspen (voir le chapitre 2). These three sites were chosen for their gentle slope, and drainage and stand composition which was dominated by spruce with a heterogeneous presence of aspen. The sampling unit used in this study was a circular plot with a 14 m diameter. The plots were distributed at every 20 m along a transect that was at least 180 m in length. At each site, the length and the number of transects established depended on the size and the shape of the spruce-aspen stand. Sites 1, 2 and 3 had respectively 28, 33 and 37 sampling plots. According to the fire map elaborated by Bergeron et al. (2004), all three sites originate from a fire that took place around 1920. More specifically and according to the tree ring counts obtained from the base (0 m) of 10 aspens on each site, sites 1, 2 and 3 most likely originate from fires that occurred in 1926, 1916 and 1916, respectively. The sites were mostly different on the basis of stand density, the proportion of aspen in the stand, the hierarchical position of aspen in the canopy, and soil texture (Table 4.1). To ensure that the properties of the mineral soil were not correlated to the presence of aspen, in each site we selected five plots in each of the three following categories (for a total of 45 plots): 1) plots dominated by black spruce with a relative basal area of less than 15% for aspen, 2) plots with a relative aspen basal area of 15 to 50%, and 3) plots with a relative aspen basal area of 50 to 75%. In each of the selected plots, we then collected three samples from the 10 first centimetres of the mineral soil (Ae horizon and the top of the B horizon). These three soil samples were then pooled, air dried, ground and analysed. Cation exchange capacity (CEC) was determined by the sum of exchangeable cations (Hendershot et al., 1993) and total N was determined colorimetrically following a H_2SO_4/H_2O_2 digestion (Keeney and

Nelson, 1982). Soil texture was determined by granulometric analyses (McKeague, 1976). None of the mineral soil properties, percent clay, sand and silt, total N and CEC were significantly correlated with aspen basal area (results not shown) thus insuring that the properties of the mineral soil were not correlated to the presence of aspen.

Table 4.1 Description of mineral soil properties, stand and tree characteristics on sites 1, 2 and 3

	Means ± standard deviations		
	Site 1	Site 2	Site 3
Site characteristics			
Stem density (stems/ha)	3220.82 ± 698.40	2013. 80 ± 602.63	1992.65 ± 707.61
Aspen relative basal area (%)	28.24 ± 18.89	38.54 ± 24.84	24.99 ± 29.55
Site index at 50 yrs (9 trees)	11.62 ± 0.83	12.18 ± 0.84	12.72 ± 1.37
Trees characteristic (selected plots)			
Aspen DBH (cm)	12.88 ± 6.39	21.06 ± 9.07	25.70 ± 12.31
Black spruce DBH (cm)	11.60 ± 0.90	14.29 ± 1.21	15.04 ± 1.27
Aspen height (m)	13.20 ± 6.36	20.33 ± 7.49	22.63 ± 9.34
Black spruce height (m)	12.12 ± 1.30	15.13 ± 1.25	15.86 ± 1.01
Black spruce age (yr)	66.76 ± 2.58	74.95 ± 2.04	77.1 ± 0.91
Mineral soil properties (selected plots)			
CEC (cmol(+)/kg)	16.18 ± 4.79	17.04 ± 11.36	15.04 ± 8.42
Total N (mg/g of soil)	1.79 ± 1.27	2.03 ± 1.09	2.68 ± 1.65
Clay (%)	50.4 ± 6.3	39.5 ± 14.9	24.5 ± 9.2
Sand (%)	14.3 ± 4.7	25.3 ± 17.1	19.1 ± 4.4
Silt (%)	35.3 ± 7.1	35.2 ± 7.0	56.5 ± 8.4

4.4.2 Overstory and understory sampling

In July 2001, we measured the diameter at the breast height (DBH) of every tree in each plot of the sampling plan to determine the basal area of each species. In August 2003, the percent cover of each understory species was estimated in 10 $1 m^2$ quadrats randomly located in each plot. Species less than 1m in height were considered understory species. Nomenclature follows Marie-Victorin (1995).

4.4.3 Light and forest floor sampling and analysis

Light and soil properties were measured in order to explore the ecological processes linked to the correlation between overstory and understory vegetation. Three samples of the FH layer (100 cm^2) were taken in three different directions at 1 m from the centre of each sampling plot. For each plot, soil samples were pooled, air dried, and ground. The pH was analysed in distilled water (McKeague, 1976). Exchangeable calcium, magnesium, and potassium were extracted with 0.1 M $BaCl_2$ and their concentrations determined by atomic absorption, while cation exchange capacity (CEC) was determined by the sum of exchangeable cations (Hendershot et al., 1993). Total N was determined colorimetrically following a H_2SO_4/H_2O_2 digestion (Keeney and Nelson, 1982) and total C was measured by ignition (Carter, 1993). To assess light availability for understory species, a LAI-2000 plant canopy analyser (LI-COR Inc., Lincoln, Nebr.) was used to measure photosynthetic photon flux density (PPFD) at 50 cm above the forest floor at four points systematically located approximately 1 m from the centre of each plot. Simultaneously, reference measurements corresponding to full light were taken every 15 seconds in an open area near the forest stand studied. Light measurements were taken during the second week of June 2002. The C-2000 software (LI-COR) was used to calculate the light ratio (%PPFD) transmitted. It associates the light measured under the forest canopy to the appropriate reference measurement.

4.4.4 Statistical analyses

Partial correspondence analysis (CA; ter Braak and Smilauer, 2002) was performed on all sites together to visualize species composition differences along the gradient of aspen

(aspen relative basal area = aspen basal area divided by total basal area and then multiply by 100). Site, plot stem density and total plot basal area were included as covariables in the correspondence analysis to control the effect of site and of stand structure on understory composition. All species sampled were included with the same weight in the partial correspondence analysis. Spearman correlation coefficients between aspen relative basal area and the first and second axes of the partial CA were calculated to test for the existence of a relationship between the proportion of aspen in black spruce dominated stands and the composition of the understory vegetation.

To explore the possible mechanisms responsible for a change in understory composition along the aspen gradient, we determined Spearman partial correlation coefficients between aspen relative basal area and some explanatory variables (light and soil properties) with plot stem density and total plot basal area as covariables. According to the Bonferroni method (Sokal and Rolf, 1995), the significant threshold was fixed at 0.0056 in order to keep an overall significant threshold of 0.05 for the 9 correlation analyses performed. Moreover, to discriminate the respective influence of nutrient cycling and light availability, we conducted a variation partitioning analysis (Bocard et al., 1992). The nutrient cycling data set consisted of the forest floor pH, organic matter thickness, total nitrogen, C:N, exchangeable Mg and Ca and CEC. Light availability was represented by %PPFD. The analysis was performed using partial canonical correspondence analyses with site, plot stem density and total plot basal area as covariables.

