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Effect of aspen (*Populus tremuloides*) as a companion species on the growth of black spruce (*Picea mariana*) in the southwestern boreal forest of Quebec

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Abstract

In the western boreal forest of Quebec, black spruce stand productivity is approximately 1 m^3/ha/year. 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 hasten 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

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1. 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 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 can be observed (Frivold and Mielikäinen, 1990; Brown, 1992; MacPherson et al., 2001; Chen and Klinka, 2003).

Since the 1990s, the forest industry has had a growing interest in the use of intolerant deciduous species. 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 et al., 1996).

Near the 49th parallel in the Quebec western boreal forest, sites are usually colonized by black spruce following a wildfire. They form even-aged stands that progressively become uneven-aged (Groot and Horton, 1994). These stands generate litter that is relatively resistant to decomposition processes and that promotes the growth of mosses and sphagnum (Flanagan and Van Cleve, 1983). In the absence of fire, the accumulation of organic matter forms a thick LFH layer dominated by feather moss and sphagnum that immobilizes nutrients (Weber and Van Cleve, 1981; Foster, 1985; Oechel and Van Cleve, 1986). It has been suggested that the paludification process could explain the low productivity of black spruce in these stands (1 m^3/ha/year; Viereck and Dyrness, 1979; Van Cleve and Viereck, 1981; Foster, 1983; Oechel and Van Cleve, 1986). However, natural stands of shade-intolerant deciduous species, which hasten nutrient cycling (Van Cleve and Noonan, 1975; Corns, 1989; Longpré et al., 1994; Paré and Bergeron, 1996), can also dominate after fire (Gauthier et al., 2000). These stands evolve into mixed-species stands that are relatively productive (2–3 m^3/ha/year). Following management activities, stands originally dominated by black spruce are invaded by deciduous species such as willow and aspen (Carleton and MacLellan, 1994; Fortin, 2000). From a management point of view, the presence of aspen in black spruce stands is often considered as a competitive species, which necessitates mechanical clearing despite the economic value of aspen. 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 et al. (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 volume and 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.

2. Material and methods

2.1. 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).

2.2. Sampling design

In a previous study (Légaré et al., 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 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 is 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 (deposits, drainage).

Three sites were chosen according to the following criteria: light slope, moderate drainage, surface deposits and stand composition dominated by black spruce with heterogeneous presence of aspen. Stands at all three sites result from wildfires that took place around 1920 according to the fire map elaborated by Bergeron et al. (2004). More precisely, stands 1, 2 and 3 originate from fires that occurred around 1926, 1916 and 1916, respectively, according to aspen base cross-sections (0 m) at each site. Sites were different on the basis of stem density, soil texture, site index and mean aspen proportion (Table 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.

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 get 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) and height of every tree in each of the 35 plots (11 or 12 at each site) of the sampling plan with a clinometer to determine the basal area covered by each species. The volume of each species was estimated with Honer's respective equation (Honer et al., 1983) and merchantable volume was calculated using stems with DBH over 9 cm only. In 2002, we conducted stem analysis in each plot on the three taller black spruces that were generally dominant or co-dominant, however, in few plots, taller black spruces were suppressed. Cross-sections were taken at the base and at 0.40, 1.0, 1.30 m and every meter to the top. Cross-sections were measured and cross-dated in the laboratory with a binocular. 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 dominant black spruces in each site were selected and cut at the base and at every meter to determine the site index, which is the height of trees at 50 years.

Table 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			
Site density	3220.82 ± 698.40	2013.80 ± 602.63	1992.65 ± 707.61
Proportion of aspen (%)	28.24 ± 18.89	38.54 ± 24.84	24.99 ± 29.55
Site index at 50 years (nine trees)	11.62 ± 0.83	12.18 ± 0.84	12.72 ± 1.37
Tree 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 (year)	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 (%)	50.40 ± 6.25	39.52 ± 14.86	24.47 ± 9.24
Sand (%)	14.34 ± 4.68	25.30 ± 17.12	19.07 ± 4.36
Silt (%)	35.26 ± 7.08	35.18 ± 7.02	56.47 ± 8.38
Oxygenated layer depth (cm)	21.49 ± 7.03	41.70 ± 18.80	34.53 ± 12.03

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).

