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Influence of aspen on forest floor properties in black spruce-dominated stands

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Abstract

In the absence of fire in black spruce-feathermoss stands, a thick forest floor layer dominated by bryophytes and sphagnum accumulates. This layer is associated with wet, cool and nutrient-poor soil conditions conducive to the paludification process and pushing the ecosystem towards an unproductive open black spruce forest. The presence of *Populus tremuloides* in theses stands may halt this process because this species has a high nutrient cycling rate and a litter that represses moss cover. The main hypothesis of this study is that, despite similar abiotic conditions (slope and drainage), the presence of *Populus tremuloides* in a stand dominated by *Picea mariana* affects surface soil nutrient availability, total N, pH as well as the decomposition process. The abundance of *Populus tremuloides* trees was associated with higher exchangeable cations, cationic exchangeable 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 *Populus tremuloides* 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 suggested that in these stands, the soil microbial community is uniformly and strongly nitrogen limited. The zone of influence of *Populus tremuloides* was evaluated in areas around the soil sampling plot ranging from 3 to 7 m. The results revealed that this zone varies with soil properties. The results suggest that the presence of *Populus tremuloides* accelerate nutrient cycling, which could affect stand productivity to some extent.

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 this species, its recalcitrant litter and the development of a sphagnum layer are all conducive to organic matter accumulation, cool soil temperature, rise of the water table and, consequently, restricted 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

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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 Bockheim et al. (1991) and Alban and Pastor (1993), 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, 2004; Longpré et al., 1994). Using forest inventory databases, Légaré et al. (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 a stand 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 test 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.

Material and methods

Study area

The study area was located in northewestwern 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 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 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). 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).

Sampling design

Three sites were chosen according to the following criteria: light 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 elaborated by Bergeron et al. (2004). More precisely, sites 1, 2 and 3 originate from 1926, 1916 and 1916 fires, respectively, according to local measures obtained from cross-sectional tree-discs of 10 *Populus tremuloides* trees taken at ground level (0 m) in 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 density and soil texture (Table 1). Site 1 had higher mean stem density, with 3220 stems* ha^{-1},

Table 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			
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 percentage	50.40 ± 6.25	39.52 ± 14.86	24.47 ± 9.24
Stand characteristics			
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)	3220 ± 698	2014 ± 603	1993 ± 708

and sites 2 and 3 had mean stem density of 2014 and 1993 stems* ha^{-1}, respectively. On each site, black spruce basal area decreases along the increasing aspen basal area and fine roots are mostly located at the interface between the A horizon and the humus layer. Humus layer thickness was lower in site 1 and higher in site 3 (Table 2). To ensure that mineral soil properties were not correlated with *Populus tremuloides* presence, we selected in each site five plots of each three following categories for further analyses (total of 45 selected plots): (1) plot dominated by *Picea mariana* with less than 15% of relative basal area of *Populus tremuloides*, (2) plot with a relative *Populus tremuloides* basal area of 15–50 %, and (3) plot with a relative *Populus tremuloides* basal area of 50–75%.

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 covered by each species. Three samples of FH layer (0.01 m^2) were taken in three different directions at 1 m of the centre of each plot and, in the same way, 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 per sites). For each plot, soil samples were pooled by horizon, air dried, and ground. Forest floor and mineral soil pH were analysed in distilled water (McKeague, 1976). Exchangeable

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

FH layer properties	Means ± standard deviations		
	Site 1	Site 2	Site 3
Humus 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

cations in the forest floor and mineral soil were extracted with 0.1 *M* $BaCl_2$ and determined by atomic absorption, while cationic exchangeable 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 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 glasses with 15–40 g of fresh soil (5 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 glasses were incubated. One glass received only deionized water (control C), another received a single dose of the nitrogen treatment (D, 1300 μg N g^{-1} dry soil added), and the last one received a double dose (DD, 2600 μg 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 2 *M* KCl solution and analysed 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).

