The responses of black spruce growth to an increased proportion of aspen in mixed stands[1]

Sonia Légaré, David Paré, and Yves Bergeron

Abstract: In the southeastern boreal forest of Canada, the presence of mixed stands of black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) 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 showed a significant relationship between the relative basal area of aspen (aspen relative basal area was determined by the ratio of aspen basal area to 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, in fact, aspen fibre. The positive effects of aspen on black spruce DBH and height were only present when the proportion of aspen 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 on the landscape, offers an example as to how commercial management of the forest can be in agreement with ecosystem management.

Résumé : Dans la forêt boréale du Sud-Est du Canada, la présence de peuplements mixtes d'épinette noire (*Picea mariana* (Mill.) BSP) et de peuplier faux-tremble (*Populus tremuloides* Michx.) croissant dans des conditions abiotiques similaires a offert l'opportunité d'étudier l'influence du peuplier faux-tremble sur le volume du peuplement et 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 relative en peuplier et le volume marchand total du peuplement. Cependant, la relation entre la surface terrière relative 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 nutriments. L'aménagement de peuplements mixtes, qui sont abondamment représentés dans le paysage forestier, pourrait offrir une situation où la mission commerciale de la forêt pourrait être en accord avec l'aménagement écosystémique.

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 enhance stand resistance to wind damage, diseases, and insect outbreaks and may represent a way to reduce economical risk by compensatory growth (Kelty 1992; Frivold and Mielikaïnen 1990). However, because of the large array of species combinations and different structure possibilities, little is known about the dynamics of mixed stands (Assmann (1961) in Frivold and Kolström (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

Received 14 March 2003. Accepted 17 October 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 18 February 2004.

S. Légaré.[2] Université du Québec en Abitibi–Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.
D. Paré. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 3800, Sainte-Foy, QC G1V 4C7, Canada.
Y. Bergeron. Chaire industrielle CRSNG–UQAT–UQAM en aménagement forestier durable, Université du Québec en Abitibi–Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9Z 5E4, Canada.

[1]This paper was presented at the 4th International Workshop on Disturbance Dynamics in Boreal Forests: Disturbance Processes and their Ecological Effects, held 9–14 August 2002, Prince George, B.C., and has undergone the Journal's usual peer review process.
[2]Corresponding author (e-mail: Sonia.Legare@uqat.ca).

 doi: 10.1139/X03-251

combinations, has been ambiguous, in part because of contrasting results and inappropriate study designs (Tarrant 1961; Tarrant and Trappe 1971; Binkley 1983; Perry et al. 1987; Frivold and Mielikaïnen 1990; Binkley 1992; Kelty 1992).

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, which maximizes 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 $m^3·ha^{-1}·year^{-1}$. 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, thus 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 mineralization, thus reducing nutrient uptake by plants (Viereck 1973; Van Cleve and Viereck 1981; Foster 1983). On the other hand, trembling aspen (*Populus tremuloides* Michx.) increases nutrient cycling because of the chemical quality of its litter (Van Cleve and Noonan 1975; Paré and Bergeron 1996). The presence of aspen in a stand dominated by black spruce could positively influence 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 stand total merchantable volume along a gradient of stands with an 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 of the ministère des Ressources naturelles du Québec, which provided observations of the growth of black spruce along a gradient of stands with various proportions of aspen. This allowed a more complete understanding of the influence of aspen on black spruce growth. On the other hand, 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.

Methods

Study area

The study area was located in the Abitibi–Témiscamingue region, in the southeastern boreal forest of Canada. The latitude of the plots varied from 47°77′N to 50°10′N, and the longitude varied 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 – 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, 920.0, and 856.8 mm, respectively, and average annual temperature is 1.2, 1.1, and 0.8 °C, respectively, according to Environment Canada (1993).

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 were 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 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 (Fig. 1). To ensure that drainage conditions were not associated with the abundance of aspen and that the two factors were not confounded, 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 mean 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 to total basal area of the stand). For the 43 plots selected, the mean density was 4475 stems/ha, varying from 1200 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). Plots with more than 10% of their total basal area occupied by species other than aspen or black spruce were also rejected. In general, selected plots were relatively young mixed stands of black spruce and aspen on well-drained soil.

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 their 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 >10 cm DBH (Perron 1985). These equations are inadequate for small stems under 10 cm 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.

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 (Heinselman 1981; Bergeron 1991; Payette 1992). In the southern part of the study area, after fires, the stands generally follow a successional path that is initiated

Fig. 1. Location of plots in Abitibi–Témiscamingue, northwestern Quebec. Each black dot represents one or more plots.

