The Contrasting Effects of Aspen and Jack Pine on Soil Nutritional Properties Depend on Parent Material

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ABSTRACT

The influence of forest stand composition on soil was investigated by comparing the forest floor (FH) and upper mineral soil (0–20 cm) nutritional properties of jack pine and aspen stands on two soil types of contrasting fertility, a coarse-textured and a fine-textured deposit, in a replicated design. The studied tree species are pioneers that are found after major disturbances in the southern boreal forest of western Quebec and that differ in their nutrient requirements but not in their growth rate. Soil organic matter as well as total and available N, P, K, Ca, Mg contents were determined and the relationships with nutrient accumulation in tree biomass were studied. On both soil types a greater total and available nutrient accumulation in the forest floor layer was observed in aspen than in jack pine whereas such differences between stand types could not be detected in the mineral soil. Differences in FH nutrient content between stand types were larger on coarse deposits than on fine-textured soils. These results support the hypothesis that tree species with greater nutrient requirements cause an enrichment of the surface soil at least in the short term. The modulation of tree species effect by soil type was contrary to the pattern observed in other studies since a greater expression of this effect was observed on poorer soils. Differences in soil nutrient content were related to levels of organic matter accumulation.

Key words: aspen; biogeochemistry; boreal forest; forest soils; jack pine; nutrient cycling; plant uptake; soil plant relationship; tree species; tree species effect.

INTRODUCTION

Common understanding of soil–plant relationships comes from conventional agricultural knowledge. It is generally believed that the growth and harvesting of productive and nutrient-demanding crop species can adversely affect soil fertility by depleting nutrient reserves. Ecological studies in forested

or other natural ecosystems are challenging this paradigm with growing evidence that species with high nutrient requirements can have a positive effect on soil nutritional properties in comparison with other species whose growth requires fewer nutrients (Alban 1982; Paré and Bergeron 1996). A recent study even showed that within a species, the vigorous growth of more productive genotypes did not deplete soil nutrients, and moreover that superior productivity increased soil calcium (Ca) availability (Bélanger and others 2004).

Among the features distinguishing forests from other ecosystems (see review by Binkley and Giardina 1998), individual trees influence soil properties at much greater spatial and temporal scales than other vegetation types. Although agricultural crop species are generally harvested after a single growing season, trees can remain in place for decades, or even centuries. Cumulative differential nutrient input, output and cycling between species of trees over time can profoundly alter soil properties.

In the southern boreal forest of western Quebec in Canada, trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) are both pioneer tree species that occur after major disturbances. Despite their similar growth rates (Longpré and others 1994), they differ in their nutrient requirements, as annual nutrient accumulation in aspen is higher than in jack pine (Alban 1982; Gower and others 2000). Jack pine forests naturally occur on acidic and coarse parent material, whereas forests dominated by aspen are mainly found on rich, fine-textured deposits. However, both species occasionally occur on coarser and finer textured soils, with the result that communities dominated by each of these two tree species can be found side by side, on the same parent material, often separated by sharp boundaries.

Alban (1982) studied the effect of nutrient accumulation in both species on soil properties in two Minnesota forests growing on sandy loam. A central conclusion of that research was that although total Ca content of the soil–vegetation complex did not differ between aspen and jack pine stands, aspen was found to redistribute Ca from the upper mineral soil to the forest floor via its litterfall with the result of a Ca enrichment of the forest floor and a parallel impoverishment of the upper mineral soil, as compared with jack pine's. Tree species effects on soil properties were significant at a depth of more than 25 cm in the mineral soil.

Alban's (1982) study was limited to two individual forest sites on parent material of similar fertility. Site fertility is an important determinant of primary production. It influences many aspects of plant physiology, such as relative allocation to roots and leaf production (see reviews by Chapin 1980; Kraus and others 2004). The chemical composition of leaf litter can vary within a single species according to site fertility, as many species produce nutrient-depleted litter in less fertile sites (Flanagan and Van Cleve 1983). Furthermore, intraspecific variations in secondary compounds in root and leaf litter may be influenced by site fertility, causing concentrations of polyphenolics, such as tannin, to be inversely associated with indices of site fertility (Cotrufo and others 1995; Kraus and others 2004; Northup and others 1998, 1995). Consequently vegetation effects on soil properties may be influenced by site fertility. Tree species effects on forest floor nutrient accumulation were higher on a richer loamy site than on a sandy site in an experimental plantation in Denmark (Raulund-Rasmussen and Vejre 1995). Finzi and others (1998b) also recorded a greater species effect on soil exchangeable Ca where soil total Ca was in greater concentration.

The main objective of the present study was to determine the effect of the colonizing tree species, jack pine and aspen, on forest floor and upper mineral soil nutrient content on two soil types of contrasting fertility, a coarse-textured deposit with more than 70% sand, and a fine-textured parent material containing more than 70% silt and clay particles. We expect that aspen, which cycles more nutrients and produces more litter will positively affect surface soil nutritional properties as compared with jack pine, because of more rapid nutrient cycling (Alban 1982; Bélanger and others 2004; Paré and Bergeron 1996). A secondary objective was to determine how the effect of tree species on soil nutrient dynamics may be influenced by site fertility. We hypothesized that tree species effects would be greater on nutrient-rich soil, because species with greater uptake would have the potential to cycle more nutrients.

MATERIALS AND METHODS

Study Area

The study was conducted in the Abitibi region of Quebec, Canada inside and in the vicinity of the Lake Duparquet Research and Teaching Forest. Climatological data are those from the La Sarre station (48° 46′ N; 79° 13′ W), located centrally relative to the study sites. Mean annual temperature and mean annual total precipitation are respectively 0.7°C and 889.8 mm; January daily minimum temperature is −24.6°C and July daily maximum is 23.5°C, freezing can occur throughout the summer (Environment Canada 2004). The region is part of the Great Clay Belt of Quebec and Ontario, a large physiographic region of lacustrine deposits left in place by pro-glacial lakes Barlow and Ojibway, at the time of their maximum expansion during the post-Wisconsinian era. The landscape is characterized by the presence of eskers that are often surrounded by reworked glacio-flu-

Table 1. Location, Upper Mineral Soil Texture, Age and Vegetation Characteristics of the 12 Studied Forest Stands

