How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions

Jérôme Laganière, David Paré, and Robert L. Bradley

Abstract: Litter quality is often considered the main driver of decomposition rate. The objective of this study was to investigate the relative contribution of two other tree-driven mechanisms, litter mixing and forest floor conditions, to foliar litter decomposition and nutrient dynamics for trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* (Mill.) BSP) using a microcosm approach. Results based on mixed linear models show that the greater influence over these processes was obtained through litter quality followed by forest floor conditions and litter mixing. Specifically, the results indicate that significantly more C and nutrients were mineralized (*i*) from aspen than from spruce litter, (*ii*) from spruce litter in mixture with aspen litter than from spruce litter applied singly, and (*iii*) from litter incubated on forest floor from the aspen stand rather than from the spruce stand, except for nutrients in the spruce litter. Collectively, our results show that the litter and forest floor material from aspen both favour decomposition and nutrient mineralization processes. Hence, we provide evidence that the effect of tree species on litter decomposition may not only be caused by the properties of its litter but also, indirectly, by the specific conditions and the decomposer community that tree species develop in their forest floor.

Résumé : La qualité de la litière est souvent considérée comme le facteur déterminant de la décomposition. L'objectif de cette étude était d'étudier la contribution relative de deux autres mécanismes contrôlés par l'arbre, soit le mélange de litière et les propriétés de la couverture morte, à la décomposition et à la dynamique des nutriments de la litière foliaire du peuplier faux-tremble (*Populus tremuloides* Michx.) et de l'épinette noire (*Picea mariana* (Mill.) BSP) en utilisant une approche en microcosme. Les résultats basés sur des modèles mixtes linéaires montrent que l'influence la plus grande sur ces processus a été obtenue via la qualité de la litière, suivie des propriétés de la couverture morte et de mélange de litière. Spécifiquement, les résultats indiquent que significativement plus de C et de nutriments ont été minéralisés (*i*) dans la litière de peuplier que dans la litière d'épinette, (*ii*) dans la litière d'épinette en mélange avec la litière de peuplier que dans la litière d'épinette seule et (*iii*) dans les litières incubées sur la couverture morte provenant du peuplement de peuplier que sur celle provenant du peuplement d'épinette, excepté pour les nutriments de la litière d'épinette. Collectivement, nos résultats montrent que la litière et la couverture morte de peuplier favorisent les processus de décomposition et de minéralisation des nutriments. Ainsi, cette étude prouve que l'influence des essences forestières sur la décomposition de la litière est non seulement reliée aux propriétés de leur litière, mais aussi, indirectement, aux conditions spécifiques et à la communauté de décomposeurs que les essences forestières développent dans leur couverture morte.

Introduction

Each tree species possesses unique functional traits that may cause distinctive effects on ecosystem functions and processes. How tree species impact soil organic matter decomposition and hence nutrient cycling has been extensively studied with the use of litter decomposition studies (reviewed in Prescott et al. 2000*a*). It is often assumed that litter chemical characteristics such as nutrient content or the presence of diverse recalcitrant compounds control the rate of litter decomposition. In the early stages of decomposition, it is generally believed that variations in decomposition rates among tree species are positively related to initial N concentrations and negatively related to initial lignin concentrations (Taylor et al. 1989). Some studies also provided evidence that litter decomposition rates were dependent on the concentration of other nutrients such as Mn or Ca (Berg 2000; Hobbie et al. 2006). Prediction of litter decomposition with litter chemistry and local soil climate has reached a certain level of confidence (Trofymow et al. 2002).

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J. Laganière.[1] Département de biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada; Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S, P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.
D. Paré. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S, P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.
R.L. Bradley. Département de biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada.

[1]Corresponding author (e-mail: jlaganie@nrcan.gc.ca).

While litter properties are often considered as the main driver of the decomposition process, tree species may affect this process by other mechanisms. It has been observed that the rates of decomposition may be altered by mixing two or more litter species together, such that certain species of litter occurring in mixtures may interact and decompose faster (or slower) than what is expected from the individual decomposition rate of each litter species (Gartner and Cardon 2004). Thus, tree species may affect decomposition rates through the reactivity of their litter to litter mixing. Potential explanations for litter mixing effects on C and nutrient dynamics include fungi-driven nutrient transfer among litter types (from nutrient-rich to nutrient-poor materials), inhibition or stimulation of microflora by specific litter compounds (e.g., phenolics), and positive feedback of soil invertebrates (e.g., activity, abundance, diversity) due to greater microhabitat and resource diversity (Hättenschwiler et al. 2005).

Finally, tree species could also influence the decomposition process through a third factor, the development of a distinct forest floor layer (LFH or O horizon) with its own chemical and biological characteristics. There are several reasons to believe that the underlying forest floor exerts some influence over this process. For example, forest floor from different stand types will differ in terms of nutrient content, pH, and moisture retention (Vance and Chapin 2001), all of which could affect decomposition rates and nutrient dynamics at the forest floor–litter interface. Similarly, the decomposer food web, composed of heterotrophic bacteria, fungi, and soil fauna, will vary beneath different tree species (Lamarche et al. 2004; Laganière et al. 2009), which should in turn affect the rate at which various litter fractions are mineralized.

While tree species effects on decomposition and nutrient dynamics through their litter chemistry have received considerable attention from a large number of laboratory and field studies (Trofymow et al. 2002; Salamanca et al. 2003), literature on tree species influence through litter mixing and through their forest floor conditions is more limited (Albers et al. 2004; Jonard et al. 2008). Furthermore, few studies have attempted to describe and isolate, within a single study, these three intrinsic components by which tree species may alter decomposition rates and nutrient dynamics.

In boreal ecosystems, where tree growth is slow and often limited by nutrient availability, the rate at which nutrients are released by litter decomposition is of particular importance for forest productivity. Thus, improving the knowledge on the mechanisms by which tree species may alter this process is valuable. Trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* (Mill.) BSP) are widespread throughout the boreal forest of Canada and are found naturally either in pure stands or in mixtures. We used these two tree species to explore species effects on early-stage leaf litter decomposition and nutrient dynamics under controlled conditions. More specifically, our objective was to determine the relative contribution of the three following components on litter decomposition rates and nutrient dynamics: (*i*) litter quality, (*ii*) litter mixing, and (*iii*) the forest floor layer with its own chemical and biological characteristics.