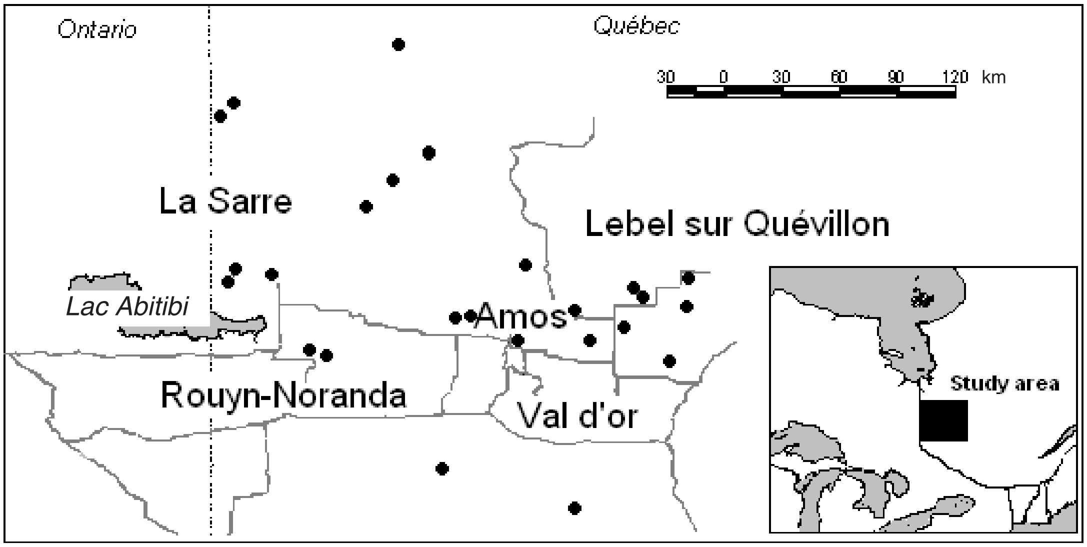


Table 1. Description of the 43 plots selected from the forest inventory database of the ministère des Ressources naturelles du Québec with 0% to 87% of relative aspen basal area.

	Mean	SD	Range
Basal area (m^2/ha)	31.41	8.62	15.29–49.53
Stand density (stems/ha)	4475.00	2741.00	1200–12 425
Merchantable volume (m^3/ha)	152.34	86.17	33.59–461.99
Dominant black spruce age (years)	55.38	13.47	23.00–75.00
Dominant black spruce height (m)	13.90	2.89	8.23–21.50
Dominant black spruce DBH (cm)	14.56	2.25	10.50–20.60

with deciduous species that are gradually replaced by tolerant coniferous species (Bergeron and Dubuc 1989). In the northern part of the study, 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 (Van Cleve and Viereck 1981; Foster 1983). In mixed stands, aspen and black spruce establish themselves at the same time after the disturbance, and either aspen or black spruce becomes the dominant species or both species are codominant, depending on site conditions, time since last disturbance, and predisturbance 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).