Site	Location	Sand (%)	Silt (%)	Clay (%)	Dominant sp.	Age (years)	Basal area ($m^2\ ha^{-1}$)		Density (# ha^{-1})		Mean DBH[a] (cm)
							Total	Dom.[a] (%)	Total	Dom.[a] (%)	
PBA C 1	48° 25′ N; 79° 23′ W	18.5	42.0	39.5	*P. banksiana*	77	ND	ND	ND	ND	ND
PBA C 2	48° 27′ N; 79° 26′ W	21.0	37.4	41.6	*P. banksiana*	77	43.6	89	1,700	76	19.1
PBA C 3	48° 26′ N; 79° 24′ W	20.3	35.9	43.8	*P. banksiana*	77	61.2	92	1,600	78	23.1
PBA S 4	48° 30′ N; 79° 08′ W	81.5	15.0	3.5	*P. banksiana*	56	34.8	100	2,800	100	12.1
PBA S 5	48° 30′ N; 79° 09′ W	79.9	18.4	1.8	*P. banksiana*	56	35.6	100	3,625	100	10.8
PBA S 6	48° 57′ N; 79° 10′ W	76.6	21.6	1.8	*P. banksiana*	89	30.9	100	1,850	100	14.1
PTR C 1	48° 25′ N; 79° 23′ W	25.0	31.5	43.5	*P. tremuloides*	77	ND	ND	ND	ND	ND
PTR C 2	48° 27′ N; 79° 26′ W	14.8	42.9	42.3	*P. tremuloides*	77	71.1	95	1,700	79	23.2
PTR C 3	48° 26′ N; 79° 15′ W	28.5	34.1	37.4	*P. tremuloides*	56	50.4	98	1,550	92	20.7
PTR S 4	48° 30′ N; 79° 08′ W	81.7	14.3	4.1	*P. tremuloides*	56	39.5	98	3,275	96	13.5
PTR S 5	48° 30′ N; 79° 07′ W	73.9	13.5	12.6	*P. tremuloides*	56	26.1	97	2,375	96	11.1
PTR S 6	48° 57′ N; 79° 10′ W	79.8	15.0	5.3	*P. tremuloides*	89	31.8	100	1,200	100	17.1

ND = not determined
[a]*Dominant species.*

vial material. The clays that sedimented in the deep waters of lake Barlow–Ojibway form a vast plain of fine-textured lacustrine clay deposit. Coarse-textured deposits are found in areas where the waters of the pro-glacial lakes were shallow in the proximity of eskers (see Rompré and Carrier 1997). Soils that evolved on lacustrine clays are classified as Grey Luvisols (Cryalfs), whereas those found on the coarse fluvio-glacial and glacio-lacustrine deposits are Humo-Ferric Podzols (Cryods) (Canada Soil Survey Committee 1978). The study area is at the southern limit of the boreal forest and forms part of the balsam fir [*Abies balsamea* (L.) Mill.]—paper birch (*Betula papyrifera* Marsh.) western bioclimatic domain (Thibault and Carrier 1983). The composition of the vegetation varies along a gradient of successional stages after fire, described by Bergeron and Dubuc (1989). On mesic sites, early successional stages after major disturbance are forests dominated by paper birch, aspen or jack pine. For further details on the vegetation of the study area, refer to De Grandpré and others (1993).

Sampling Site Descriptions

Three individual forest stands, dominated by each of the two species, jack pine and aspen, were selected on each of the two parent materials, coarse-textured deposits (with more than 70% sand) and fine-textured deposits (more than 70% silt plus clay). All plots were on mesic drainage conditions.

On sand, aspen sites appeared as small clumps within pine stands with no changes in topography or drainage, whereas on clay, large stands of both forest types were found. The presence of mixed stands of these two species in this area (Longpré and others 1994) further suggests that both species have the potential to colonize these site types following a major disturbance. The coarse-textured deposits, comprising loamy sand and sandy loam textural classes will be hereafter referred to as "sand", whereas the finer textured soil, including a range of textural classes (clay, silty clay loam, clay loam and silty clay) will be referred to as "clay". The major abiotic and overstory vegetation characteristics of the 12 individual forest stands are listed in Table 1. The post-fire age of the stands was determined from previous studies using dendrochronological methods (Bergeron and others 2004) and ranged from 56 to 89 years (Table 1). The diameter at breast height (DBH) of all trees greater than 5 cm in diameter was measured in two randomly selected 10 m × 10 m plots per site for sites on clay, and in four 10 m × 10 m plots per site for sites on sand.

Measurements of the vegetation on two sites (PBAC1 and PTRC1) could not be taken because these two stands had been clear-cut before the vegetation data could be collected, resulting in an unbalanced model for the vegetation, but not for the soil data. All stands had a homogenous overstory vegetation composition with the dominant

tree species, whether aspen or jack pine, representing a large percentage of the total basal area and density (Table 1). Stands growing on sand generally had a higher dominance than on clay, with the dominant tree species occupying more than 90% of the overstory layer. Forest stands on sand also had a higher number of smaller trees, resulting in a lower basal area and higher density than forest stands on clay. Variation in overstory between sites of the same type was mainly due to differences in the post-fire age of the stands.

Soil Sampling and Analyses

Analyses of texture and total nutrient content of the surface mineral soil (0–20 cm) were conducted to verify that there was no association between a certain stand type and intrinsic soil mineralogical composition for a given deposit.

The forest floor mass (FH mass) of each site was determined in a parallel in situ isotopic ^{15}N dilution experiment (Ste-Marie 2006) that required coring the FH layers in 32 individual locations in each site with a sharpened ABS cylinder (15.2 cm diameter, 25 cm length). Eight individual samples of the FH layers of the organic horizons were sampled by gently sweeping the litter layer until the material started adhering to the soil surface, and then cutting portions of forest floor with a knife until a composite sample of approximately 300 g was obtained. Within 24 h, samples were passed through a 1-cm sieve to remove roots and coarse woody debris, mixed by hand, and then kept at 4°C. In five of the eight locations where the FH was removed, the upper mineral soil (0–20 cm) was sampled with a 7-cm diameter corer. Mineral soil samples were air-dried prior to analysis and sieved at 2 mm.