We wanted to test for the influence of aspen on understory cover groups (shrubs, herbs, mosses and sphagnum (Appendix 1)) without the influence of plot stem density and total plot basal area which affect light availability above the forest floor. Hence, a first regression analysis was performed between the understory cover groups, plot stem density and total plot basal area. A second regression analysis was then performed between aspen relative basal area and the residuals of the first regression analysis. Site effects on the relationship between understory cover groups, stem density and total basal area were included in the first regression analysis by the use of two dummies variables (dummy1 and dummy2). Shrub cover was log transformed to obtain a normal distribution. The relationship between aspen basal area and species richness, evenness and diversity was also tested with this procedure. Terricolous bryophytes and sphagnum were included at the genus taxonomical level for the study of richness, evenness and diversity. Shannon's diversity indices were calculated from the mean percent cover of each species (or genus in the case of mosses or sphagnum) in the plot (Scherrer, 1984). The correspondence analysis and the variance partitioning analysis were performed using CANOCO for Windows (GLW-CPRO, Centre for Biometry Wageningen, The Netherlands) and all other statistical analyses were performed using the SAS software (SAS Institute Inc., Cary, N.C.).

4.5 Results

4.5.1 Relationship between overstory and understory composition

The eigenvalues for the two first axes and the total inertia of the partial correspondence analysis were respectively 0.365, 0.287 and 3.133. In the illustration of the partial CA (Figure 4.1), most of the site 1 plots are located near the centre of the first axis while the plots of sites 2 and 3 are located all along the axis. This reflects the lower aspen gradient observed in site 1 in comparison to the two other sites (0 to 40 m^2/ha in site 1 compared with 1 to 60 m^2/ha in sites 2 and 3). Despite similar abiotic conditions among sites and the absence of any correlation between the mineral soil properties and aspen relative basal area, the Spearman correlation coefficients obtained indicate that the first axis of the partial CA was significantly correlated with aspen basal area (Rho=-0.47, $p<0.0001$). However, the second axis was not significantly correlated with aspen relative basal area (Rho=-0.16, $p<0.1118$). Plots at the top left of the magnify "square" of the ordination are dominated by *Galium triflorum* Michx., *Rubus idaeus* L., *Lonicera canadensis* Bartr., *Actaea rubra* (Ait.) Willd. and *Ribes* species (Figure 4.2; Figure 4.3). Generalist species such as *Aster macrophyllus* L., *Cornus canadensis* L. and *Maianthemum canadense* Desf. progressively take the dominance of the communities at the centre of the ordination. At the bottom right, communities are mainly dominated by ericaceous plants, mosses, and sphagnum species (Figure 4.3). Exploratory Spearman partial correlations were performed to investigate the mechanisms possibly responsible for the association of overstory and understory vegetation. They revealed that aspen relative basal area was significantly positively correlated with forest floor pH, total nitrogen, exchangeable K, Mg and Ca, and %PPFD while it was negatively correlated to organic matter thickness and the forest floor C:N ratio (Table 4.2). In the variance partitioning analysis, all of the explanatory variables together accounted for 13.82 % of the variance in the understory vegetation data set (Figure 4.4). Soil properties alone accounted for 12.80 % while %PPFD accounted for 0.99 %.

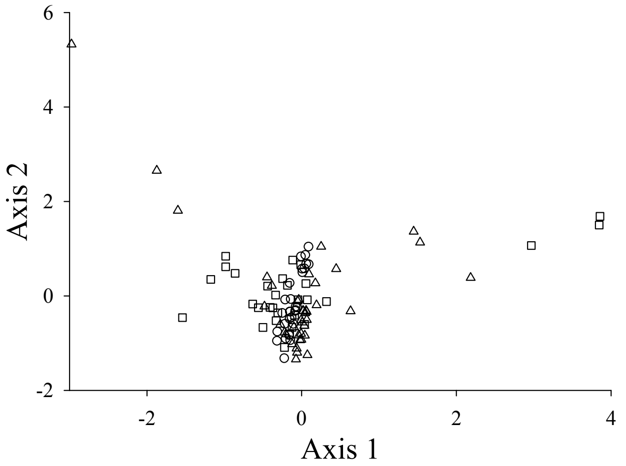


Figure 4.1 Partial correspondence analysis of all sites. Covariables : stem plot density and total plot basal area. Site 1 = o, site 2 = □, site 3 = Δ (N = 98).

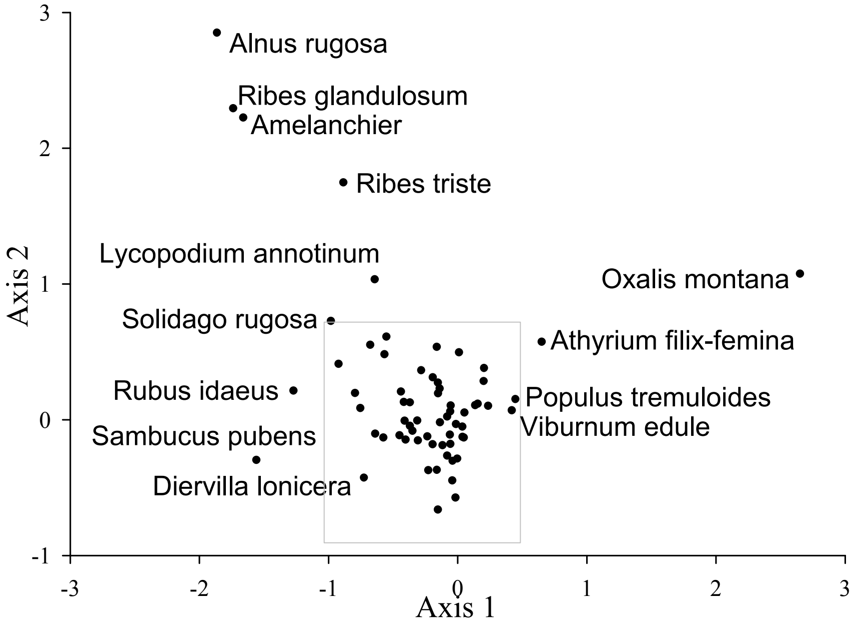


Figure 4.2 Correspondence analysis on all sites, covariables : stem plot density and total plot basal area, species illustration (see Figure 4.3 for grey square details).