Statistical analysis

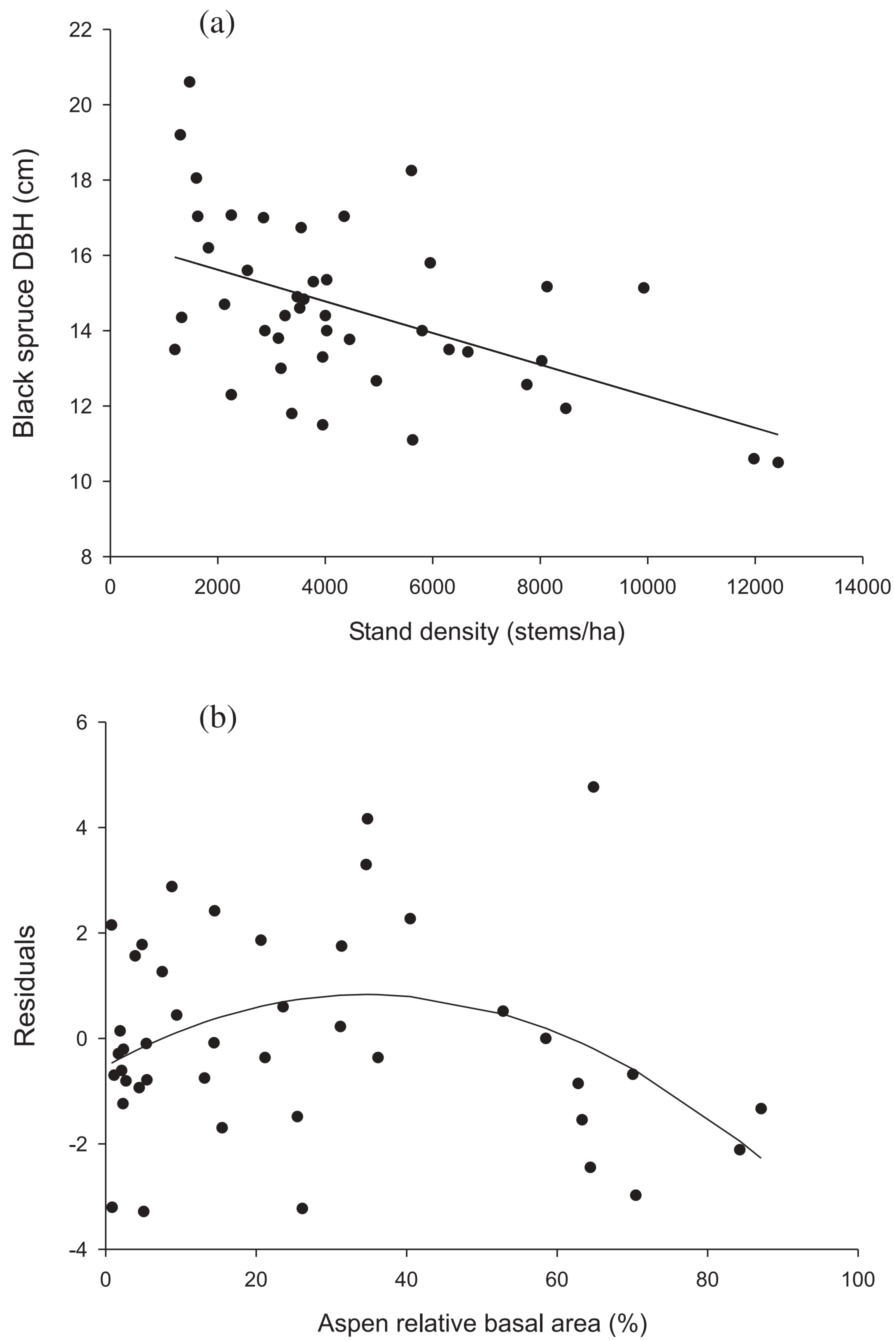
Individual-species scale

To explore the relationships between aspen relative basal area and black spruce mean 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 mean DBH and stem density. Polynomial regression was performed as a multiple regression with the relative basal area of aspen and 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 mean 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 the regressions analysis between stem density and both DBH and height of black spruce. 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:

$$y = b_0 + b_1x, \quad \text{if } x < \tau$$
$$y = b_0 + (b_1 + b_2)x - b_2\tau, \quad \text{if } x \geq \tau$$

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 nonlinear and involved

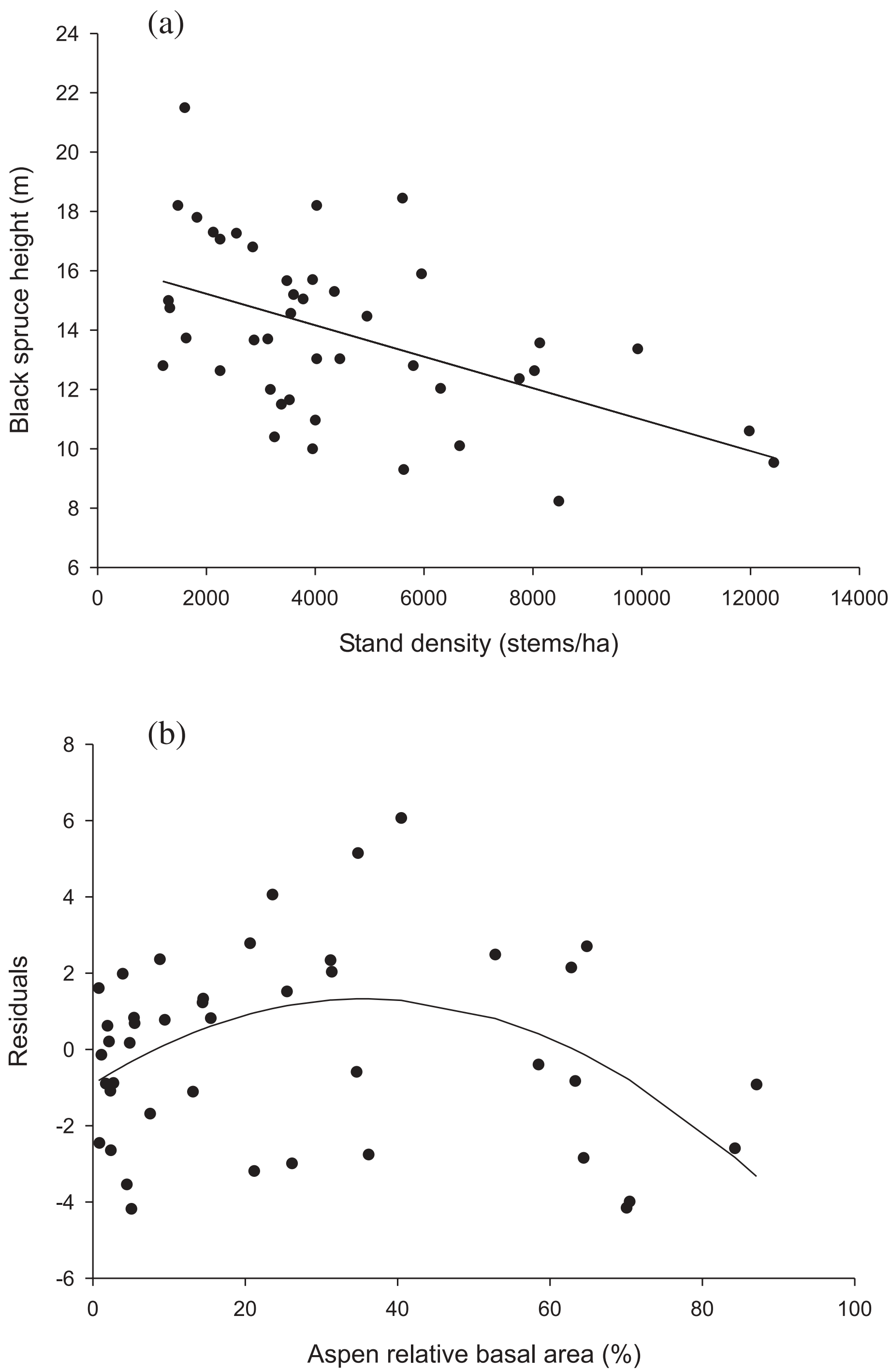
Fig. 2. (*a*) Regression analysis of black spruce mean DBH against stem density, $Y = -0.0004X + 16.456$ ($R^2 = 0.2657$, $p = 0.0004$, $N = 43$), and (*b*) polynomial regression analysis of residuals from the precedent regression against the full gradient of relative basal area of aspen, $Y = -0.0011X^2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