Mineral soil particle size distribution was determined using the hydrometer method (Sheldrick and Wang 1993). The pH of all soil samples was determined in distilled water at a 1:4 soil:water volume ratio with a glass electrode. Total nitrogen (N_T) and organic carbon (C_{ORG}) content was analyzed on FH samples and mineral soil samples by direct combustion with an elemental analyzer (Carlo-Erba CNS 1500). Soil extractions of inorganic N (N_{INORG}) (2 M KCl, 1:15; dry soil:solution weight ratio) were done in situ immediately after sampling for all forest floor samples, whereas for mineral soil, air-dried samples were extracted. Concentrations of ammonium (NH_4^+) and nitrate (NO_3^-) were determined by flow injection analysis (Tecator FIAStar 5020), NH_4^+ being determined by the gas diffusion method and NO_3^- by the

cadmium reduction method. Nitrate (NO_3^-) represented a very small faction of N_{INORG} in both soil compartments, therefore only the sum of NH_4^+ and NO_3^- is presented. An index of P availability ($P_{BRAY II}$) of all soil samples was determined using the Bray II procedure (McKeague 1976). For total phosphorus (P_T) determination, samples were burnt at 470°C and the ashes were washed with 5N HCl and concentrated HNO_3 (Kalra and Maynard 1992). Measurements of P_T were performed by colorimetric determination (882 nm) on a Lachat Quikchem 8000 (Zellweger Analytics Inc., Lachat Instruments Division, Milwaukee, WI, USA). Exchangeable cations (Ca_{EXCH}, K_{EXCH}, Mg_{EXCH}, Al_{EXCH} and Fe_{EXCH}) were analyzed in all soil samples by atomic absorption spectrometry (Perkin-Elmer model PC5100, Perkin-Elmer, Norwalk, CT, USA) on 0.1 M $BaCl_2$ extracts following the method of Hendershot and others (1993). Exchangeable iron (Fe_{EXCH}) concentrations were below the detection limit for both soil layers. Total potassium (K_T), calcium (Ca_T) and magnesium (Mg_T) contents of the forest floor were determined with an atomic absorption spectrometer (Perkin Elmer 5100 PC) in atomic absorption mode for Ca_T and Mg_T, and in flame emission mode for K_T. For the mineral soil, the elemental composition was determined on 32-mm diameter fused beads prepared from a 1:5 soil–lithium tetraborate mixture using an automated X-ray fluorescence spectrometer system (Philips PW2440 2kW) with a Rhodium 60-kV end window X-ray tube.

Calculations

Bulk density of the mineral soil of the sand deposit was estimated from linear regression models developed from data on similar soils near Maniwaki, Quebec (Bélanger 2000) using the percent content of sand, silt and clay and the C_{ORG} concentration of the top mineral soil. On clay, the upper mineral soil bulk density was estimated using the equations of Saxton and others (1986), using the percent content of sand, silt and clay.

The biomass equations of Evert (1985) were used to estimate the biomass of four components in individual trees: stem wood, stem bark, foliage and branches. These equations had been validated on a number of trees in the same region (see Paré and Bergeron 1995) and required two variables, DBH and height. The DBH was measured on all individual trees (DBH > 5 cm). Tree height was estimated using local equations (unpublished results, ministère des Ressouces naturelles et de la Faune du Québec) using individual tree DBH (in cm),

stand mean DBH (MDBH in cm) and stand mean tree height (MH in m):

For aspen stands PTRC 2, PTRC 3, PTRS 4 and PTRS 5 ($n = 579$, $R^2 = 0.9462$),

$$H = -0.4618 + 0.3269\,DBH - 0.0022\,DBH2 \tag{1}$$
$$- 0.2137\,MDBH + 0.9639\,MH$$

For aspen stand PTRS 6 which had the most northern location ($n = 270$, $R^2 = 0.9584$),

$$H = -0.7011 + 0.3363\,DBH - 0.0016\,DBH2 \tag{2}$$
$$- 0.2542\,MDBH + 0.9873\,MH;$$

For jack pine stands PBAC 2, PBAC 3, PBAS 4 and PBAS 5 ($n = 392$, $R^2 = 0.9342$),

$$H = -0.7564 + 0.3522\,DBH - 0.0026\,DBH \tag{3}$$
$$- 0.2809\,MDBH + 1.0295\,MH;$$

For jack pine stand PBAS 6 which had the most northern location, a simplified equation was used because no equations using stand mean height were available, ($n = 147$; $R^2 = 0.5299$),

$$H = -0.3509 + 1.3494\,DBH - 0.0209\,DBH^2. \tag{4}$$

Calculated values were validated with the measurement of the height of three dominant trees on each site (D'Astous 2000). Nutrient concentrations for each biomass component were taken from Paré and others (2002).

Statistical Analyses

For all analyses, the site was considered to be the experimental unit, so that all the results of one forest site were pooled and mean values for each variable were used for statistical analysis ($n = 3$ per forest and soil type). For each variable, the normality of the distribution was tested with the Shapiro–Wilk W test and homoscedasticity was tested using Bartlett's procedure. When necessary, data were transformed to root square or natural logarithm to meet assumptions. All statistical analyses were performed on SAS (SAS Institute Inc. 2001). Two-way analyses of variance with complete balanced design were used to determine the contribution of the independent categoric variables tree species (SP), deposit type (SOIL) and the interaction between the two. The ''slice'' option was used to test for significant effects of the dominant tree species on a given deposit, as well as effects of deposit for a given tree species on soil properties.

RESULTS

Upper Mineral Soil

No significant differences where found between stand types for all mineral soil properties that were assessed. This included soil pH, C:N ratio, total as well as SOM and available forms of nutrient (N, P, K, Ca, Mg) concentrations as well as contents (Statistical tests not presented, see Table 2 for values). With the exception of exchangeable Mg, no stand type × soil type interactions were significant either. Soil type was identified as the major determinant of mineral soil properties (Table 2). There was no significant difference in mineral soil pH according to soil type or tree species (Table 2). Clay soils had a significantly lower C:N ratio and were significantly richer than sandy soils in all total and available nutrients, with the exception of the contents of SOM, P_T and P_{BRAYII} that were similar on both deposits as well as Ca_T but for jack pine only (Table 2).

Significant tree species effects that were responsible for interactions between tree species and soil type were found for C:N and Mg_{EXCH}, that were, respectively, lower and higher under aspen than jack pine but only on sand (Table 2). On sand, Ca_{EXCH} was also significantly higher under aspen than under jack pine (Table 2). However, for all other exchangeable as well as total nutrients, tree species was not a significant source of variation in the upper mineral soil nutritional properties suggesting that species colonization was independent of mineral soil properties.

Forest Floor (FH)

The dominant tree species had a significant effect on the FH mass (Table 3). The FH was generally thicker under aspen than jack pine but differences were significant only for the sandy soil (Table 4) as revealed by the significant interaction between the two factors (Table 3). Both soil type and tree species significantly affected forest floor pH and C:N ratio (Table 3). The FH material of aspen had significantly higher pH and lower C:N than that of jack pine on both soil types (Table 4), whereas the FH material on clay soils had significantly higher pH than on sand for both tree species (Table 4). The jack pine FH layer C:N ratio was significantly lower on clay than on sand but was similar on both soil types for aspen (Table 4).