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, 5 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, 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 a strong evidence that they are not significant. Thus, a *P*-value over 0.40 or a negative coefficient of correlation were considered to be evidences 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. Then, we 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, and interaction between site and *Populus tremuloides* basal area in each area around the sampling point was also considered for the following distances: 0–3, 3–5 and 5–7 m of 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 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 were $\log_{10}$ transformed for normal distribution except forest floor pH.

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.

Results

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. 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 cationic 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), cationic 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 (Table 3). Clay percentage of mineral soil was significantly correlated with aspen basal area at 5 m of the sampling point on site 3.

Humus layer chemical properties and aspen basal area relationships

On all sites, forest floor pH increased significantly along the basal area of aspen within 7 m (Figure 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 with a $P = 0.0537$ 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). 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 4). Total nitrogen increased while C:N ratio decreased along the gradient of aspen basal area within 7 m of the sampling point (Figure 3).

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

Organic matter thickness was influenced by aspen trees located within 7 m of the sampling point while decay rates was 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 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 4). Organic matter thickness decreased along the gradient of aspen basal area within 7 m of the sampling point (Figure 4).

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

Variables	ρ (P > |r|) AABA3	ρ (P > |r|) AABA5	ρ (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)

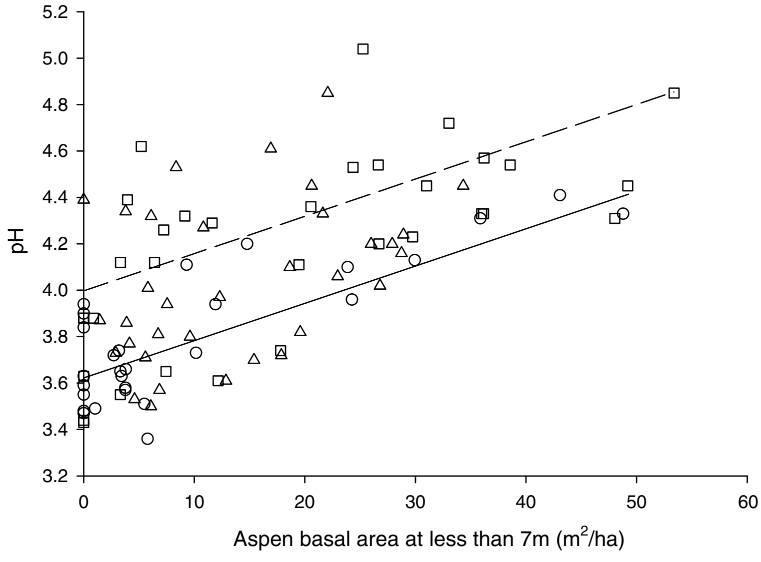

Figure 1. Relationship between pH and aspen basal area within 7 m (ABA7) of the sampling point; pH = 3.6241 + 0.0160 ABA7 + 0.3767 dummy2, R^2: 0.5972, $P = <0.0001$, $N = 95$, △ = site 1 (solid line), □ = site 2 (long dash line), ○ = site 3 (solid line).

