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LIST OF ABBREVIATIONS

AFD	Aménagement forestier durable
AM	Arbuscular mycorrhiza
ANOVA	Analysis of variance
BA	Basal area
BS	Black spruce
C	Carbon
CEC	Cation exchange capacity
CEF	Centre d’étude de la forêt
C:N	Carbon to nitrogen ratio
CRSNG	Conseil de recherche en sciences naturelles et génie du Canada
DBH	Diameter at breast height
DPR	Diversity-productivity-relationship
ECM	Ectomycorrhizae
EDB	Laboratoire Évolution et diversité biologique
EFM	Ecosystem-based forest management
FAO	Food and agricultural organisation
FERLD	Forêt d’enseignement et de recherche du lac Duparquet
FRB	Fine root biomass
FRQNT	Fonds de recherche du Québec – Nature et technologies
GEOTOP	Centre de recherche en géochimie et géodynamique de Montréal

IRF	Institut de recherche sur les forêts
IRMS	Isotope ratio mass spectrometer
K	Potassium
LFC	Laurentian forestry center
MFFP	Ministère des forêts, de la faune et des parcs du Québec
N	Nitrogen
NH_4^+	Ammonium
NO_3^-	Nitrate
P	Phosphorous
RDMC	Root dry matter content
RTD	Root tissue density
TA	Trembling aspen
UQAM	Université du Québec en Abitibi-Témiscamingue
UQAT	Université du Québec à Montréal

RÉSUMÉ

Les études montrent que les coupes totales, utilisées sur plus de 85% des forêts affectées à l'exploitation du bois au Canada, pourraient impacter négativement la biodiversité et la productivité futures des forêts boréales du pays. L'épinette noire et le peuplier faux-tremble sont les deux espèces les plus abondantes à haute valeur marchande dans la forêt boréale de l'est du Canada. La valeur marchande plus élevée de l'épinette noire par rapport à celle du peuplier faux-tremble, la supposé exclusion compétitive du tremble par l'épinette au cours de la succession forestière, ainsi que l'absence de consensus sur le type de relation (positive, négative ou non significative) diversité-productivité dans le biome forestier boréal, incitent les aménagistes forestiers à orienter les opérations sylvicoles (éclaircie commerciale et pré-commerciale) de façon à exclure le peuplier faux-tremble des peuplements. Les relations dans les sols entre les espèces, généralement omises des études diversité-productivité en forêt boréale, semblent être la clé pour une meilleure compréhension des interactions entre ces deux espèces.

Cette thèse explore les interactions dans les sols entre l'épinette noire et le peuplier faux-tremble afin de déterminer si elles sont complémentaires vis-à-vis de l'utilisation des nutriments du sol dans les peuplements mixtes de la forêt boréale du Nord-Ouest du Québec. Dans un premier temps (Chapitres II et III), je caractérise les stratégies d'acquisition des ressources des deux espèces le long du profil du sol. J'insiste par la suite (Chapitre IV) sur l'azote (N) qui représente la ressource la plus limitante à la croissance des arbres en forêt boréale. A cet effet, les attributs racinaire (biomasse, densité de tissus et symbioses mycorrhiziennes) et foliaire (teneur en N, rapports isotopiques du N ($\delta^{15}N$)) de l'épinette et du tremble ont été mesurés pour déterminer si les deux espèces absorbe les nutriments dans des horizons de sol différents. Une expérience *in situ* d'ajouts de deux formes d'isotopes stables de l'azote (ammonium et nitrate) a également été mise en place pour déterminer si les deux espèces ont des préférences différentes pour les deux formes minérales de l'azote.

L'analyse des attributs racinaire et foliaire a montré que l'épinette tire l'essentiel de sa nutrition azotée dans l'horizon organique tandis que celle du peuplier provient de l'horizon minéral. Les résultats montrent que l'épinette bénéficie d'un effet facilitateur du tremble sur les propriétés chimiques du sol pour adopter une stratégie intensive d'absorption des nutriments. Cette stratégie confère à l'épinette un avantage concurrentiel sur le tremble dans la couche organique. La diversité et l'abondance plus élevées des communautés mycorhiziennes associées aux racines de l'épinette que celles du peuplier faux-tremble dans l'horizon organique des peuplements mixtes démontrent une domination compétitive des communautés associées à l'épinette sur celle du peuplier faux-tremble; suggérant une exclusion compétitive du tremble par l'épinette dans l'horizon organique. Le peuplier faux-tremble maintenait la même biomasse de racines fines dans l'horizon organique et l'augmentait de 25% dans l'horizon minéral des peuplements mixtes par rapport aux peuplements purs. J’ai interprété ce patron comme un mécanisme d'évitement de la compétition, car l'augmentation de la biomasse de racines fines dans le sol minéral n'était pas le résultat de l'effet du mélange d'espèces sur les propriétés chimiques du sol. La diversité et l'abondance plus élevées des communautés mycorhiziennes du tremble que celles de l'épinette dans l'horizon minéral des peuplements mixtes suggéraient une domination compétitive du tremble sur l'épinette dans le sol minéral des peuplements mixtes. L’expérience d’ajouts d’isotopes a révélé une claire préférence de l’épinette pour l’ammonium et du peuplier faux-tremble pour le nitrate dans leur peuplement pur respectif. Ces préférences étaient inexistantes dans les peuplements mixtes où la cinétique d’absorption ou le facteur de fractionnement des deux formes d’isotopes de l’azote ajoutées ne différait pas entre les deux espèces.

Contrairement aux précédentes études, cette étude montre que l’épinette bénéficie de la présence du tremble sans impacter négativement l’acquisition des ressources de ce dernier. Les résultats suggèrent une exclusion compétitive du tremble par l'épinette qui ne se produit probablement que dans la couche organique du sol dans les peuplements mixtes. Une séparation spatiale plus forte des racines de l'épinette et du tremble dans les peuplements mixtes contribue à un partitionnement spatial de leur absorption de nutriments le long du profil du sol. La biomasse de racines fines plus faible de l'épinette dans les peuplements mixtes que purs a montré que l'épinette alloue plus de carbone (C) à sa croissance aérienne dans les peuplements mixtes que dans les peuplements purs où le C est principalement alloué dans le sol pour la recherche de nutriments. Ces résultats sont conformes à l'observation précédente selon laquelle les peuplements mixtes d’épinettes et de trembles ont un volume plus élevé de biomasse marchande avec un volume d'épinettes dont les tiges sont plus grosses que les peuplements purs d’épinettes (Légaré *et al.*, 2004).

Ainsi, cette thèse suggère aux aménagistes forestiers du Québec de diversifier les pratiques sylvicoles à travers le paysage forestier selon les types de peuplements. Plus spécifiquement, je recommande de maintenir le tremble pendant l'éclaircie pré-commerciale dans les peuplements à dominés par l'épinette. La présence de trembles assurera une certaine stabilité aux peuplements dominés par l’épinette et réduira leur susceptibilité aux pertes de productivité liée à la paludification des sols. Dans les peuplements de trembles purs et mixtes, je recommande de promouvoir le mélange d'épinettes et de trembles. L’étude suggère qu’au-delà de leur coexistence en raison du partitionnement de leur absorption de nutriments dans les horizons de sol différents, l'épinette et le tremble utiliseraient aussi efficacement les nutriments disponibles dans le sol.

Mots clés : rapport isotopique δ^{15}N, relation diversité-productivité, relations souterraines des espèces, azote du sol, sylviculture

ABSTRACT

Studies show that clearcuttings, used in more than 85% of forests designated for tree harvest in Canada could negatively impact the biodiversity and productivity of boreal forest. Black spruce and trembling aspen are the two most abundant species with high merchantable value in the boreal forest of eastern Canada. The higher merchantable value of spruce compared to aspen, the hypothesized competitive exclusion of aspen by spruce during the forest succession, as well as the lack of consensus on the type of diversity-productivity relationship (positive, negative or insignificant) in the boreal forest, have led forest managers to orient silvicultural practices (commercial and pre-commercial thinning) to exclude aspen from stands. The underground relationships between species, generally omitted from diversity-productivity studies in the boreal forest, seem to be the key to a better understanding of the interactions between these species in order to promote their mixture.

This thesis explores the underground interactions between spruce and aspen to determine if they are complementary with regard to the use of soil nutrients in mixed stands in the boreal forest of northwestern Quebec. First (Chapters II and III), we characterize the resource acquisition strategies of the two species along the soil profile. We further (Chapter IV) focus on nitrogen (N), the most limiting resource for tree growth in the boreal forest. For this purpose, the root (biomass, tissue density and mycorrhizal symbiosis) and leaf attributes (N content and N isotopic ratios (δ^{15}N)) of the two species were measured to determine whether the two species take up nutrients in different soil horizons. Second, an *in situ* ^{15}N labelling experiment (addition of two forms of ^{15}N (ammonium and nitrate) was conducted to determine if the two species have different preferences for the two mineral forms of nitrogen.

The analysis of root and leaf traits showed that spruce derives its N from the organic horizon whereas aspen N derives from the mineral horizon. The results showed that spruce benefits from the facilitative effect of aspen on the chemical properties of the soil to adopt an intensive nutrient uptake strategy in mixed stands. This strategy provides spruce a competitive advantage over aspen in the organic layer. The higher diversity and abundance of root-associated mycorrhizal communities of spruce than those of aspen roots in the organic horizon of mixed stands also suggests a competitive dominance of communities associated with spruce over that of aspen; supporting the hypothesized competitive exclusion in the organic horizon. Aspen maintained the same fine root biomass in the organic horizon and increased it by 25% in the mineral horizon of mixed stands compared to pure stands. I interpreted this pattern as competition avoidance mechanism, since the increased fine roots biomass in the mineral soil did not result from the species mixture effect on soil chemical properties. The higher diversity and abundance of root-associated mycorrhizal communities than those of spruce in the mineral horizon of mixed stands suggested a competitive dominance of aspen over spruce in the mineral soil. The ^{15}N labelling experiment showed a clear preference of spruce for ammonium and trembling aspen for nitrate in their respective pure stands. These preferences were not observed in mixed stands where the two species took up the two added ^{15}N forms in the same proportions.

Unlike previous studies, this study shows that spruce benefits from the presence of aspen without negatively impacting the nutrient acquisition of the latter. The results suggested a competitive exclusion of aspen by spruce which likely occurs only in the organic layer of the soil in mixed stands. Stronger spatial separation of spruce and aspen roots in mixed stands contributes to partitioning of their nutrient uptake along the soil profile. The lower fine root biomass of spruce in mixed stands than pure showed that spruce allocates more carbon (C) to its aboveground growth in mixed stands than in pure stands where its C is mainly allocated in the soil for nutrients search. The results are consistent with previous observation (Légaré *et al.*, 2004) that mixed stands of spruce and aspen have a higher marketable volume of spruce biomass than pure spruce stands.

I therefore recommend that forest managers in Quebec should diversify silvicultural practices across the forest landscape according to stand types. More specifically, I recommend maintaining aspen within stands during pre-commercial thinning in pure spruce stands. The presence of aspen will provide some stability to spruce-dominated stands and reduce their susceptibility to productivity losses due to paludification of soils. In pure and mixed aspen stands, I recommend promoting the mixture of spruce and aspen. This study suggests that beyond their coexistence due to the partitioning of their nutrient uptake at different soil depth, spruce and aspen also efficiently use the available nutrients in the soil.

Keywords: isotopic ratio $\delta^{15}N$, diversity-productivity relationship, species underground interactions, soil nitrogen, silviculture

CHAPTER I

GENERAL INTRODUCTION

1.1 Background

1.1.1 The boreal forest in Canada

The boreal forest is the largest terrestrial carbon reservoirs representing 33% of the world's forest lands (FAO, 2010). It stretches from Greenland to Newfoundland and across northern Canada into Alaska in North America (Bradshaw *et al.*, 2009; Brandt *et al.*, 2013). The boreal forest has a subarctic climate, which is characterized by cold and snowy winters with a short growing season (Burton *et al.*, 2010). Average daily temperatures are above 10°C for 30 to 120 days of the year (Walter, 1985). Precipitations vary greatly along longitudinal gradients; with averages ranging from 150 to 450 mm/year (Walter, 1985). According to the World Reference Base for soil resources (WRB), boreal soils are mostly cryosols (27%), podzols (15%), cambisols (8%) and leptosols (8%); being relatively humid and cold (Jones *et al.*, 2010).

Wildfires are the most dominant disturbances influencing forest composition and carbon storage in boreal forests (Bergeron *et al.*, 2014; Ito, 2005; Sukhinin *et al.*, 2004; Weber et Flannigan, 1997). Their size and frequency strongly control the relative abundance and distribution of tree species, forest composition, internal structure and dynamics (Johnstone et Chapin, 2006). Many other natural drivers of ecosystem dynamics such as long-term climate variability and insect outbreaks are also of importance for the dynamics of the boreal forests. The two most disruptive defoliators in Canadian boreal forests are the spruce budworm (*Choristoneura fumiferana* Clemens, SBW), which mostly defoliates balsam fir and spruce species, and the forest tent caterpillar (*Malacosoma disstria* Hübner; FTC) that attacks trembling aspen, balsam poplar and paper birch as its main hosts (Chen et Popadiouk, 2002; Moulinier *et al.*, 2011). These disturbances play an important role in the recruitment of species, biogeochemical cycling of nutrients and maintenance of forest productivity (Brandt *et al.*, 2013). At the landscape scale, these disturbances affect species composition, structure and forest successional dynamics (Bergeron et Dansereau, 1993; Brassard et Chen, 2010).

Boreal forests are generally dominated by one to two species per stand, with single-species stands being quite common (Zasada *et al.*, 1997). In Northeastern Canada, the boreal forests are dominated by black spruce (*Picea mariana* Mill., referred hereafter as spruce) (Brandt, 2009; Liu et Yang, 2014). There are also large areas covered by shade-intolerant deciduous trees such as trembling aspen (*Populus tremuloides* Michx., referred hereafter as aspen), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marshall), either in pure or mixed stands with conifers such as eastern larch (*Larix laricina* (Du Roi) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.) and jack pine (*Pinus banksiana* Lamb.) (Brandt *et al.*, 2013). According to the vegetation zones and bioclimatic domains of Quebec in eastern Canada (Saucier *et al.*, 1998), these mixed stands of conifers and broadleaf tree species are located in the southern part of the black spruce – moss and the balsam fir – white birch domains (Figure 1.1). The latter being referred to as *boreal mixedwoods*.

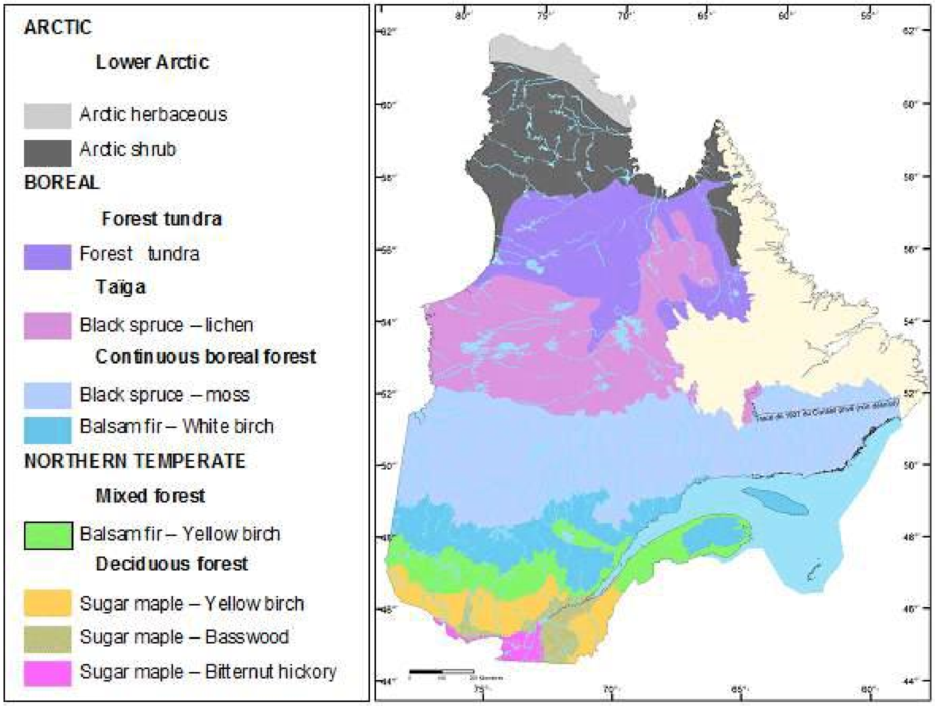


Figure 1.1 Vegetation zones and bioclimatic domains in Quebec (Saucier *et al.*, 1998).

The successional dynamics of the forest, from which the diversity of stand types in the southern part of the black spruce - moss bioclimatic domain originated, also makes the forests of this part of the boreal forest qualify as boreal mixedwoods. Boreal mixedwoods are defined in terms of characteristic site types to provide a stable frame of reference for a complex and dynamic forest (Chen et Popadiouk, 2002; MacDonald et Weingartner, 1995). Essential elements defining mixedwood sites include the abundance, diversity, and relative position of associated species at each successional stage depending on the disturbance type and pre-disturbance stand composition (Towill *et al.*, 2004). Other characteristics include unrestricted drainage of soils, well-drained fertile soils on mid-slope positions, deep soils (medium to fine textures) from glacial lacustrine or alluvial origin (McClain, 1981; Pierpoint, 1981). These characteristics prevail in the southern part of the black spruce-moss bioclimatic zone of Quebec (Saucier *et al.*, 1998).