parameter estimation (NLIN procedure, version 8, SAS Institute Inc., Cary, N.C.). 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 decided to test the influence of aspen on the residuals of black spruce mean 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 mean 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

Fig. 3. (*a*) Regression analysis of black spruce mean 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 the full gradient of relative basal area of aspen, $Y = -0.0018X^2 + 0.1256X - 0.9181$ ($R^2 = 0.1650$, $p = 0.0272$, $N = 43$).



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 analy-

Table 2. Piecewise regressions performed between aspen relative basal area and the residuals of both regressions 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 two segments)	0.2310	0.2950
p value	<0.0001	<0.0001

Note: $R^2 = SS_{regression}/SS_{corrected\ total}$; slope second segment = $b_1 + b_2$.

sis was performed on three ranges (0%–5%, 5%–15%, 15%–45%), but there was no significant difference between these categories.

Stand scale

Because preliminary results suggested a negative impact of aspen on black spruce growth when it accounted for 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 preceding analysis. 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. 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., Cary, N.C.), and the significance threshold was fixed at 5%.

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).

Results

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; Fig. 2). 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; Fig. 3). Relative basal area was positively related to DBH and dominant height of black spruce when aspen accounted for less than 40% of the stand basal area, but was negatively related when the proportion of aspen was greater than 40% of the total stand basal area (Table 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; Fig. 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; Fig. 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 3; Fig. 6).

Stand scale

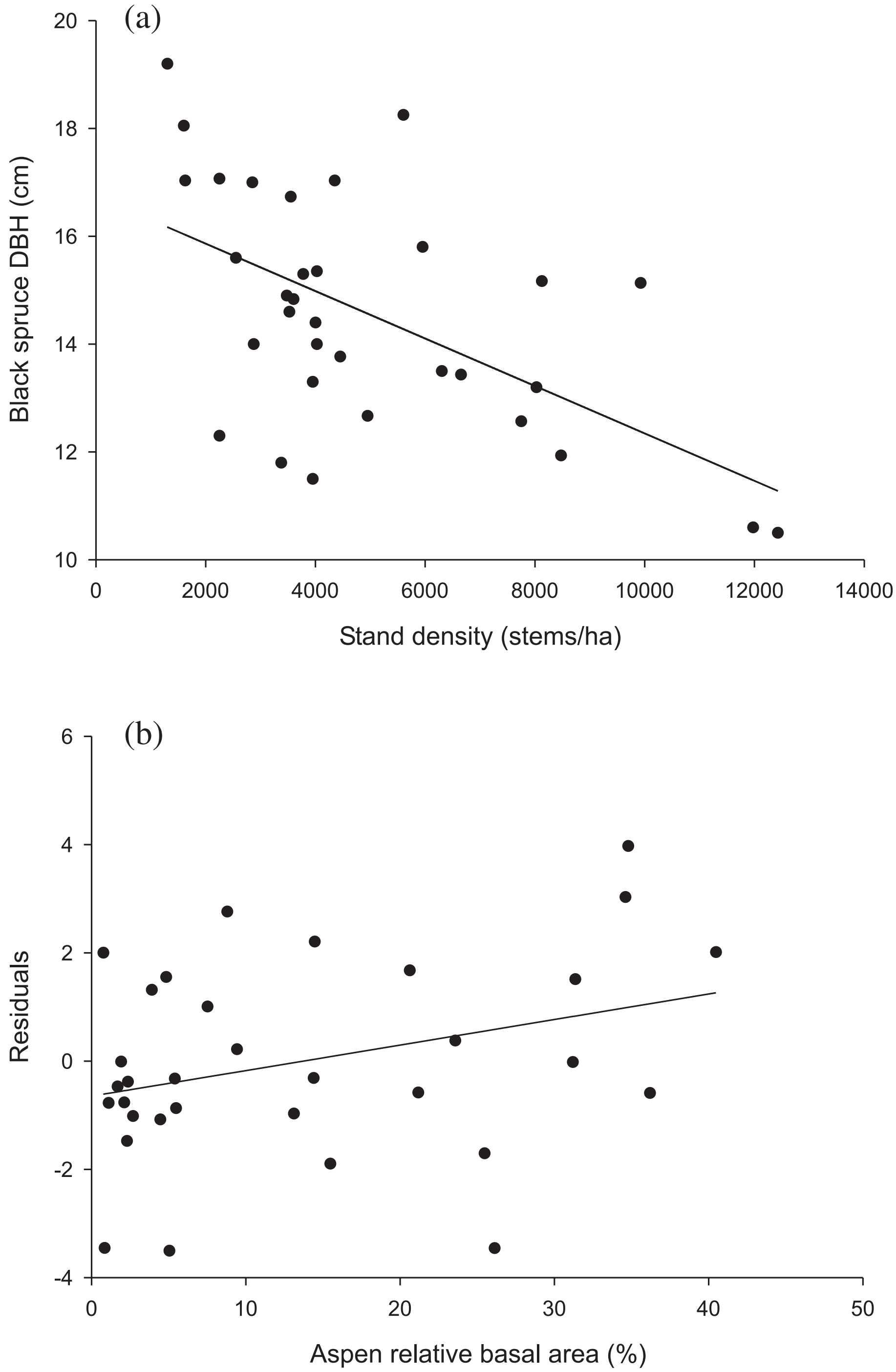
Residuals from the significant regression analysis performed on total (all species) merchantable volume and stem density were significantly affected by aspen basal area when the proportion of aspen varied between 0% and 41% of the total stand basal area. However, the residuals from the significant regression analysis of black spruce merchantable volume and stem density were not significantly affected by aspen (0%–41%; Fig. 7).