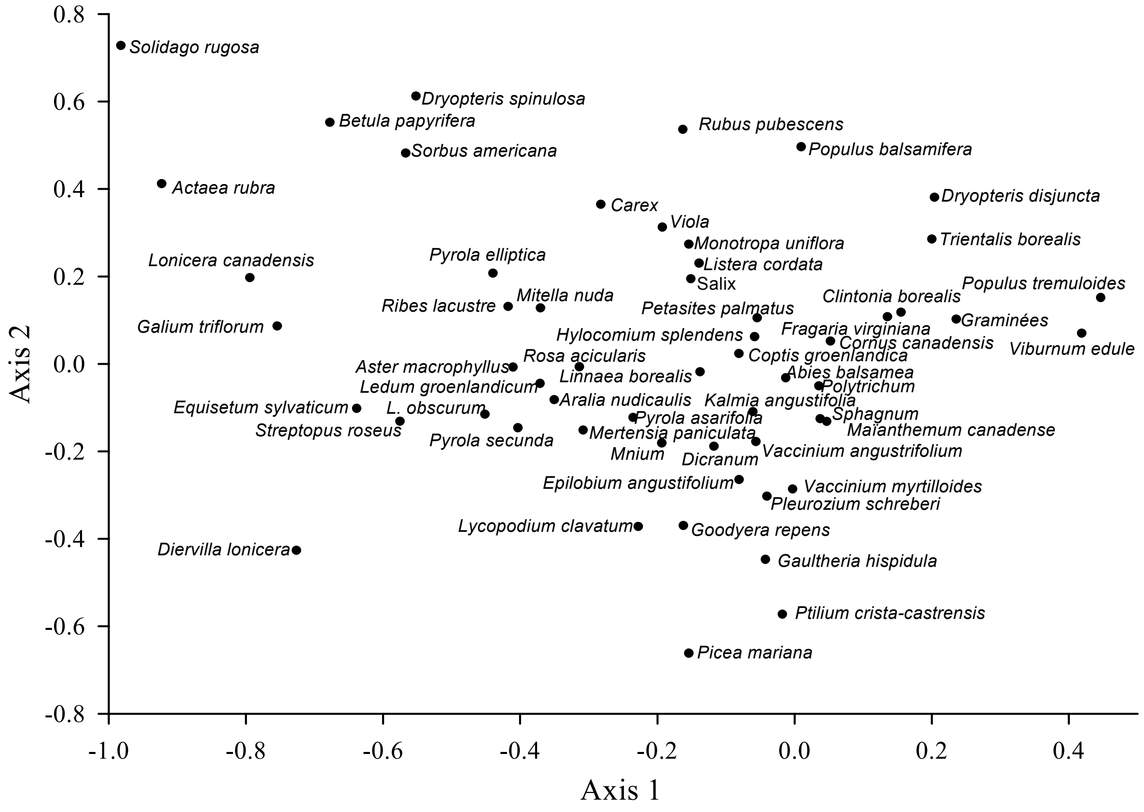


Figure 4.3 Correspondence analysis on all sites, covariables : stem plot density and total plot basal area, magnification of species illustration for the grey square on Figure 4.2.

Table 4.2 Spearman partial correlation coefficients between aspen relative basal area and explanatory variables (light and soil properties) with plot stem density and total plot basal area as covariables (H0: r =0). Significant threshold was fixed at 0.0056 to keep an overall significant threshold of 0.05 for the 9 correlation coefficients tested

Explanatory variables	Rho (p > |r|) between aspen relative basal area and variables
Forest floor pH	0.65 (<0.0001)
C:N ratio	-0.63 (<0.0001)
Organic matter thickness (cm)	-0.62 (<0.0001)
Total nitrogen (mg/g of soil)	0.53 (<0.0001)
Exchangeable Ca (cmol(+)/kg)	0.41 (<0.0001)
% PPFD	0.41 (<0.0001)
Exchangeable Mg (cmol(+)/kg)	0.38 (<0.0002)
Exchangeable K (cmol(+)/kg)	0.36 (0.0004)
CEC (cmol(+)/kg)	0.22 (0.0328)

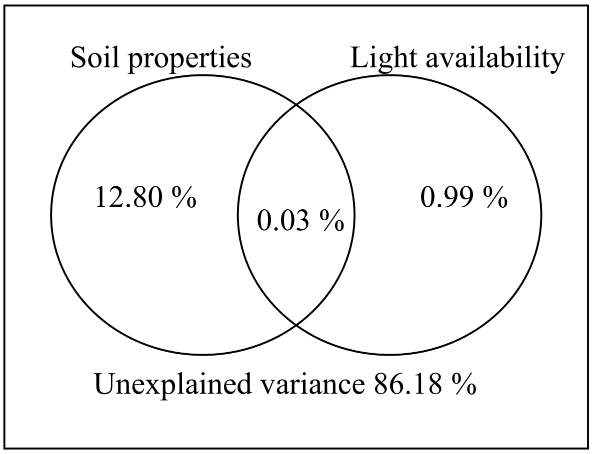


Figure 4.4 Partitioning of the understory data set variance using soil properties and light availability as subsets of explanatory variables and stem plot density and total plot basal as covariables (N=98).

4.5.2 Cover, richness, evenness and diversity

According to the regression analysis, the cover of moss and sphagnum species increased significantly with plot stem density while it decreased with increasing total plot basal area. The residuals from this regression were significantly negatively affected by aspen basal area (Table 4.3; Figure 4.5). The cover of woody and herb species decreased significantly with an increasing plot stem density, however, the residuals from these regressions were not significantly affected by aspen basal area (Table 4.3). The richness of the understory layer was significantly affected by plot stem density but the residuals from this regression were not significantly affected by aspen basal area (Table 4.4). Understory layer evenness decreased significantly with plot stem density while it increased significantly with total plot basal area. The Shannon diversity index significantly increased with both plot stem density and total plot basal area. The residuals from these two last regressions were not significantly affected by aspen basal area (Table 4.4).