In boreal mixedwoods, early successional stages following fire are generally dominated by shade-intolerant broadleaf species such as aspen (Bergeron, 2000; Bergeron et Dubuc, 1989). During subsequent years following the fire, shade-tolerant species such as black- and white spruce seed-in gradually and dominate the understory (Galipeau *et al.*, 1997). Because of their differences in mode of regeneration, shade-tolerance and growth dynamics, aspen attain optimal merchantable size before spruce and dominates the canopy. Although the crown hierarchy of spruce and aspen benefits to spruce (spruce prefers diffuse light for its photosynthesis while aspen in the upper strata effectively captures direct light), it has been reported that the absence of canopy gaps negatively impacts the growth of spruce (Smith *et al.*, 2016). However, the shade-tolerant character of spruce and the progressive accumulation of its recalcitrant litter in the forest floor contributes to acidifying and increasing the thickness of the organic layer that slows aspen growth and inhibits its regeneration (Lafleur *et al.*, 2015a). Thus, when spruce reach optimal size, aspen biomass has often decreased as a result of mortality from senescence (Pothier *et al.*, 2004). This phenomenon leads to spruce-dominated stands and is commonly interpreted as the competitive exclusion of aspen by spruce during the forest succession. These spruce-dominated stands feature low diversity of vascular plants, animals and insects (Cavard *et al.*, 2011a) and are more susceptible to productivity losses (Lafleur *et al.*, 2015b) than mixed stands.

Boreal forests provide numerous goods and services to Canadian populations. These are classified as (1) provisioning (timber, pulp, fuelwood, food, and freshwater); (2) regulating (climate regulation, flood regulation, disease regulation, and water purification); (3) cultural (spiritual, educational, recreational, and aesthetics); and (4) supporting (primary production, nutrient cycling, and soil formation) services (Hassan *et al.*, 2005). In particular, the boreal forest plays an important role in supporting the regional and global forest industry and carbon sequestration (Conard et Davidenko, 1998; Kuusela, 1992). Both human activities and climate change influence these functions (Flannigan *et al.*, 2009; Liu *et al.*, 2012) and it is of paramount importance to supply forest management with a good understanding of ecological drivers of ecosystem structure and function (e.g. biodiversity-productivity relationship, BPR).

1.1.2 Sustainable management of the boreal forest in Quebec

In Quebec, forest management has undergone significant evolution since its onset in the second half of the 19th century (Mercier, 2017). This evolution is a product of multiple factors, the knowledge accumulation on the functioning of the boreal ecosystem, and the interest of the government to perpetuate the forest resource. In 2013, the implementation of a new forest regime took place through the Sustainable Forest Development Act (Gouvernement du Québec, 2010) that recommended ecosystem-based forest management (EFM) as the approach to be used to establish sustainable forest management.

The EFM is currently widely accepted as a means of conciliating industrial demands for timber and biodiversity concerns (Davey *et al.*, 2003; Patry *et al.*, 2013; Raum, 2017; Steenberg *et al.*, 2019; Vaillancourt *et al.*, 2009). Its implementation aims to ensure the maintenance of the biodiversity as an essential prerequisite for the world's population to continue to have access to the many benefits and products derived from forests, and the viability of forest ecosystems by reducing the gaps between the managed forest and the natural forest. It also aims to meet socio-economic needs, while respecting the social values linked to the forest environment (Gauthier *et al.*, 2008). From this definition emerges three main issues (ecological, economic and social) related to the three dimensions of sustainable management.

The success of EFM in the boreal forest relies on good knowledge of its ecological issues (Grondin *et al.*, 2003; Jetté *et al.*, 2013; Saucier *et al.*, 2010). In Quebec, the boreal forest in the north can still be considered natural compared to the temperate forest in the south. Knowledge of past historical variations as well as the effects of industrialization are necessary to understand and describe the natural forest in the southern Quebec (Grenon *et al.*, 2010; Patry *et al.*, 2013). By definition, a natural forest is a forest that has evolved according to a dynamic generated by natural disturbances, climate and physical environment in the absence of large-scale human intervention (Brassard et Chen, 2010; Grondin *et al.*, 2010). EFM in the boreal forest will therefore consist of making management decisions, based on the knowledge of the ecological mechanisms that govern the natural dynamics of boreal forest stands while meeting the needs of the society.

The EFM recommends using different management strategies and silvicultural practices at forest landscape and stand scales, respectively (Larouche *et al.*, 2013). The application of this recommendation is, however, not mandatory. Forest managers can adopt or rather draw inspiration from it to meet EFM's ecological issues (Grenon *et al.*, 2010). Given the sites specificity (Laflèche *et al.*, 2013) and the diversity of forest types at the landscape scale (Saucier *et al.*, 2010), EFM recommends that silvicultural practices (generally grouped into two main categories, namely monosilviculture, mixed silviculture) should be carried out at the stand scale and diversified at landscape scale in order to address the compositional problems that can be caused by past forest harvest (Jetté *et al.*, 2013). Such approach should eventually help prevent or reverse the observed trend, which is the scarcity of mixed stands and old-growth forests (Bergeron et Harper, 2009; Jetté *et al.*, 2013).

Broadly different habitat requirements and successional trajectories of conifers and broadleaves and their hypothesized temporal coexistence in the stands in the absence of fire have led forest managers to opt for clearcuts on ~85% of the total harvested area in Canada (Statistics Canada, 2018). The higher market value of black spruce compared to that of aspen also prompts forest managers to orient monosilvicultural practices (commercial and pre-commercial thinning) so as to exclude trembling aspen from stands. These approaches do not fully address the complexity of the forest landscape in the boreal mixedwoods.

Unlike monosilviculture, mixed silvicultural practices have been reported to have less impact on biodiversity by recreating plant and animal assemblages consistent with a range of natural variability (Drever *et al.*, 2006; Puettmann *et al.*, 2015). This results from the premise that maintaining stand structures consistent with biological legacies after natural disturbance will serve as refugia and habitat for forest species (Attiwill, 1994; Drapeau *et al.*, 2002, 2008; Puettmann *et al.*, 2009). Moreover, silvicultural practices relying on mixed stands are hypothesized to encourage the development of old-growth structural features and the assemblages of old-growth adapted species (Jetté *et al.*, 2013; Kuuluvainen, 2009). Undertaking such practices, however, requires a better knowledge of diversity-productivity relationships (DPR) and mechanisms that shape the coexistence of species.

1.1.3 Context of diversity-productivity relationship studies in boreal forests

Natural disturbances shape the forest landscape and influence stand species diversity, composition and structure in boreal forests (Chen *et al.*, 2009; Chen et Popadiouk, 2002). As results, tree species in boreal forests differ strikingly in their rates of growth, nutrient uptake strategies, transpiration, litter chemistry and flammability (Flanagan et Van Cleve, 1983; Pastor *et al.*, 1996; Van Cleve *et al.*, 1991) which confer them a higher functional diversity. All these changes occurring in different stand developmental stages determine the productivity of stands in the boreal forest (Chapin III *et al.*, 1998, 2000) but their heterogeneity across the forest landscape could make productivity modelling more complex.

The lower species diversity and the dynamic aspect of stands in the boreal mixedwoods, led DPR studies in boreal forests to generally focus on how changes in stand species composition affect tree growth and stand productivity (Goulden *et al.*, 2011; Paré et Bergeron, 1995; Taylor *et al.*, 2014); particularly with regard to the productivity of commercial tree species with high merchantable value (Légaré *et al.,* 2004; Légaré *et al.*, 2005a; Felipescu et Comeau 2007; Cavard *et al.*, 2010).

The type of DPR (positive, negative or nonsignificant) in boreal forests depend on mechanisms underlying facilitation, competition and niche partitioning; particularly when the species involved belong to different functional groups (broadleaf versus conifers, referred hereafter as stand compositional diversity) (e.g. Légaré *et al.*, 2004; Felipescu et Comeau, 2007; Cavard *et al.*, 2010; Cavard *et al.*, 2011a; Drobyshev *et al.*, 2013; Aussenac *et al.*, 2016). On one hand, Légaré et al. (2004), Felipescu et Comeau (2007) and Cavard et al. (2010) suggested facilitation and higher interspecific competition to explain the variability in the influence of companion species with respect to nutrient availability (facilitation) and utilization (competition). On the other hand, Drobyshev et al. (2013) and Aussenac et al. (2016) suggested niche partitioning to explain the growth variability among functional groups. These studies, however, fail in giving more insight into mechanisms underlying DPR since they do not account for the diversity of traits between and within species both above- and belowground. Since these studies mostly used species aboveground traits to test these links in boreal forests, exploring belowground interactions between species will help identify traits that can be included in DPR models in boreal forests.

1.1.4 Belowground interactions between species

The soil represents the most complex compartment to study in forest ecosystems. It is the place where several ecosystem processes playing an important role in the growth of trees occur. Besides being trees' feeding substrate, it also constitutes a living medium for several microorganisms' communities. These microorganisms (microbes and fungi) play a fundamental role in the decomposition of dead organic matter and in the biogeochemical cycle of nutrients (Hooper *et al.*, 2000; van der Heijden *et al.*, 2008). Both plants and microorganisms interact in the soil. The type of interaction they maintain, either positive (facilitation and niche partitioning) or negative (competition), determines the structure, composition, and productivity of plant communities (Frontier *et al.*, 2008).

- Facilitation

Research on plant community dynamics generally aims at predicting fluctuations in the abundance of species in their environment. These predictions are based on models focusing on the factors behind the distribution of species, including biotic and abiotic factors (Barry et Elith, 2006; Bertness *et al.*, 1999; Graham *et al.*, 2007). Regarding belowground biological interactions, facilitation is the major mechanism causing large fluctuations in soil chemical properties. Theoretically, the facilitation is observed when an organism, called “facilitator” modifies the initial environmental conditions (biotic or abiotic) of its community while making it more favorable for other organisms (Bruno *et al.*, 2003); either directly (by reducing thermal stress due to exposure to wind and light or by reducing stress related to low availability of limiting nutrients) or indirectly (by eliminating competitors or parasites) (Bertness et Callaway, 1994; Stachowicz, 2001). The facilitation therefore consists in the fact that in a given plant community, the presence of one species positively impact the growth, the survival and the regeneration of another species (Bertness et Callaway, 1994). This is the case between aspen and spruce in the boreal mixedwoods.

In the boreal mixedwoods, the compositional diversity of stands changes during forest succession and affects the environmental conditions and energy supply of soil microbes through the functions of the roots, above- and below-ground litter production, light interception and leaching processes in the canopies (Bauhus *et al.*, 1998; Côté *et al.*, 2000; Klimek *et al.*, 2016; Légaré *et al.*, 2005b; Merilä *et al.*, 2002; Ohtonen et Väre, 1998; Taylor *et al.*, 2014). Evidence of the importance of species mixture in maintaining ecosystem functioning and the existence of potential complementary relationships between co-occurring species reported in these studies suggest that aspen has significant positive effects on belowground processes. Aspen and spruce generally differ in their litter quality (Côté *et al.*, 2000; Légaré *et al.*, 2005b), coarse and fine roots distribution within soil profiles (Brassard *et al.*, 2009, 2013). These studies shown that the presence of aspen within stands in boreal forests positively influences soil properties and activity of soil microorganisms which benefit spruce. Through its effect on the composition of soil microorganisms, aspen plays a fundamental role in the decomposition of dead organic matter and in the biogeochemical cycle of nutrients, including carbon and nitrogen cycle (Légaré *et al.*, 2005b). By positively modifying environmental conditions, aspen makes additional resources (light, nutrients and water) in mixed stands compared to pure spruce stands; which has a direct effect on spruce recruitment, survival and growth rates (Cavard *et al.*, 2010, 2011; Légaré *et al.*, 2004, 2005a). Analyzing the functional traits of both tree species therefore emerge as an important way to understand how ecosystem processes playing a key role in their growth are generated.

- Competition

Unlike aboveground competition which mainly involves a single resource (light), belowground competition is very complex. It encompasses a wide variety of resources including water and essential nutrients which differ in their forms (organic and mineral) molecular size, level of oxidation and mobility in soil (Casper et Jackson, 1997). Belowground competition also affects several physiological mechanisms (Kiaer *et al.*, 2013; Wilson, 1988), is asymmetric as the understory vegetation (mosses, *Ericaceae* and vascular plants) can also interfere with tree nutrient uptake (Weiner *et al.*, 1997).

Each species adopts different growth strategies to cope with belowground competition. These strategies are morphological and physiological adjustments that plants make in response to competition (Craine, 2005; Tilman, 1988, 2007). These growth strategies and the rate of competition for resources differ between species and according to the succession stage of forest stands (Bazzaz, 1979; Messier *et al.*, 1999). Although still poorly understood and less studied in the boreal forest, it is suggested that a good knowledge of the differences in nutrient uptake strategies are as important in explaining the coexistence of species as the differences in tree aboveground growth (Bauhus et Messier, 1999).

Competition is detected where there are interactions between several tree species. It can cause a decrease in the growth, survival or regeneration of co-occurring tree species. Conceptually, there is competition when the roots of species overlap in depletion zones along the soil profile (Brisson et Reynolds, 1994; Robinson, 1996); decreasing species-specific nutrient uptake (Casper et Jackson, 1997; Tilman, 1982). It is therefore proposed that two species competing for the same limiting resources cannot coexist because the most competitive species will eliminate the less competitive over time (Craine et Dybzinski, 2013; Dybzinski et Tilman, 2007, 2009; Gause, 1934; Tilman, 1982).

Trees take up nutrients from the soil through their root system and their association with fungi (mycorrhizae). The root system of a tree is made up of two types of roots; (1) coarse and (2) fine roots (Drénou, 2006; McClaugherty *et al.*, 1982). The coarse roots, by their annual growth (length and diameter), as well as their branching, ensure anchoring and increase tree resistance to wind damage (Drénou, 2006; Robinson *et al.*, 2003). Coarse roots bear fine roots (diameter < 2 mm) whose main function is to ensure the uptake of water and nutrients (Gilman, 1990; White *et al.*, 2013). Fine roots are generally mycorrhized (mycorrhizae are symbiosis between tree roots and fungi (Brundrett, 2002, 2009; Drénou, 2006). Fine roots develop where nutrients are the most available (Crabtree et Bernston, 1994; Forde et Lorenzo, 2001; Pacé *et al.*, 2017). Therefore, the root response to a depletion zone is generally used as an indicator of competition for nutrients (Craine, 2005; Grime, 2007; Tilman, 2007).

In contact with the roots of other species, the roots of some plants release secondary substances (exudates), which may regulate the soil microorganism communities, favor symbiosis, change the soil chemical properties or inhibit the growth of other plant species (Chaparro *et al.*, 2013; Nardi *et al.*, 2000). This mechanism is called interference competition. Also known as allelopathy, interference competition has deleterious effects on plant growth or survival (Bais *et al.*, 2004; Flores, 1999); thus, playing an important role in the establishment and maintenance of plant communities (Walker *et al.*, 2003).

Physical space is also considered an important resource for the development and growth of plants (Casper *et al.*, 2003; McConnaughay et Bazzaz, 1991, 1992). For plants growing in a spatially limited environment, the allocation of roots of some species could constrain the root allocation of other species, thereby reducing their nutrient uptake capacity. In response to competition for space, some species modify the structure of their root system (McConnaughay et Bazzaz, 1992) to avoid competition for space and resources (Mou *et al.*, 1997). Competition avoidance generally consists of architectural adjustments (local changes in topology, root length or in the angle or number of root branching (Berntson, 1994; Brassard *et al.*, 2009, 2013) or selective allocation of root biomass in areas where the competition rate is the lowest (Grams et Andersen, 2007). This mechanism is common in species forming root grafts such as trembling aspen (DesRochers *et al.*, 2003; Grams et Andersen, 2007; Gray, 2000), and most often results in spatial segregation between potentially competitive species (niche partitioning).

- Niche partitioning

Niche partitioning has been a primary focus of many population and community ecology studies, as it resolves the paradox of competitive exclusion and the fact that many ecosystems have ecologically similar species that do not drive one another extinct. The ecological niche is a term for the position of a species within an ecosystem (MacArthur et Levins, 1967). It therefore describes both the range of resources and conditions necessary for persistence of the species, and its ecological role in the ecosystem (Hutchinson, 1959, 1961). Theoretically, if two species have the same niche, one species will exclude the other. The term niche partitioning therefore refers to the process by which natural selection drives competing species into different patterns of resource use or different niches (Chesson, 2000; Hector et Hooper, 2002; MacArthur, 1958). Species partition belowground resources in a variety of ways (spatial, temporal or in the species' preferences for different forms of available resources), most often taking advantage of environmental heterogeneity (Mou *et al.*, 1997).