Tree species generally explained a greater percentage of the variation than soil type in the amount of nutrients contained in the forest floor (Table 3). For almost all total and exchangeable

Table 2. Surface Mineral Soil pH, CN Ratio, Organic Matter and Element Content on an Area Basis

	Clay				Sand				Soil type effect	
	Jack pine		Aspen		Jack pine		Aspen		Jack pine	Aspen
pH	4.59 (0.15)	NS	4.74 (0.22)		4.37 (0.04)	NS	4.40 (0.1)		NS	NS
C:N	13.9 (0.4)	NS	14.6 (0.8)		28.8 (3.1)	*	21.1 (1.2)		***	*
Total (mg ha^{-1})										
SOM	74.3 (9.4)	NS	72.9 (1.1)		45.1 (7.5)	NS	61.4 (18.9)		NS	NS
N_T	3.79 (0.39)	NS	3.57 (0.15)		1.11 (0.10)	NS	2.03 (0.51)		***	*
P_T	3.83 (0.35)	NS	3.64 (0.94)		2.14 (0.64)	NS	1.95 (0.62)		NS	NS
K_T	87.3 (2.6)	NS	80.6 (10.9)		46.4 (1.5)	NS	49.1 (1.2)		***	**
Ca_T	36.4 (2.4)	NS	39.7 (9.7)		54.5 (0.6)	NS	60.7 (7.2)		NS	*
Mg_T	68.8 (2.4)	NS	62.9 (9.1)		15.4 (1.2)	NS	21.2 (5.3)		***	**
Available (kg ha^{-1})										
N_{INORG}	30.7 (3.4)	NS	29.6 (3.1)		15.5 (0.3)	NS	19.2 (3.9)		**	*
$P_{BRAY\ II}$	79.0 (4.6)	NS	81.6 (50.5)		31.6 (10.3)	NS	36.5(17.9)		NS	NS
K_{EXCH}	608 (214)	NS	512 (146)		8 (8)	NS	60 (34)		**	*
Ca_{EXCH}	3,368 (686)	NS	3,362 (1,143)		54 (34)	*	219 (70)		***	**
Mg_{EXCH}	552.8 (78.7)	NS	427.8 (133.7)		8.6 (1.2)	**	34.6 (10.6)		***	***

Values are means of three site means (SE). The level of significance of tree species effect on a given soil type (t-test) as well as differences between soil type are given.
NS = not significant
* Significant at P ≤ 0.05, ** significant at P ≤ 0.01, *** significant at P ≤ 0.001.

Table 3. Proportion of the Variation (R^2) in Forest Floor Soil Properties, Nutrient Content on an Area Basis and Nutrient Concentration Explained by the Factors Dominant Tree Species (SP), Soil Type (Soil) and their Interaction (X)

	Model	SP	Soil	X	Model	SP	Soil	X
FH mass	0.9152***	0.6350***	0.0260 NS	0.2543**				
pH	0.8594***	0.4928***	0.3630**	0.0035 NS				
C:N	0.8973***	0.4954***	0.3260***	0.0758*				
Total	**Area basis**				**Concentration**			
SOM	0.8868***	0.6815***	0.0092 NS	0.1962**	0.7158*	0.0678 NS	0.5810**	0.0670 NS
N_T	0.9135***	0.7515***	0.0613*	0.1006*	0.9290***	0.2629***	0.6642***	0.0019 NS
P_T	0.9466***	0.6286***	0.1910***	0.1269**	0.8298**	0.0532 NS	0.7642***	0.0123 NS
K_T	0.7254*	0.2881*	0.2784*	0.1589 NS	0.5995 NS	0.0122 NS	0.5617*	0.0256 NS
Ca_T	0.9353***	0.6201***	0.2782***	0.0370 NS	0.9223***	0.3574***	0.5588***	0.0061 NS
Mg_T	0.6214*	0.3653*	0.2168 NS	0.0393 NS	0.6407*	0.0758 NS	0.5579**	0.0069 NS
Available								
N_{INORG}	0.9480***	0.3979***	0.5293***	0.0207 NS	0.9542***	0.0669**	0.8040***	0.0834**
$P_{BRAY\ II}$	0.8619***	0.6418***	0.2140**	0.0060 NS	0.7184*	0.0819 NS	0.6134**	0.0231 NS
K_{EXCH}	0.9205***	0.8001***	0.0334 N.S.	0.0870*	0.5686 NS	0.2405 NS	0.2284 NS	0.0997 NS.
Ca_{EXCH}	0.9806***	0.5902***	0.3716***	0.0180*	0.9731***	0.4287***	0.5442***	0.0002 NS
Mg_{EXCH}	0.9626***	0.6217***	0.2721***	0.0689**	0.9706***	0.4082***	0.5125***	0.0498**

NS = not significant
* Significant at P ≤ 0.05, ** significant at P ≤ 0.01, *** significant at P ≤ 0.001.

nutrients, accumulation in aspen forest floor was significantly greater than in that of jack pine on both soil types (Table 4). On clay sites, total FH layer contents of N_T, P_T and Ca_T were significantly higher for aspen than for jack pine whereas on sand, differences in FH total nutrient content between stand types were significant for all tested elements (Table 4). For available nutrients, tree species effect was significant for all elements on both soil types (Table 4). In jack pine stands, soil

Table 4. Forest Floor (FH) Mass, pH and C:N Ratio, Organic Matter and Element Content on an Area Basis

	Clay			Sand			Soil type effect	
	Jack pine		Aspen	Jack pine		Aspen	Jack pine	Aspen
FH mass (mg ha^{-1})	42.6 (2.3)	NS	54.9 (4.2)	28.2 (2.5)	***	82.8 (6.7)	*	**
PH	5.09 (0.21)	**	6.15 (0.22)	4.34 (0.08)	**	5.23 (0.19)	*	**
C:N	31.2 (3.2)	*	24.8 (0.2)	47.4 (0.8)	***	28.9 (1.4)	***	NS
SOM (mg ha^{-1})	29.9 (2.2)	NS	38.5 (3.4)	17.7 (1.0)	***	46.3 (3.4)	*	NS
Total (kg ha^{-1})								
N_T	668 (27)	**	1,067 (96)	258 (16)	***	1,118 (112)	**	NS
P_T	49.6 (1.6)	**	67.5 (3.4)	17.2 (4.2)	***	64.2 (3.7)	***	NS
K_T	146 (43)	NS	195 (83)	37 (9)	**	137 (8)	**	NS
Ca_T	326 (51)	***	1,002 (109)	95 (29)	**	505 (12)	*	***
Mg_T	63.2 (19.9)	NS	93.5 (15.9)	13.7 (3.6)	*	73.6 (19.7)	NS	NS
Available (kg ha^{-1})								
N_{INORG}	0.43 (0.01)	***	0.82 (0.06)	0.13 (0.01)	**	0.38 (0.05)	***	***
$P_{BRAY\ II}$	7.67 (0.58)	**	13.61 (1.93)	3.25 (0.32)	**	10.45 (0.69)	*	NS
K_{EXCH}	28.8 (2.4)	**	53.7 (9.9)	17.7 (0.6)	***	58.2 (1.4)	**	NS
Ca_{EXCH}	190 (11)	***	908 (59)	30 (2)	***	293 (64)	***	***
Mg_{EXCH}	21.4 (1.3)	***	60.5 (6.8)	4.7 (0.7)	***	37.3 (7.2)	***	*