Materials and methods

Site description

Two stands of approximately 1 ha in size (approximately 300 m apart), the first predominantly composed of black spruce and the other of trembling aspen, were selected for forest floor and leaf litter collection near the town of Villebois (49°03′N, 79°08′W) in the northern part of the Abitibi region, Quebec, Canada. This area is part of the black spruce – feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Quebec (Grondin 1996). The parent material is lacustrine clay left by the proglacial Lakes Barlow and Ojibway at the time of their maximum expanse in the Wisconsinian glacial age (Vincent and Hardy 1977). Soils are generally classified as Grey Luvisols (Soil Classification Working Group 1998).

Both stands originated from the same wildfire that took place in 1926 according to dendrometric measurements (Légaré et al. 2005*b*). At the time of sampling, each stand had produced a distinct organic layer (i.e., forest floor) that mainly reflects the litter quality of the dominant vegetation, with several other site variables being similar (climate, parent material, drainage, topography, etc.). Thus, the spruce stand had produced a lignin-rich acidic litter, which had generated a thick layered forest floor (i.e., a mor humus) (Soil Classification Working Group 1998) and a soil faunal community based on fungivorous microarthropods (Flanagan and Van Cleve 1983; Wardle 2002; Lindo and Visser 2003). On the other hand, the aspen stand had produced a relatively nutrient-rich leaf litter, which had generated a thinner organic layer qualified as "Lamimoder" (Fons et al. 1998) that harbours earthworm communities (González et al. 2003). The spruce understory included mainly Labrador tea (*Ledum groenlandicum* Oeder) and *Vaccinium* spp. *Pleurozium schreberi* was the dominant ground cover and an important input of organic matter to the soil (DeLuca et al. 2002). The aspen understory included herbs and isolated clumps of speckled alder (*Alnus rugosa* (Du Roi) Spreng.). The site characteristics of each stand type are shown in Table 1.

Forest floor samples

In August 2004, forest floor (LFH or O horizon) was collected at 12 random sampling locations in each stand. The samples were sieved (6.5 mm mesh) and gently mixed to yield a single composite forest floor sample (approximately 60 L) from each stand. Major invertebrate taxa were included in the forest floor samples, but large surface-dwelling predators such as spiders, carabid beetles, and staphylinid beetles were too big to be present in such small units. The two forest floor samples were stored in coolers under ice packs and returned to the Laboratoire d'écologie des sols (Université de Sherbrooke) where they were stored at 4 °C until the beginning of the experiment. The initial chemical characteristics and faunal abundances of both forest floor samples are reported in Table 2.

Litter samples

Senesced leaf litters from each stand were collected during the litterfall season in October of the same year. Freshly fallen aspen leaves were collected from the forest floor by

Table 1. Site characteristics of the adjacent stands located in the northern part of the Abitibi region, Quebec, Canada.

	Stand type	
Site characteristics	Trembling aspen	Black spruce
Topography	Flat	Flat
Stand origin	Wildfire (1926)	Wildfire (1926)
Climate	Boreal	Boreal
Parent material	Lacustrine clay	Lacustrine clay
Soil type	Grey Luvisol	Grey Luvisol
Soil texture	Clayey	Clayey
Soil C (%)	0.23±0.03	0.28±0.02
Soil N (%)	0.013±0.001	0.015±0.003
Soil C:N ratio	17.6±1.8	19.1±3.3

Note: Each value for soil C and N is the mean of five subsamples ± SD taken at a depth of 0.75 m (C horizon).

Table 2. Initial chemical properties and faunal abundance of forest floor from both stand types.

	Forest floor	
	Trembling aspen	Black spruce
Chemical properties		
C (%)	23.44±0.75	45.90±0.55
N (%)	1.20±0.04	0.95±0.03
C:N ratio	19.62±0.80	48.7±1.52
$P_{extractable}$ (μg/g)	13.97±1.94	31.49±5.54
CEC (cmol(+)/kg)	51.4±2.84	42.29±11.81
pH (H_2O)	5.01±0.03	3.65±0.02
pH ($CaCl_2$)	4.72±0.02	3.11±0.01
Faunal abundance (no./kg forest floor dry mass)		
Oribatida	2022±588	2871±910
Gamasida	64±59	243±198
Acari larva	0	0
Collembola	195±101	408±181
Lubricus rubellus	0	0

Note: Each value is the mean of five subsamples ± SD. Invertebrates were extracted by placing fresh soil subsamples (approximately 330 cm^3) into modified Berlese–Tullgren funnels until completely dried. Acari larva and *L. rubellus* failed to be detected by the extraction method, probably because they were present in inactive forms (e.g., egg or cocoon).

hand whereas spruce needles were collected by striking trees with a bludgeon and collecting the fallen needles in a plastic sheet placed over the forest floor. Litter materials were transported to the laboratory and further sorted by hand to remove impurities. Leaves and needles that appeared to be colonized by fungi or invertebrates were discarded. Both litter types were defaunated by drying for 24 h at +80 °C, freezing for 24 h at –80 °C, and redrying for 24 h at +80 °C (Bardgett et al. 1998). The initial chemical quality of both litter species is reported in Table 3.

Litter incubation

To test the effect of litter quality, we used polyvinyl chloride litter baskets (9 cm diameter) equipped with a 1.4 mm mesh size screen at the bottom to retain the litter in the basket and allow upward colonization of the litter by soil organisms (i.e., bacteria, fungi, small invertebrates). Since there was no screen on top of the litter baskets, macroinvertebrates such as earthworms were able to colonize the litter from above. A 4 g subsample of each litter species (aspen or spruce) was transferred into 36 litter baskets (18 "aspen" and 18 "spruce") and placed in boxes containing the forest floor samples, as described below. To test the effect of the presence of another litter species on litter decomposition (called hereafter "litter mixing" for simplicity while litter species were not thoroughly mixed), 18 additional litter baskets were prepared in which 2 g of spruce litter was placed at the bottom, covered with a second screen, and overlaid with 2 g of aspen litter. Although the design of these mixed baskets prevented a thorough mixing of the two litter species, it would allow us to measure litter species-specific responses to litter mixing. We did not alternate the position of the litter species in the mixture because spruce needles tend to lie under the aspen leaf litter during the early stages of decomposition under natural conditions. To test tree species effects through the component "forest floor conditions", approximately 750 g (dry weight equivalent) of each forest floor type (aspen or spruce) was transferred into each of three plastic boxes (42 cm × 28 cm × 15 cm) for a total of six boxes (three "aspen" and three "spruce"). Three baskets of each litter treatment (aspen, spruce, and mixture) were randomly placed on the surface of the forest floor for a total of nine litter baskets per box (Fig. 1). The boxes were covered with a polyethylene film to limit evaporation and left to incubate in darkness for 17 weeks at 20 °C. The litter was further kept moist by adding 15 mL of distilled water to each basket once a week.