Differences in the rooting depth of species may contribute to vertical partitioning of trees' nutrient uptake in the boreal forest. Despite the fact that tree roots are predominantly restricted to the upper soil layers (Brassard *et al.*, 2009), different rooting patterns have been reported between spruce and aspen (Brassard *et al.*, 2013); particularly with regard to fine roots (Brassard *et al.*, 2013; Ma et Chen, 2017; Pacé *et al.*, 2017). Fine roots are crucial for tree nutrient uptake (White *et al.*, 2013) whereas coarse roots increase tree resistance to wind damage and are most involved in water uptake (Robinson *et al.*, 2003). Most conifers in the boreal forest of Canada have a shallow rooting systems (e.g. black spruce, white spruce) while hardwood tree species have a deep rooting system (Kabzems et Louisier, 1992; Ouimet *et al.*, 2008; Pregitzer *et al.*, 2002; Strong et La Roi, 1983).

The ecology of mycorrhizal fungi provides a good understanding of forest soil functioning and tree species' autecology with regard to their survival, nutrition, and productivity (Kranabetter *et al.*, 2008). Roots associations with mycorrhizal fungi have been shown to decrease competition and increase yield when species are mixed (Perry *et al.*, 1992). The fundamental aspect of mycorrhizae ecology is the relationship between soil nitrogen (N) supply and their diversity and distribution. In the boreal forest, ectomycorrhizal fungi can facilitate organic N availability and uptake (Chalot et Brun, 1998; Read *et al.*, 2004; Read et Perez-Moreno, 2003) especially in cold and less fertile soils (Lipson et Näsholm, 2001) where the partitioning of N uptake may favor the coexistence of species.

Trees generally take up soil nutrients in their mineral forms (Tamm, 1991). However, some conifer species such as black spruce in the boreal forest are able to absorb and utilize organic nitrogen (Kielland *et al.*, 2006, 2007). This may suggest a remarkable partitioning nutrient uptake between boreal tree species; whether between conifers or between conifers and hardwoods. Houle *et al.* (2014) used leaf traits (nitrogen isotopic signature and concentration) to reveal nitrogen partitioning (N uptake at different soil depths) between jack pine and black spruce and suggested that this resource partitioning may have implications on the productivity of boreal forests. A similar situation may exist for aspen and spruce in mosaic of mixed stands of both species and may be used to understand their long-term coexistence in the black spruce – moss bioclimatic domain of Quebec.

In summary, facilitation, competition and niche partitioning are closely related and can simultaneously occur in a given plant community. Facilitation could favor competition (by altering the root traits of species (Callaway *et al.*, 1991 ; Dickie *et al.*, 2005)) which, in turn may result in niche partitioning (Callaway, 1995 ; Gause, 1934). Although the beneficial part of facilitation has received considerable research interest, some studies have reported its bidirectional nature; in particular, the physiological and fitness consequences for both beneficiaries (neighboring species) and facilitators (Schöb *et al.*, 2012, 2014). By modifying the local environmental conditions, facilitators may create new niche space, which favor some new species while excluding others. However, this bidirectional nature of the facilitation is generally neglected. Most studies focus solely on either facilitation (overlooking the positive effect of the facilitator species on beneficiaries), competitive exclusion or niche partitioning. Addressing these three mechanisms is therefore critical in determining whether species are complementary in a plant community.

Two hypotheses (niche complementarity and sampling effect) have been proposed to support positive diversity-productivity relationship (DPR) in terrestrial ecosystems

(Huston, 1997 ; Loreau, 1998 ; Loreau et de Mazancourt, 2013 ; Tilman, 1999 ; Tilman *et al.*, 1997, 2006). The sampling as well as complementarity effects generally implies that plant community productivity strongly depends on the functional traits of the constituent species (Roscher *et al.*, 2012). The sampling effect hypothesis proposes that diverse communities with high productivity are those where there is a greater chance to find more productive species with specific functional traits that allow greater resource use, in higher proportion. The niche complementarity hypothesis proposes that species-rich communities are able to access and utilize limiting resources efficiently because they contain species with a diverse array of ecological attributes. Complementarity effects occur when interspecific niche differences lead to more efficient acquisition of limiting resources and, therefore, higher productivity. The niche complementarity hypothesis has been suggested as the main hypothesis supporting positive DPR in ecosystems with harsh environmental conditions such as the boreal forest (Paquette et Messier, 2011). Good understanding of belowground interactions between tree species is therefore critical to provide a mechanistic interpretation of DPR to determine whether mixed silviculture could be promoted in the boreal forest.

1.2 Problem statement

This study focuses on black spruce and trembling aspen, two of the most dominant and economically valuable species in the boreal forests of eastern Canada (Armstrong, 2014; Zhang et Pearse, 2012). Forest managers' penchant for monosilvicultural practices, as described in the above sections, is likely supported by studies such as Cavard *et al.* (2011b) while there appear to be misunderstandings about interactions between black spruce and trembling aspen in mixed stands of boreal forest. Recent studies (Aussenac *et al.*, 2016; Cavard *et al.*, 2011b) have shown a negative effect of species mixing on tree growth compared to tree growth in pure stands. Cavard *et al.* (2011b) showed that low productivity of mixed stands of aspen and spruce resulted in the decline of aspen growth and slowed growth of spruce over time. These studies suggested that the decline of aspen growth may be related to a decrease in soil fertility due to a gradual accumulation of spruce litter which have a very low rate of decomposition. However, early studies in the same type of stands were showing positive effects of TA on both spruce growth (Légaré *et al.*, 2004, 2005a) and soil fertility (Légaré *et al.*, 2005b). A picture emerging from this research suggests that soil nutrition may be the key factor controlling productivity that likely interacts with complementary of these species to climatic fluctuations (Drobyshev *et al.*, 2013).

The 2009 report of the Sustainable forests Management Network of Canada has indicated that forest productivity will decline in areas with precipitation deficit and there will be short-term increases in the northern regions where black spruce is the most dominant species (McKenney *et al.*, 2007; Williamson *et al.*, 2009). These previsions also indicate that site quality may become more favorable to early succession species (Logan et Ouranos (Consortium de recherche), 2012; Prato, 2008) such as trembling aspen which already coexists with black spruce (hereafter spruce), forming boreal mixedwoods. This could lead to dominance of trembling aspen (hereafter aspen) within forest stands in these regions over time. Conversely, most widely used management practices in the boreal mixedwoods (clear-cuts, cuts with protection of regeneration and planting) tend to favor the development of BS-dominated stands and disfavour mixed spruce and aspen stands; while the latter would be more productive (Légaré *et al.*, 2004) and resilient to climate change (Drobyshev *et al.*, 2013).

The question is whether the overlooked climate complementarity of the two studied species is equally observable in the soil where several mechanisms (competition, niche partitioning and facilitation (Neufeld *et al.*, 2014)) governing the coexistence of species may occur? These mechanisms play an important role in the growth and dynamics of mixed stands (Filipescu et Comeau, 2007; Man et Lieffers, 1999). Knowledge of these mechanisms in natural forest ecosystems is still limited. In this context, it is necessary to improve our understanding of the factors controlling growth, resource partitioning and the way these two species interact in mixed stands.

1.3 Objectives and hypotheses

This thesis explores the belowground interactions between black spruce and trembling aspen to determine if they are complementary with regard to the use of soil nutrients in mixed stands in the boreal forest of northwestern Quebec. We test the "resources partitioning hypothesis" (Turner, 2008) which proposes that competing species are more likely to coexist when they use resources in different ways. The main body of the thesis is structured around three chapters grouped into two main parts. The first part (Chapters II and III) explores the resource acquisition strategies of the two species whereas chapter IV focuses on nitrogen (N) to validate the conclusions of the first part.

Chapter II examines the functional traits of the roots (fine roots biomass and root tissue density) to understand how the use of soil resources help these species to persist in mixed stands in the boreal forest. We hypothesized (1) that the two species have different rooting depth (shallow for spruce and deep for aspen) in pure stands. Second, based on the concept of "functional equilibrium" (Iwasa et Roughgarden, 1984), we hypothesized (2) that the fine root biomass (FRB) of spruce will decrease in mixed stands, and that (3) the fine root biomass of aspen will increase in mixed stands. The functional equilibrium hypothesis assumes that in ecosystems subject to nutrient stress, plants will allocate more biomass towards the roots to enhance the uptake of resources when nutrient availability becomes limiting, and contrarily when soil fertility increases. Since the nutrient content increases mostly in the organic layer of mixed stands compared to pure spruce stands (Légaré *et al.*, 2005b), we hypothesized that (4) the spruce would exhibit lower FRB and higher root tissue density, and that the opposite pattern would be observed in aspen in the organic layer of mixed stands, compared to pure spruce and pure aspen stands. We expected, therefore, an intensive nutrient uptake strategy for spruce and extensive strategy for aspen, which is characterized by generally low and high carbon investments in root production, respectively (Addo-Danso *et al.*, 2018; Grime, 1977; Grime *et al.*, 1986; Lõhmus *et al.*, 1989). Finally, we hypothesized that (5) the increasing aspen FRB in mixed stands compared to pure aspen stands would lead to a stronger spatial separation of spruce and aspen roots (shallower for spruce and deeper for aspen), and consequently, contrasting nutrient uptake strategies in different soil horizons.

Considering the fact that mycelial network of mycorrhizae increases the surface area of the root, Chapter III analyses the structure and composition of the root-associated mycorrhizal communities of spruce and aspen to determine whether the stand compositional tree diversity affects the ability of the two tree species to take up nutrients by impacting individual mycorrhizal community composition of these tree species. We first hypothesized (1) that the root-associated mycorrhizal community structure (diversity, similarity and distribution along the soil profile) of spruce and aspen differs between pure spruce and pure aspen stands. We further hypothesized (2) that mixing the two species within a stand means a higher α-diversity of root-associated mycorrhizal community and a change in mycorrhizal species composition, resulting from changes in soil chemical properties and increased competition. Finally, we hypothesized (3) that mixing of two species leads to a stronger spatial separation of mycorrhizal communities along the gradient in soil depth, i.e. a shallower location of spruce-associated communities and deeper location of aspen-associated communities, as compared to pure stands.

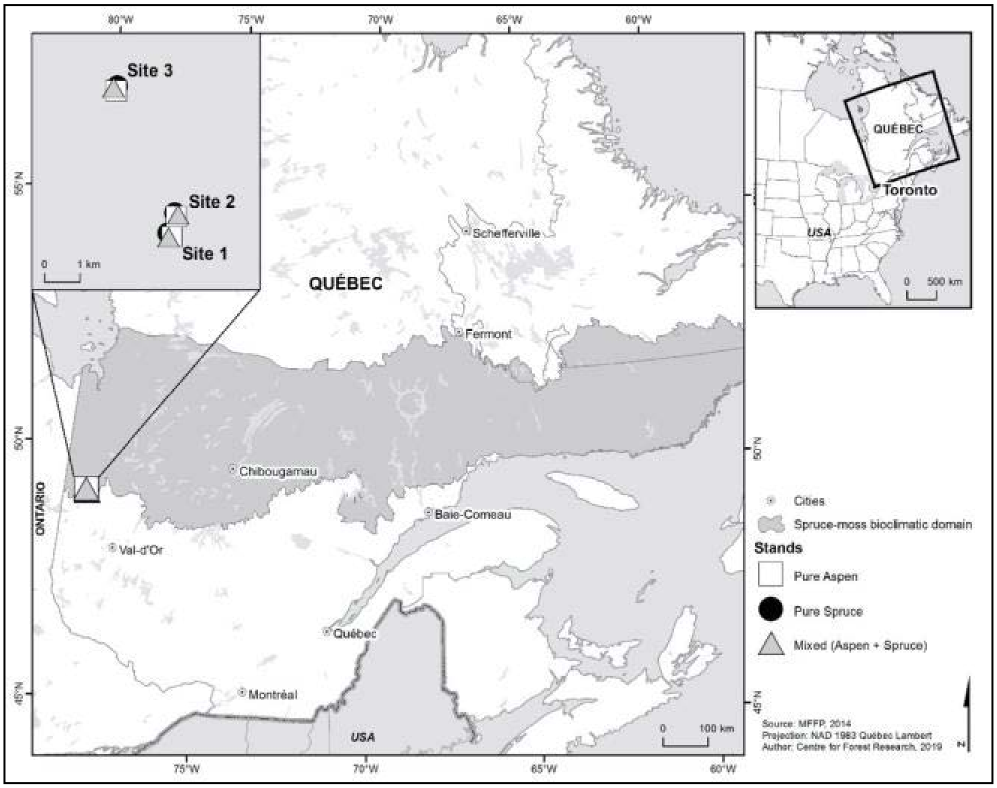
The second part of the thesis has only one chapter. Chapter IV focuses on nitrogen, which represents the most limiting resource for tree growth in the boreal forest. The isotopic geochemistry approaches are used to determine whether the coexistence of the two species results from the fact that they absorb nitrogen at different soil horizons or because they have different preferences for the two mineral forms of nitrogen (ammonium and nitrate). First, to test for the N spatial partitioning, we compared the ^{15}N natural abundance in the soils and in the foliage of spruce and aspen in pure and mixed stands. We hypothesized (1) that the two species takes up the N at different soil depth (shallower N-uptake in spruce and deeper in aspen) in both pure and mixed stands. Second, to test for partitioning of N-inorganic forms, we performed a 30 day *in-situ* ^{15}N-labeling experiment in pure and mixed stands. We hypothesized (2) that in their respective pure stands, black spruce would prefer ammonium and aspen would prefer nitrate. In mixed stands, we expected (3) the N-form preference of both species to be more pronounced as the two species will seek to distance themselves to avoid competition. Finally, since the nutrient content increases mostly in the organic layer of mixed stands, as compared to pure spruce stands (Légaré *et al.*, 2005), we hypothesized (4) that spruce will benefit of a better N nutrition in mixed than in pure stands while the net effect will be neutral for aspen.

These three chapters are followed by a general conclusion in which I summarize the underground interactions between spruce and aspen in the boreal mixedwoods. I also discuss the implications for the growth of spruce and aspen between pure and mixed stands. I use this information to recommend sylvicultural practices that may help limit competition for resources and prevent biodiversity and productivity losses in boreal forest stands. I also discuss what these results imply for the development of future research protocols in the context of DPR studies in boreal forests.

1.4 Study area

The study area is located in the southern part of the black spruce-feathermoss bioclimatic domain in North-Western Quebec (49°08’N to 49°11’N and 78°46’W to 78°53’W). The boreal mixedwood in the area is dominated by black spruce, which grows on deep clay soils developed from proglacial deposits of Barlow and Ojibway lakes at the time of their maximum expansion during the Wisconsonian glaciation (Veillette, 1994). The mean annual temperature and total annual precipitation of the study area are 1.5°C and 675.7 mm, respectively (Environment Canada, 2016). Fires and insect outbreaks are primary factors of natural forest dynamics in the area. Selected stands (three sites in total) were growing on moderately dry clay dominated soil (Brais et Camiré, 1992), and originated from the same fire that occurred in the area ca. 1916 (Légaré *et al.*, 2005b).

The three studies sites were between 2 and 15 km away from each other. On each site we selected one pure (monodominant) stand of trembling aspen (TA), one pure black spruce (BS), and one mixed stand (Figure 1.2). These were 20 x 50 m^2 (0.1 ha) rectangular samples plots established in each site so that each plot represents a stand type which was uniform in terms of topography and vegetation. We defined pure stands as those with the proportion of stems and basal area of the most abundant tree species exceeding respectively 75 % and 60 % in the total count of individuals with diameter at 1.3 m above 10 cm. Mixed stands were those with the number of trees of individual species representing 30 % to 50 % of the total number of stems in the stand (MFFP, 2015).



Source: MFFP, 2014
Projection: NAD 1983 Québec Lambert
Author: Centre for Forest Research, 2019

Figure 1.2 Location of the study sites in the spruce-moss bioclimatic domain of Quebec.

CHAPTER II

CONTRASTING ROOT SYSTEM STRUCTURE AND BELOWGROUND INTERACTIONS BETWEEN BLACK SPRUCE (*Picea mariana* (Mill.) B.S.P) AND TREMBLING ASPEN (*Populus tremuloides* Michx) IN BOREAL MIXEDWOODS OF EASTERN CANADA

(STRUCTURE CONTRASTÉE DU SYSTÈME RACINAIRE ET INTERACTIONS SOUTERRAINES ENTRE L'ÉPINETTE NOIRE (*Picea mariana* (Mill.) B.S.P) ET LE PEUPLIER FAUX-TREMBLE (*Populus tremuloides* Michx) DANS LES FORÊTS BORÉALES MIXTES DE L'EST DU CANADA)

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2.1 Résumé

Cette étude explorait les interactions souterraines entre l'épinette noire et le peuplier faux-tremble dans les peuplements purs et mixtes pour comprendre comment l’utilisation des ressources du sol aide ces espèces à coexister dans les forêts boréales mixtes de l'ouest du Québec. Nous avons analysé les stratégies d’acquisition de ressource des racines fines de chaque espèce (biomasse racinaire et densité des tissus racinaires) le long de trois couches de sol (organique, couches supérieure 0-15 cm et inférieure 15-30 cm du sol minéral), en utilisant 180 carottes de sol. Les carottes ont été collectées dans trois sites, contenant chacun trois parcelles de 20 × 50 m^2 pur d'épinette, purs de tremble et mixte d'épinette et de tremble. L'épinette avait un enracinement superficiel, tandis que le tremble avait un enracinement profond dans les deux types de peuplements. Par rapport aux peuplements purs d'épinette, l'épinette avait une biomasse de racines fines (FRB) plus faible et une densité de tissu racinaire (RTD) plus élevée dans la couche organique des peuplements mixtes. Ces deux traits indiquaient une stratégie d’utilisation intensive des ressources par l’épinette et son avantage concurrentiel sur le tremble dans cette couche. La FRB de tremble dans le sol organique ne différait pas significativement entre les peuplements purs et mixtes, mais augmentait dans le sol minéral des peuplements mixtes. Puisque nous n'avons pas observé de différence significative dans la teneur en éléments nutritifs de la couche de sol minéral entre le peuplier faux-tremble pur et les peuplements mixtes, nous avons conclu que le peuplier faux-tremble peut subir une exclusion compétitive dans la couche organique par l'épinette. Le peuplier faux-tremble a présenté une stratégie extensive d'absorption des nutriments dans la couche organique des peuplements mixtes: FRB plus élevée et RTD plus faible que l'épinette. Dans les peuplements mixtes, les différences dans la structure d'enracinement du tremble entre les couches organiques et minérales suggèrent l'utilisation de stratégies contrastées d'absorption des nutriments le long du profil du sol. Nous supposons qu’une séparation spatiale plus marquée des racines de l'épinette et du tremble dans les peuplements mixtes contribue probablement à un partitionnement de leur absorption d'éléments nutritifs le long du profil du sol. Ces résultats indiquent une exclusion compétitive du tremble par l'épinette dans les sols des forêts boréales mixtes tout en suggérant que cette exclusion compétitive ne se produit probablement que dans la couche organique du sol.