Table 4.3 Regression analyses of shrub cover, herb cover, and bryophyte and sphagnum cover over stand density, total stand basal area, and sites (dummy variable 1 and dummy variable 2). A subsequent regression analysis was performed on the residuals obtained from previous regression analyses over the aspen relative basal area (ARBA). Only significant terms were included in the model

Sources	R^2	Parameters	T value	*p*
Shrub cover (Log_{10})	0.4189			
Dummy 2		0.3445	4.25	<0.0001
Stand density		-1.3384	-5.58	<0.0001
Residuals	0.0017			
ARBA		0.1772	0.41	0. 6857
Herb cover	0.4428			
Dummy 2		13.9283	3.12	0.0024
Stand density		-0.0166	-6.76	<0.0001
Residuals	0.0290			
ARBA		13.0108	1.69	0.0938
Mosses and sphagnum cover	0.5056			
Dummy 1		-26.0546	-3.80	0.0003
Dummy 2		-25.3251	-4.85	<0.0001
Stand density		0.0235	6.80	<0.0001
Total basal area		-1.3147	-5.02	<0.0001
Residuals	0.1401			
ARBA		-30.9629	-3.95	0.0001

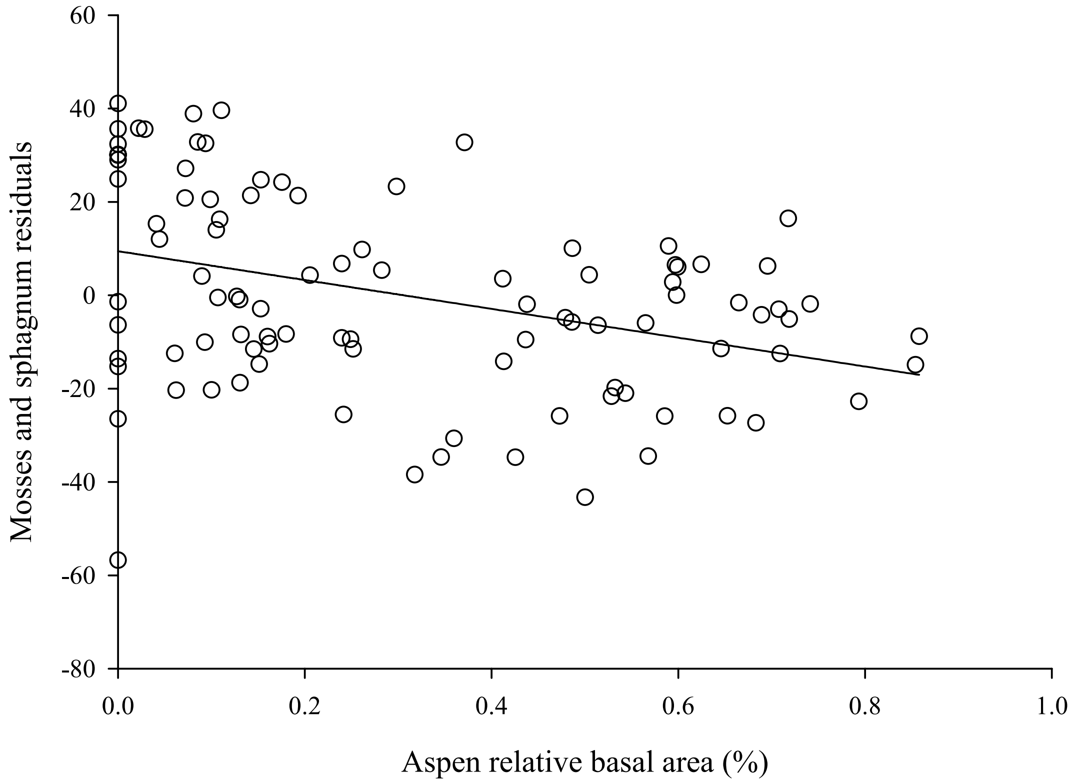


Figure 4.5 Regression analysis on the residuals of the initial regression analysis (cover of moss and sphagnum against stem density and total plot basal area) and relative basal area of aspen. Site effect on the relationship between the cover of moss and sphagnum species and stem density and total basal area were included in the regression analysis by two dummies variables (dummy1 and dummy2).

Table 4.4 Regression analyses of understory richness, evenness and its Shannon index by stand density, total stand basal area, and sites (dummy variable 1 and dummy variable2). The residuals from the previous regression analyses were submitted to a subsequent regression analysis as a response to aspen relative basal area (ARBA)

Sources	R^2	Parameters	T value	*P*
Richness	0.4076			
Dummy 1		2.9438	2.02	0.0463
Dummy 2		6.1300	5.40	<0.0001
Stand density		-0.0033	-4.54	<0.0001
Residuals	0.0222			
ARBA		2.7078	1.48	0.1430
Evenness	0.4487			
Dummy 2		0.2045	3.59	0.0005
Stand density		-0.0002	-6.10	<0.0001
Total basal area		0.0083	2.80	0.0061
Residuals	0.0049			
ARBA		0.0674	0.69	0.4915
Shannon index	0.4969			
Dummy 2		0.4280	4.66	<0.0001
Stand density		0.0003	-6.24	<0.0001
Total basal area		0.0120	2.51	0.0138
Residuals	0.0149			
ARBA		0.1887	1.20	0.2315

4.6 Discussion

4.6.1 Composition

A correlation between the composition of overstory and understory vegetation was observed in our study, despite the absence of any slope or drainage gradient. The lack of correlation between mineral soil properties and aspen basal area suggests that the observed overstory-understory correlation cannot be explained by a similar response of the two strata to an environmental gradient. Plots with a low aspen component had an understory mainly composed of ericaceous, bryophyte and sphagnum species which are generally associated to stands with a low nutrient status (Al-Mufti et al., 1977; Chen, Légaré and Bergeron, 2004; Gilliam and Robert, 2003; Monk, 1966; Small, 1972). *Gaultheria hispidula* (L.) Mühl (Bergeron and Bouchard, 1983) as well as *Coptis groenlandica* (Oeder) Fern., *Cornus canadensis* and *Oxalis montana* Raf. (Glaser, Janssens and Siegel, 1990; Siccama, Bormann and Likens, 1970) are associated with a poorly decomposed humus and are common on soils with an acidic humus. Plots with a higher component of aspen had an understory composed of generalist species such as *Equisetum sylvaticum* L., *Rubus pubescens* Raf., *Galium triflorum*, *Ribes lacustre* (Pers.) Poir. and *Ribes triste* Pallas. which are associated with mesotrophic conditions (Bergeron and Bouchard 1983). *Galium triflorum* was also found as an indicator species of fertile conditions by Légaré et al. (2001). Generally, the communities identified by the partial CA plot seem to represent a fertility gradient going from mesotrophic-highly saturated in bases conditions to oligotrophic conditions. The second axis also seemed associated with oligotrophic conditions at the top and mesotrophic ones at the bottom. The presence of aspen, which is believed to act as a cation pump (Corns, 1989), can be associated to a higher total nitrogen content and higher Mg and Ca availability, thus supporting the presence of species with higher nutrient requirements. Moreover, forest floor pH (Légaré et al., 2001; Tyler, 1989) and litter pH (Saetre et al., 1997) were identified as important soil properties for understory composition and our results showed a highly significant correlation between forest floor pH and aspen relative basal area. Our results are consistent with others studies that have shown that forest composition affects understory composition mainly through its influence on nutrient cycling (Légaré et al., 2001; Qian et al., 2003; Saetre et al., 1997). However, despite the fact that the understory vegetation accounts for a low proportion of the total stand biomass, it could also affect nutrient cycling through a retroactive effect by yearly contributing an important input of litter to the forest floor. In this sense it would expand the influence of stand composition (Yarie, 1980).