Litter and forest floor analyses

Initial litter composition was characterized on eight subsamples previously ground with a ball mill. Total C and total N were determined by dry combustion using a LECO CNS 2000 analyzer (LECO Corporation, St. Joseph, Michigan). Total P was determined by H_2SO_4/H_2O_2 digestion (Keeney and Nelson 1982) followed by colorimetric analysis using a Quikchem 8000 AE flow injection autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin). Total K, Ca, and Mg concentrations were analyzed after H_2SO_4/H_2O_2 digestion by atomic absorption spectrophotometry (Perkin Elmer 5100 PC, Boston, Massachusetts). At the end of the incubation period, the litter of each basket was dried, weighed, defaunated, and analyzed for the same chemical characteristics as the initial (i.e., non-incubated) litter.

Prior to analyses, five forest floor subsamples were air dried, ground, and sieved (2 mm). Total C and total N were determined as described above. Available P was extracted with Bray's II extractant (0.03 mol/L NH_4F plus 0.1 mol/L HCl) (McKeague 1976) followed by colorimetric analysis (Lachat Instruments). Cationic exchange capacity (CEC) was determined by summing exchangeable cations (Carter 1993) extracted with 0.1 mol/L $BaCl_2$ and by atomic absorption spectrophotometry. The pH was determined both in water and in 0.5 mol/L $CaCl_2$ using a PHM82 pH meter (Radiometer Copenhagen) (Carter 1993).

Soil faunal communities

At the end of the incubation period, forest floor invertebrates colonizing litter baskets were immediately extracted from the litter by transferring each basket into a modified Berlese–Tullgren funnel equipped with 25 W bulbs and the

Table 3. Initial chemical properties of both litter species.

	Litter species	
	Trembling spen	Black spruce
C (%)	51.06±0.29	53.14±0.38
N (%)	0.56±0.03	0.28±0.01
C:N ratio	91.45±5.31	193.35±9.06
P total (mg/g)	0.42±0.04	0.31±0.05
K total (mg/g)	2.81±0.52	1.62±0.22
Ca total (mg/g)	18.93±1.37	10.68±0.34
Mg total mg/g)	2.69±0.15	0.92±0.02

Note: Each value is the mean of eight subsamples ± SD.

extracted fauna was preserved in 70% ethanol. All organisms were sorted, identified, and counted under a stereoscopic binocular microscope. The fauna was sorted as either Collembola, suborders of Acari (Oribatida, Gamasida, and Actinedida), Acari larva, or Lumbricidae (*Lumbricus rubellus* Hoffmeister) according to Dindal (1990).

Data analyses

Because of the hierarchical structure of the data, linear mixed models with random intercepts and slopes were used to test the effects of experimental factors (litter quality, litter mixing, and forest floor conditions) and their interaction terms on remaining post-incubation litter C and nutrient contents (SAS PROC MIXED). We identified two hierarchical levels, or potential sources of variation, in the data: (*i*) between boxes and (*ii*) within boxes and between incubation baskets; these were treated as random factors in the models. Covariables with estimates equal to zero were removed from the model. This analysis was complemented by planned contrast *F* tests to compare various treatment combinations and to separate the components of the interaction terms. To meet the assumptions of normality and homogeneity of variances, response variables were transformed using a Box–Cox power transformation (Box and Cox 1964). To test for differences in soil invertebrate accumulation among different litter baskets and different forest floors after the incubation period, we used mixed models with Poisson distributions (SAS PROC GLIMMIX). This latter analysis was also complemented by planned contrast *F* tests. All analyses were performed with SAS software v. 9.1 (SAS Institute Inc., Cary, North Carolina).

Results

Tree species effects through litter quality

While C concentrations of both litter species were comparable, the N concentration of the aspen litter was twice higher than that of spruce, yielding a C:N ratio two times lower for the aspen litter (Table 2). All other elemental concentrations (P, K, Ca, and Mg) were higher in the litter from aspen than in that from spruce.

Results from the mixed linear models showed that litter quality had a significant influence on litter decomposition and the rates of five nutrient dynamics (Table 4). Significantly more C was mineralized (i.e., higher decomposition) in the aspen litter than in the spruce litter. Aspen litter lost 59% of its initial C content, while spruce litter lost only 30%, a difference of 29% (Fig. 2). Net mineralization occurred in the aspen litter for all of the nutrients considered, except for N, where the net mineralization was negligible. Conversely, net mineralization in the spruce litter occurred only for K and Ca. All other nutrients (N, P, and Mg) were rather strongly immobilized in the spruce litter during the course of the incubation.

Tree species effects through the reactivity of their litter to litter mixing

Litter mixing had a very weak influence on litter elemental dynamics (Table 4). Figure 2 indicates that only the N and P dynamics of the litter mixture (mixed observed) were significantly different from what was expected from the combined elemental dynamics of each litter species (mixed predicted). Both observed N and P contents remaining in the mixture were higher than those predicted (i.e., higher net N immobilization and lower net P mineralization).

Tree species effects through their forest floor conditions

Forest floor from the aspen stand had lower C and higher N concentrations compared with those from the spruce stand (Table 3). The C:N ratio of the forest floor from aspen was two times lower than that from spruce, indicating a poorer substrate quality for the latter. Extractable P concentration was higher in the spruce forest floor, while cationic exchange capacity and pH (H_2O and $CaCl_2$) were lower compared with those of the aspen forest floor. Forest floor from the spruce stand harboured higher abundances of microarthropods, but the variability of the data remained quite high.