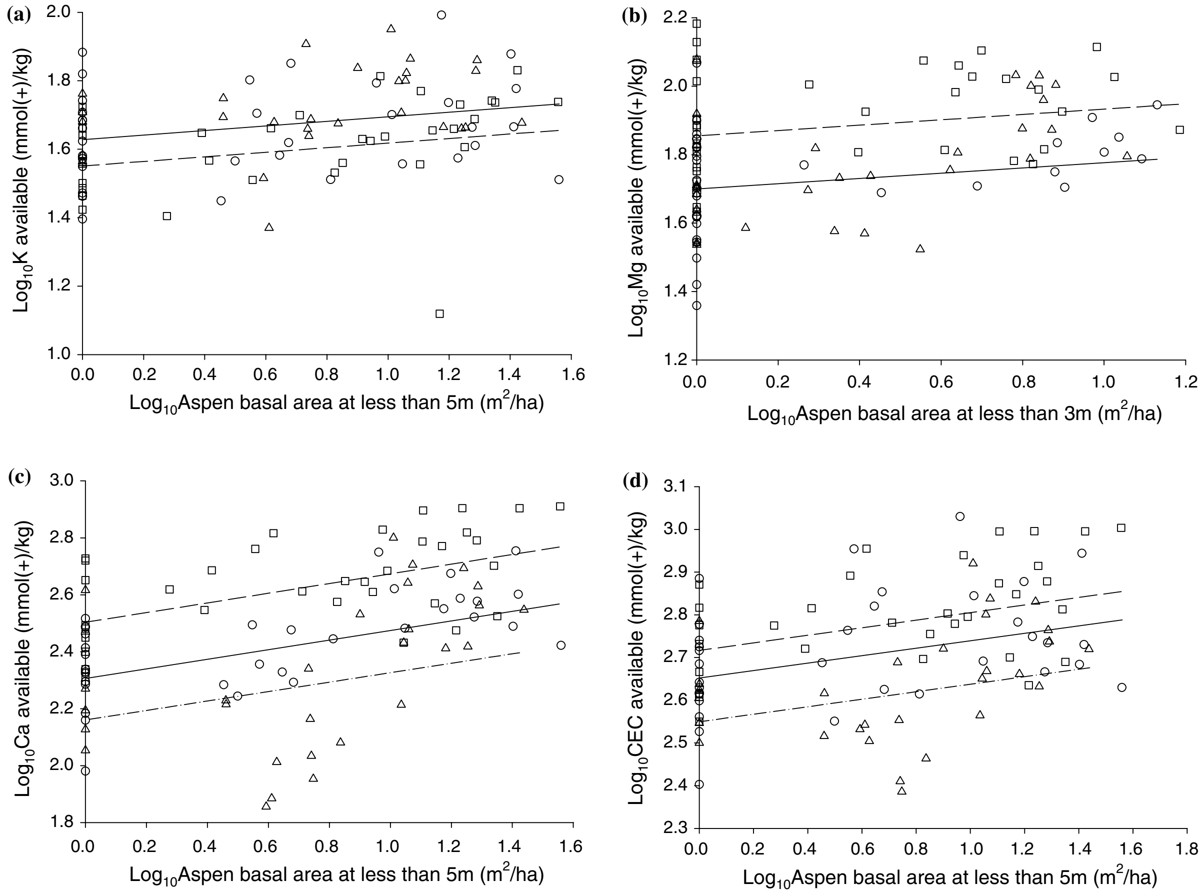

Figure 2. (a) Relationship between K and aspen basal area within 5 m (ABA5) of the sampling point; $\log_{10}K = 1.6267 + 0.0672 \log_{10}ABA5 - 0.0772$ dummy2, R^2: 0.1564, $P = 0.0004$, $N = 95$, △ = site 1 (solid line), □ = site 2 (long dash line), ○ = site 3 (solid line). (b) Relationship between 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, $P < 0.0001$, $N = 95$.

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 sites (Table 5, Figure 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 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 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 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**				
	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*

+ P = 0.0660, all soil properties are $\log_{10}$ transformed except forest floor pH.

Discussion

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 mostly accepted in the scientific community (Bergeron and Bouchard, 1984; Carleton and Maycock, 1978; Gauthier et al., 2000). It is however possible to find different forest communities on sites sharing similar soil conditions (Gauthier et al., 2000), which allows 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, the study was conducted on three large sites which we presumed to be homogeneous in terms of mineral soil characteristics, with each showing a gradient in aspen–black spruce composition. Only three mineral soil properties (clay percentage, 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. According to the fact that all forest floor properties were affected by aspen at 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.