Although light availability is also affected by forest composition (Anderson, Loucks and Swain, 1969; Constabel and Lieffers, 1996; Federer and Tanner, 1966; Messier, Parent and Bergeron, 1998; Tasker and Smith, 1977), this process does not seem to play a dominant role in understory composition in our study. Nevertheless, light availability in the understory strata can influence composition to a lesser extent, as suggested by Légaré et al. (2001). However, we did not assess the distribution of sunflecks and light quality among forest types a consideration which is neglected in the literature but could be valuable for a better understanding of understory dynamics (Gilliam and Roberts, 2003).

4.6.2 Cover

As we hypothesised, among the understory cover groups, only the cover of mosses and sphagnum was significantly related to aspen relative basal area. The decrease in moss and sphagnum abundance that was observed along the gradient of aspen is consistent with the results obtained by Ewald (2000), Saetre et al. (1997) and Simmons and Buckley (1992). Saetre et al. (1997) suggested a lower risk of desiccation of bryophytes under spruce stands with low light intensity. This is supported by a positive relationship between aspen relative basal area and %PPFD in this study. Also, aspen leaf litter can reduce the presence of bryophytes by shade and/or chemical inhibition (Barkman, 1992; Clymo, 1973; Oechel and Van Cleve, 1986; Økland, 1995). Our results showed that the presence of bryophytes is associated with conditions of low nutrient availability which occur in stands with a low aspen component. We hypothesised that the presence of bryophytes also affects nutrient cycling through the interception and immobilization of nutrients, a retroactive process which exacerbates the influence of forest composition.

Contrary to what was expected, we did not find any statistically significant relationships between the cover of woody and herb species and aspen basal area. Light availability was significantly correlated with aspen basal area. Messier, Parent and Bergeron (1998) found that shade tolerant tree species attenuate more light than shade intolerant species in pure stands. These results suggest that, on the strict basis of forest composition, an aspen relative basal area of 60% is not sufficient to induce a change in shrub and herb cover. Understory cover is strongly associated with stand structure attributes (Légaré, Bergeron and Paré, 2002; Whittaker and Likens, 1973) that affect light availability. Our results support the idea that structural attributes such as stand density and total basal area affect all of the understory cover groups (shrubs, herbs, and mosses and sphagnum).

4.6.3 Richness, evenness and diversity

The increasing presence of aspen in a stand dominated by black spruce was expected to increase the heterogeneity of light and soil conditions, and thus increase the diversity of understory layer. However, according to our results, the influence of aspen basal area on richness, evenness and diversity of the understory layer was not significant. This concords with Légaré et al. (2001) but not with Berger and Puettmann (2000) and Qian et al. (2003). This discordance could be explained by the lower overstory composition gradient tested in our study which may have affected the variability observed in the composition of the understory vegetation. Moreover, Qian et al. (2003) suggested that some composition differences observed in their study may also be attributed to ecological differences between study sites. Furthermore, to ensure that we looked at the influence of aspen only, we conducted a partial regression to control for the total basal area and the stem density of plots which was not the case of other studies that examined understory richness and diversity (e.g. Qian et al. 2003). However, our study does not assess the influence of the composition and structure of the midstory which was suggested to have an influence on understory diversity (Berger and Puettmann, 2000; Robert, 1992). Despite the absence of a significant change of understory richness and diversity along the gradient of aspen, the significant change of understory composition between overstory types suggests that, at a higher spatial scale, understory species richness and diversity is higher in mixed stands than in pure stands.

4.7 Conclusion

Our results suggest that while understory composition is affected by a nutrient status associated with the presence of aspen, it is more important to consider canopy structure in order to explain the cover and diversity of understory communities. The great variability in the results observed in the literature concerning the relationship between forest composition and the diversity and richness of the understory layer could be linked to the influence of stand density, basal area and the degree of mixture of the different tree species.

4.8 Acknowledgments

This study was supported by the Fonds Québécois de la Recherche sur la Nature et les Technologies, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Tembec Inc., the Canadian Forest Service, the Natural Sciences and Engineering Research Council of Canada and Canada Economic Development. We are grateful to Annie Belleau for field assistance, Alain Courcelles for the laboratory work and Thuy Nguyen Xuan for revising the manuscript.

APPENDIX 1

List of plant species recorded in the understory layer (< 1 m).