Results from the mixed linear models showed that forest floor conditions had a significant influence on litter decomposition and on nutrient dynamics (Table 4). Significantly more C was mineralized when the leaf litter was incubated on the forest floor from the aspen stand (Fig. 2). Overall, litter incubated on aspen forest floor lost 62% of its initial C content, while that incubated on spruce forest floor lost only 27%, a difference of 35% (Fig. 2). Net mineralization of P, K, and Ca was higher for litter incubated on aspen forest floor, while no difference was observed between forest floors from both stand types in the case of Mg. Net N immobilization was more pronounced on litter incubated on aspen forest floor compared with that incubated on spruce forest floor.

Differences in invertebrate assemblages among litter baskets were detected between forest floors from different stand types (Fig. 3). Higher abundances of microarthropods (Oribatida, Gamasida, and Acari larva) were found in litters incubated on the forest floor from the spruce stand whereas the earthworm *L. rubellus* was present exclusively in the forest floor from the aspen stand. Also, higher numbers of Gamasida, Acari larva, and Collembola found in the spruce forest floor were observed in the mixed litter baskets.

Tree species effects through the interactions between factors

The interaction between litter quality and litter mixing (litter quality × litter mixing) significantly influenced litter decomposition and nutrient dynamics (Table 4). Spruce litter applied in mixture with aspen decomposed more rapidly, mineralized more K, and immobilized less Mg than when

Fig. 1. Schematic view of the experimental design used in this study.

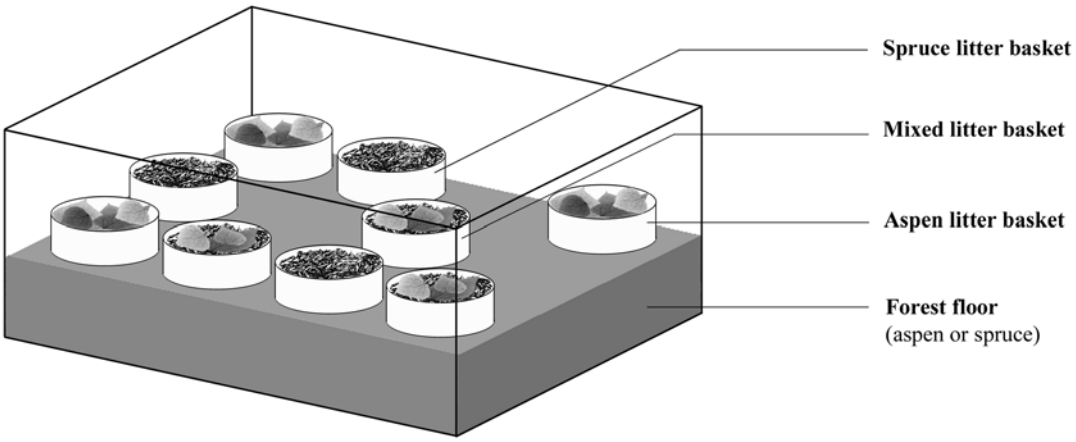


Table 4. Effects of three experimental factors (litter quality, litter mixing, and forest floor type) and their interaction terms through which tree species affect elemental contents remaining (%) in litter after 17 weeks of incubation.

		F					
Mechanism	df	C	N	P	K	Ca	Mg
Litter quality (L)	1	1010.04***	368.36***	214.06***	647.80***	133.92***	643.32***
Litter mixing (M)	1	0.00	5.36*	5.79*	0.18	0.37	0.45
Forest floor (F)	1	852.37***	13.20**	20.03*	42.32**	24.23**	0.94
L × M	1	15.14***	0.05	1.17	37.29***	9.90**	14.15***
L × F	1	731.56***	298.98***	98.46***	11.08**	47.76***	293.62***
M × F	1	0.09	2.43	13.43***	2.56	1.69	1.10
L × M × F	1	3.49	2.19	0.31	6.21*	0.16	7.79**

Note: *F* statistics derived from mixed linear models (random intercept-slope models with boxes, incubation baskets, and litter sample locations as random factors). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

applied singly (Fig. 4). Aspen litter decomposition and nutrient mineralization were also affected by the presence of spruce litter, but in the opposite way. In contrast, aspen litter mixed with spruce decomposed less rapidly and mineralized less K, Ca, and Mg.

The interaction between litter quality and forest floor conditions significantly influenced litter decomposition and nutrient dynamics (Table 4). Net losses of C and nutrients from leaf litter were faster on the aspen than on the spruce forest floor (Fig. 2) but, as illustrated in Fig. 5, this effect was more pronounced for aspen than for spruce litter. About 60% more C was lost from aspen litter decomposing over the aspen forest floor than over the spruce forest floor; in comparison, spruce litter C loss was only 8% greater on the aspen forest floor than on the spruce forest floor (Fig. 5). Net N mineralization was only observed in the aspen litter incubated on aspen forest floor. Net N, P, and Mg immobilization was greatest for spruce litter decomposing on aspen forest floor.