Mots-clés: relation diversité-productivité; stratégie d'absorption des nutriments; biomasse de racines fines; densité de tissu racinaire; diversité compositionnelle du peuplement

2.2 Abstract

This study explored the underground interactions between black spruce and trembling aspen in pure and mixed stands to understand how their soil resource use help these species coexist in the boreal mixedwoods of Western Quebec. We analyzed species-specific fine root foraging strategies (root biomass and root tissue density) along three soil layers (organic, top 0–15 cm, and bottom 15–30 cm mineral soil), using 180 soil cores. We collected cores in three sites, each containing three 20 × 50 m^2 plots i.e. pure spruce, pure aspen, and mixed spruce and aspen stands. Spruce had a shallow rooting, whereas aspen had a deep rooting in both types of stands. Compared to pure spruce stands, spruce had a lower fine root biomass (FRB) and a higher root tissue density (RTD) in the organic layer of mixed stands. Both patterns were indicative of spruce's more intensive resource use strategy and competitive advantage over aspen in that layer. Aspen FRB in the organic soil did not differ significantly between pure and mixed stands, but increased in the mineral soil of mixed stands. Since we did not observe a significant difference in the nutrient content of the mineral soil layer between pure aspen and mixed stands, we concluded that aspen may experience competitive exclusion in the organic layer by spruce. Aspen exhibited an extensive nutrient uptake strategy in the organic layer of mixed stands: higher FRB and lower RTD than spruce. In mixed stands, the differences in aspen rooting patterns between the organic and mineral layers suggested the use of contrasting nutrient uptake strategies along the soil profile. We speculate that the stronger spatial separation of the roots of spruce and aspen in mixed stands likely contribute to a higher partitioning of their nutrient uptake along the soil profile. These results indicate the competitive exclusion of aspen by spruce in boreal mixedwoods, which likely occurs in the soil organic layer.

Keywords: diversity-productivity relationships; nutrient uptake strategy; fine root biomass; root tissue density; stand compositional diversity

2.3 Introduction

Understanding the relationship between diversity and productivity in forest ecosystems is critical to quantifying ecosystem responses to past and future environmental variability. A consistent and positive relationship between these two variables has been demonstrated on the global scale (Liang *et al.*, 2016; Zhang *et al.*, 2012, 2016) in temperate and tropical forests (Morin *et al.*, 2011; Ratcliffe *et al.*, 2015; Roscher *et al.*, 2012; Ruiz-Benito *et al.*, 2014). Forest stands with high structural and species richness support a greater diversity of species (understory vascular plants, birds, insects, and mammals) and functions (Franklin et Van Pelt, 2004; Hunter, 1999), and have greater productivity (Légaré *et al.*, 2005; Lei *et al.*, 2009; Paquette et Messier, 2011; Wang *et al.*, 2011). More diverse stands have been shown to exhibit a higher resilience to environmental variability (Aussenac *et al.*, 2016; Morin *et al.*, 2014; Yachi et Loreau, 1999). On the other hand, a few studies have highlighted an insignificant or even negative effect of species diversity on forest productivity (Cavard *et al.*, 2010; Chen *et al.*, 2003) and tree growth (Aussenac *et al.*, 2016). Earlier studies of diversity–productivity relationships (DPR) in boreal mixedwoods focused primarily on the effects of variability in climate (Aussenac *et al.*, 2016; Drobyshev *et al.*, 2013) and light conditions (Cavard *et al.*, 2010). Evaluating variability in tree diameter and volume growth, these studies indicated the potential role of competition, facilitation, and niche complementarity in shaping tree productivity (Cavard *et al.*, 2011a; Filipescu et Comeau, 2007; Paquette et Messier, 2011). Apart from theoretical interest, a mechanistic model explaining DPR in the boreal forest could be of critical importance in developing silvicultural practices in boreal mixedwoods.

Black spruce and trembling aspen are two of the most dominant and economically-valuable species in the boreal forests of eastern Canada (Armstrong, 2014; Zhang et Pearse, 2012). These species have broadly different habitat requirements and successional trajectories and are hypothesized to temporally coexist in the stands in the absence of fire (Bergeron *et al.*, 2014) because of the competitive exclusion of aspen by spruce over time. These ecological considerations, the absence of a general trend concerning DPR (Cavard *et al.*, 2011a; Légaré *et al.*, 2004), and the concern of operationalizing tree harvest in mixed stands of the two species have led forest managers to opt for clearcutting on ~85% of the total harvested area in Canada (Statistics Canada, 2018). The growing evidence of a positive species mixing effect on stand productivity (Paquette et Messier, 2011) and resilience to major disturbances, such as fire (Wirth, 2005) and insect outbreaks (Bergeron *et al.*, 1995; Bouchard *et al.*, 2006), including the projected northward shift in the range of distribution of aspen with future climate conditions (McKenney *et al.*, 2007, 2011), calls for the consideration of silvicultural practices focused on mixed stands.

Aspen (TA) and spruce (BS) can modify their environment through the impact of their litter and root system on soil chemistry (Légaré *et al.*, 2005). As compared to pure spruce stands, mixed stands of spruce and aspen have higher soil fertility, due to increases in soil temperature, humidity, nutrient content, and pH. In turn, this leads to a positive relationship between aspen abundance in mixed stands and the total stand productivity (Légaré *et al.*, 2004), despite a negative effect of spruce on aspen growth (Cavard *et al.*, 2011a). The accumulation of spruce litter and reduced rates of its decomposition in mixed stands of spruce and aspen compared to pure aspen stands

(Légaré *et al.*, 2005) could be among the factors behind such a negative effect on aspen growth. The use of soil nutrients appears to be the central element in species interactions affecting growth rates, species geographic distribution, and nutrient cycling within forest stands. However, the contribution of underground interactions has seldom been quantified, and their effects on productivity remain to be demonstrated.

Underground interactions between tree species occur through the effect on the availability of resources, chemical signaling, and the secretion of allelochemical compounds (Callaway, 2002). These can either be positive, neutral, or negative (Kuebbing et Nuñez, 2015). Positive interactions exhibit themselves when one species has a positive effect on other species by increasing the availability of soil nutrients (Callaway, 1995; Callaway *et al.*, 2002), whereas negative interactions occur through resource depletion, allelopathy, or interference competition (de Kroon *et al.*, 2003, 2012; Goldberg, 1990). These mechanisms can simultaneously occur in the same plant community (Holzapfel et Mahall, 1999). Therefore, there is a need to consider resource competition and the physiological response of plants to competition in order to better understand the underground interactions between species in mixed forest stands.

Fine roots are of immediate importance for tree nutrient uptake (Pregitzer *et al.*, 2002), and their biomass, tissue density, nutrient content, and distribution along the soil profile have been viewed as proxies for nutrient uptake strategies (Brassard *et al.*, 2009; Craine, 2005; Lõhmus *et al.*, 2006; Ostonen *et al.*, 2007a; White *et al.*, 2013). The filling of soil volume by fine roots (hereafter referred to as *fine root biomass*) has been shown to reflect nutrient availability (Ostonen *et al.*, 2007a, 2007b), and has an impact on tree aboveground biomass production (Brassard *et al.*, 2013), ultimately determining tree competitive ability for resources (Tilman, 1982, 2007). On the other hand, the root tissue density (RTD, the amount of structural material invested by the unit volume of roots) is related to the availability of nutrients, and reflects the response of species to competition for resources (Grime, 1977). Root biomass and tissue density are, therefore, essential metrics which define species' underground niche, in terms of its resource use (Craine, 2005; Tilman, 2007).

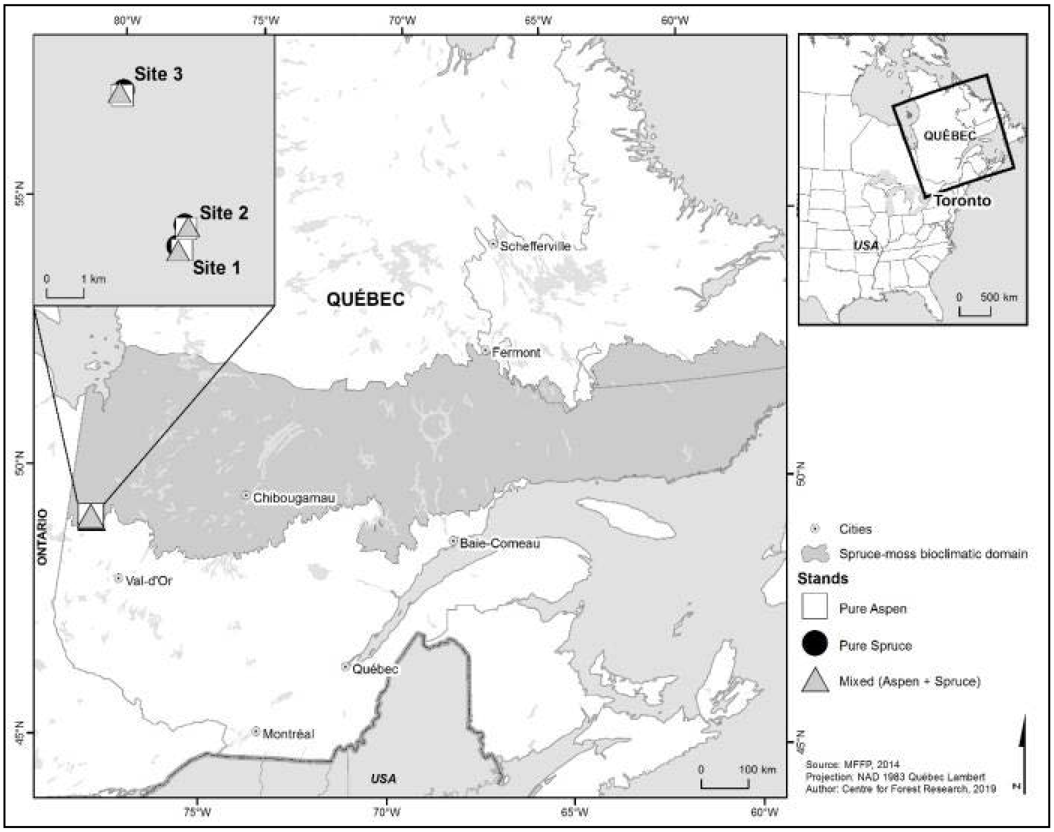
We tested for differences in root foraging strategies between black spruce and trembling aspen, by analyzing their fine root biomass and tissue density along the soil profile in pure and mixed stands. We tested the general hypothesis that species coexistence in ecosystems is maintained through differences in resource use (Turner, 2008). More specifically, we first hypothesized (H1) that the two species have different rooting depth (shallow for spruce and deep for aspen) in pure stands. Second, based on the concept of "functional equilibrium" (Iwasa et Roughgarden, 1984), we hypothesized (H2) that the fine root biomass of spruce will decrease in mixed stands, and that (H3) the fine root biomass of aspen will increase in mixed stands. The functional equilibrium hypothesis assumes that in ecosystems subject to nutrient stress, plants will allocate more biomass towards the roots to enhance the uptake of resources when nutrient availability becomes limiting, and contrarily when soil fertility increases. Since the nutrient content increases mostly in the organic layer of mixed stands compared to pure spruce stands (Légaré *et al.*, 2005), we hypothesized that (H4) the spruce would exhibit lower FRB and higher root tissue density, and that the opposite pattern would be observed in aspen in the organic layer of mixed stands, compared to pure spruce and pure aspen stands. We expected, therefore, an intensive nutrient uptake strategy for spruce and extensive strategy for aspen, which are characterized by generally low and high carbon investments in root production, respectively (Addo-Danso *et al.*, 2018; Grime, 1977; Grime *et al.*, 1986; Lõhmus *et al.*, 1989). Finally, we hypothesized that (H5) the increasing aspen FRB in mixed stands compared to pure aspen stands would lead to a stronger spatial separation of spruce and aspen roots (shallower for spruce and deeper for aspen), and consequently, contrasting nutrient uptake strategies in different soil horizons. Knowledge about such a pattern will help guide future forest management decisions in the boreal zone of Quebec.

2.4 Materials and Methods

2.4.1 Study Area

The study area was located in the black spruce-feathermoss bioclimatic domain in north-western Quebec (49°08′ N to 49°11′ N and 78°46′ W to 78°53′ W). The boreal forest in the area is dominated by black spruce, which grows on deep clay soils developed from proglacial deposits of Barlow and Ojibway lakes at the time of their maximum expansion during the Wisconsonian glaciation (Veillette, 1994). The mean annual temperature and total annual precipitation of the study area are 1.5 °C and 675.7 mm, respectively (Environment Canada, 2016). Fires and insect outbreaks are the primary factors of natural forest dynamics in the area. Selected stands were growing on moderately dry, clay-dominated soil (Brais et Camiré, 1992), and originated from the same fire that occurred in the area in ca. 1916 (Légaré *et al.*, 2005).

The studied sites (three in total) were between 2 and 15 km away from each other (Figure 2.1). We established three 20 × 50 m^2 (0.1 ha) rectangular samples plots in each site, whereby each represented a stand which was uniform in terms of topography and vegetation. These comprised one pure (monodominant) stand of trembling aspen, one pure black spruce, and one mixed stand (Figure 2.1).



Source: MFFP, 2014
Projection: NAD 1983 Québec Lambert
Author: Centre for Forest Research, 2019

Figure 2.1 Location of the study sites in the spruce feathermoss bioclimatic domain of Quebec.

The selection criteria for stand types were similar to those of the previous studies investigating tree species' mixing effects in natural forest stands, i.e., pure stands had more than 80% of the stand basal area made up by a single species, whereas in mixed stands, none of the species had a basal area beyond 80% of the total stand basal area (Brassard *et al.*, 2013; Ma et Chen, 2017). Our selection criteria also followed the definition of pure stands in the Quebec forest resource inventory. There, a single conifer species should contribute to more than 75% of stand basal area for the stand to be classified as *pure*, while in mixed stands, 25% to 50% stand basal area should be composed of coniferous trees (MFFP, 2015). To validate the attribution of stand type, we recorded diameter at breast height (DBH), i.e., at 1.3 m, for all trees above 10 cm, and calculated the basal area (BA) and density of each species (Table 2.1).

2.4.2 Sample Collection and Preparation

Selected stands had an overstory dominated by healthy aspen or/and spruce, the same age of the dominant canopy cohorts (100 years; (Légaré *et al.*, 2005)), low proportions of jack pine (*Pinus banksiana* Lamb.) in the canopy (<15%) and balsam fir (*Abies balsamea* (L.) Mill.) in the understory (field observation), and low abundance of *Sphagna* on the forest floor. These stand properties have been reported to influence the biomass of fine roots (Ma et Chen, 2017; Pacé *et al.*, 2017) and nutrient partitioning (Houle *et al.*, 2014) in boreal forests. The selected plots were at least 150 m away from any other sampled point in a given site (Figure 2.1). We selected mixed stands within a transition zone of two pure stands of BS and TA. The 150 m distance between the two stands was designed to avoid border effects. To this end, we kept in mind the results of an earlier study, where the effect of aspen on the soil's physical and chemical properties was reported to persist within a distance of 7 m from a trembling aspen-dominated stand (Légaré *et al.*, 2005).

Table 2.1 Characteristics of sampled stands. BS, TA, and M refer to pure spruce, pure aspen, and mixed stands, respectively.