Discussion

Despite the presence of similar abiotic conditions, black spruce growth changed 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 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 stand basal area 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 indexes for black spruce in Quebec's commercial forest vary from 9 to 18 m (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 stand with a site index of 12 m is 80 m^3/ha compared with 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%)

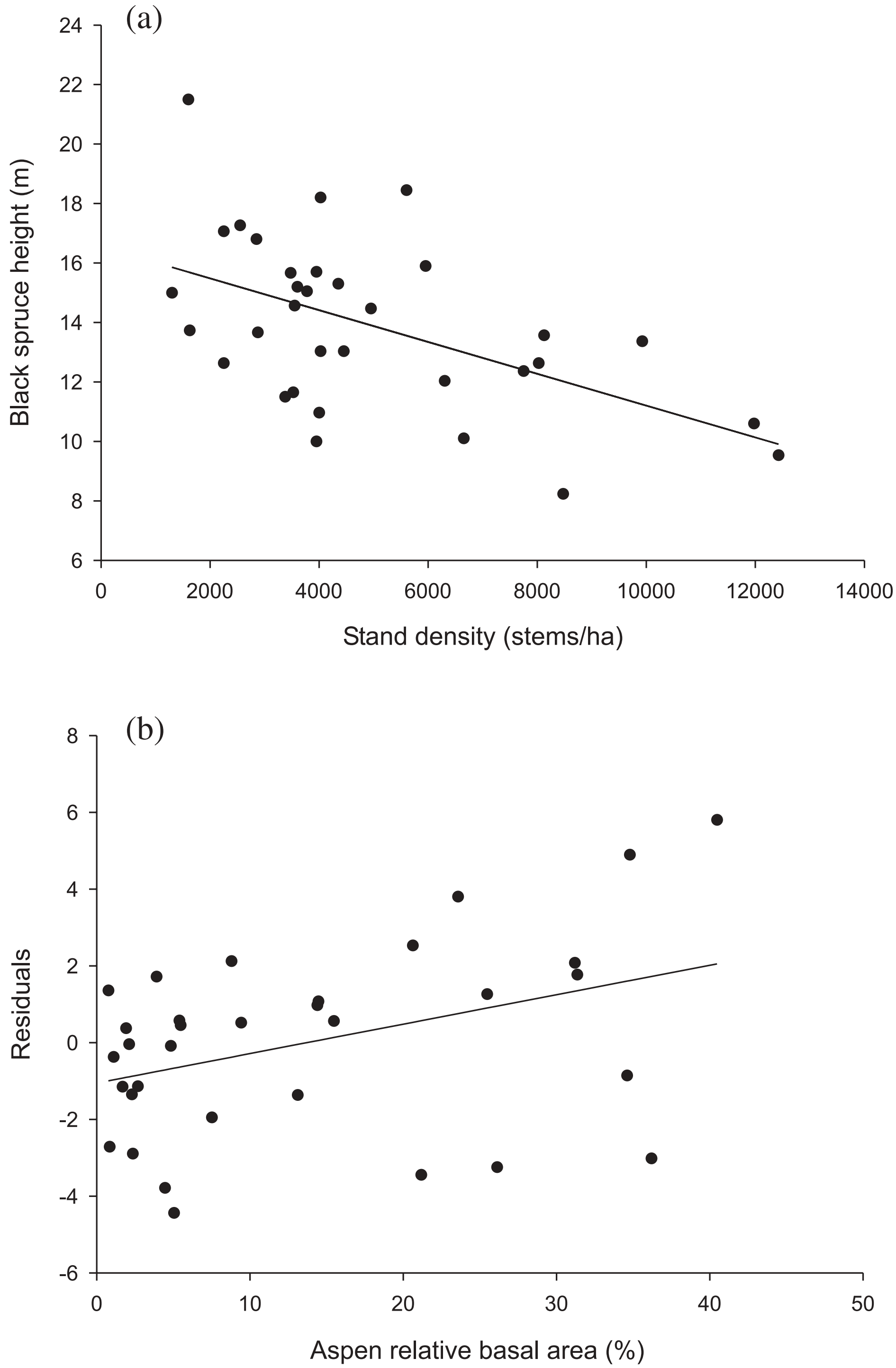
Fig. 4. (*a*) Regression analysis of black spruce mean DBH against stem density, $Y = -0.0004X + 16.742$ ($R^2 = 0.3180$, $p = 0.0006$, $N = 33$), and (*b*) regression analysis of residuals from the precedent regression against restricted gradient of relative basal area of aspen (0%–41%), $Y = 0.0472X - 0.648$ ($R^2 = 0.1051$, $p = 0.0657$, $N = 33$).