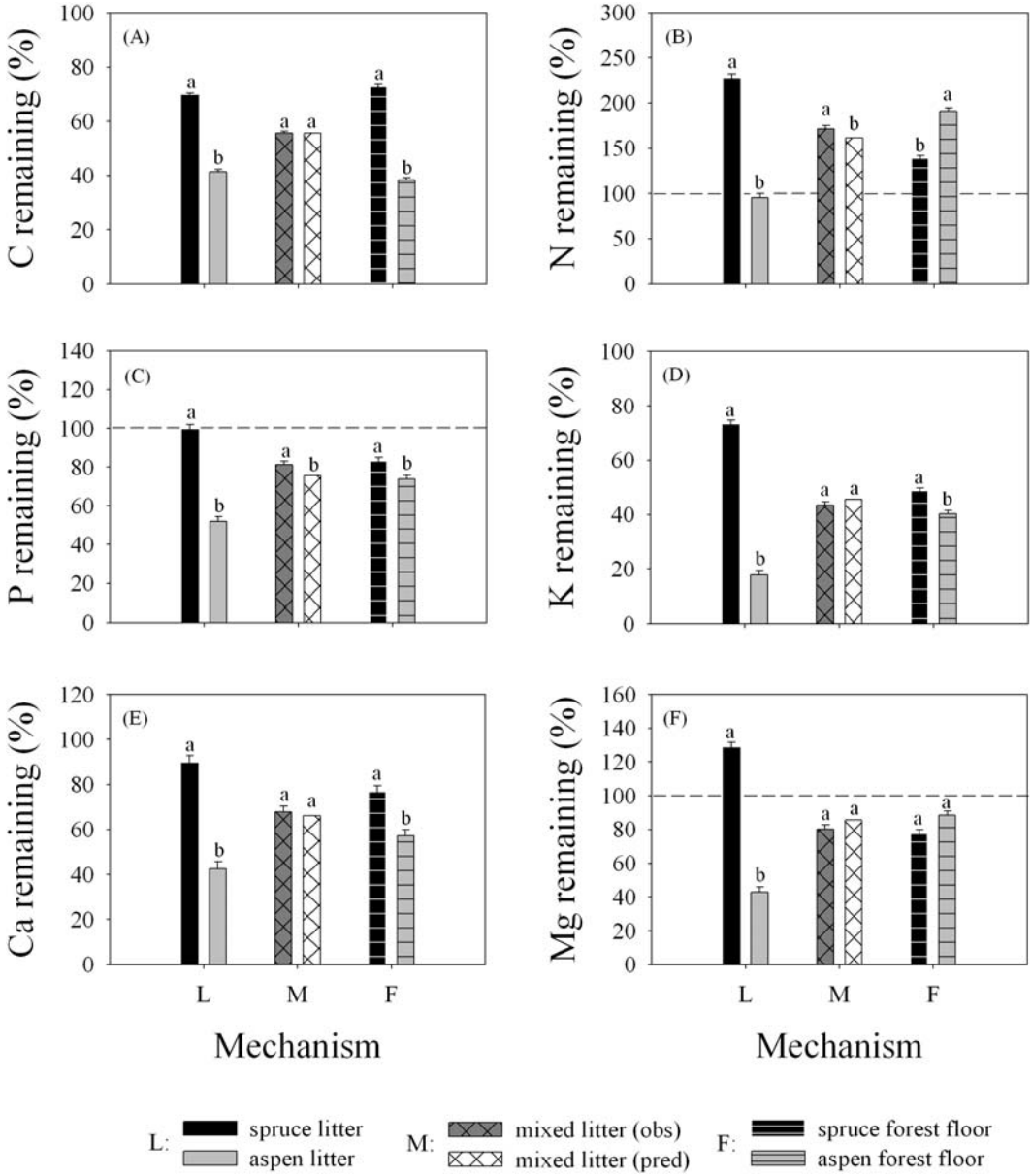
The other interaction terms (litter mixing × forest floor conditions and litter quality × litter mixing × forest floor conditions) will not be discussed here, since their contribution to explaining the total variance of the different parameters was negligible (Table 4).

Discussion

The results of our experiment confirmed the influence of all three considered components by which tree species could affect litter decomposition and nutrient dynamics. While their influence over these processes was already known, especially for the litter quality component, the present study proposed an original approach to separate their relative contributions and made it possible to weigh their importance in terms of variance partitioning. Their influence ranked in the following order: litter quality followed by forest floor conditions and, to a lesser extent, litter mixing. Interactions between factors, namely litter quality × forest floor conditions and litter quality × litter mixing, also significantly influenced these processes.

It is generally believed that the early phase of decomposition is regulated by nutrient level and readily available C (Berg 2000). Hence, on the one hand, the slower decomposition observed for spruce litter might be related to the lower quantity of nutrients present in its litter chemistry. However, that these litter-induced nutrient deficiencies could actually delay decomposition remains unlikely given that heterotrophic growth is generally limited by C availability (energy) and that there is very little evidence for a direct positive effect of nutrient addition on litter decomposition. Nutrient fertilization trials have consistently been shown to either delay or have no effect on microbial biomass and activity and on litter decomposition (Prescott 1995; Treseder 2008). On the other hand, the slower decomposition of spruce litter might be explained by a lower amount of readily available C. Organic matter from aspen stands generally contains more labile material than that from spruce stands. For exam-

Fig. 2. Components through which tree species affect elemental contents remaining in the litter after 17 weeks of incubation through litter quality (L), through the reactivity of litter to litter mixing (two litter species combined) (M), and through forest floor influence (F). The broken line, when present, represents the limit between net mineralization and net immobilization of the element. Error bars represent 1 SE (n = 18); different lowercase letters represent significantly different means according to planned contrast F tests ($p < 0.05$).