Values are means of three site means (SE). The levels of significance of the effect of dominant tree species on a given soil type and of the soil type for a given tree species (t-test) are given.
NS = not significant
* Significant at P ≤ 0.05, ** significant at P ≤ 0.01, *** significant at P ≤ 0.001.

type had a significant effect on forest floor nutrient content, with clay soils showing greater accumulation of nutrients in this layer than on sandy soils (Table 4). In aspen stands, the amount of nutrients contained in the forest floor was generally similar on both deposits, except for Ca_T, N_{INORG}, Ca_{EXCH} and Mg_{EXCH} pools that were higher on clay than on sand (Table 4).

The effect of soil type relative to tree species became stronger when considering nutrient concentrations rather than nutrient contents and generally explained a greater percentage of the variation than tree species (Table 3). The dominant tree species actually remained a significant source of variation only in the concentrations of N_T, Ca_T, N_{INORG} (on clay only), K_{EXCH} (on clay only), Ca_{EXCH} and Mg_{EXCH} (Tables 3, 5). However, for all other nutrients, the concentrations where higher in aspen forest soils but these differences were not significant (Table 5).

The significant interaction between tree species and soil type for SOM, N_T and P_T as well as for K_{EXCH}, Ca_{EXCH} and Mg_{EXCH} contents of the forest floor (Table 3) is due to a greater tree species effect on sand than on clay (Table 4). The higher FH mass in aspen forests growing on sand resulted in a higher SOM, N_T and K_{EXCH} content of aspen FH on the poor sandy soil compared with the rich clay soil (Table 4). Considering nutrient concentrations of

the FH layer, tree species effects seemed more important on clay than on sand for N_{INORG}, K_{EXCH} and Mg_{EXCH} (Table 5), and interactions were significant for N_{INORG} and Mg_{EXCH} only (Table 2).

Organic Matter and Nutrient Pools

The distribution of organic matter in the four different stand types is illustrated in Figure 1A. Most of the organic matter is immobilized in the woody biomass of trees (stems, bark and branches) with clay sites having greater standing biomass than sandy sites. Tree standing biomass was larger for aspen than for jack pine on clay, whereas on sand the standing biomass of jack pine was slightly higher than that of aspen. The amount of soil organic matter (FH and upper mineral soil) was lower in jack pine on sand than in any other stand type, which all had relatively similar values. The foliage and the forest floor are larger organic matter pools under aspen than jack pine, especially on sand.

Nitrogen distribution among soil and tree compartments is presented in Figure 1B. The soil represented the major N reservoir containing more than 80% of all assessed N pools. Clay soils contained much more N_T and tree species had a much greater impact on stand N_T content on sandy soils than on clay soils. The forest floor and the aboveground biomass of aspen, especially the foliage,

Table 5.   Forest Floor (FH) Organic Matter and Element Concentrations

	Clay			Sand		
	Jack pine		Aspen	Jack pine		Aspen
Total (g kg^{-1})						
SOM	701 (20)	NS	700 (9)	633 (21)	NS	564 (40)
N_T	15.8 (1.2)	**	19.4 (0.3)	9.2 (0.4)	**	13.5 (0.6)
P_T	1.17 (0.05)	NS	1.24 (0.08)	0.59 (0.09)	NS	0.79 (0.11)
K_T	3.37 (0.86)	NS	3.45 (1.31)	1.30 (0.21)	NS	1.67 (0.08)
Ca_T	7.58 (0.87)	**	18.16 (0.66)	3.25 (0.71)	**	6.18 (0.50)
Mg_T	1.45 (0.40)	NS	1.68 (0.18)	0.47 (0.08)	NS	0.90 (0.23)
Available (mg kg^{-1})						
N_{INORG}	10.1 (0.9)	***	14.9 (0.2)	4.9 (0.8)	NS	4.6 (0.5)
$P_{BRAY II}$	181 (15)	NS	257 (59)	115 (6)	NS	128 (15)
K_{EXCH}	708 (43)	*	977 (151)	665 (21)	NS	709 (19)
Ca_{EXCH}	4,553 (537)	***	16,192 (857)	1,130 (73)	***	3,949 (682)
Mg_{EXCH}	503 (15)	***	1,068 (52)	180 (16)	**	453 (56)

Values are the means of three site means (SE). The degree of significance of the effect of dominant tree species on a given soil type and of the soil type for a given tree species (t-test) are given.
NS = not significant
* Significant at P $\leq$ 0.05, ** significant at P $\leq$ 0.01, *** significant at P $\leq$ 0.001.

contained more N than jack pine. On sand, the mineral soil of aspen contained more N_T than that of jack pine. Aspen stands on sand differed from other stand types by having a higher percentage of N_T in the forest floor (32% of measured ecosystem N compared with 15–20% for other stand types). Jack pine on sand had very low N_T content compared with other stand types.

The contents of P, K, Ca and Mg of the different pools is illustrated in Figure 1C–F. Available, rather than total, nutrient content of both soil layers are presented. For P, K, Mg and Ca, major differences in the content of the soil–tree systems between the two deposits lie in the mineral soil, which represented a much greater pool on clay than on sand and in the case of Ca and Mg was the main ecosystem reservoir. On sand, the mineral soil contained extremely small amounts of exchangeable K, Ca and Mg, especially for jack pine stands. The P, K, Ca and Mg contents of the soil–tree system are much greater on clay than on sand, and generally greater in aspen than in jack pine. On both soil types, aspen accumulated more nutrients in its biomass than jack pine and greater amounts of P, K, Ca and Mg were found in foliage and forest floor in aspen than in jack pine stands. On clay, aspen upper mineral soil appeared to be depleted in available base cations (K, Ca and Mg) as compared with jack pine upper mineral soil whereas the opposite was observed on sand, with aspen mineral soil containing more available nutrients than that of jack pine.