2.3. Statistical analyses

To test the homogeneity of mineral soil properties and water regime (clay, silt and sand percentage, 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 (Mantel, 1967; Douglas and Endler, 1982). 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, NC), and the significance threshold was fixed at 0.05.

3. Results

3.1. 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 2).

3.2. 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). 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, Fig. 1).

3.3. 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 black spruce volume and merchantable volume of black spruce decreased significantly (Table 3, Figs. 2 and 3). Stand density positively influenced stand volume,

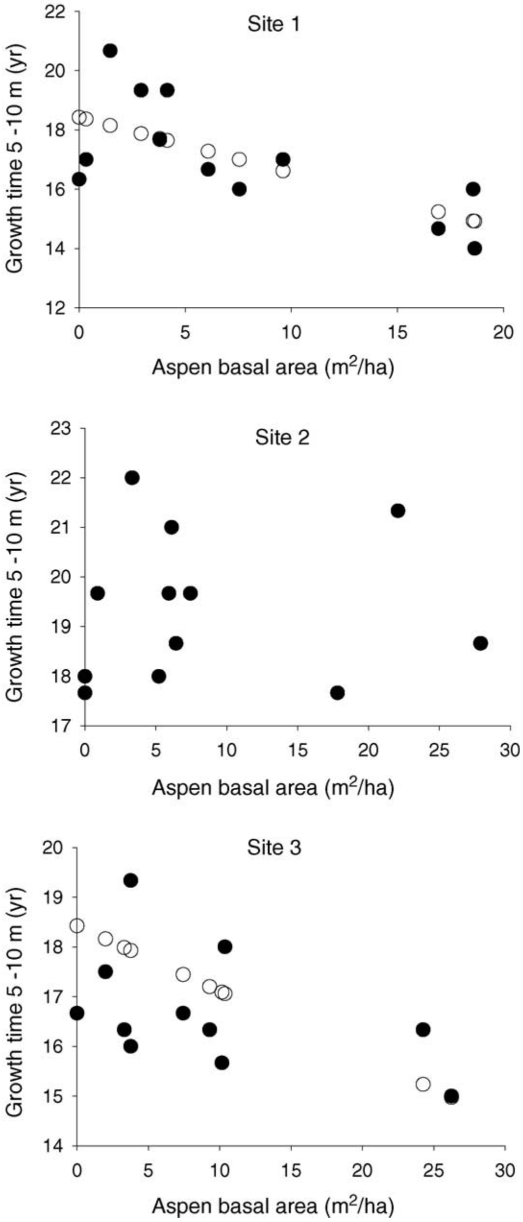

Fig. 1. Relationships between aspen basal area and black spruce TTG510 in sites 1 (a), 2 (b) and 3 (c) ($N = 12$, 12 and 11, respectively; ●: observed, ○: predicted by the GLM procedure).

Table 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.

Table 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	15.07 (<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: 0.4747)	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	26067.34	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; $^{*}P < 0.01$, $^{**}0.01 \leq P < 0.001$, $^{***}P < 0.001$; $Y = b_0 + b_1$ (stand density) + b_2 (aspen basal area (site)).