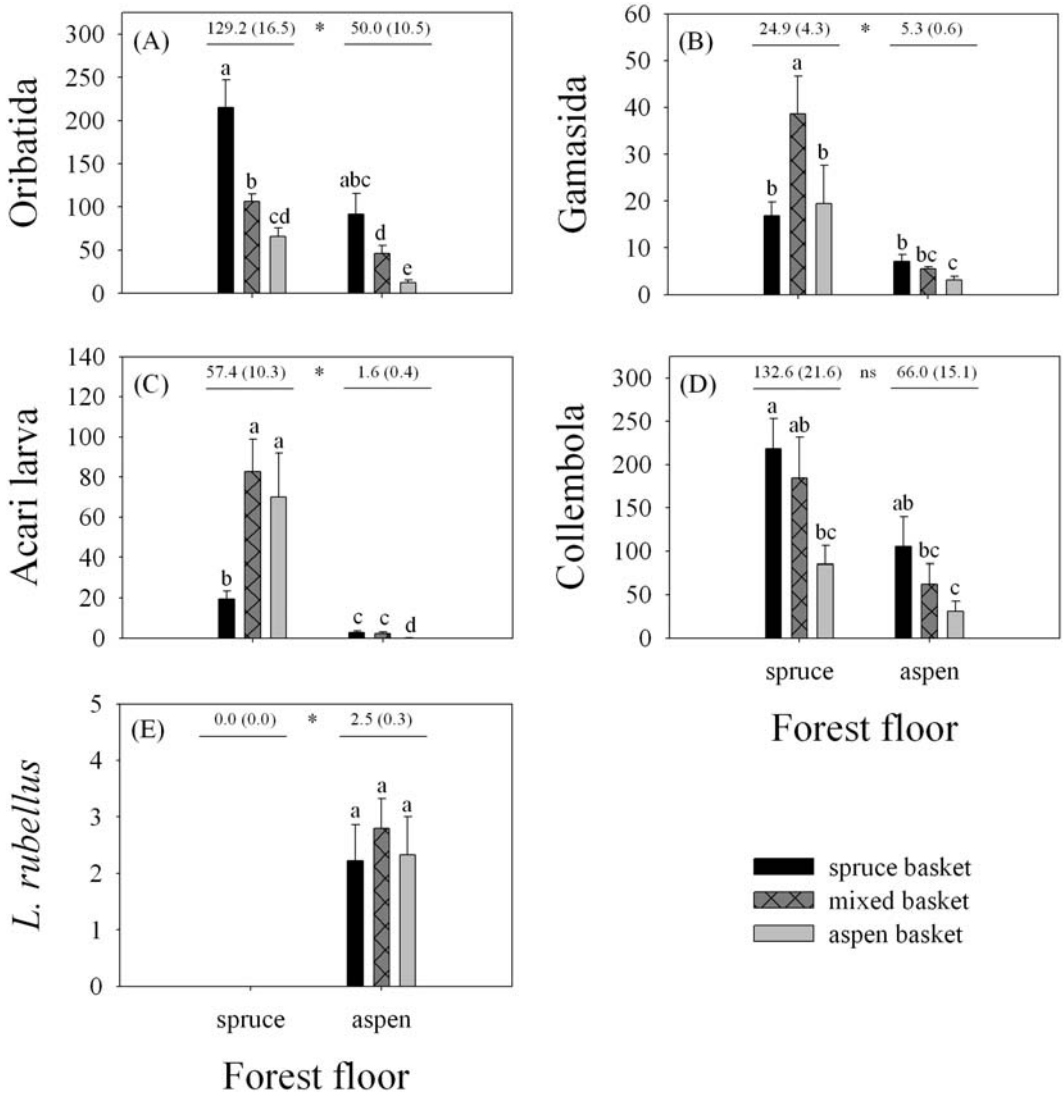


ple, aspen litter from the Canadian Intersite Decomposition Experiment contained 8.7%, 35.4%, 33.7%, and 14.4% nonpolar (i.e., soluble fats, waxes, and oils), water-soluble (i.e., simple sugars and water-soluble phenolics), acid-soluble (i.e., cellulose and hemicellulose), and acid-unhydrolyzable (i.e., Klason lignin) fractions, respectively, while black spruce litter contained 10.9%, 19.9%, 37.0%, and 28.3% (Trofymow and CIDET Working Group 1998). Moreover, unlike nutrient fertilization trials, work to date mostly suggests that a supply of readily available C induces a positive effect on organic matter decomposition rates (Fontaine et al. 2007), a phenomenon called positive "priming effect" (Bingeman et al. 1953).

The present study suggests that whatever the limitation, whether it originates from a lack of labile C, from a lack of nutrients, or from both, it could be partly counteracted by mixing the slowly decomposing litter species (e.g., spruce) with another litter species, aspen in this case. While the combined reactivity of spruce and aspen litter to litter mixing yielded a weak effect on mineralization rates (Table 4, factor litter mixing), a positive reactivity of spruce litter to the presence of aspen litter was apparent when the two components of the litter mixture were isolated (Table 4, interaction litter quality × litter mixing), as was possible with our experimental setup.

Several mechanisms have been proposed to explain how a litter species may interact with another so as to increase the C and nutrient mineralization rates of the second one

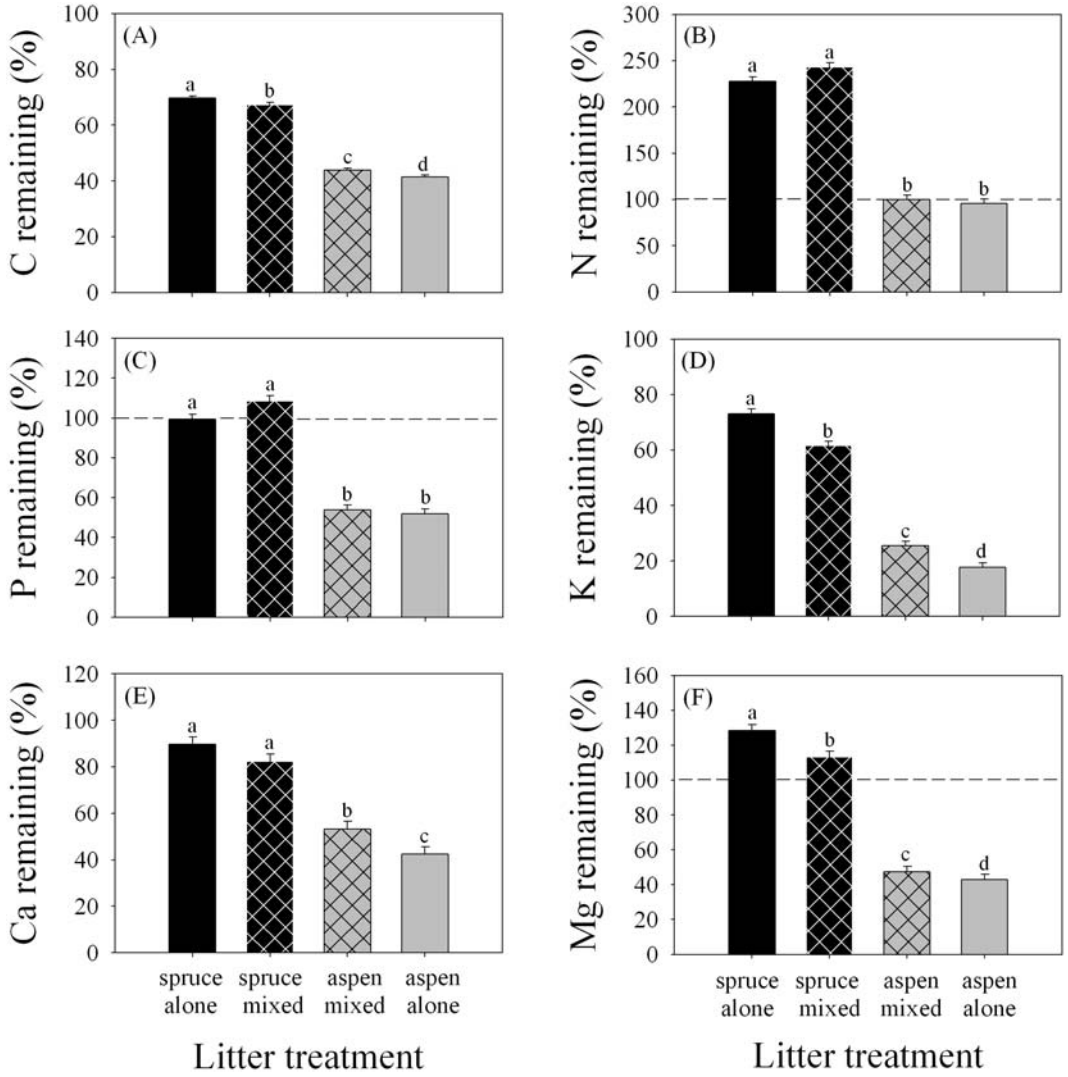
Fig. 3. Invertebrate abundances (individuals per basket) in single species and mixed litter baskets after 17 weeks of incubation on both forest floor types. Mean abundances (SE) for each forest floor type are shown on the upper part of each graph and a significant difference ($p < 0.05$) is indicated by an asterisk. Error bars represent 1 SE ($n = 9$); different lowercase letters represent significantly different means according to planned contrast F tests ($p < 0.05$).