DISCUSSION

Because there are strong ties between soil types and forest composition in natural ecosystems, common garden experiments are useful in determining the influence of forest composition on soils. Problems with common gardens are that they cannot include the entire complex biota of a natural forest. Also the time between the conception of the design and the production of results can be longer than a researcher's career. In the present study we tried to ensure that the soil conditions for a given soil type did not vary with tree species. We also used a replicated design to maximize the confidence level of our results even if replication at the site level can limit the significance of statistical tests because of the inherent intersite variability combined with the small number of studied sites per forest type ($n = 3$) (Augusto and others 2002; Binkley and Menyailo 2005). The soil conditions including drainage, the upper mineral soil texture and its total element content did not differ between stands dominated by the two different tree species (Tables 1, 2) suggesting that stand type was independent of initial site fertility. Given the proximity of their locations, sites can be assumed not to be subject to important differences in climate conditions and atmospheric deposition. Forest stand history can significantly affect humus quality and nutrient availability (Muys 1995), but these stands have never been subjected to commercial management practices such as planting, fertilization or intensive vegeta-
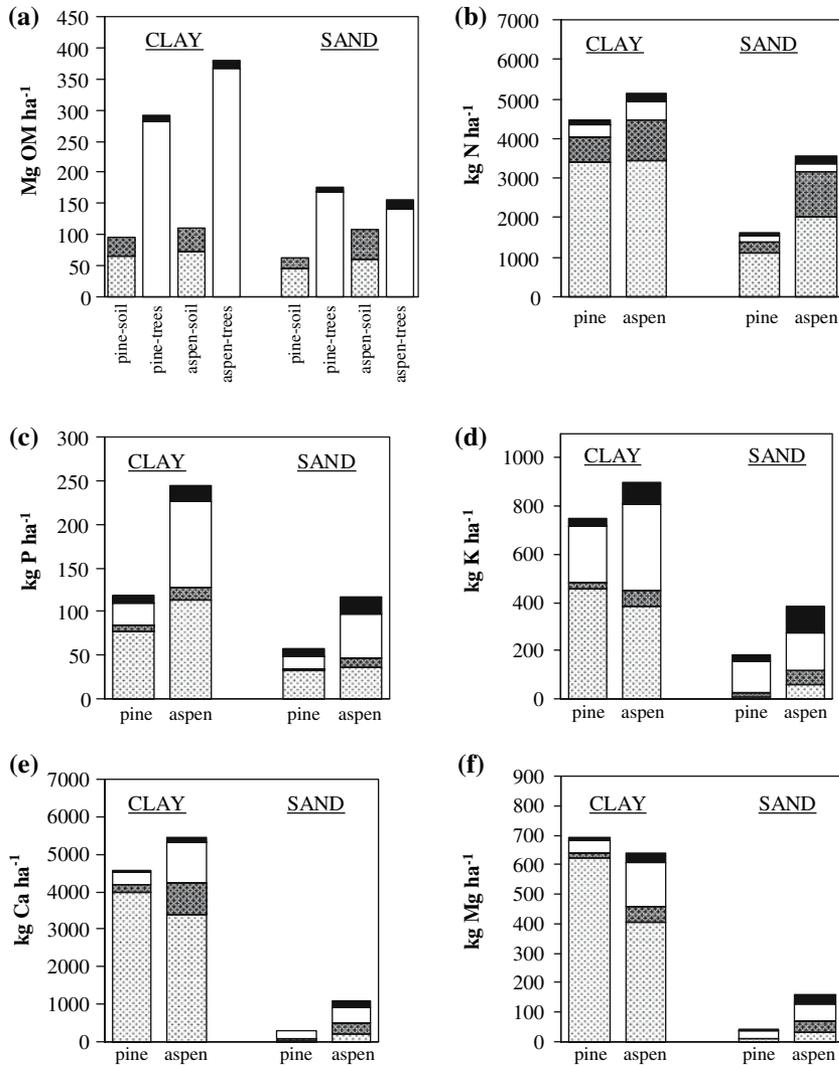
Figure 1. Organic matter and nutrient content of the soil and trees of the dominant species. Values are means of two sites for clay sites and of three sites for sites on sand. Soil Ca, K, Mg and P content are in available forms [*light dotted bar* upper 20 cm mineral soil, *dark dotted bar* FH layers, *open bar* woody biomass (stem, branches and bark), *filled bar* foliage].

tion harvesting. All of these conditions indicate that variations in the forest floor properties, as well as in the exchangeable cation contents of the mineral soil, most likely result from differences in stand vegetation composition. Furthermore, the charcoal layer at each site was at the bottom of the organic soil horizon, suggesting that the humus layer was burned during the last fire episode and that most of the humus, if not all of it, originates from the present stands.

The total amounts of OM and nutrients present in the available form in the soil and in the vegetation are much higher for aspen than for jack pine, irrespectively of deposit type, with the exception of Mg on clay (Figure 1). The nutrient content in these pools is greater on clay soil than on sand (Figure 1). However, the proportional increase in the nutrient content of these pools from jack pine to aspen ranged from 100 to 200% on sand, whereas they were less than 30% on clay, except

for P. For a given soil type, the differences in tree aboveground biomass between the two stand types were rather small (Figure 1), indicating that the difference in vegetation nutrient content is mainly caused by differences in nutrient concentrations between the two species (Alban 1982; Gower and others 2000). On the contrary, the differences in total and available nutrient contents in the forest floor of the two species were mainly due to differences in the thickness of this soil layer, specifically on sandy deposits where the FH layer mass was roughly three times greater in aspen than in jack pine stands, whereas nutrient concentrations were only slightly different. Such important differences in FH mass have also been reported between species within a forest stand (Binkley and Giardina 1998; Finzi and others 1998a). We can only speculate on the reasons for such important differences in FH mass because no direct measurements of litterfall and decomposition rates were made. Esti-