Woody species	Herb species	Herb species (continued)
Abies balsamea (L.) Mill.	*Actea rubra* (Ait.) Willd.	*Maianthemum canadense* Desf.
Alnus rugosa (Duroi) Spreng.	*Aralia nudicaulis* L.	*Mertensia paniculata* (Ait.) G Don.
Amelanchier spp.	*Aster macrophyllus* L.	*Mitella nuda* L.
Betula papyrifera Marsh.	*Athyrium filix-femina* (L.) Roth	*Monotropa uniflora* L.
Diervilla lonicera Mill.	*Carex* spp.	*Oxalis montana* Raf.
Kalmia angustifolia L.	*Clintonia borealis* (Ait.) Raf.	*Petasites palmatus* (Ait.) Gray
Ledum groenlandicum Retzius	*Coptis groenlandica* (Oeder) Fern.	*Pyrola asarifolia* Michx.
Picea mariana (Moench) Voss	*Cornus canadensis* L.	*Pyrola elliptica* Nutt.
Populus balsamifera L.	*Dryopteris disjuncta* (Ledeb.) Morton.	*Pyrola secunda* L.
Populus tremuloides Michx.	*Dryopteris spinulosa* (O.F. Muel.) Watt.	*Rubus pubescens* Raf.
Ribes glandulosum Grauer.	*Epilobium angustifolium* L.	*Solidago rugosa* Mill.
Ribes lacustre (Pers.) Poir	*Equisetum sylvaticum* L.	*Streptopus roseus* Michx.
Ribes triste Pallas	*Fragaria virginiana* Duchesne	*Trientalis borealis* Raf.
Rosa acicularis Lindl.	*Gaultheria hispidula* (L.) Mühl	*Viola* spp.
Rubus idaeus L.	*Galium triflorum* Michx.	Moss species
Salix spp.	*Goodyera repens* (L.) R. Br.	*Dicranum* spp.
Sambucus pubens Michx.	Graminées	*Hylocomium splendens* (Hedw.) B.S.G.
Sorbus americana Marsh.	*Linnaea borealis* L.	*Mnium* spp.
Vaccinium angustifolium Ait.	*Listera cordata* (L.) R. Br.	*Pleurozium schreberi* (Brid.) Mitt.
Vaccinium myrtilloides Michx.	*Lonicera canadensis* Bartr.	*Polytrichum* spp.
Viburnum edule (Michx.) Raf.	*Lycopodium annotinum* L.	*Ptilium crista-castrensis* (Hedw.) De Not.
	Lycopodium clavatum L.	*Sphagnum* spp.
	Lycopodium obscurum L.	

CONCLUSION GENERALE

INFLUENCE DE LA PRESENCE DU PEUPLIER FAUX-TREMBLE SUR LA PRODUCTIVITE DES PEUPLEMENTS DOMINES PAR L'EPINETTE NOIRE

La conclusion générale de cette thèse a été soumise comme fiche technique à la Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable.

5.1 Introduction

Les industries forestières qui utilisent principalement les essences résineuse, ont souvent recours à des traitement sylvicoles afin de réduire la proportion peuplier faux-tremble des peuplements d'épinettes noires. Malgré la valeur commerciale du peuplier faux-tremble, l'invasion des territoires aménagés par le peuplier faux-tremble inquiète certains aménagistes et une question se pose quant au contrôle de cette espèce si bien adaptée aux perturbations. Cependant, l'influence positive d'une proportion cible de peuplier faux-tremble sur la disponibilité des éléments nutritifs et sur la croissance de l'épinette noire a été rapportée dans la littérature scientifique. D'autre part, certaines études ont montré le potentiel des conifères à favoriser un couvert de mousses et d'éricacées qui peut réduire la température du sol, occasionner une remontée de la nappe phréatique et produire une litière de faible qualité favorisant ainsi une baisse de la fertilité du sol à moyen ou long terme. Sachant que la productivité des pessières voisinant le 49e parallèle est généralement inférieure à 1 m^3/ha/an alors que la productivité des peuplements mixtes dans la même région varie entre 2 et 3 m^3/ha/an, une nouvelle question émerge, y aurait-il un intérêt écologique et économique à viser une certaine proportion de peuplier faux-tremble dans les peuplements aménagés d'épinette noire ?. De plus, l'aménagement de peuplements mixtes, qui occupe une proportion importante du paysage, est suggéré par l'aménagement écosystémique. Cette approche, qui prône la conservation de trois cohortes de structures différentes en proportion variable, propose que le maintien de la structure forestière à l'échelle du paysage pourrait permettre le maintien de la biodiversité. Ainsi, l'aménagement mixte pourrait représenter une situation où les objectifs commerciaux de la forêt sont en accord avec l'aménagement écosystémique.

5.2 Hypothèse

La présence du peuplier augmente la concentration en azote dans le sol organique, ralentit le processus de paludification et augmente le volume marchand total du peuplement ainsi que la productivité de l'épinette noire.

5.3 Description de l'aire d'étude

L'étude a été réalisée au nord de La Sarre (Abitbi-Témiscamingue, Québec), dans les cantons Bourque et Rousseau (région écologique 6a). Trois peuplements dominées par l'épinette noire et ayant une présence variable de peuplier faux-tremble ont été sélectionnés. En plus de l'homogénéité des conditions de drainage et de faible pente dans ces peuplements, les analyses en laboratoire révèlent que le pourcentage d'argile, de sable, la concentration d'azote total et la capacité d'échange cationique (CEC, mesure donnant un indice de la fertilité du site) du sol minéral ne sont pas significativement corrélés avec la surface terrière de peuplier faux-tremble (Tableau 5.1).

Tableau 5.1 Description du sol minéral, des caractéristiques des peuplements et des espèces dans les sites 1, 2 et 3

	Moyenne ± erreur type		
	Site 1	Site 2	Site 3
Caractéristiques des peuplements			
Densité moyenne des tiges (nombre de tiges / ha)	3220 ± 698	2013± 602	1992 ± 707
Proportion de PET (%)	28,24 ± 18,89	38,54 ± 24,84	24,99 ± 29,55
Caractéristiques des espèces			
Hauteur moyenne PET (m)	13,20 ± 6,36	20,33 ± 7,49	22,63 ± 9,34
Hauteur moyenne EPN (m)	12,12 ± 1,30	15,13 ± 1,25	15,86 ± 1,01
Âge moyen de l'EPN (années)	66,76 ± 2,58	74,95 ± 2,04	77,1 ± 0,91
Propriétés du sol minéral			
Azote total (mg/g de sol)	1,8 ± 1,3	2,0 ± 1,1	2,7 ± 1,7
Argile (%)	50,4 ± 6,3	39,5 ± 14,9	24,5 ± 9,2
Sable (%)	14,3 ± 4,7	25,3 ± 17,1	19,1 ± 4,4

5.4 Méthodes

Dans chacun des 3 peuplements, un certain nombre de parcelles circulaires de 7 m de rayon ont été installées selon la grandeur et la forme du peuplement mixte de peuplier et d'épinette (28 parcelles dans le site 1, 33 dans le site 2 et 37 parcelles dans le site 3). Un inventaire de la végétation arborescente incluant toutes les tiges (dhp et hauteur) dans chacune des parcelles circulaires de chaque site ainsi que des analyses de tige (les 3 plus hautes épinettes noires de la parcelle) ont été effectuées dans le but d'évaluer les variations du volume marchand total, du volume marchand et de la productivité de l'épinette noire le long du gradient de peuplier faux-tremble. Le recouvrement des bryophytes (mousses terricoles) et sphaignes a été estimé dans 10 quadrats de $1m^2$ dans chacune des parcelles circulaires de 7m de rayon afin de déterminer leur recouvrement le long du gradient de peuplier faux-tremble. Un échantillonnage du sol organique suivi par des analyses en laboratoire a permis de déterminer la concentration en azote total dans le sol organique.