		Site 1			**Site2**			**Site 3**		
		BS	**TA**	**M**	**BS**	**TA**	**M**	**BS**	**TA**	**M**
Species proportion (% number of stems)	*Populus tremuloides*	2	60	34	2	70	38	2	74	43
	Picea mariana	83	33	50	89	22	51	97	20	54
	Abies balsamea		6	3		2			6	1
	Pinus banksiana	15	1	10	9	5	11	1		1
	Betula papyrifera Marshall			1						1
	Populus balsamifera L.			2		1				
Density (stems ha^{-1})		3100	1410	1160	3000	1220	1610	2382	900	1680
Organic soil layer properties	pH	3.8	4.0	4.9	4.2	5.0	4.7	3.6	5.01	4.4
	Total C (g kg^{-1})	311	194.2	301.2	337.7	321.5	321.2	376.2	287.2	348.7
	Total N (g kg^{-1})	7.8	10.5	13.7	10.67	11.5	11.8	7.7	17.3	11
	Mineral N (mg kg^{-1})	29.2	31.7	27.5	34.2	43.5	42.0	22.5	72.0	37.2
	C:N ratio	39.9	18.3	21.8	31.6	26.6	27.1	48.8	16.6	31.7
	P (mg kg^{-1})	81.5	36.2	59.7	69.5	79.0	61.5	129.7	90.5	161.2
	K (mg kg^{-1})	407	331	444.7	552.2	585.7	480.7	460.7	524.2	635.7
Basal area (BA, m^2 ha^{-1})		61.42	113.46	61.63	66.6	91.6	78.55	65.48	78.07	74.53
Basal area percentage per species (%)	*Populus tremuloides*	3.32	81.93	58.82	5.50	87.05	63.52	2.86	90.47	68.93
	Picea mariana	72.9	16.11	26.83	80.00	7.50	24.26	96.02	8.47	29.14
	Abies balsamea		0.94	0.78		0.27			1.06	0.20
	Pinus banksiana	23.78	1.02	12.21	14.50	4.35	12.22	1.12		0.78
	Betula papyrifera			0.46						0.25
	Populus balsamifera			0.90		0.83				0.70
Organic layer depth (cm)		17.3	6.2	10.16	20.0	7.5	11.5	14.2	9.76	13

C, N, P, and K in soil properties denote carbon, nitrogen, phosphorus, and potassium, respectively.

At each plot, 20 soil cores were extracted using a 7-cm diameter manual auger every 10 m along four 50 m long transects, spaced 4 m apart from each other. The sampling took place between July 15 and August 20, 2016. The chosen timing broadly corresponded to the period when fine roots are at their maximum length in this part of the boreal forest (Brassard *et al.*, 2013). We collected samples from the organic horizon (F and H layer combined) and from the top 0–15 cm (later referred to as *Min1*) and bottom 15–30 cm (*Min2*) of the mineral soil. The samples were placed in plastic bags, transported to the laboratory in an ice-filled cooler, and stored at a temperature of −20 °C prior to analyses.

The 180 soil cores were pooled per transect and for each soil horizon to form a set of 12 composite samples for each plot. The composite samples were allowed to thaw over six hours and then soaked in water for at least one hour. The mixture was then stirred carefully to separate roots from the soil particles and poured through a 750 µm mesh round sieve. The sieve was suspended under a distilled water bath and shaken continuously until the roots were free from any soil particle. The roots were collected and live and dead roots were separated, based on visual appearance and a manual extension test (Brassard *et al.*, 2013). Live roots were light in color and resistant to breakage, whereas dead roots were a grey to dark color and were easily fragmented. We discarded dead roots from further analyses. Live fine roots were sorted by species, using a combination of morphological characteristics established from prior root reference samples collected on known younger and older trees of each studied species in the study stands. The morphological criteria used were color, size, ramification, and presence/absence of root hairs (Brassard *et al.*, 2013). Aspen roots were less ramified, with colors ranging between white and pale, whereas the roots of coniferous trees were ramified, finer in structure, and of a color ranging between red and brown. Compared to other coniferous trees, spruce roots were more reddish in color with a black bark. Balsam fir (*Abies balsamea* (L.) Mill.) had roots with bark color ranging from yellowish to orange, whereas jack pine had roots with a texture similar to spruce but with a lighter, brown bark color. The presence of root hairs was mostly used to separate nontree roots (commonly with root hairs) from tree roots. We extracted only the roots of spruce and aspen based on these criteria. We discarded roots larger than 2 mm in diameter, measuring them with a caliper. The separated fine roots were gently dried between two filter papers at room temperature to remove water, and were immediately weighed to obtain the fine roots' fresh mass. A representative fresh root subsample per soil layer was subsequently taken per transect in each stand, in such a way that their weight would be comparable among transects (Birouste *et al.*, 2014). Following this protocol, we took two grams of fresh live roots in the FF and in the top *Min1* soil section, whereas only 0.5 g was taken in the lower *Min2*, where fine root weights in the samples were the lowest. The composite samples were oven-dried at 60 °C for 48 h and reweighed to obtain the root dry mass.

2.4.3 Chemical Analysis

An aliquot (50 g) was taken from each soil sample taken per transect and air-dried to a constant weight for a week (Carter et Gregorich, 2008), ground, and sieved (<2 mm). For each soil horizon layer, soils were extracted with 2M KCl (10:1 solution soil ratio, 30 min). Nitrate (NO_3) and ammonium (NH_4) concentrations were measured, respectively, by ion chromatography (Dionex2120i, Thermo Fisher Scientific Inc., Sunnyvale, CA, USA) and colorimetrically with a Technicon Autoanalyzer (Technicon AA2, Seal Analytical Inc., Mequon, WI, USA). Since the observed nitrate concentrations were close to the detection limit (limit of <1 mg kg^{-1} for extractable NO_3), we only report NH_4 results. Total C and N concentrations were measured with an elemental analyzer (Carlo Erba, Milan, Italy). The bulk soil pH in water was analyzed following the method described by Carter and Gregorich (2008) using a Thermo Scientific Orion 2 pH meter (Thermo Fisher Scientific, Waltham, MA, USA). Exchangeable cations and phosphorus (P) were measured by extraction in Mehlich-3 solution (Mehlich, 1984), and were further summed to estimate the effective cation exchange capacity (CEC). A summary of these soil chemical properties is provided in Appendix A Table S2.1. Chemical analyses were conducted at the laboratory of organic and inorganic chemistry of the Ministry of Forests, Wildlife and Parks of Quebec.

2.4.4 Data Analysis

2.4.4.1 Metrics Calculation

Four metrics were used to test the hypotheses. The fine root biomass (FRB) was calculated as the dry mass of living fine roots per volume of soil ($kg \cdot m^{-3}$) in each sample. The vertical heterogeneity index (VHI) was assessed as the standard deviation of fine roots biomass percentages in each of the three soil horizon layers over transect. VHI indicates how fully and evenly fine roots occupy the belowground space (Brassard *et al.*, 2011). The mixture effect ratio (Ro) was calculated as the ratio between the observed biomass (B_o) to the expected biomass (B_{exp}) of fine roots in mixtures. B_{exp} was calculated by multiplying the fine root biomass of each species in pure stands by their respective basal area proportion in mixed stands (Loreau et Hector, 2001). Finally, the root dry matter content (RDMC) was derived as the ratio between root dry mass and root fresh mass, in $g \cdot g^{-1}$. This metric is used as a proxy of root tissue density (RTD, (Birouste *et al.*, 2014)), and represents the amount of structural material invested by unit volume of roots. RDMC is an easily measurable and less susceptible to errors metric, as compared to metrics based on image analysis (Birouste *et al.*, 2014). A potential increase in the volume of data for roots may advance our understanding of underground interactions between plant species (Pierret *et al.*, 2016; Zobel et Zobel, 2002).

2.4.4.2 Statistical Analysis

We used several approaches to test our hypotheses. First, we used (1) a repeated measures analysis of variance (repeated measures ANOVA) to analyze differences in species-specific FRB, and a Kruskal-Wallis rank test to analyze differences in species-specific RDMC. We ran layer-wise comparisons between pure and mixed stands, and comparisons of soil layers within mixed stands. We regarded data collected on the transects as "multiples samples" (repeated measures). The ANOVA consisted of a mixed model with FRB as the response variable. Stand types and transects were fixed-effect factors, and the site identity was the random factor. The normality and the homoscedasticity assumptions were met for FRB data. In contrast, for the RDMC, we performed the Kruskal-Wallis and Dunn tests using R package *dunn.test*, since the normality and the homoscedasticity was not met, even after log10 transformation. Second, we assessed the spatial heterogeneity of fine root distribution by comparing species-specific roots VHI between pure and mixed stands (H1). Lower VHI values are indicative of a more even distribution of fine roots with soil depth (Brassard *et al.*, 2013). Third, we tested for the effect of species mixing on the total fine root biomass within each soil horizon layer by comparing computed Ro values with the threshold value 1 (H2 and H3). Values of Ro greater than one indicate a positive effect of mixture on fine root biomass, while values below one indicate a negative effect (Loreau et Hector, 2001). The Ro value helped, therefore, to assess the effect of mixing upon tree rooting patterns. Fourth, to test hypotheses H4 and H5, we performed a principal component analysis (PCA) on the species rooting attributes (FRB and RDMC) and soil chemical properties of the three soil layers over transect to characterize species-specific rooting strategies in pure and mixed stands (Roumet *et al.*, 2016). The analyzed soil chemistry included C:N ratio, pH, carbon (C), total nitrogen (N_{tot}), ammonium (N_m), phosphorus (P), potassium (K), and exchangeable cation (CEC) content. Finally, we performed an analysis of covariance (ANCOVA) to compare the explanatory power of each nutrient on the variation of FRB and RDMC between stand types. The ANCOVA assessed the effect of stand types (pure vs. mixed) on variation of species FRB and RDMC while considering the variability of nutrient content from one stand type to another. The analysis was performed independently for each nutrient and soil layer, since the method considers only linear association between one response variable and one explanatory variable (McDonald, 2014). As a regression model, the ANCOVA compared the slopes (i.e., the mixed effect) and the intercept of the regression lines (i.e., the effect of stand type) between pure and mixed stands. The model allowed us to determine whether differences in species rooting between pure and mixed stands resulted from the species mixture effect on nutrient availability. Ultimately, the analysis allowed us to test whether the two species in mixed stands retain the same rooting and nutrient uptake strategy as in their respective pure stands.

All statistical analyses were conducted with R, version 3.4.4 (R Core Team, 2016). The normality and homoscedasticity assumptions were tested for all analyses, using Shapiro–Wilk and Levene tests (R package *car*), respectively.

2.5 Results

2.5.1 Fine Root Biomass

Spruce and aspen FRB showed a decreasing gradient with increasing soil depth (Figure 2.2a). Spruce FRB differed significantly between the organic and the top mineral layers in both pure spruce ($F = 34.91, p < 0.001$) and mixed ($F = 62.72, p < 0.001$) stands. As for spruce, aspen FRB was significantly different among the three soil layers in pure aspen ($F = 51.51, p < 0.001$) and mixed ($F = 36.9, p < 0.001$) stands.

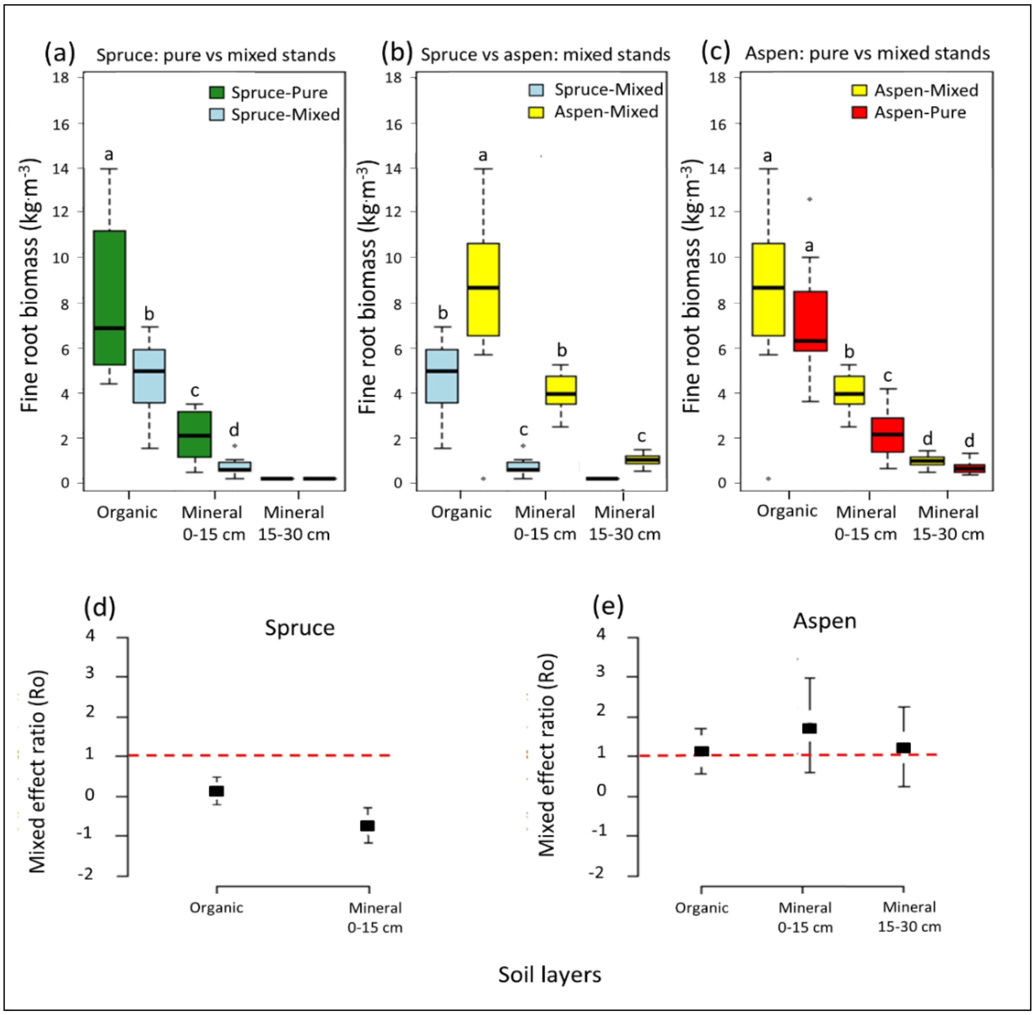


Figure 2.2 Differences in soil volume filling by fine roots of black spruce and trembling aspen in the three sampled soil horizon layers (**a**,**c**) between pure and mixed stands, and (**b**) within mixed stands. Species mixture effect on fine roots biomass of (**d**) black spruce and (**e**) trembling aspen in different soil horizon layers. In (**a**–**c**), the box represents 50% of the data set, distributed between the 2nd and 3rd quartiles. The median divides the box into the interquartile range. The lower and upper whiskers represent the minimum and maximum quartiles. For each soil layer, the number of samples $n = 12$ (i.e., 3 sites x 4 transects). Null values indicate that no root biomass was recorded in the soil layer on the transect. In (**b**), points represent average Ro values ($n = 3$), bars the 95% confidence interval, and the red dotted line the threshold under or over which the effect is considered as negative or positive. Statistical differences among pairwise comparison at $p = 0.05$ within each soil layer are denoted by letters.

The FRB of spruce decreased, while aspen FRB increased in mixed stands, compared to respective pure stands (Figure 2.2). The decreased spruce FRB and increased aspen FRB in mixed stands varied along soil profile (Figure 2.2b), and resulted from the species mixture effect (Figure 2.2d and 2.2e). Spruce FRB in the organic layer and in the top mineral layer was higher in pure spruce stands, and differed significantly from that of their corresponding soil layers in mixed stands (Figure 2.2a, 2.2b and 2.2c). Unlike spruce, aspen FRB in the organic and the bottom mineral layers did not differ between pure aspen and mixed stands, except in the top mineral layer (Figure 2.2c).

Aspen roots were more evenly distributed along soil profile than spruce roots (Figure 2.3). Spruce root VHI did not differ significantly between pure and mixed stands ($t = -0.95$, $p > 0.05$). However, the VHI values of spruce roots exhibited lower variability in mixed than in pure stands. Like spruce, aspen root VHI did not show significant difference between pure aspen and mixed stands ($t = 0.17$, $p > 0.05$). The VHI values of aspen roots showed lower variability in pure stands, compared to mixed stands (Figure 2.3).

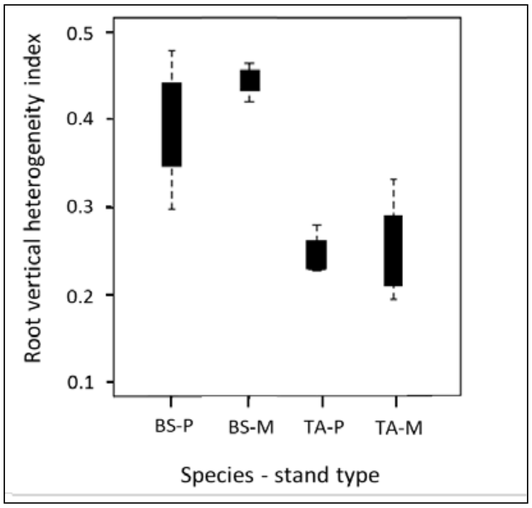


Figure 2.3 Fine roots vertical heterogeneity index describing how fully and evenly fine roots of black spruce (BS) and trembling aspen (TA) are distributed with soil depth in pure (P) and mixed (M) stands.

Overall, the PCA showed a shift in rooting patterns of spruce in mixed stands, compared to pure spruce stands, whereas aspen rooting did not differ between the two stand types (Figure 2.4).