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 confounded 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 vol-

Fig. 5. (*a*) Regression analysis of black spruce mean 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%), $Y = 0.7674X - 1.055$ ($R^2 = 0.1549$, $p = 0.0235$, $N = 33$).



ume gain in the stand is aspen fibre. This suggests that aspen uses a different ecological niche than black spruce, thus reducing the competition between the species. In addition to providing an "extra cubic metre" 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 (*Picea glauca* (Moench) Voss) 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

Fig. 6. Covariance analysis comparing the relative importance of stem density and the relative basal area on the variation of black spruce mean stem volume (cubic metres per stem). The black line shows the relationship between density and black spruce volume in stands with 5% to 15% of aspen basal area, and the grey line shows the relationship between density and black spruce volume in stands with 0% to 5% of aspen basal area.

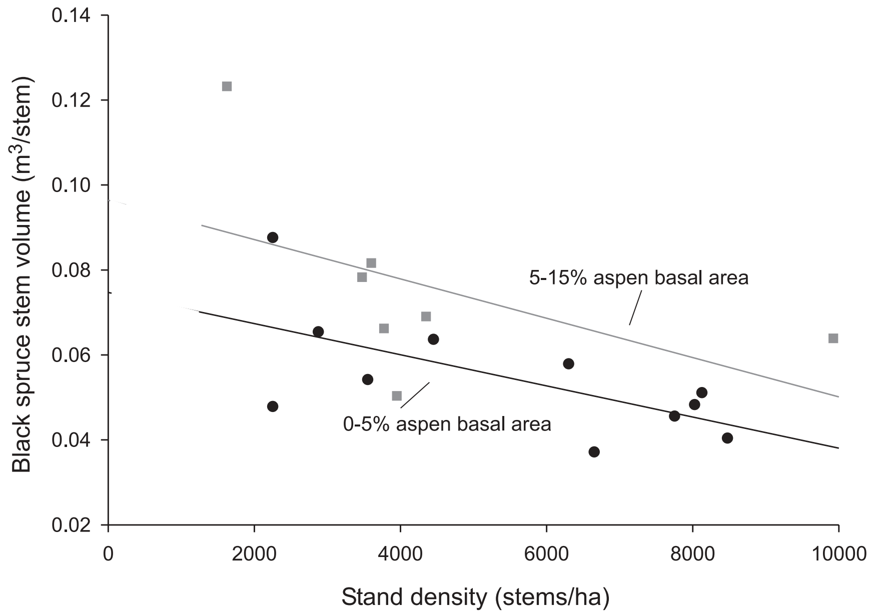


Table 3. Covariance analysis comparing the relative importance of stem density and relative basal area of aspen on the variation of volume by stem of black spruce (cubic metres per stem).

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	6.72*
Stem density	1	0.0017	1.56
Relative basal area	1	0.0039	0.09
Stem density × relative basal area	1	0.0000	
Model testing for homogeneity of intercept point, 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*