5.5 Résultats et Discussion

Malgré l'absence de corrélation entre la présence de peuplier faux-tremble et les propriétés physiques et chimiques du sol minéral, la présence croissante du peuplier faux-tremble est associée avec l'augmentation de la concentration en azote total dans le sol organique (horizon LFH) dans les 3 sites à l'étude (figure 5.1). Ce résultat suggère que la présence de peuplier faux-tremble pourrait augmenter la fertilité du site par son influence sur les propriétés physiques (température, taux d'humidité) et chimiques (disponibilité des éléments nutritifs, pH) du sol organique ce qui pourrait favoriser une augmentation du taux de décomposition et ainsi accroître la concentration d'azote et les éléments disponibles pour la croissance de la végétation (voir chapitre 2).

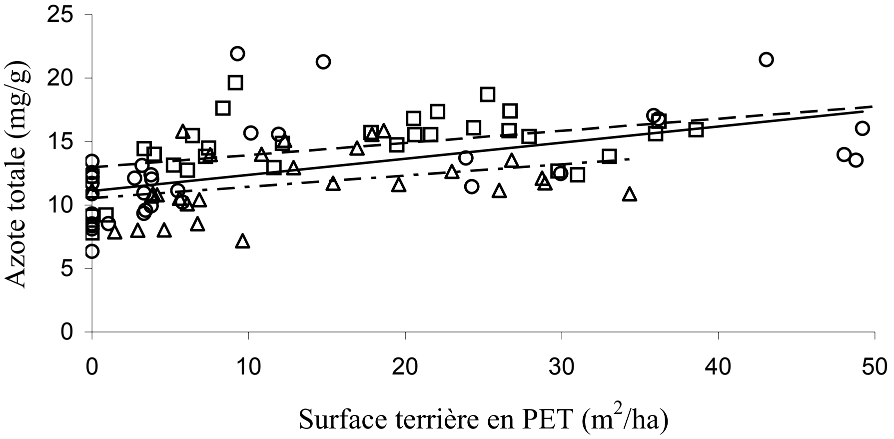


Figure 5.1 Concentration en azote totale en fonction de la surface terrière en peuplier faux-tremble. Δ = site 1 (dash dotted line), □ = site 2 (long dash line), o = site 3 (solid line).

Dans les trois sites échantillonnés, le recouvrement de mousses et de sphaigne diminue avec l'augmentation de la surface terrière de peuplier faux-tremble (Figure 5.2). L'accumulation d'une épaisse couche de mousses et de sphaignes est souvent associée à une baisse de productivité expliquée par l'immobilisation des éléments nutritifs par cette couche relativement résistante à la décomposition. D'autre part, une concentration élevée en calcium pourrait défavoriser la survie des sphaignes. Ainsi, notre résultat suggère que la présence de peuplier faux tremble dans un peuplement dominé par l'épinette noire, par son influence sur le cycle des éléments nutritifs et la composition de la strate de sous-bois, pourrait ralentir le processus de paludification.

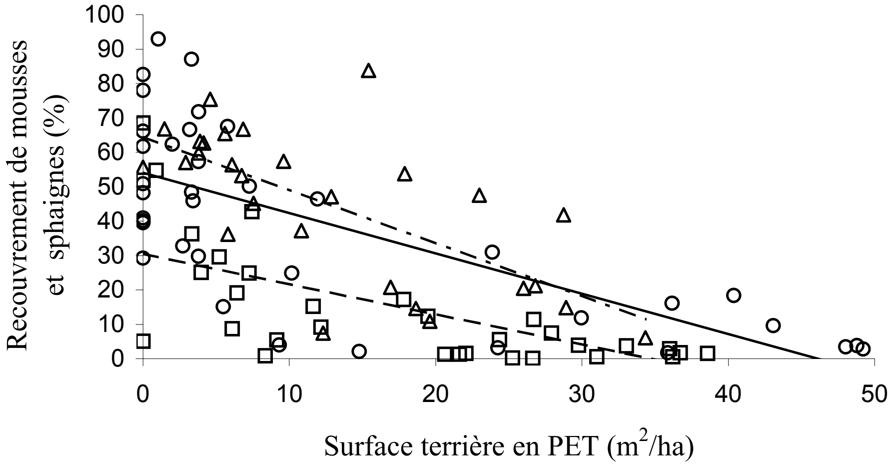
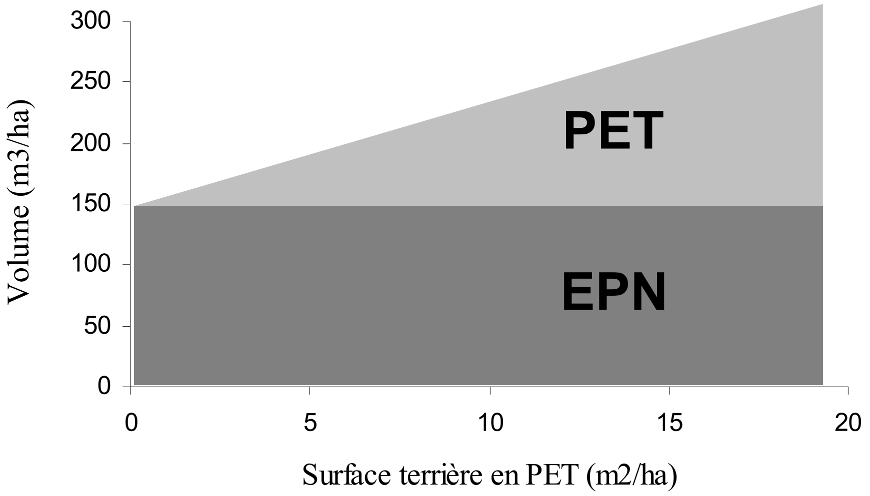


Figure 5.2 Recouvrement de mousses et de sphaignes en fonction de la surface terrière en peuplier faux-tremble. Δ = site 1 (dash dotted line), □ = site 2 (long dash line), o = site 3 (solid line).