At the species-specific level, the FRB of the two species was strongly related to the variation in soil chemical properties (Figure 2.5, Appendix A Figure S2.1). In the organic and top mineral layers, spruce FRB correlation with pH, total N, C:N ratio, NH4, and P was stronger in pure than in mixed stands (Figure 2.5a). These correlations were negative for pH, total N, NH4, K, and CEC, and positive for P. Spruce FRB in mixed stands was mostly influenced by the nutrient content of the organic layer, whereas in pure stands, it depended on both nutrient content of the organic and the top mineral horizons.

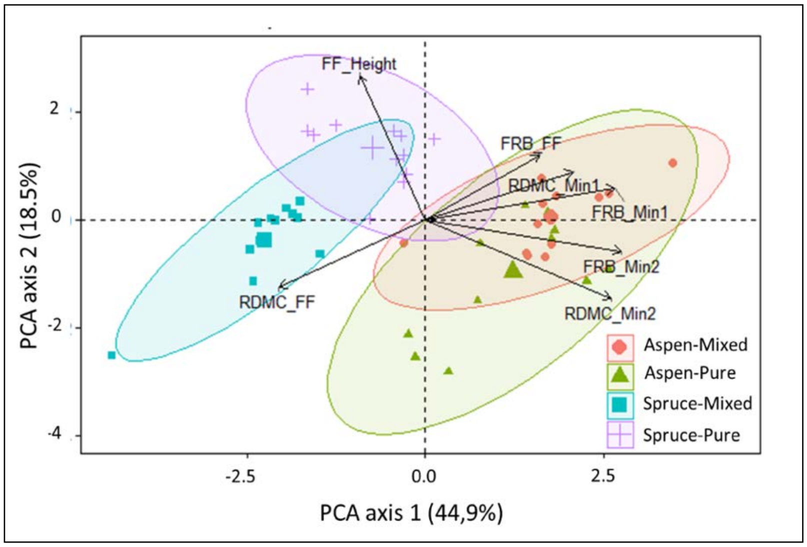


Figure 2.4 Principal component analysis of fine root biomass (FRB) and root dry matter content (RDMC) characterizing the rooting system of black spruce and trembling aspen in pure and mixed stands. The depth of organic horizon (FF_Height) was included in the analysis as a supplementary variable. FF, Min1, and Min2 refer to organic, mineral soil at 0–15 cm, and mineral soil at 15–30 cm, respectively.

Spruce FRB showed a stronger correlation with C, P, NH_4, K, and CEC in the pure than in the mixed stand (*p* for the effect of stand types <0.05; Appendix A Table S2.2 and Figure 2.1). A similar pattern was observed for the effect of the depth of organic layer on spruce FRB between the two types of stands. In contrast, the pH and C:N ratio showed a stronger correlation with spruce FRB in mixed than in pure stands. The observed differences were, however, not the result of species mixture effect on the availability of those nutrients (*p* for the mixed effect >0.05; Appendix A Table S2.2), except for NH_4 (*p* for the mixed effect <0.05; Appendix A Table S2.2).

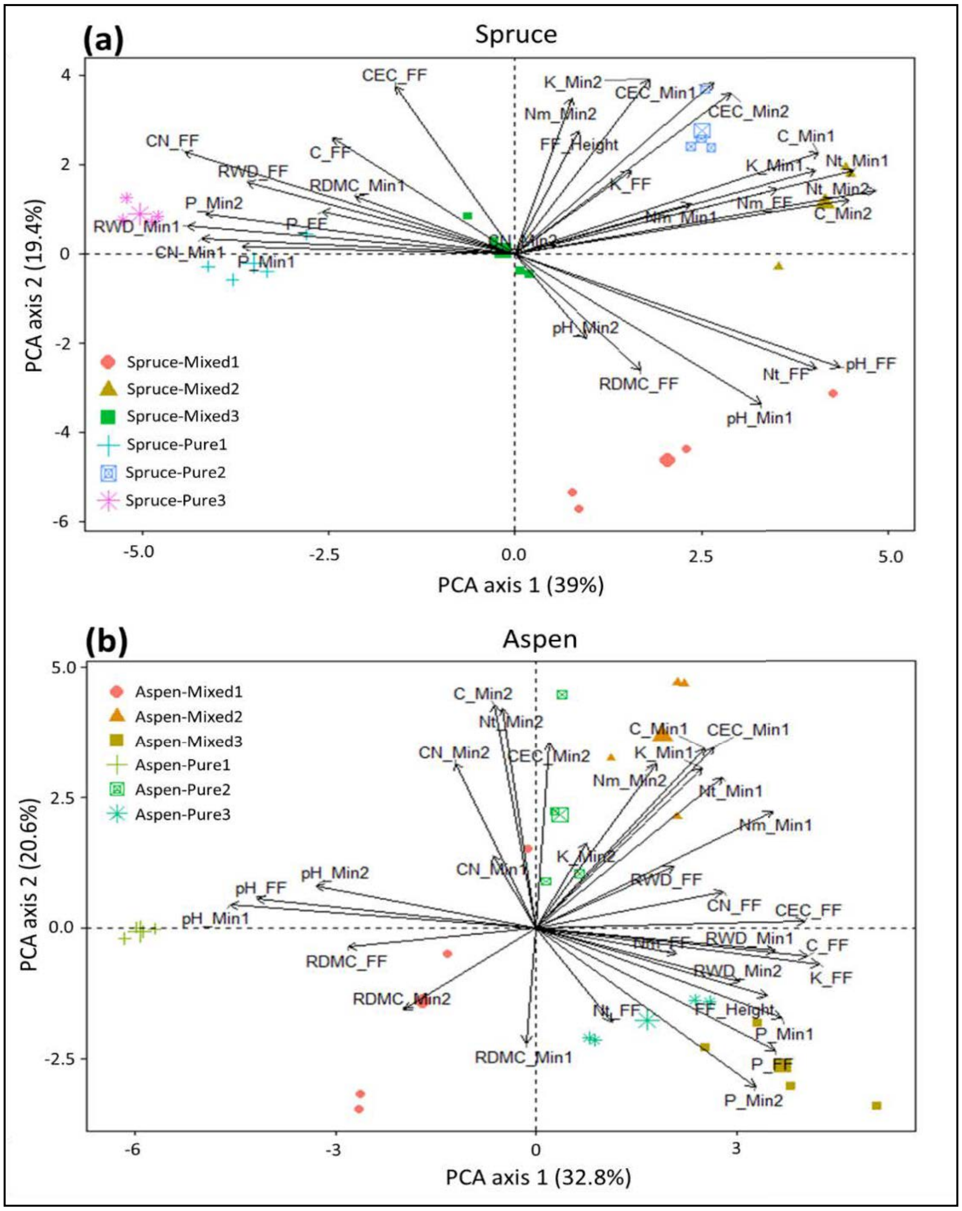


Figure 2.5 Principal component analysis comparing rooting patterns of black spruce (**a**) and trembling aspen (**b**) between pure and mixed stands. Variables included in the analyses are C:N ratio, pH, total carbon (C), total nitrogen (Nt), Ammonium (Nm), phosphorus (P), potassium (K), exchangeable cations (CEC) and depth of the organic layer (FF height), fine root biomass (FRB), and root dry matter content (RDMC) of the two species in respective pure and mixed stands affected by site (1–3). FF, Min1, and Min2 refer to organic, mineral soil at 0–15 cm, and mineral soil at 15–30 cm, respectively.

Aspen FRB was independent of nutrient content of the organic layer in pure and mixed stands, as suggested by PCA and ANCOVA (Figures 2.5b and Appendix A Figure S2.1). However, aspen FRB in the top and bottom mineral layers was more strongly correlated to total N, NH_4, P, pH, K, and CEC in mixed than in pure stands (p for mixed effect <0.05; Appendix A Table S2.3 and Figure S2.1).

2.5.2 Root Dry Matter Content

The RDMC of spruce in mixed stands was significantly higher in the organic layer than in the top mineral (Figure 2.6a). However, in pure stands, spruce RDMC did not show a significant difference between the organic and the top mineral layers, despite the increasing trend with soil depth (Figure 2.6a).

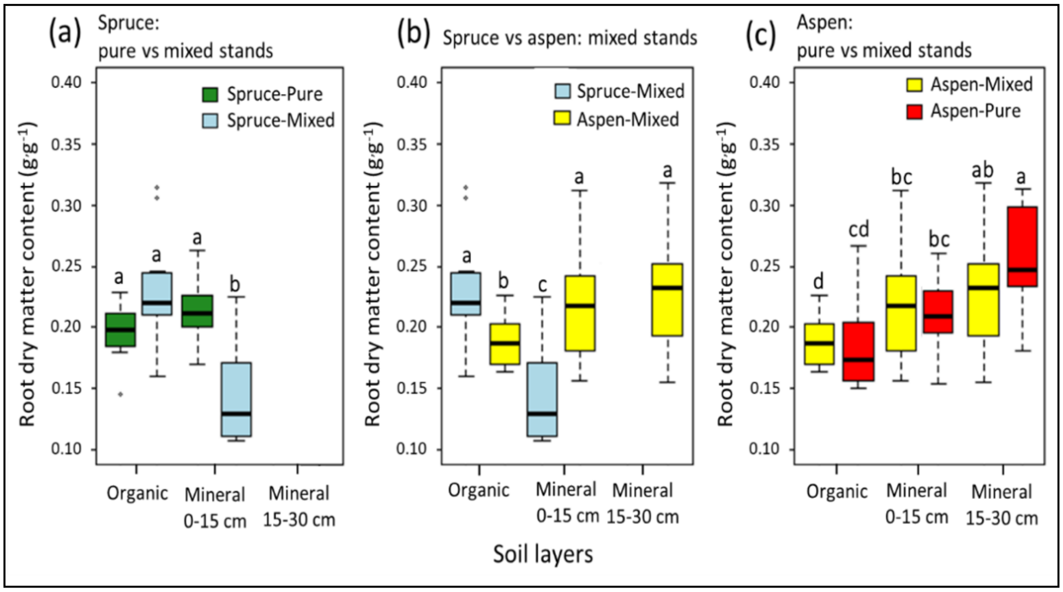


Figure 2.6 Differences in the root dry matter content (RDMC) of fine roots of black spruce and trembling aspen in the three sampled soil horizon layers (a,c) between pure and mixed stands, and (b) within mixed stands. The box represents 50% of the data set, distributed between the 2nd and 3rd quartiles. The median divides the box into the interquartile range. The lower and upper whiskers represent the minimum and maximum quartiles. Statistical differences among pairwise comparison at $p = 0.05$ within each soil layer are denoted by letters.

The RDMC of spruce in the organic layer was higher, with a greater variability in mixed than in pure stands (Figure 2.6a). In contrast, in the top mineral layer spruce RDMC was smaller in mixed than in pure stands (Figure 2.6a). No RDMC data was recorded for spruce roots in the 15–30 cm mineral layer of the soil, since spruce roots were limited in the organic and top 0–15 cm mineral layers.

In aspen, the RDMC increased with increasing soil depth (Figure 2.6c). Aspen RDMC was smaller in the organic layer than in the top mineral and bottom mineral layers in both pure and mixed stands (Figure 2.6c). There were, however, no significant differences in soil layer-specific RDMC between pure aspen and mixed stands (Figure 2.6c). Overall, spruce had a higher RDMC than aspen in the organic layer. By contrast, in the top mineral layer in mixed stands, spruce RDMC was lower than aspen RDMC (Figure 2.6b). Aspen RDMC was the highest in the bottom mineral layer (Figure 2.6b and 2.6c) and did not differ between pure and mixed stands (Figure 2.6c).

Spruce RDMC was correlated with the C:N ratio, total N, NH4, K, and pH. The effects of those nutrients on spruce RDMC varied with stand type and soil layer (Figure 2.5a; Appendix A Table S2.2). The correlation between spruce RDMC was stronger for C, C:N ratio, and NH4 content in the organic layer in mixed than in pure spruce stands. In contrast, in pure stands, those nutrients were strongly correlated with spruce RDMC in the top mineral horizon, as compared to mixed stands. Most of the nutrient concentrations did not differ significantly between pure aspen and mixed stands, which argued against the difference in the availability of soil nutrients as a driver of differences in aspen RDMC between the two types of stands (Appendix A Table S2.3).

2.6 Discussion

Our results showed a shallow rooting for spruce and a deep rooting for aspen in pure stands (Figures 2.2 and 2.3), supporting hypothesis H1, i.e., that the two species have a contrasted rooting depth in their respective pure stands. We found a lower spruce fine root biomass in both the organic (23% decrease) and mineral layers (45% decrease) in mixed stands, compared to pure stands. The result supported the hypothesis that mixing decreases the spruce root biomass (H2). Although aspen root biomass in the organic and the bottom mineral layers did not differ significantly between pure and mixed stands, the 25% increase in FRB recorded in the top mineral layer of mixed stands indicated a positive effect of mixing on aspen root biomass, supporting hypothesis H3. For spruce, lower root biomass and higher RDMC were associated with shallower rooting in mixed than in pure stands. We speculate that the pattern was a response of spruce to increased nutrient availability in mixed, compared to pure, spruce stands, and was indicative of an intensive resource acquisition strategy, with a more efficient use of soil resources. The result, therefore, supported H4. By contrast, aspen had deeper rooting and exhibited a contrasting nutrient uptake strategy in the organic layer in both mixed and pure aspen stands, as compared to spruce. The similarity between the rooting pattern (fine root biomass and RDMC) of aspen in the top mineral soil with that of spruce in the organic layer pointed to the use of an intensive resource acquisition strategy by aspen in the mineral layer. This observation supported the hypothesis suggesting more contrasting rooting patterns along the soil profile with mixing of species (H5).

We found an increase of spruce FRB in pure stands in response to lower nutrient availability, and its decline in mixed stands as a result of increased nutrient availability compared to pure stands (Figure 2.5a). This indicated an anisotropic response of spruce root biomass production towards nutrient-rich patches of soil (Brassard *et al.*, 2009). The higher spruce FRB in the organic and top mineral horizon in pure stands, compared to mixed stands (Figure 2.2a), suggested more stressful conditions for spruce in pure stands (Steele *et al.*, 1997). This situation may result from nitrogen limitation (Tamm, 1991) and competition with mosses and ericaceous species (Pacé *et al.*, 2017; Zackrisson *et al.*, 1997). Mosses and *Ericaceae* were more abundant in pure spruce stands, while they were only found in small patches in mixed stands (field observations). Both groups immobilize and cycle nutrients at the top of the organic layer, making them less accessible to trees (Légaré *et al.*, 2005; Schenk, 2006). In mixed stands, the higher root and litter turnover (short lifespan and high decomposition rate) of vascular plants (Pellegrini *et al.*, 2017) and aspen (Brassard *et al.*, 2013; Steele *et al.*, 1997) maintain a higher fertility within the organic layer (Cavard *et al.*, 2011b; Légaré *et al.*, 2001, 2005; McClaugherty *et al.*, 1982; Vogt *et al.*, 1991), thereby modulating interspecific competition among understory plants and trees. The higher turnover of aspen roots in the organic layer results mainly from their lower RDMC, common to deciduous species in temperate and boreal forests (McClaugherty *et al.*, 1982; Morrow, 1950; Paula et Pausas, 2011).

The shift in spruce rooting patterns between pure and mixed stands (Figures 2.4 and 2.5a) points to its plastic response to nutrient availability and competition (morphological plasticity, census Bradshaw (Bradshaw, 1965)), which is indicative of the use of both intensive and extensive nutrient uptake strategies (Grime *et al.*, 1986). An intensive strategy is generally associated with low C cost for root production to the plant, and the reverse for the extensive strategy (higher C cost to the plant) (Addo-Danso *et al.*, 2018; Lõhmus *et al.*, 1989). The spruce intensive strategy prevails in mixed stands, and resulted in lower FRB (Figure 2.2a) and higher RDMC (Figure 2.4) in the organic layer of mixed stands, as compared to pure stands. This indicates a reduced carbon allocation into root biomass (Bauhus et Messier, 1999; Eissenstat *et al.*, 2015). In pure stands, the extensive strategy exhibited itself through higher spruce FRB, its strong and negative correlation with nutrient content (N, NH_4, K, CEC), and higher RDMC in both the organic and the top mineral layers (Figure 2.6) (Craine, 2005; Tilman, 1982, 2007).

The decline in spruce root biomass in mixed stands might also indicate a higher competitive ability of aspen in these stands, as has been suggested for mixed Norway spruce (*Picea abies* (L.) H. Karst) and beech (*Fagus sylvatica* L.) stands in Europe (Schmid, 2002). The inter-site variability observed in the rooting patterns of spruce in mixed stands (Figure 2.5a) might indicate that the interspecific competition may increase with a higher aspen basal area. However, the limited number of sites in our study did not allow us to test such a hypothesis. To do so, it would be necessary to increase the sampling size to ensure adequate coverage of a range of canopy compositions. We speculate that the negative impact of aspen on spruce nutrient uptake would be minimal, due to the facilitative effect of aspen on soil nutrient availability compared to multiple competitive mechanisms (intraspecific competition, interference with Ericaceae and nutrient immobilization by moss layer) which are at play in pure stands (Peltzer *et al.*, 1998).