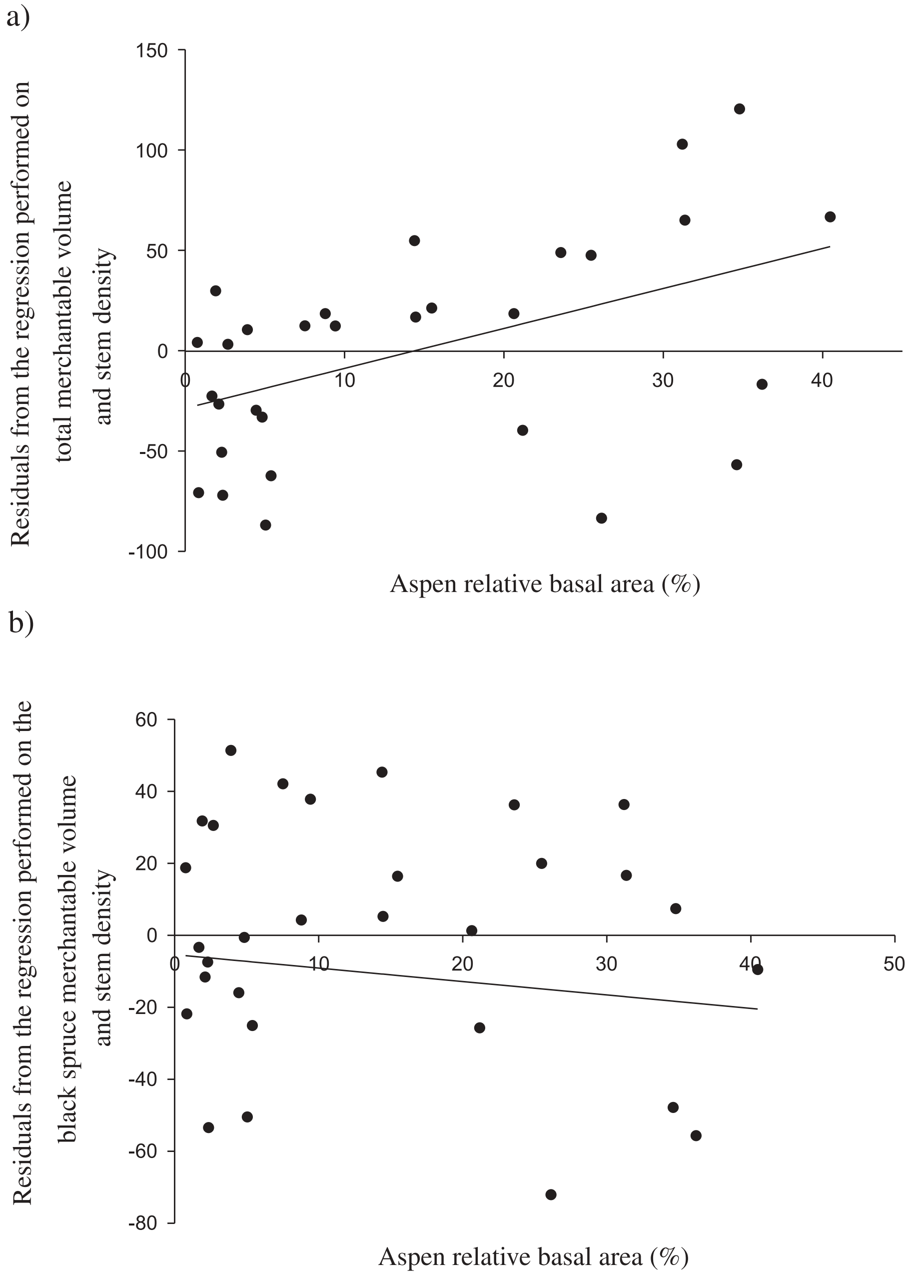
Note: *, $0.01 < P < 0.05$; **, $0.001 < P < 0.01$; ***, $P < 0.001$.

positive influence of one species on another (Vandermeer 1989). Similarly 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 without, or with less, competition for water and nutrients (Constabel and Lieffers 1996). However, aspen shade could limit 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 because of niche separation. In fact, some studies have observed that early-successional species have deeper root systems than late-successional species (Grier et al. 1981; Gale and Grigal 1987), and this root stratification could be a competition avoidance strategy (Strong and La Roi 1983; Kabzems and Lousier 1992; Perry et al. 1992). However, 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 et al. 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 (Longpré et al. 1994; Brais et al. 1995; 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 deteriorates 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 better 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 growth 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, aspen could improve the growth of the stand and the growth of black spruce.

Fig. 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 a restricted gradient of relative basal area of aspen (0%–41%), $Y = -0.3731X + 5.3957$ ($R^2 = 0.0209$, $p = 0.4464$, $N = 30$).



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 invasion of aspen in the managed landscape, which has been observed by Fortin (2000), worries the industry, and a question is raised among foresters: 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 time 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 in agreement with ecosystem management.

Acknowledgments

We thank the ministère des Ressources naturelles du Québec for letting us use their database. This work was supported by the Fonds québécois de la recherche sur la nature et les technologies, the Chaire industrielle CRSNG–UQAT–UQAM en aménagement forestier durable, and the Natural Sciences and Engineering Research Council of Canada.

References

Assmann, E. 1961. Waldertragskunde. BLV Verlagsgesellschaft, Munich.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**: 1980–1992.

Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio, **79**: 51–63.

Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**: 235–242.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. **75**: 49–54.

Binkley, D. 1983. Ecosystem production in Douglas-fir plantations: interaction of red alder and site fertility. For. Ecol. Manage. **5**: 215–227.

Binkley, D. 1992. Mixtures of $nitrogen_2$-fixing and non-$nitrogen_2$-fixing tree species. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malclom, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. Brit. Ecol. Soc. Spec. Publ. 11. pp. 99–123.

Brais, S., Camiré, C., Bergeron, Y., and Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manage. **76**: 181–189.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**: 137–166.

Constabel, A.J., and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. **26**: 1008–1014.

Environment Canada. 1993. Canadian climate normals 1961–90. Canadian Climate Program, Atmospheric Environment Service, Downsview, Ont.