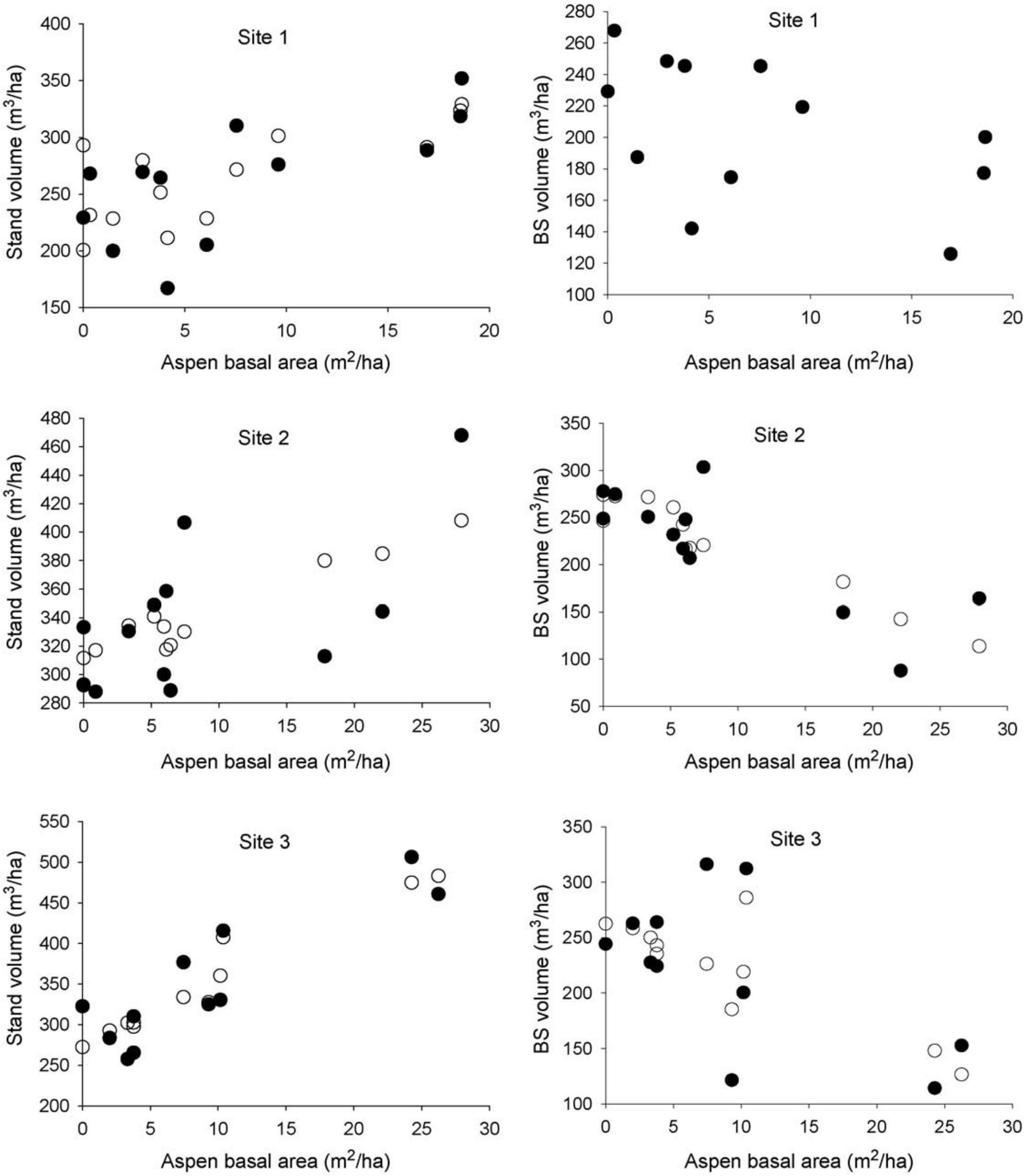

Fig. 2. Relationships between aspen basal area and volume (black spruce (BS) and stand) in sites 1, 2 and 3 ($N = 12$, 12 and 11, respectively; ●: observed, ○: predicted by the GLM procedure).