mates of foliage biomass and nutrient content were much higher in aspen stands than in jack pine stands (Figure 1). Furthermore, on sand, foliage represented a greater proportion of total aspen biomass (9%) than in other stand types (3–4%) indicating a greater relative production of ephemeral tissues. A greater production of root biomass (Steele and others 1997) and of litterfall (Gower and others 2000, 1997) was also observed in a comparison of jack pine and aspen stands of the BOREAS project, although in these studies, soil type varied with species composition. Considering that annual litterfall is approximately equal to total foliage biomass in aspen and to 33% of jack pine foliage (Reich and others 1998), the difference in humus buildup between the two species on sand is equivalent to the difference of cumulative litterfall for a period of less than 4 years. Considering also the contribution of root litter and that produced by understory plants, which are more abundant in aspen than in jack pine on the sandy deposit (D'Astous 2000), the buildup of a thick humus in aspen stands on sandy soil over a 60 year period is feasible. Nevertheless as pointed out by Greene and Johnson (1999) there is very little forest composition change following fire in stands of aspen, jack pine or black spruce. It is therefore likely that the tree species effect had been in effect for a time period extending beyond the current stand age. Besides a potential important difference in litter production between species, the literature reports a tendency for high-quality litter to produce more humus, presumably because litter's high N concentrations slow late-stage organic matter decay (see review by Prescott 2005). These results do not however explain why the FH mass was not as contrasted on clay between the two stand types as it was on sand. Many studies have shown that total phenolics and tannin concentrations are inversely related to nutrient availability within a species (Kraus and others 2004; Northup and others 1998), including aspen (Bryant and others 1987) and that these secondary compounds have an adverse effect on decomposition (see Kraus and others 2004; Cotrufo and others 1995). Raulund-Rasmussen and Vejre (1995) also found that humus accumulation under a given tree species was negatively related to site fertility. Also the abundant understory vegetation in both stand types on clay soils could have alleviated tree species effect, whereas the understory in jack pine stands on sand was very sparse.

Although tree species effect was mainly observed for the forest floor layer, the higher amounts of nutrients immobilized in aspen biomass and forest floor did not translate into lower fertility of the top portion of the mineral soil, but actually led to an increase in mineral soil exchangeable Ca and Mg on sandy soils. These results, which are consistent with Bélanger and others (2004), may be explained by two mechanisms that can both be effective: the results of greater input of nutrients (increased mineral weathering or interception of atmospheric deposition, N fixation) or the results of better nutrient retention in aspen ecosystems (Cole 1995). The more acidic conditions found in the surface soil layers of jack pine, were associated with lower exchangeable cations concentrations and lower CEC, which could lead to a poorer retention of base cations. The thicker forest floor with greater cation exchange capacity together with the greater evapotranspiration of aspen stands compared with jack pine stands (Blanken and others 2001; Kimball and others 1997) may also be responsible for better nutrient retention through reduced leaching in aspen stands. In the case of N, the presence of N fixing species (*Alnus* spp.) in all three aspen stands on sand as opposed to jack pine stands (C. Ste-Marie, personal observation) could be responsible for higher N_T.

Results of this study suggest that whether aspen or jack pine re-colonize a disturbed site, it will lead to divergent soil conditions. There was a greater content of almost all nutrients in the FH of aspen than of jack pine on both soil types, as a result of both greater FH mass and of higher nutrient concentrations. Aspen forest floor also had significantly higher pH and lower C:N ratio than jack pine forest floor, two properties generally considered as good indicators of soil quality and they influence nutrient availability and soil organic matter mineralization (Thomas and Prescott 2000; Howard and others 1998; Kelly and others 1998).

A greater species effect on soil in the poorer site is contrary to what was observed by Finzi and others (1998b) and Raulund-Rasmussen and Vejre (1995). They suggested that richer soils may have a greater potential for species to express their differences in nutrient cycles. Our results showed that this pattern is not universal as we observed a greater contrast in soil properties between species on poor soil. This effect may be caused by understory community effects, which were strikingly different on sandy pine sites compared with all the other ones. Binkley and Menyailo (2005) point out that tree species effects on soil properties might be reduced or increased by the influence of canopy trees on understory vegetation. Prescott and others (2000) suspected that differences in the composition of the understory vegetation, and particularly the amount of the ericaceous shrub salal was

masking tree species effect on net N mineralization. In the present study, jack pine understory on sand was strongly dominated by mosses [mainly *Pleurozium schreberi* (Brid.) Mitt.] and ericaceous shrubs (mainly *Kalmia angustifolia* L. and *Vaccinium angustifolium* Ait.) (D'Astous 2000), both of which are known for their low nutrient requirements and effective uptake and sequestration of nutrients(Bending and Read 1996; Cornelissen and others 2001; Jalal and others 1982; Read and others 2004).

In conclusion, we found that species had a significant effect on soil. Aspen was associated with a richer humus layer and the greater immobilization of nutrients in tree biomass and in the humus layer did not appear to create a decline in the surface mineral soil stocks of available elements. A stronger species effect was found on poor coarse-textured soils. The composition of plant understory, which was strikingly different between stand types on sand but not on clay, could play a role in the modulation of species effect by soil type. Finally, because differences between stand types in the nutrient content of the forest floor were more dependant on forest floor mass than on forest floor nutrient concentrations, mechanisms for organic matter buildup appear to be key to explaining differences in soil properties between stand and soil types.

ACKNOWLEDGEMENTS

REFERENCES

Alban DH. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci Soc Am J 46:853–61.

Augusto L, Ranger J, Binkley D, Rothe A. 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann For Sci 59:233–53.

Bélanger N. 2000. Investigating the long-term influence of atmospheric acid deposition and forest disturbance on soil chemistry and cation nutrient supplies in a forested ecosystem of southern Quebec. Ph.D. thesis, McGill University, Montréal, Québec.

Bélanger N, Paré D, Bouchard M, Daoust G. 2004. Is the use of trees with superior growth a threat to soil nutrient availability? A case study with Norway spruce. Can J For Res 34:560–72.

Bending GD, Read DJ. 1996. Effects of the soluble polyphenol tannic acid on the activities of ericoid and ectomycorrhizal fungi. Soil Biol Biochem 28:1595–602.

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

Bergeron Y, Gauthier S, Flannigan M, Kafka V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–32.

Binkley D, Giardina C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106.

Binkley D, Menyailo O. 2005. Gaining insights on the effects of tree species on soils. In: Binkley D, Menyailo O, Eds. Tree species effects on soils: implications for global change. Dordrecht: NATO Science Series, Kluwer. pp 1–16.

Blanken PD, Black TA, Neumann HH, den Hartog G, Yang PC, Nesic Z, Lee X. 2001. The seasonal water and energy exchange above and within a boreal aspen forest. J Hydrol 245:118–36.

Bryant JP, Clausen TP, Reichardt PB, McCarthy MC, Werner RA. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortix (*Choristoneura conflictana* (Walker)). Oecologia 73:513–7.