Finér, L., Messier, C., and De Grandpré, L. 1997. Fine-root dynamics in mixed boreal conifer broad-leafed forest stands at different successional stages after fire. Can. J. For. Res. **27**: 304–314.

Flanagan, P.W., and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res. **13**: 795–817.

Forêt Québec. 2000. Normes d'inventaire forestier : les placettes-échantillons temporaires, peuplements de 7 m et plus de hauteur. Direction des inventaires forestiers, ministère des Ressources naturelles du Québec, Québec, Que.

Fortin, S. 2000. Expansion du tremble (*Populus tremuloides* Michx.), au cours du XXième siècle, dans le bassin de la Rivière York en Gaspésie, Québec. M.Sc. thesis, Université du Québec à Chicoutimi, Chicoutimi, Que.

Foster, D.R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. **61**: 2459–2471.

Frivold, L.H., and Kolström, T. 1999. Yield and treatment of mixed stands of boreal tree species in Fennoscandia. *In* Management of mixed-species forest: silviculture and economics. *Edited by* A.F.M. Olsthoorn, H.H. Bartelink, J.J. Gardiner, H. Pretzsch, H.J. Hekhuis, and A. Franc. Institute for Forestry and Nature Research, Wageningen, Netherlands. IBN Sci. Contrib. 15. pp. 37–45.

Frivold, L.H., and Mielikaïnen, K. 1990. The effects of hardwoods on softwood growth in mixed stands in Fennoscandia. *In* The Silvics and Ecology of Boreal Spruces. IUFRO Working Party S1.05-12 Symposium Proceedings, 12–17 August 1989, Newfoundland. *Edited by* B.D. Titus, M.B. Lavigne, P.F. Newton, and W.J. Meades. For. Can. Nfld. For. Cent. Inf. Rep. N-X-271. pp. 75–82.

Gale, M.R., and Grigal, D.F. 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. For. Res. **17**: 829–834.

Grier, C.C., Vogt, K.A., Keyes, M.R., and Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. **11**: 155–167.

Grondin, P. 1996. Écologie forestière. *In* Manuel de foresterie. *Edited by* J.A. Bérard and M. Côté. Les Presse de l'Université Laval, Québec, Que. pp. 133–279.

Grondin, P., Noël, J., Hotte, D., Tardif, P., and Lapointe, C. 2000. Croissance potentielle en hauteur et dynamique des espèces forestières sur les principaux types écologiques des régions écologiques 5a – 6a (Abitibi). Ministère des Ressources naturelles du Québec, Québec, Que. Rapport interne 461.

Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. *In* Forest succession: concepts and applications. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 374–405.

Kabzems, R., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the boreal white and black spruce zone. British Columbia Ministry of Forests, Victoria, B.C. For. Resour. Dev. Agree. Rep. 176.

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed-species stands. *In* The ecology and silviculture of mixed-species forests. *Edited by* M.J. Kelty. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 125–141.

Légaré, S., Bergeron, Y., Leduc, A., and Paré, D. 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. Can. J. Bot. **79**: 1019–1027.

Lehman, C.L., and Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. Am. Nat. **156**: 534–552.

Longpré, M.-H., Bergeron, Y., Paré, D., and Béland, M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can. J. For. Res. **24**: 1846–1853.

Man, R., and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. **75**: 505–513.

Paré, D., and Bergeron, Y. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can. J. For. Res. **26**: 1022–1031.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, Cambridge, U.K. pp. 145–169.

Perron, J.-Y. 1985. Tarif de cubage : volume marchand brut. Ministère des Ressources naturelles du Québec, Québec, Que.

Perry, D.A., Choquette, C., and Schroeder, P. 1987. Nitrogen dynamics in conifer-dominated forests with and without hardwoods. Can. J. For. Res. **17**: 1434–1441.

Perry, D.A., Bell, T., and Amaranthus, M.P. 1992. Mycorrhizal fungi in mixed-species forests and others tales of positive feedback, redundancy and stability. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and

P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. Br. Ecol. Soc. Publ. 11. pp. 151–179.

Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Gouvernement du Québec, Québec, Que.

Rothe, A., and Binkley, D. 2001. Nutritional interactions in mixed species forests: a synthesis. Can. J. For. Res. **31**: 1855–1870.

Seber, G.A.F., and Wild, C.J. 1989. Nonlinear regression. John Wiley & Sons, New York.

Strong, W.L., and La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. **13**: 1164–1173.

Tarrant, R.F. 1961. Stand development and soil fertility in a Douglas-fir–red alder plantation. For. Sci. **7**: 238–246.

Tarrant, R.F., and Trappe, J.M. 1971. The role of *Alnus* in improving the forest environment. Plant Soil, **19**: 335–348.

Van Cleve, K., and Noonan, L.L. 1975. Litter fall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res. **5**: 626–639.

Van Cleve, K., and Viereck, L.A. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *In* Forest succession: concepts and application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 185–211.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge University Press, Cambridge, U.K.

Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quat. Res. **3**: 465–495.

Vincent, J.-S., and Hardy, L. 1977. L'évolution et l'expansion des lacs glaciers Barlow et Ojibway en territoire québécois. Géogr. Phys. Quat. **31**: 357–272.