The lack of a strong correlation between aspen FRB, RDMC, and nutrients in the organic layer in both types of stands (Figures 2.5b and Appendix A Figure S2.1) suggested a strong selective placement of aspen roots within soil patches, pointing to an extensive nutrient uptake strategy (Campbell *et al.*, 1991). A similar lack of correlations has been reported for aspen in pure aspen and mixed jack pine-aspen stands (Brassard *et al.*, 2013), two deep-rooted boreal species.

Aspen responded to tree species mixture by a greater allocation of roots to the mineral horizon (Figure 2.2), apparently avoiding competition with spruce in the organic layer (Grams et Andersen, 2007). The increasing aspen FRB and its higher RDMC in the mineral horizon, as well as the similarity between these rooting patterns of spruce with those of spruce as observed in the organic layer of mixed stands, pointed to an intensive strategy in nutrient acquisition (Grime *et al.*, 1986). Under such a strategy, roots exhibit competition avoidance, which generally leads to the specialization of the part of the root system free from interspecific competition in the uptake of locally abundant resources (Hutchings et Wijesinghe, 1997; Stuefer, 1998; Stueffer *et al.*, 1996). Indeed, a higher nutrient content in the mineral soil of mixed stands (Appendix A Table S2.1) and their correlation with aspen FRB indicated that aspen nutrient uptake mainly takes place in the mineral horizon in mixed stands. This corroborates the significant correlation observed between the natural isotopic abundance of N in aspen leaves and that of the top mineral soil in mixed stands and the lack of such correlation in pure aspen stands (see Chapter IV). However, it should be noted that, overall, compared to total root biomass of aspen in pure stands, the increased root biomass of aspen in mixed stands might suggest that aspen would allocate more biomass to fine roots compared to aboveground biomass in the mixed stands. These results suggest that two species with different types of root foraging strategies and competitive ability are more likely to coexist in a heterogeneous environment (Hutchings *et al.*, 2003).

Mycorrhizae also play an important role in the nutrition of trees species in boreal forests. Spruce and aspen are known as obligate mycorrhizal species, with spruce linking exclusively with ectomycorrhizae (Robertson *et al.*, 2006), and aspen with both ecto- and arbuscular mycorrhizae (Neville *et al.*, 2002). They extend the uptake zone of their host beyond their root-soil interface, and their diversity and uptake capacity varies with stand tree species composition (Kalliokoski *et al.*, 2010; Pierret *et al.*, 2016). Although they were not studied here, a good understanding of their composition and distribution along the soil profile might be critical for an appropriate characterization of belowground interactions between spruce and aspen in mixed stands.

2.7 Conclusion

Overall, the results suggest that spruce and aspen accentuate their differences in rooting depth when mixed together. The process is likely controlled by tree-soil feedbacks and the intensity of interspecific competition, as has been suggested (Berger *et al.*, 2004, 2009; Bhatti *et al.*, 1998; Rosengren *et al.*, 2006; Schmid, 2002). We provide new insight into underground interactions between the two species in boreal mixedwoods in northwestern Quebec, supporting the hypothesis of a competitive exclusion of aspen by spruce, as suggested in earlier studies (Bergeron *et al.*, 2014), while emphasizing that the hypothesis is valid only in the organic layer of the soil. The facilitative effect of aspen on nutrient availability, however, might contribute to minimizing the impact of spruce competitive pressure on aspen. Aspen respond to mixing by increasing their root biomass in the mineral soil, and the process likely contributes to a partitioning of the use of soil resources by both species along the soil profile. These findings, therefore, suggest that spruce may benefit from the presence of aspen by increasing its nutrient uptake in the organic soil layer while not limiting aspen nutrients acquisition. We speculate, based on the concept of "*functional equilibrium*", that increased spruce nutrient uptake in mixed stands would lead to higher aboveground total stand biomass. The observation that mixed spruce–aspen stands have a higher volume of spruce merchantable biomass, compared to pure spruce stands (Légaré *et al.*, 2004), is in agreement with this hypothesis.

2.8 Acknowledgments

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CHAPTER III

NUTRIENT PARTITIONING BETWEEN BLACK SPRUCE AND TREMBLING ASPEN IN THE BOREAL MIXEDWOODS OF EASTERN CANADA: CAN MYCORRHIZAL COMMUNITIES EXPLAIN IT?

(PARTITIONNEMENT DES ABSORPTIONS DE NUTRIMENTS ENTRE L'ÉPINETTE NOIRE ET LE PEUPLIER FAUX-TREMBLE DANS LES FORÊTS BORÉALES MIXTES DE L'EST DU CANADA: LES COMMUNAUTÉS DE MYCORHIZES PEUVENT-ELLES L'EXPLIQUER?)

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3.1 Résumé

Les champignons mycorhiziens sont essentiels à la croissance et à la survie des arbres. Cependant, les connaissances sur l'étendue de leur association avec différentes espèces d'arbres de la forêt boréale restent limitées. Nous avons examiné la distribution verticale et la composition des communautés mycorhiziennes des racines de l'épinette noire (*Picea mariana* (Mill.) BSP) et du peuplier faux-tremble (*Populus tremuloides* Michx) le long de trois couches de sol (organique, couches supérieure 0-15 cm et inférieure 15-30 cm du sol minéral) dans les peuplements purs et mixtes en utilisant des techniques de séquençage de nouvelle génération. Les résultats ont montré que la composition de leurs communautés mycorhiziennes de l'épinette noire et du peuplier faux-tremble diffèrent entre leurs peuplements purs respectifs. Cette différence était maintenue dans les peuplements mixtes malgré le changement observé dans la composition des communautés mycorhiziennes spécifiques de chacune des deux espèces entre les peuplements purs et mixtes. Dans les peuplements mixtes, l'abondance relative des mycorhizes spécialistes de l'épinette était plus élevée que l'abondance relative des mycorhizes spécialistes du peuplier faux-tremble dans la couche organique tandis que le schéma inverse était observé dans le sol minéral. Ce résultat suggère une domination compétitive des communautés mycorhiziennes de l'épinette noire sur les communautés mycorhiziennes du peuplier faux-tremble dans le sol organique et inversement dans le sol minéral. Nous spéculons que ces différences dans la richesse et l'abondance des communautés mycorhiziennes individuelles de l'épinette noire et de peuplier faux-tremble le long du profil du sol pourraient contribuer à un partitionnement de leur absorption de nutriments dans des horizons de sol différents dans les peuplements mixtes.

Mots-clés: forêt boréale, champignons mycorhiziens, diversité compositionnelle des peuplements, compétition, partitionnement des nutriments

3.2 Abstract

Mycorrhizal fungi are critical for the growth and survival of trees although the knowledge on the extent of their association with different tree species in the boreal forest remains limited. We examined the vertical distribution and composition of the root-associated mycorrhizal communities of black spruce (Picea mariana (Mill.) B.S.P) and trembling aspen (Populus tremuloides Michx) along three soil layers (organic, minerals top 0-15 cm and bottom 15-30 cm) in pure and mixed stands, using next generation sequencing. We found that spruce and aspen differ in the composition of their mycorrhizal communities in respective pure stands. The difference was maintained in mixed stands despite a shift in the composition of species-specific mycorrhizal communities between pure and mixed stands. In mixed stands, the relative abundance of spruce-specialist mycorrhizae was higher than the relative abundance of aspen specialists in the organic layer while the opposite pattern was observed in the mineral soil. This result suggests a competitive dominance of spruce mycorrhizal communities over aspen mycorrhizal communities in the organic soil and reversely in the mineral soil. We speculate that the differences in the richness and abundance of individual mycorrhizal communities of spruce and aspen along the soil profile could contribute to a strong partitioning of their nutrient uptake with soil depth in mixed stands.

Keywords: Boreal forest, mycorrhizal fungi, stand compositional diversity, competition, nutrient partitioning

3.3 Introduction

Boreal soils represent the world's largest belowground carbon (C) sink (Myneni *et al.*, 2001), but have the potential to become a C source under projected global climate change (Hayes *et al.*, 2011; IPCC, 2007). These soils constitute a living medium for diverse communities of bacteria and fungi (Torsvik *et al.*, 1996), which in turn play a fundamental role in biogeochemical cycles of elements, including carbon and nitrogen cycle (Hooper *et al.*, 2000; van der Heijden *et al.*, 1998, 2008). Their biomass, species composition, diversity (species richness and abundance) and activity are all influenced by soil physicochemical properties, which highly depend on soil type, the age and the compositional diversity of stands (Aikio *et al.*, 2000; de Gannes *et al.*, 2016; Merilä *et al.*, 2002; Ohtonen et Väre, 1998). Understanding plant-soil feedback is therefore critical for understanding the temporal and spatial patterns of forest productivity and development of sustainable management of boreal forests.

Among microorganisms of the boreal forest ecosystems, the fungi are the principal decomposers of organic matter, and are also engaged in several types of intimate relationships with plants (Brundrett, 2002; Smith et Read, 2008). As heterotrophic organisms, fungi have developed different modes of nutrition to feed on simple sugars allowing grouping into three main functional groups: saprotrophic, mycorrhizal and parasitic fungi. Saprotrophic fungi are primary decomposers of plant litter and are key drivers of nutrient cycle (especially carbon and nitrogen) in boreal ecosystems (Hobbie et Horton, 2007; Lindahl *et al.*, 2007; Thormann, 2006). Mycorrhizal fungi rely on symbiotic relationships with plant roots (Tedersoo et al. 2014), benefiting from carbon (C) provided by their host plants in exchange for soil-derived nutrients, primarily - nitrogen and phosphorous. The symbiosis has been shown to be essential for host trees growth (Khasa *et al.*, 2001; Smith et Read, 2008; van der Heijden *et al.*, 2008) and survival through reducing deleterious effects of pathogens (Borowicz, 2001), and increasing host resistance to abiotic stresses (Coleman-Derr et Tringe, 2014; Grover *et al.*, 2011).

Several guilds of mycorrhizae have been recognized, including arbuscular mycorrhizae, ectomycorrhiza, ericoid mycorrhizae, arbutoid mycorrhizae and orchid mycorrhizae. *Arbuscular mycorrhizae* and *Ectomycorrhizae* are the most thoroughly studied and ecologically important guilds of mycorrhizae (Smith et Read, 2008). *Arbuscular mycorrhizae* (AM) are the most common and widespread of all mycorrhizae and are found in approximately 85%-90% of the world's plant species across diverse plant taxa (Oehl *et al.*, 2011 ; Schüβler *et al.*, 2001). They are obligate mutualist symbionts occurring inside the cells of the plant root, relying entirely on carbon supply from their host (Smith et Read, 2008). In contrast, *ectomycorrhizae* (ECM) occurs on the roots of about 5% of the world's plants. ECMs have been reported as the most abundant and widespread mycorrhizal guild in boreal forests because of their high adaptation to harsh environmental conditions (Chalot et Brun, 1998). Underground, the main body of mycorrhizae is made up of fine branching called hyphae which intertwine to make up a tangled web called the mycelium. This extensive thin mycelial network increases the surface area of the root while changing soil chemistry by their enzymatic activity (Van der Heijden et Sanders, 2002). Despite major advances in our understanding of the ecology of mycorrhizae (Tedersoo *et al.*, 2010, 2014), the extent and significance of mycorrhizal root symbiosis in boreal ecosystems warrants further research.

The distribution patterns of mycorrhizae among host species in forest stands may have major consequences for stand productivity, especially in the context of competitive interactions of co-occurring tree species. Studies of ecologically and economically important tree taxa (e.g. *Betulaceae*, *Pinaceae* and *Salicaceae*) have indicated a high spatial variation in their root-associated mycorrhizal communities, with most species showing an aggregated distribution of such communities at local (e.g. stand, canopy gap and forest edges) scale (Bidartondo *et al.*, 2000; Gardes et Bruns, 1996; Kranabetter *et al.*, 2008; Kranabetter et Wylie, 1998). Some tree species associate with only ECM (e.g. black spruce (Robertson *et al.*, 2006)) whereas others form both ECM and AM (e.g. trembling aspen (Neville *et al.*, 2002)).

A significant number of ECM and AM fungi were shown to be generalists, i.e. associated with several tree species including those naturally coexisting (Kennedy *et al.*, 2003; Smith *et al.*, 2009). Both mycorrhizal guilds have been reported to compete on roots of the same host tree species (Lodge et Wentworth, 1990). This competition results in some variability in the spatial distribution of ECM and AM communities. In particular, ECMs exhibits a high diversity and abundance in shallower roots, while AM does so in deep roots, indicating niche differentiation. In case of different hosts, such pattern may lead to partitioning of resources between host trees at different soil depths.

Black spruce and trembling aspen are two of the most dominant and economically valuable species in the boreal mixedwoods of eastern Canada (Armstrong, 2014; Zhang et Pearse, 2012). The two species have broadly different habitat requirements and successional trajectories and are hypothesized to temporally coexist in the stands in the absence of fire (Bergeron *et al.*, 2014) because of the competitive exclusion of aspen by spruce over time. In terms of stand dynamics, early successional stages following fire are generally dominated by shade-intolerant broadleaf species such as trembling aspen (Bergeron, 2000; Bergeron et Dubuc, 1988). Subsequent years following the fire, shade-tolerant species such as black spruce seed-in gradually and dominate the understory (Galipeau *et al.*, 1997). The shade-tolerant character of spruce and the progressive accumulation of its recalcitrant litter in the forest floor contributes to soil acidification and increasing the thickness of the organic layer that, in turn, slow aspen growth and inhibit its regeneration (Lafleur *et al.*, 2015a). When spruce reaches optimal size, aspen biomass has often decreased as a result of mortality from senescence (Pothier *et al.*, 2004). The resulting spruce-dominated stands feature low diversity of vascular plants, animals and insects (Cavard *et al.*, 2011b) and are more susceptible to productivity losses than mixed stands (Lafleur *et al.*, 2015b). Promoting mixed stands, however, requires a better knowledge of mechanisms that shapes the coexistence of species.

Studies of diversity vs. productivity relationship studies in the boreal mixedwoods suggest that the partitioning of the use of soil nutrients by spruce and aspen is the central element in species nutrient acquisition strategies that may allow the two species to persist within mixed stands (Cavard *et al.*, 2011a; Drobyshev *et al.*, 2013; Légaré *et al.*, 2004, 2005a). Our recent study in the boreal mixedwoods of eastern Canada suggested that differences in the root distribution of aspen and spruce along the soil profile contribute to a strong partitioning of resource use at different soil depth (Ghotsa Mekontchou *et al.*, 2020). At the same time, the spatial pattern of root tissue density and root biomass of both tree species indicated a strong dependence upon mycorrhizae.

The mycelial network of mycorrhizae increases the surface area of roots and promote the transfer of nutrients between tree species (Simard *et al.*, 1997), challenging the interpretation of trees underground interactions based solely on their root distribution. However, knowledge about the use mycorrhizal networks by trees remains limited (Bruns *et al.*, 2002; Ishida *et al.*, 2007). Data on composition and the vertical distribution of the mycorrhizal communities may help quantify and interpret underground interactions between tree species. A significant step forward in our understanding of community structure of mycorrhizal fungi would be uncovering of different mechanisms responsible for maintaining fungal diversity across a range of spatial scales (Dahlberg, 2001).

This study examined the spatial structure of the mycorrhizal communities of black spruce and trembling aspen along soil profile in pure and mixed stands of boreal mixedwoods in Northwestern Quebec. We were interested in determining whether stand compositional tree diversity affects the ability of these species to take up nutrients by impacting the mycorrhizal composition of fine roots. We first hypothesized (H1) that the root-associated mycorrhizal community structure (diversity, similarity and distribution along the soil profile) of spruce and aspen differs between pure spruce and pure aspen stands. We further hypothesized (H2) that mixing of two species within a stand means a higher α-diversity of root-associated mycorrhizal community and a change in mycorrhizal species composition, resulting from changes in soil chemical properties and increased competition. Finally, we hypothesized (H3) that mixing of two species leads to a stronger spatial separation of mycorrhizal communities along the gradient in soil depth, i.e. a shallower location of spruce-associated communities and deeper location of aspen-associated communities, as compared to pure stands.

3.4 Material and methods

3.4.1 Study area

The study area was located in the black spruce-feathermoss bioclimatic domain within the Clay Belt of northern Quebec and Ontario, Canada (49°08'N to 49°11'N and 78°46'W to 78°53'W). We established three sites each featuring three stand types: black spruce dominated (BS), trembling aspen dominated (TA), and mixed black spruce – trembling aspen (MXT) stands. These were 20 x 50 m^2 (0.1 ha) rectangular plots, each of them being uniform in terms of topography and vegetation, and representing a particular stand type. Selection criteria for each stand type and stand characteristics including species percentage and soil chemical properties are described in Ghotsa Mekontchou et al. (2020). The three sites were 2 to 15 km away from each other, and originated from the same fire that occurred in the area in ca. 1916 (Légaré *et al.*, 2005).

3.4.2 Sampling

At each plot, 20 soil cores were extracted using a 7 cm diameter auger at every 10 m along four 50 m long transects, spaced 4 m apart from each other. The sampling took place between July 15 and August 20, 2016. The chosen timing broadly corresponded to the period when fine roots are at their maximum length in this part of the boreal forest (Brassard *et al.*, 2013). We collected samples from the organic horizon (F and H layer combined) and from the top 0-15 cm (later referred to as *Min1*) and bottom 15-30 cm (*Min2*) of the mineral soil. The samples were placed in plastic bags, transported to the laboratory in an ice-filled cooler and stored at -20°C temperature prior to analyses.