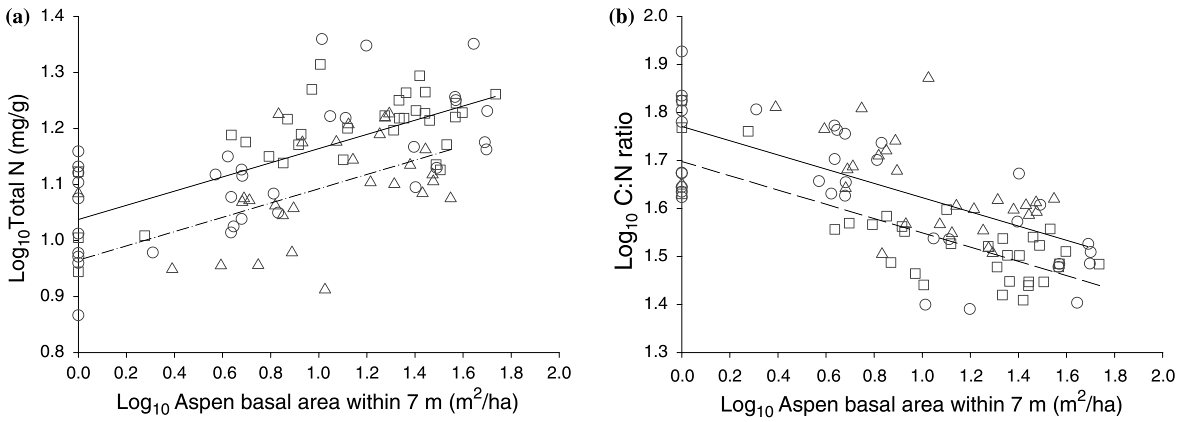

Figure 3. (a) Relationship between total nitrogen and aspen basal area within 7 m (ABA7) of the sampling point; $\log_{10}\text{TN} = 1.0379 + 0.1262 \log_{10}\text{ABA7} - 0.0713$ dummy1, R^2: 0.4764, $P < 0.0001$, $N = 95$, △ = site 1 (dash dotted line), □ = site 2 (solid line), ○ = site 3 (solid line).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

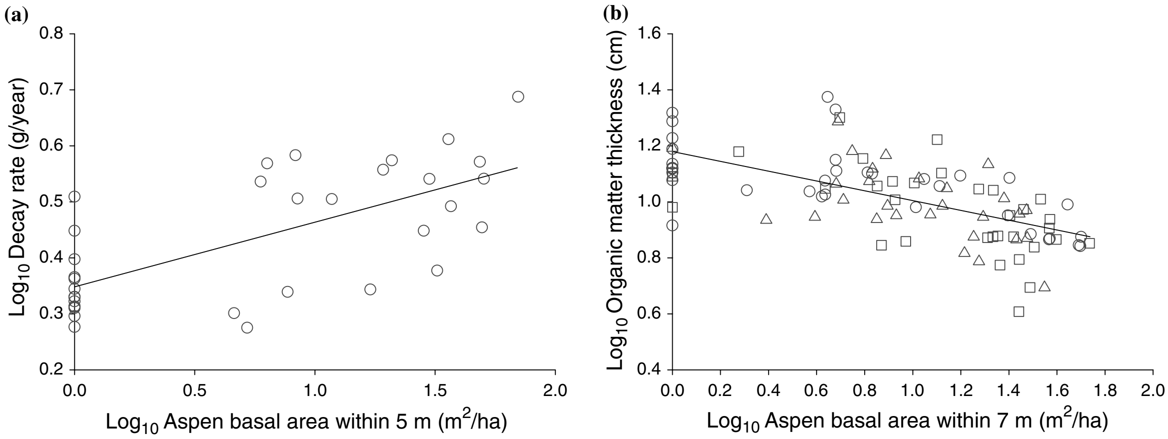

Figure 4. (a) Relationship between decay rate and aspen basal area within 5 m (ABA5) of the sampling point; $\log_{10}\text{DECAY} = 0.3483 + 0.1151 \log_{10}\text{ABA5}$, R^2: 0.4638, $P < 0.0001$, $N = 34$, ○ = site 3 (solid line). (b) Relationship between organic matter thickness (OM) and aspen basal area within 7 m (ABA7) of the sampling point; $\log_{10}\text{OM} = 1.1771 - 0.1750 \log_{10}\text{ABA7}$, R^2:0.3905, $P < 0.0001$, sites 1, 2 and 3 (solid line).