Le volume marchand total augmente avec la surface terrière en peuplier faux-tremble dans tous les sites. Cependant, le volume en épinette est maintenu le long du gradient de peuplier faux-tremble seulement dans le site 1 et le volume marchand en épinette noire diminue dans les sites 2 et 3 (figure 5.3). Les peuplements mixtes dans notre aire d'étude semble fournir un plus grand rendement à hectare par rapport aux peuplements purs d'épinette noire. Cependant, dans certain cas, la composante en épinette n'est pas maintenue, ce qui pourrait être le résultat de la compétition interspécifique. Le temps de passage de 5 à 10 m de hauteur pour l'épinette noire diminue dans les sites 1 et 3 avec la surface terrière croissante de peuplier faux-tremble, tandis que le temps de passage n'est pas significativement influencé dans le site 2 (figure 5.4). Ainsi, la productivité de l'épinette noire augmente avec la présence de peuplier faux-tremble selon le site (voir le chapitre 3). Nous posons l'hypothèse que la qualité du site, la proportion et la distribution du peuplier faux-tremble dans le peuplement devrait influencer l'intensité de la compétition entre les deux espèces et devrait ainsi influencer le rendement du peuplement. En effet, la distribution du peuplier faux-tremble dans le site 2 était corrélé dans l'espace, ce qui signifie que le peuplier faux-tremble était plutôt distribué en bouquet dans ce site comparativement à une présence aléatoire dans les sites 1 et 3. De plus, la hauteur moyenne du peuplier faux-tremble est d'approximativement 5 m supérieur à la hauteur moyenne de l'épinette noire dans les sites 2 et 3 et la proportion de peuplier faux-tremble dans le site 2 est d'environ 38% comparativement à 28% et 24% pour les sites 1 et 3 respectivement. Une étude menée dans la même aire d'étude conclue qu'au-delà d'un seuil, évalué à approximativement 40% de la surface terrière totale d'un peuplement en peuplier faux-tremble, la présence de peuplier faux-tremble influence négativement la croissance de l'épinette noire (voir le chapitre 1). Concrètement, dans le site 1 où la compétition semble relativement faible entre les deux essences (proportion de surface terrière couverte par le peuplier faux-tremble à 44%), la composante d'épinette noire (180 m^3/ha) semble maintenue tout en obtenant 100 m^3/ha de peuplier faux-tremble. Tandis que dans le site 2, où la compétition est relativement forte, pour une proportion de surface terrière équivalente de peuplier faux-tremble (42%), le volume marchand total est supérieur d'environ 75 m^3/ha, cependant, la composante en épinette noire est réduite d'approximativement 100 m^3/ha pour être remplacée par du peuplier faux-tremble (figure 5.3).

a)



b)

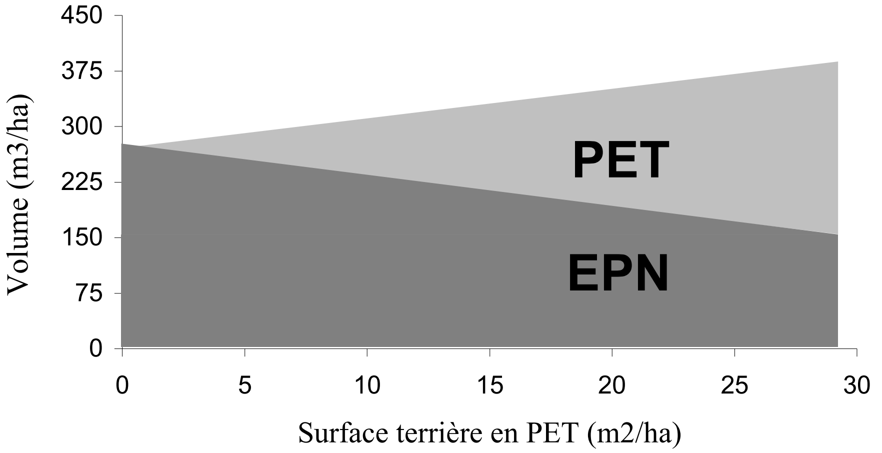


Figure 5.3 Volume marchand total par esspèce en fonction de la surface terrière en peuplier faux-tremble dans le a) site 1 et b) les sites 2 et 3.

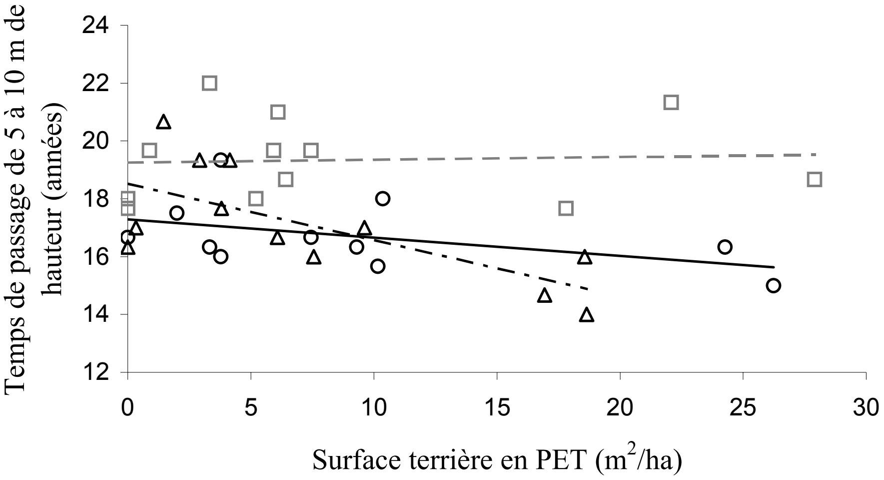


Figure 5.4 Temps de passage de l'épinette noire en fonction de la surface terrière en peuplier faux-tremble. Δ = site 1 (dash dotted line), □ = site 2 (long dash line), o = site 3 (solid line).

5.6 Conclusion

Bien que les résultats obtenus ne proviennent que de trois sites, ils suggèrent tout de même que l'aménagement de peuplements mixtes pourrait être économiquement intéressant, pour le moins sur des sites spécifiques ayant une proportion limitée de peuplier faux-tremble. Dans un contexte d'échange des bois entre les usines utilisant les différentes espèces, le maintien de peuplements mixtes pourrait maintenir une certaine diversité de paysages et ainsi favoriser les multiples usagers de la forêt.

5.7 Remerciements

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