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

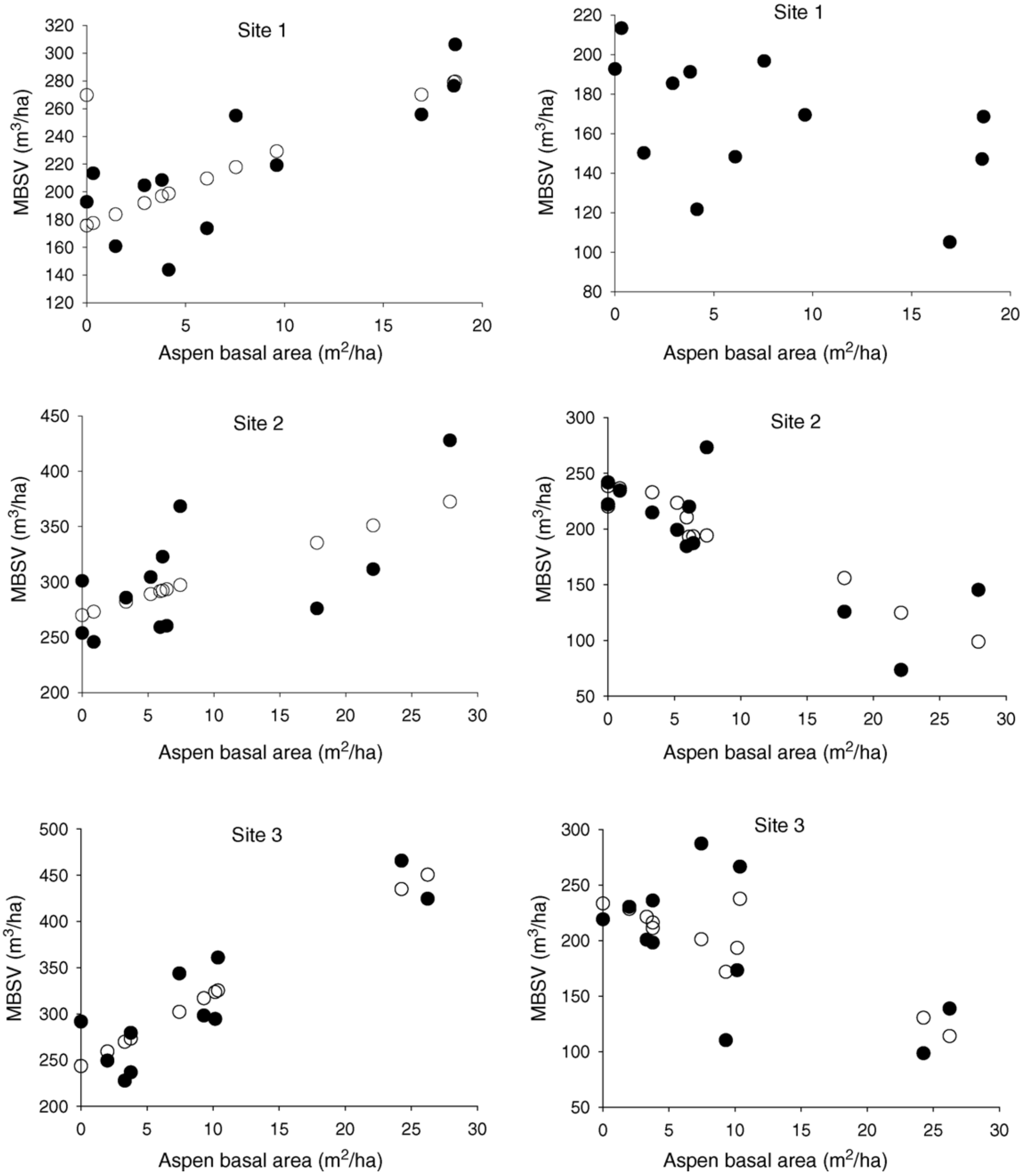

Fig. 3. Relationships between aspen basal area and merchantable volume (black spruce (BS) and stand) in sites 1, 2 and 3 ($N = 12$, 12 and 11, respectively; ●: observed, ○: predicted by the GLM procedure).

significantly related to plot localization (results not shown).

4. Discussion

4.1. 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. The decrease of total nitrogen concentrations in the mineral soil with increasing aspen relative basal area loosely suggest 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 in the needles of balsam fir seedlings on site 2 and aspen basal area (Légaré et al., unpublished data).

4.2. Competitive reduction principle

As observed by Légaré et al. (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 a 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 et al. (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 et al. (2004) reported a 5 m greater height for stands having an aspen relative basal of 40% compared with 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 stand merchantable volume in site 1 varied from approximately 180–280 m^3/ha along the increasing gradient of aspen basal area (0–18.64 m^2/ha). This corresponds to an aspen proportion of 0–43.67% 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 aspen basal area proportion similar to that of site 1 (0–41.29%), 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 being replaced by aspen (Fig. 3).

4.3. Facilitation

In two of our sites (1 and 3), black spruce TTG510 was positively affected by the 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 rate in pure and mixed stands, which is well documented (Corns, 1989; Longpré et al., 1994; Brais et al., 1995; 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 that 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 (Corns, 1989; Longpré et al., 1994; Brais et al., 1995; 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 et al., 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 a 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 structure of the canopy.

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 species' respective proportions 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 unit nutrient 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 (Légaré et al., unpublished data). 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 7 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 guidelines including a non-negligible range of variation.

4.4. 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 et al., 2001), which is close to the mean stand volume calculated for sites 1, 2 and 3 (262.43 ± 53.75, 339.33 ± 53.36, 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 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 alternative pure stands of aspen and black spruce could also affect stand diversity and productivity in time, thus representing another management option.

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