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 et al., 1997) and that the influence of tree species depends on the soil properties explored (Rothe et al., 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 (deposits, slope, drainage), the presence of aspen trees on the three sites was associated with higher

Table 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
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		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***
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	141.47***
	Treatment	2	6436.13	7.88**
	ABA7	1	179.20	

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

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). Zinke (1962) and Lodhi (1977) 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 pointed out 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) is rapidly cycling 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. Size of the crown area projection on the soil surface was identified as a major variable corresponding to the influence of

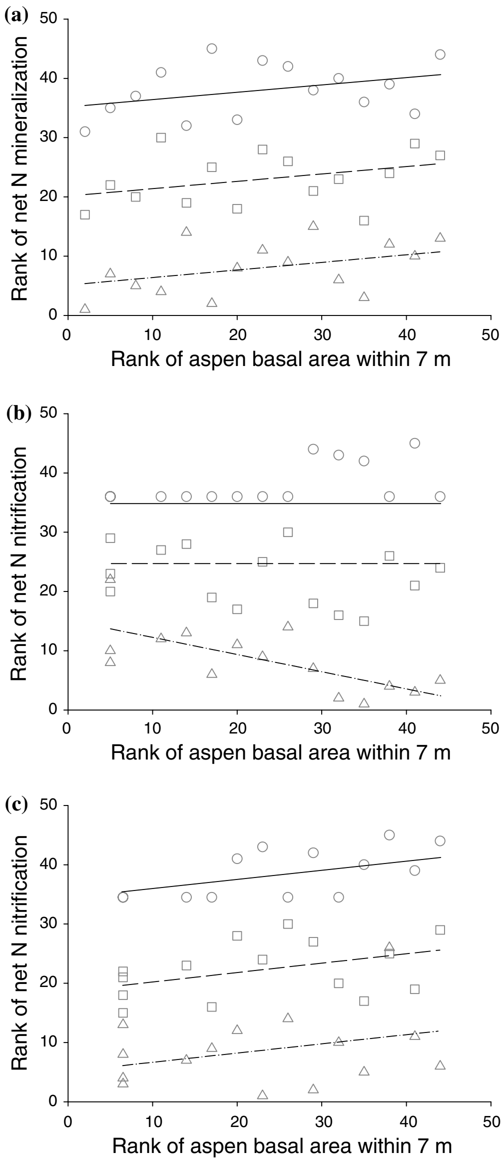

Figure 5. (a) Relationship between rank of net N mineralization and rank of aspen basal area within 7 m (ABA7) of the sampling point in site 1. Relationship between rank of net N nitrification and rank of aspen basal area within 7 m (ABA7) of the sampling point in (b) site 2 and (c) site 3. ○ = Control treatment (solid line), □ = single dose treatment (long dash line), △ = double dose treatment (dash dotted line), see details in Table 5.

individual trees on soil properties according to Zinke (1962). Moreover, aspen leaves dispersion could also be affected by wind and steep slope (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.

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 hastens 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 others studies conducted in the Canadian boreal forest (Boudreault et al., 2002; Yu et al., 2002) following approximately 80 years of forest growth, and that 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. This suggests that most of the forest floor is newly formed and that the possibility of a carry-over from the previous stand is minimal.

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,

Table 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.

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 aspen could have a greater impact on relatively poorer sites.

Laboratory incubation was conducted under standard conditions of temperature and water content for all samples. These conditions may differ from the ones 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 relationship between total C:N and N mineralization that was observed in the present study, with the exception of site 3, suggests that the experiment, considering the low temperature of incubation (10 °C), was not conducted for a period of time long enough to evaluate the true soil potential for N nutrition. 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 hastens 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.