Canada Soil Survey Committee. 1978. The Canadian system of soil classification. Ottawa: Supply and Services Canada.

Chapin FS. 1980. The mineral nutrition of wild plants. Ann Rev Ecol Syst 11:233–60.

Cole DW. 1995. Soil nutrient supply in natural and managed forests. Plant Soil 168–169:43–53.

Cornelissen J, Aerts R, Cerabolini B, Werger M, van der Heijden M. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. Oecologia 129:611–9.

Cotrufo MF, Ineson P, Roberts JD. 1995. Decomposition of birch leaf litters with varying C-to-N ratios. Soil Biol Biochem 27:1219–21.

D'Astous M-O. 2000. Caractérisation de la transmission de la lumière en forêt boréale: effets de la richesse, la composition et la structure du peuplement forestier. M.Sc. thesis, Université du Québec à Montréal, Montréal, Québec.

De Grandpré L, Gagnon D, Bergeron Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J Veg Sci 4:803–10.

Environment Canada. 2004. Canadian climate normals or averages 1971–2000. (http://www.climate.weatheroffice.ec.gc.ca/climate_normals/results_f.html). (Accessed 9 May 2006).

Evert F. 1985. Systems of equations for estimating oven-dry mass of 18 Canadian tree species. Canadian Forestry Service, Petawawa National Forestry Institute, Chalk River, Ontario, Information Report PI-X-59.

Finzi AC, Van Breemen N, Canham CD. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecol Appl 8:440–6.

Finzi AC, Canham CD, Van Breemen N. 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. Ecol Appl 8:447–54.

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

Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele SJ, Stow TK. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J Geophys Res 102:29029–42.

Gower ST, Hunter A, Campbell J, Vogel J, Veldhuis H, Harden J, Trumbore S, Norman JM, Kucharik CJ. 2000. Nutrient dynamics of the southern and northern BOREAS boreal forests. Ecoscience 7:481–90.

Greene DF, Johnson EA. 1999. Modelling recruitment of Populus tremuloides, Pinus banksiana, and Picea mariana following fire in the mixedwood boreal forest. Can J For Res 29:462–73.

Hendershot WH, Lalande H, Duquette M. 1993. Ion exchange and exchangeable cations. In: Carter MR, Eds. Soil sampling and methods of analysis. Boca Raton: Canadian Society of Soil Science, Lewis Publishers. pp 167–76.

Howard PJA, Howard DM, Lowe LE. 1998. Effects of tree species and soil physico-chemical conditions on the nature of soil organic matter. Soil Biol Biochem 30:285–97.

Jalal MAF, Read DJ, Haslam E. 1982. Phenolic composition and its seasonal variation in *Calluna vulgaris.*. Phytochemistry 21:1397–1401.

Kalra YP, Maynard DG. 1992. Méthodes d'analyse des sols forestiers et des tissus végétaux. Forêts Canada, Centre de foresterie du Nord, Edmonton, Alberta. Information Report NOR-X-319-F.

Kelly EF, Chadwick OA, Hilinski TE. 1998. The effect of plants on mineral weathering. Biogeochemistry 42:21–53.

Kimball JS, Thornton PE, White MA, Running SW. 1997. Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region. Tree Physiol 17:589–99.

Kraus TEC, Zasoski RJ, Dahlgren RA. 2004. Fertility and pH effects on polyphenol and condensed tannin concentrations in foliage and roots. Plant Soil 262:95–109.

Longpré M-H, Bergeron Y, Paré D, Béland M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can J For Res 24:1846–53.

McKeague JA. 1976. Manual of soil sampling and methods of analysis. Canadian Society for Soil Science, Ottawa, Ontario.

Muys B. 1995. The influence of tree species on humus quality and nutrient availability on a regional scale (Flanders, Belgium). In: Nilsson LO, Hüttl RF, Johansson UT, Eds. Nutrient uptake and cycling in forest ecosystems. Dordrecht: Kluwer. pp 649–60.

Northup RR, Yu Z, Dahlgren RA, Vogt KA. 1995. Polyphenol control of nitrogen release from pine litter. Nature 377:227–9.

Northup RR, Dahlgren RA, McColl JG. 1998. Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback?. Biogeochemistry 42:189–220.

Paré D, Bergeron Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J Ecol 83:1001–7.

Paré D, Bergeron Y. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can J For Res 26:1022–31.

Paré D, Rochon P, Brais S. 2002. Assessing the geochemical balance of managed boreal forests. Ecol Indic 1:293–311.

Prescott CE. 2005. Decomposition and mineralization of nutrients from litter and humus. In: BassiriRad H, Eds. Nutrient acquisition by plants an ecological perspective. Ecological studies, vol. 181. Berlin: Springer. pp 15–41.

Prescott CE, Vesterdal L, Pratt J, Venner KH, de Montigny LM, Trofymow JA. 2000. Nutrient concentrations and nitrogen mineralization in forest floors of single species conifer plantations in coastal British Columbia. Can J For Res 30:1341–52.

Raulund-Rasmussen K, Vejre H. 1995. Effect of tree species and soil properties on nutrient immobilization in the forest floor. Plant Soil 168–169:345–52.

Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can J Bot 82:1243–63.

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct Ecol 12:395–405.

Rompré M, Carrier D. 1997. Étude pédologique des sols défrichés de l'Abitibi-Témiscamingue. Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec. IRDA, Québec, Canada.

SAS Institute Inc. 2001. JMP start statistics—a guide to statistics and data analysis using JMP and JMP IN software. Second edition. Pacific Grove: Duxbury-Thomson Learning.

Saxton KE, Rawls WJ, Romberger JS, Papendick RI. 1986. Estimating generalized soil-water characteristics from texture. Soil Sci Soc Am J 50:1031–6.

Sheldrick BH, Wang C. 1993. Particle size distribution. In: Carter MR, Eds. Soil sampling and methods of analysis. Boca Raton: Canadian Society of Soil Science, Lewis Publishers. pp 499–511.

Steele SJ, Gower ST, Vogel JG, Norman JM. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol 17:577–87.

Ste-Marie C. 2006. Relations entre le couvert forestier et les sols dans la détermination des flux d'azote et autres macronutriments. Ph.D. thesis, Université du Québec à Montréal, Montreal, Quebec.

Thibault M, Carrier L. 1983. Les régions écologiques du Québec méridional. Service de recherche forestière, ministère de l'Énergie et des Ressources, Québec.

Thomas KD, Prescott CE. 2000. Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. Can J For Res 30:1698–706.