(Seastedt 1984; Hättenschwiler et al. 2005). As mentioned earlier, a plausible explanation would be that aspen litter improves decomposition rates by providing more available C to the bacterial and fungal decomposer communities. By relieving the C stress, aspen litter may switch the energy-limited status of soil microbes to a nutrient-limited status, thereby increasing "nutrient-acquisition mechanisms" and thus the decomposition rates (Bradley and Fyles 1995). Furthermore, even if the "nutrient-transfer hypothesis" seems to be an intuitively compelling mechanism for synergistic effect among litter species, this process is rarely convincingly demonstrated according to the recent literature (Hoorens et al. 2003; Hättenschwiler et al. 2005). A second hypothesis would be that decomposing aspen leaves have a higher moisture retention capacity than decomposing spruce needles (Hansen 1999; Prescott et al. 2000*b*), which may in turn increase decomposition rates (Prescott et al. 2004). In the litter mixture baskets, the purported higher moisture conferred by decomposing aspen leaves may have increased decomposition rates in the underlying spruce needles. If such is the case, it then remains to be shown whether a more thorough mixing of aspen and spruce litters, as opposed to the stratified mixtures that we used in the present study, would result in more favourable moisture conditions for spruce needle decomposition. A third hypothesis suggesting that the litter mixture favours higher abundances of microarthropods, and hence increased litter comminution and (or) microbial stimulation (Hättenschwiler et al. 2005), is not supported by our data (Fig. 3).

Besides the better chemical properties of the forest floor layer found below aspen, an explanation for the higher rates of mineralization observed for litters decomposing on the forest floor from aspen would be that the forest floor harboured a decomposer community that was distinctly more efficient than that of the spruce forest floor. Lamarche et al. (2007) provided evidence that microbial communities from

Fig. 4. Percentage of initial element content remaining in single species and mixed litter after 17 weeks of incubation showing the interaction between litter quality and litter mixing. The broken line, when present, represents the limit between net mineralization and net immobilization of the element. Error bars represent 1 SE (n = 18); different lowercase letters represent significantly different means according to planned contrast F tests ($p < 0.05$).