Conclusion

Our results suggest that the presence of aspen at different time and spatial scales could hasten nutrient cycling, which may improve or preserve the productivity of the stand. These results support the hypothesis that presence of aspen could enhances black spruce productivity. However, our results are not sufficient to conclude about the possible success of mixed management for this type of stand. This success will depend on the species selected, on the proportion of each species, and on site characteristics. It could also depend on ecological niche separation, which reduces competition between species. The number of possible combinations of species and the property-specific responses could also explain the variety of responses observed about forest composition on soil properties in the scientific literature.

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References

Alban D H 1982 Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci. Soc. Am. J. 46, 853–861.

Alban D H and Pastor J 1993 Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23, 1744–1749.

Bergeron Y and Bouchard A 1984 Use of ecological groups in analysis and classification of plant communities in a section of western Quebec. Vegetatio 56, 45–63.

Bergeron Y, Gauthier S, Kafka V, Lefort P and Lesieur D 2001 Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31, 384–391.

Bergeron Y, Gauthier S, Flannigan M and Kafka V 2004 Fire regimes at the transition between mixedwoods and conifer boreal forest in northwestern Quebec. Ecology (in press).

Binkley D 1986 Forest Nutrition Management. John Wiley & Sons, New York, 290 pp.

Binkley D 1995 The influence of tree species on forest soils: Processes and patterns. *In* Proceedings of the Tree and Soil Workshop. Eds. D J Mead and I S Cornforth. pp. 1–33. Agronomy Society of New Zealand, Canterbury, Special Publication No. 10.

Bockheim J G, Jepsen E A and Heisey D M 1991 Nutrient dynamics in decomposing leaf litter of four tree species on a sandy soil in northwestern Wisconsin. Can. J. For. Res. 21, 803–812.

Boettcher S E and Kalisz P J 1991 Single-tree influence on earthworms in forest soils in eastern Kentucky. Soil Sci. Soc. Am. J. 55, 862–865.

Boudreault C, Bergeron Y, Gauthier S and Drapeau P 2002 Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Can. J. For. Res. 32, 1080–1093.

Carleton T J and Maycock P F 1978 Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56, 1157–1173.

Carter M R 1993 Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Boca Raton, FL. 461 pp.

Corns I G W 1989 Ecosystems with potential for aspen management. *In* Managing for aspen, a shared responsibility: Proceedings of the Joint Technical Session of the Forest Ecology, Silviculture and Tree Improvement Forest Management, and Forest Economics and Policy Working Groups. For. Chron. 65, 16–22.

Côté L, Brown S, Paré D, Fyles J and Bauhus J 2000 Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biol. Biochem. 32, 1079–1090.

Environment Canada 1993 Canadian Climate Normals, 1961–1990. Atmospheric Environment Service, Ottawa, Ont.

Finzi A C and Canham C D 1998 Non-additive effects of litter mixtures on net N mineralization in a southern New England forest. For. Ecol. Manage. 105, 129–136.

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.

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

Foster D R 1985 Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of southeastern Labrador, Canada. J. Ecol. 73, 517–534.

Gauthier S, De Grandpré L and Bergeron Y 2000 Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. 11, 781–790.

Grondin P 1996 Écologie forestière. *In* Manuel de foresterie. Eds. J Bérard and M Côté. pp. 133–278. Les Presses de l'Université Laval, Québec.

Hendershot W H, Lalande H and Duquette M 1993 Ion exchange and exchangeable cations. *In* Soil Sampling and Methods of Analysis. Ed. M R Carter. pp. 167–176. Canadian Society of Soil Science. Boca Raton, FL.

Hobbie S E 1992. Effects of plant species on nutrient cycling. Trends Ecol. Evol. 7, 336–339.

Keeney D R and Nelson D W 1982 Nitrogen-inorganic forms. *In* Methods of Soil Analysis. Part 2, Chemical and Microbiological Properties. Eds. A L Page and R H Miller. pp. 643–698. American Society of Agronomy, Madison, WI.

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.

Légaré S, Paré D and Bergeron Y 2004 The response of black spruce growth to an increased proportion of aspen in mixed stands. Can. J. For. Res. 34, 405–416.

Lodhi M A K 1977 The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. Am. J. Bot. 64, 260–264.

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.

MacLean D A, Woodley S J, Weber M G and Wein R W 1983 Fire and nutrient cycling. *In* The Role of Fire in Northern Circumpolar Ecosystems. Eds. R W Wein and D A MacLean. pp. 11–132. John Wiley & Sons Ltd., New York.

McClaugherty C A, Pastor J, Aber J D and Melillo J M 1985 Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66, 266–275.

McKeague J A 1976 Manual on Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Ottawa, Ont.

Moore T R, Trofymow J A, Taylor B, Prescott C, Camiré C, Duchesne L, Fyles J, Kozak L, Kranabetter M, Morrison I, Siltanen M, Smith S, Titus B, Visser S, Wein R and Zoltai S 1999 Litter decomposition rate in Canadian forests. Global Change Biol. 5, 75–82.

Oechel W C and Van Cleve K 1986 The role of bryophytes in nutrient cycling in the taiga. *In* Forest Ecosytems in Alaskan Taiga. Eds. K Van Cleve, F S Chapin III, P W Flanagan, L A Viereck, C T Dyrness. pp. 121–137. Springer-Verlag, New York.

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. 25, 1022–1031.

Riha S J, James B R, Senesac G P and Pallant E 1986 Spatial variability of soil pH and organic matter in forest plantations. Soil Sci. Soc. Am. J. 50, 1347–1352.

Rhoades C C 1997 Single-tree influences on soil properties in agroforestry: Lessons from natural forest and savanna ecosystems. Agrofor. Syst. 35, 71–94.

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

Rothe A, Kreutzer K and Küchenhoff H 2002 Influence of tree species composition on soil and soil solution properties in two mixed spruce-beech stands with contrasting history in Southern Germany. Plant Soil 240, 47–56.

Soil Classification Working Group 1998 The Canadian System of Soil Classification, Third Edition. Agriculture and Agri-Food Canada, Research Branch, Publication 1646. 187 pp.

Staelens J, Nachtergale L, Luyssaert S and Lust N 2003 A model of wind-influenced leaf litterfall in a mixed hardwood forest. Can. J. For. Res. 33, 201–209.

Thomas K D and Prescott C E 2000 Nitrogen availability in forest floors of three tree species on the same site: The role of litter quality. Can. J. For. Res. 30, 1698–1706.

Trofymow J A, Moore T R, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M and Visser S 2002 Rates of litter decomposition over 6 years in Canadian forests: Influence of litter quality and climate. Can. J. For. Res. 32, 789–804.

Turner D P and Franz E H 1985 The influence of western hemlock and western redcedar on microbial numbers, nitrogen mineralization, and nitrification. Plant Soil 88, 259–267.

van Breemen N, Finzi A C and Canham C D 1997 Canopy tree – soil interactions within temperate forests: Effects of soil elemental composition and texture on species distributions. Can. J. For. Res. 27, 1110–1116.

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. Eds. D C West, H H Shugart and D B Botkin. pp. 185–211. Springer-Verlag, New York.

Viereck L A and Dyrness C T 1979 Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska. USDA For. Serv., Gen. Tech. Rep. PNW-90.

Vincent J S and Hardy L 1977 L'évolution et l'expansion des lacs glaciaires Barlow et Ojibway en territoire québécois. Géogr. Phys. Quatern. 31, 357–372.

Weber M G and Van Cleve K 1981 Nitrogen dynamics in the forest floor of interior Alaska black spruce ecosystems. Can. J. For. Res. 11, 743–751.

Wedin D A and Tilman D 1990 Species effects on nitrogen cycling: A test with perennial grasses. Oecologia 84, 433–441.

Yu Z, Apps M J and Bhatti J S 2002 Implications of floristic and environmental variation for carbon cycle dynamics in boreal forest ecosystems of central Canada. J. Veg. Sci. 13, 327–340.

Zinke P J 1962 The pattern of influence of individual forest trees on soil properties. Ecology 43, 130–133.

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