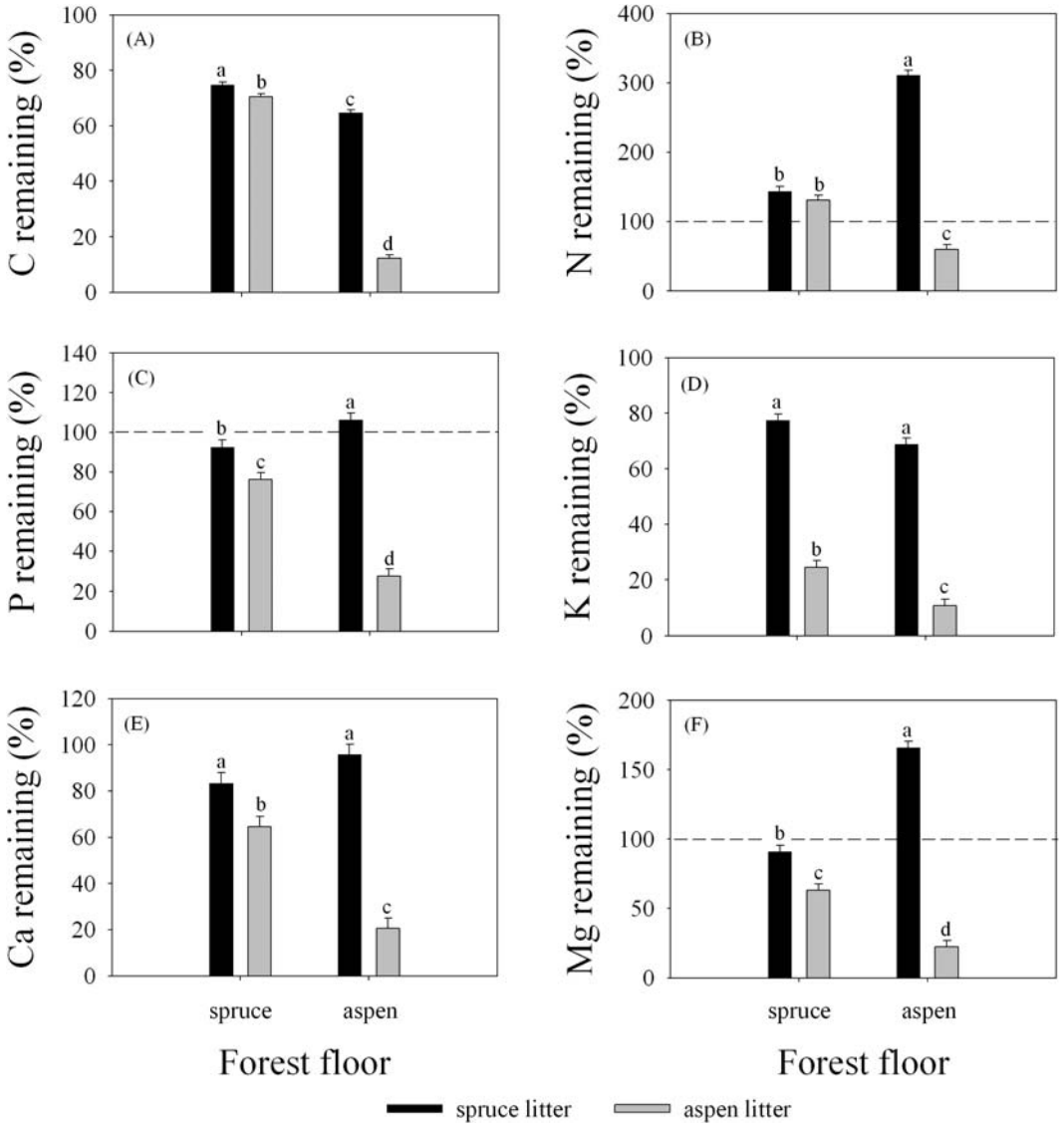


aspen and spruce stands in the Abitibi region were indeed functionally and genetically distinct. In the same region, Laganière et al. (2009) provided evidence that the same may be true for the soil faunal community: macroinvertebrates were more related to the forest floor below aspen, whereas microarthropods were more related to black spruce forest floor. Their results further suggested that aspen favours the development of a macrofaunal community, which in turn accelerates the rates of decomposition. Likewise, in this experiment, while the forest floor from the spruce stand developed greater abundances of microarthropods, macroinvertebrates (i.e., earthworms) were an exclusive component of the forest floor from the aspen stand, where litter mineralization was faster.

Earthworms are probably the most important comminuting soil organism (Edwards 1998), but their presence in boreal forest soils is limited by their intolerance to low pH and their high Ca requirements (Bohlen 2002). Aspen litter increases both of these variables compared with black spruce and other boreal conifer species (Lamarche et al. 2004; Légaré et al. 2005*a*). Epigeic earthworm species such as *L. rubellus* are known to facilitate the breakdown and mineralization of surface litter by increasing contact surfaces for microbial attack (Bohlen 2002). Although microbes are responsible for most of the final steps in soil organic matter decomposition (Bardgett 2005), it is likely that the presence of *L. rubellus* in the aspen forest floor material is a key factor that provides a faster mineralization of C and nutrients from both aspen and spruce litters. Furthermore, the effect of aspen forest floor on the decomposition rates of aspen litter (interaction litter quality × forest floor conditions) was much more dramatic than that of spruce litter (Fig. 5), which may indicate a much greater ability of *L. rubellus* to process deciduous litter.

Both aspen and spruce litters decomposed faster on aspen forest floor material. These results do not support, therefore, the hypothesis that tree species will select a decomposer community that is most efficient in decomposing the litter

Fig. 5. Percentage of initial element content remaining in the litter after 17 weeks of incubation showing the interaction between litter quality and forest floor. The broken line, when present, represents the limit between net mineralization and net immobilization of the element. Error bars represent 1 SE (n = 9); different lowercase letters represent significantly different means according to planned contrast F tests ($p < 0.05$).



from that particular species, as some have suggested (e.g., Hunt et al. 1988; Wardle 2002). Instead, our results are in accordance with those of Ayres et al. (2006) who found that litter from different tree species does not systematically decompose at faster rates in the presence of indigenous soil communities. In our study, the so-called "home-field advantage" (Hunt et al. 1988) seems to apply to aspen litter and forest floor material but not to spruce. Our results suggest that the suitability of aspen forest floors to sustain populations of *L. rubellus*, or what might be a "keystone soil species", may be the catalyzing factor behind the asymmetric feedback between the litter and forest floor of aspen and spruce stands. In various types of ecosystems, several authors observed the same positive influence that certain species of plants may have on the abundance of earthworms and, ultimately, on the decomposition rates of leaf litter (e.g., Hobbie et al. 2006; Laganière et al. 2009). Finally, it is important to note that most of the "home-field advantage" work comes from litter bag studies that exclude soil fauna. In contrast, this work underscores the importance of including soil fauna.

A microcosm study was necessary to ensure identical climatic conditions and to better identify the relative contribution of litter quality, litter mixing, and forest floor effects, which was the purpose of this study. Another advantage of using microcosms to compare with an in situ litterbag approach was that the macrofauna was not excluded from the decomposition process. Macroinvertebrates such as earthworms were able to colonize litter baskets from above and to participate in litter decomposition. Nevertheless, the microcosm approach may create artificial conditions that could affect the extrapolation of results to field conditions. For example, the forest floor was disturbed during collection, sieving, and mixing, the temperature of incubation was

maintained constant and was much higher than in situ, the leaf litter was defaunated by a freeze–thaw cycle, etc. However, given that our results are in line with those of other studies that took place in situ, these apparent limitations of the microcosm approach seem minor. Jonard et al. (2008) developed a similar approach in situ to evaluate the relative importance of the different factors whereby tree species can influence litter decomposition and obtained results that are consistent with our findings. In a field experiment in Denmark, spruce litter was also less affected by the incubation environment than a broadleaf species (Vesterdal 1999). Moreover, Prescott et al. (2000*b*) and Laganière et al. (2009) found rates of decomposition to be faster in aspen than in spruce stands, which is consistent with our study. In addition, both studies concluded that this effect was not simply due to differences in litter quality but to the distinct forest floor properties found under aspen, namely the composition of the decomposer community.

Conclusion

This study provided evidence that the effect of tree species on litter decomposition was mediated through several components. First, the C and nutrient mineralization rates of aspen litter were faster than those of black spruce litter in all conditions, indicating a major role of litter quality consistent with the results of Aerts et al. (2003) and Verhoeven and Toth (1995). Second, aspen litter modestly increased C and nutrient mineralization rates of spruce litter in mixture. Third, forest floor from the aspen stand increased C mineralization of both litter types, and it also increased nutrient mineralization of aspen litter. The latter effect could possibly be explained by the fact that the earthworm *L. rubellus* was an exclusive component of the aspen forest floor community. Hence, we propose that the effect of tree species on litter decomposition may not only be caused by the properties of its litter but also, indirectly, by the specific conditions and the decomposer community that tree species develop in their forest floor. In this case, the presence of a keystone macrofaunal species in aspen soils may be a major trigger for tree species effect.

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