The 180 soil cores were pooled per transect and for each soil horizon to form a set of 12 composite samples in each plot. The composite samples were let to thaw over six hours and then soaked in water for at least one hour. The mixture was then stirred carefully to separate roots from the soil particles and poured through a 750 µm mesh round sieve. The sieve was suspended under a distilled water bath and shaken continuously until the roots were free from any soil particle. The roots were collected and separated between live and dead roots, based on visual appearance and a manual extension test (Brassard *et al.*, 2013). Live fine roots were sorted by species using a combination of morphological characteristics established from prior root reference samples collected on younger and older trees of each studied species in the study stands as described in Ghotsa Mekontchou et al. (2020). An aliquot was taken from each soil sample and air-dried to constant weight for a week (Carter et Gregorich, 2008), ground and sieved (< 2 mm) for further soil analyses. Soil chemical properties (C:N ratio, total N, exchangeable P and K, CEC, pH and NH_4^+) measurement methods are described in Ghotsa Mekontchou et al. (2020).

For each species, the roots extracted were gently washed with distilled water to remove organic and mineral soil. They were pooled to constitute a composite root sample from each of the three soil layers taken per transect. We selected 15-50 root tips of 2 cm long from each composite root sample for molecular analysis, based on published reference characteristics for macroscopic and microscopic mycorrhizal morphotypes (Ingleby *et al.*, 1990; Massicotte *et al.*, 2010; Robertson *et al.*, 2006). These characteristics included colour, texture, lustre, dimensions, tip shape, branching pattern, and presence of rhizomorphs (Robertson *et al.*, 2011). The 2 cm root tip length was previously successfully used to sample for both ECM and AM (Toju et Sato, 2018). A total of 50 root tips were collected for each sample from the organic layer. The number of root tips ranged from 30-50 in the top 0-15 cm of mineral soil to 15-30 in the bottom 15-30 cm, reflecting low root biomass at that depth. The root tips collected were conserved in a buffer (pH 8) to prevent DNA denaturation and stored at -20°C temperature for further molecular analysis.

3.4.3 DNA extraction and library preparation

The genomic DNA was extracted from each sample using the QIAamp® genomic DNA extraction kit (Qiagen, Hilden, Germany), then eluted with 40 µL of Buffer AE and stored at -30 °C until used. DNA concentrations were assessed using fluorometric quantitation with a Qubit dsDNA HS Assay Kit and Qubit Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). Library preparation for Illumina sequencing was performed according to the manufacturer's instructions for user-defined primers (Illumina, 2013)[1], with some modifications. All sample concentrations were standardized to 5 ng/µL, and each sample was amplified in triplicate to ensure reproducibility (Kennedy *et al.*, 2014; Schmidt *et al.*, 2013). The ITS1 region of the

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[1] https://support.illumina.com/content/dam/illumina-support/documents/documentation/chemistry_documentation/16s/16s-metagenomic-library-prep-guide-15044223-b.pdf

fungal ribosomal DNA was amplified using Fwd: ITS5 GGAAGTAAAAGTCGTAACAAGG (White *et al.*, 1990) and a modified version of Rev.:5.8S_Fungi CAAGAGATCCGTTGTTGAAAGTK, which improves taxonomic resolution and specificity to the fungal kingdom (Epp *et al.*, 2012). Polymerase chain reactions (PCR) were performed by first mixing 37.5 µl of HotStarTaq Plus Master Mix (contains 1000 units of HotStarTaq Plus DNA Polymerase, PCR Buffer with 3 mM MgCl2, and 400 µM of each dNTP), 27 ul RNase-Free Water (QIAGEN Inc., Germantown, MD, USA), 1.5 µl of each 10 µM primer and 7.5 µL of gDNA at 5 ng/µL. The final volume of 75 µL was then equally distributed in three 96-well plates placed in distinct thermocyclers. Thermal cycling conditions were as follows: initial denaturation at 95°C for 5 minutes; 40 cycles at 94°C for 30 s, 50°C for 30 s, 72°C for 1 minute; and a final elongation at 72°C for 10 minutes. PCRs were done on a C1000 Touch Thermal Cycler (Bio-Rad Laboratories, Hercules, Canada) and triplicate products were pooled and visualized on GelRed-stained 1% agarose gels using the Chemigenius Bioimaging System (Syngene, Cambridge, UK). PCR products were purified using 81 µL of magnetic beads solution (Agencourt AMPure XP, Beckman Coulter Life Science, Indianapolis, IN, USA) according to Illumina's protocol (Illumina, 2013). Unique codes were added to each sample by amplifying 5 µL of the purified PCR product with 25 µL of KAPA HIFI HotStart Ready Mix (Kapa Biosystems, MA, USA), 5 µL of each Nextera XT Index Primer (Illumina Inc., San Diego, CA, USA) and 10 µL of UltraPure™ DNase/RNase-Free Distilled Water for a total volume of 50 µL. Thermal cycling conditions were as follows: 3 minutes at 98°C, 8 cycles of 30 s at 98°C, 30 s at 55°C, 30 s at 72°C, and a final elongation step of 5 minutes at 72°C. Indexed amplicons were purified with the magnetic beads as previously described, quantified using a Qubit dsDNA BR Assay Kit (Life Technologies) and combined at equimolar concentration. Paired-end sequencing (2 × 250 bp) of the pools was carried out on an Illumina MiSeq at the Genomic Sequencing and Genotyping Platform (Centre de Recherche du Centre Hospitalier de l'Université Laval, Québec, QC, Canada).

3.4.4 Bioinformatics and taxonomic identification

The bioinformatic analysis of raw sequencing data was performed with the *OBITools* package, a set of python programs developed to simplify the manipulation of sequence files for DNA metabarcoding (Boyer *et al.*, 2016). The raw sequence data were first converted into FASTQ files. A read-pairing assembly was performed, and the subsequent read assigned to corresponding samples. A cleaning step was performed to remove low-quality reads that could involve some biases in the data analysis. The low-quality sequences were those shorter than the empirical sequence length distribution (< 50 bp), containing ambiguous nucleotides (other characters than A, C, G or T), displaying low score paired-end alignments (paired-end alignment score < 50), and singleton sequences i.e. observed once over the whole dataset. Clustering at 97% identity (Nilsson *et al.*, 2008) was performed with the OBITool Sumaclust using the raw number of mismatches (deletions account as mismatches) as a measure of the sequence dissimilarity.

The taxonomic identification was performed with BLAST (Altschul *et al.*, 1990) against the Genbank (genbank.com) database. The most similar sequence was reported for each OTU (Operational Taxonomic Unit). OTUs were assigned to taxonomic rank using the OBITool Ecotag function, which analyzed our sequences with Genbank sequences, formed clusters of most similar sequences, and assigned sequences to the closest ancestor that was shared with the most similar sequences in a cluster. With the Ecotag function based on taxonomical distant between similar sequences, approximately 70% of OTUs were assigned to a species, genus and family, 21% to a higher taxonomic level (order, class, kingdom and phylum), and 9% not ranked. Taxonomic assignation allowed to attribute functional groups to OTUs using the FUNGuild program (Nguyen *et al.*, 2016), the mycological database of Quebec (Mycoquebec, https://www.mycoquebec.org/bas.php?l=l) and other published data on the ecology of fungi taxa (Bent *et al.*, 2011 ; Robertson *et al.*, 2006 ; Smith et Read, 2008 ; Tedersoo *et al.*, 2010 ; Tedersoo et Smith, 2013). We used many sources of information because the FUNGuild program often output multiple guilds for a single OTU. Levels of classification used to infer functional guilds were species, genes, family, and to some extent order and class (e.g. *Glomeromycetes*). The output guild's information was grouped into six categories namely arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), ericoid mycorrhizal, saprotrophic/endophytic, pathogen/parasite and unknown type. We grouped saprotrophic and endophytic fungi in the same group based on recommendations of Porras-Alfaro and Bayman (2011).

3.4.5 Statistical analysis

All statistical analyses were coded within R environment (R Core Team, 2016). We used R package *vegan* (Oksanen *et al.*, 2018) for community analyses.

Prior to analyses, we removed doubletons, tripletons, quadrupletons and all OTUs with a total frequency count ≤ 10 reads in the dataset to reduce among-sample variance in diversity metrics that resulted from variance in sequencing effort, i.e. variance in the sequencing reads among samples. The threshold of 10 reads was defined following a Procrustes correlation analysis using the *protest* function which tests the non-randomness (significance) between two community configurations (Peres-Neto *et al.*, 2006). The resulting OTUs abundance matrix data was further standardized using a Hellinger transformation (Borcard *et al.*, 2011).

We first assessed the fungal OTU α-diversity by calculating the observed and expected species richness estimates (number of OTUs, Chao and Jacknife (Chao et Chiu, 2016)), and the Shannon-Wiener diversity index (Shannon, 1948) using the *specpool* and *diversity* functions of R package *vegan*, respectively. To test the effect of stand type on OTU α-diversity and differences among soil layers, we used a one-way analysis of variances (ANOVA) followed by a Tukey post hoc test. The similarities in the composition of mycorrhizal communities were quantified by a non-metric multidimensional scaling (NMDS) using *metaMDS* and *s.class* functions of the R packages *vegan* and *ade4*, respectively. Four NMDS were performed, each of them comparing (1) the individual mycorrhizal communities of spruce and aspen between respective pure stands, (2) spruce mycorrhizal communities between pure spruce and mixed stands, (3) aspen mycorrhizal communities between pure aspen and mixed stands, and (4) the individual mycorrhizal communities of spruce and aspen in mixed stands. The function *envfit* was further used to test the goodness of fit of environmental variables (C:N ratio, total N, exchangeable P and K, CEC, pH, NH_4^+ and the root density) on each NMDS ordination of mycorrhizal community, based on 999 random permutations. We further assessed the dissimilarities in root-associated mycorrhizal communities of the two species (a) along the soil profile and (b) among stand types, using the permutational analysis for the multivariate homogeneity of dispersion (Anderson, 2006) which compare β-diversity metric (hereafter Bray-Curtis distance) computed from OTUs abundance matrix data (Chase *et al.*, 2011). Finally, we assessed the preference of root-associated mycorrhizal fungi for spruce or aspen based on the multinomial species classification method (CLAM test). The method allowed a robust statistical classification of habitat or host specialists and generalists, without excluding rare species *a priori* (Chazdon *et al.*, 2011). A specialization threshold value of 2/3 (supermajority rule) and an α *value* of 0.001 was used because the Benferroni correction in the CLAM analysis generally returns too stringent results (Chazdon *et al.*, 2011). Regarding ECMs and AMs preference for spruce or aspen, mycorrhizal OTUs were classified in four categories i.e. (a) spruce specialists, (b) aspen specialists, (c) generalists, i.e. commonly found on roots of both spruce and aspen, and (d) too rare to be statistically classified with confidence. The same procedure was applied for mycorrhizae's stand type preference at host species scale. Competitive interactions between root-associated mycorrhizal communities of the two tree species were drawn from differences in OTUs' richness and abundance within each soil layer (Kennedy *et al.*, 2011). The richest and most abundant communities were referred to as competitively dominant over those with the lower richness and abundance.

3.5 Results

3.5.1 Sequencing output

A total of 6 096,696 DNA sequences clustered into 3,219 OTUs passed the quality control following the bioinformatic analysis of sequencing data. Of these, 34% of OTUs (1108 OTUs) were identified as mycorrhizal guilds and 66% as saprophytic/endophytic, parasites/pathogens, and non-fungal species. Out of this, the mycorrhizal guild constituted approximately 82% of the total number of sequences (5 001,836 reads) although representing a small proportion of the total number of OTUs. After the second quality filtering step, 436 rare OTUs (< 10 reads) were discarded. Consequently, the remaining 672 abundant OTUs (total number of sequences of 4 975,218 reads) were used for subsequent analyses. From these, 42%, 34%, 21% and 3% were taxonomically classified down to family, genus, species and class rank, respectively. The 3% identified at class level were members of *Glomeromycetes*. Our data confirmed that spruce formed mycorrhiza exclusively with ECMs fungi whereas aspen formed mycorrhiza with both ECM and AM fungi (Appendix B Figure S3.1).

3.5.2 Mycorrhizal richness and diversity

The richness and diversity of mycorrhizal communities associated with tree roots in our dataset were significantly higher in aspen than in spruce irrespectively of the stand type (pure or mixed, Table 3.1). Mycorrhizal OTUs richness decreased with increasing soil depth. This pattern was more pronounced in mixed and pure aspen stands than in spruce stands. In contrast, in pure spruce stands there was no significant difference between the observed OTUs richness between the organic and the mineral soil layers. Conversely, the expected OTUs richness indexes (Chao and Jacknife) predicted an increased diversity with increasing soil depth (Table 3.1) in pure spruce stands.

The Shannon-Wiener index calculated at the stand type level showed a significantly higher OTUs diversity on aspen roots in mixed than in pure stands, irrespectively of soil layers considered (Table 3.1). No significant difference was detected between the OTU diversity of communities associated with spruce roots in pure and mixed stands. In spruce, when partitioned between soil layers, the OTU diversity was significantly lower in mixed than in pure stands in both the organic and the mineral soil layers (Table 3.1). Similarly, aspen exhibited a higher OTUs diversity in mixed than in pure stands in both the organic and the top mineral soil layers.

Table 3.1 Root-associated mycorrhizal community (ECM and AM combined) alpha diversity indexes (Means and SEM) of spruce and aspen by stand type and soil layer.

			Alpha diversity estimates			
			Richness estimators			Diversity index
			Observed	Expected		
Stand type	Soil layer	Host	Nber of OTU	Chao	Jacknife	Shannon-Wiener
Pure Spruce	Total stand		191	246.33 ± 18.6	249.9 ± 19.75	2.41 ± 0.4 **AB**
	Organic	Spruce	143	172.14 ± 11.34	184.81 ± 13.61	2.57 ± 0.26 **abc**
	Mineral 0-15cm	Spruce	142	273.75 ± 43.6	210.44 ± 27.78	2.21 ± 0.46 **bc**
Mixture	Total stand	Spruce	225	325.26 ± 28.28	310.94 ± 26.68	2.37 ± 0.44 **AB**
		Aspen	359	464.95 ± 24.43	484.51 ± 28.3	2.65 ± 0.41 **A**
	Organic	Spruce	191	280.1 ± 26.22	267.36 ± 29.4	2.61 ± 0.35 **ab**
		Aspen	260	362.67 ± 25.7	363.58 ± 34.16	2.9 ± 0.25 **a**
	Mineral 0-15cm	Spruce	121	200.26 ± 26.46	179.28 ± 25.01	1.99 ± 0.24 **c**
		Aspen	225	364.06 ± 36.07	326.81 ± 33.86	2.65 ± 0.38 **ab**
	Mineral 15-30cm	Spruce	-	-	-	-
		Aspen	98	138.07 ± 15.89	136.33 ± 18.12	2.17 ± 0.35 **bc**
Pure Aspen	Total stand		248	404.63 ± 40.01	358.72 ± 26.77	2.18 ± 0.55 **B**
	Organic	Aspen	193	308.01 ± 33.12	276.41 ± 27.5	2.3 ± 0.56 **bc**
	Mineral 0-15cm	Aspen	144	324.62 ± 59.4	220.5 ± 28.18	2.05 ± 0.52 **c**

For the Shannon-Wiener index, statistical differences among pairwise comparison at $p = 0.05$ within each soil layer among stand types are denoted by lowercase and by capital letters for total stand diversity comparison.

3.5.3 Mycorrhizal communities' composition

The NMDS showed that the mycorrhizal communities in the study sites were structured according to the chemical properties of soils, stand types, soil layers and the host tree species identity (Figure 3.1). The root-associated mycorrhizal communities of spruce and aspen significantly differed from each other in both pure (Figure 3.1a) and mixed (Figure 3.1b) stands. These differences were observed in both the organic and the mineral soil layers. However, the differences in the composition of mycorrhizal communities between the two tree species were more pronounced in pure stands than in mixed stands.

Regarding the differences in the community composition between pure stands of both species, the most informative factors explaining the differences in community composition were the soil C:N ratio, the pH, and the tree species identity (Table 3.2). In mixed stands, the differences in root-associated mycorrhizal community composition between the two tree species depended greatly on the host tree identity, the soil nutrient content (NH4+, total N, K and CEC) and C:N ratio within the stands (Table 3.2). The differences in root density, pH, C:N ratio, P, NH_4^+, and CEC content between pure spruce and mixed stands were the most significant explanatory factors of differences in the composition of mycorrhizal communities associated with spruce roots between pure and mixed stands (Table 3.2). The pH was the only informative factor explaining the differences in the composition of mycorrhizal communities associated with aspen roots between pure and mixed stands (Table 3.2).

The level of similarities between mixed and pure stands of species-specific mycorrhizal communities varied along the layers of the soil profile (Figure 3.1c and 3.1d). In the organic soil, spruce root-associated ectomycorrhizal communities exhibited a strong similarity between pure spruce and mixed stands (Figure 3.1c, Appendix B Table S3.2).

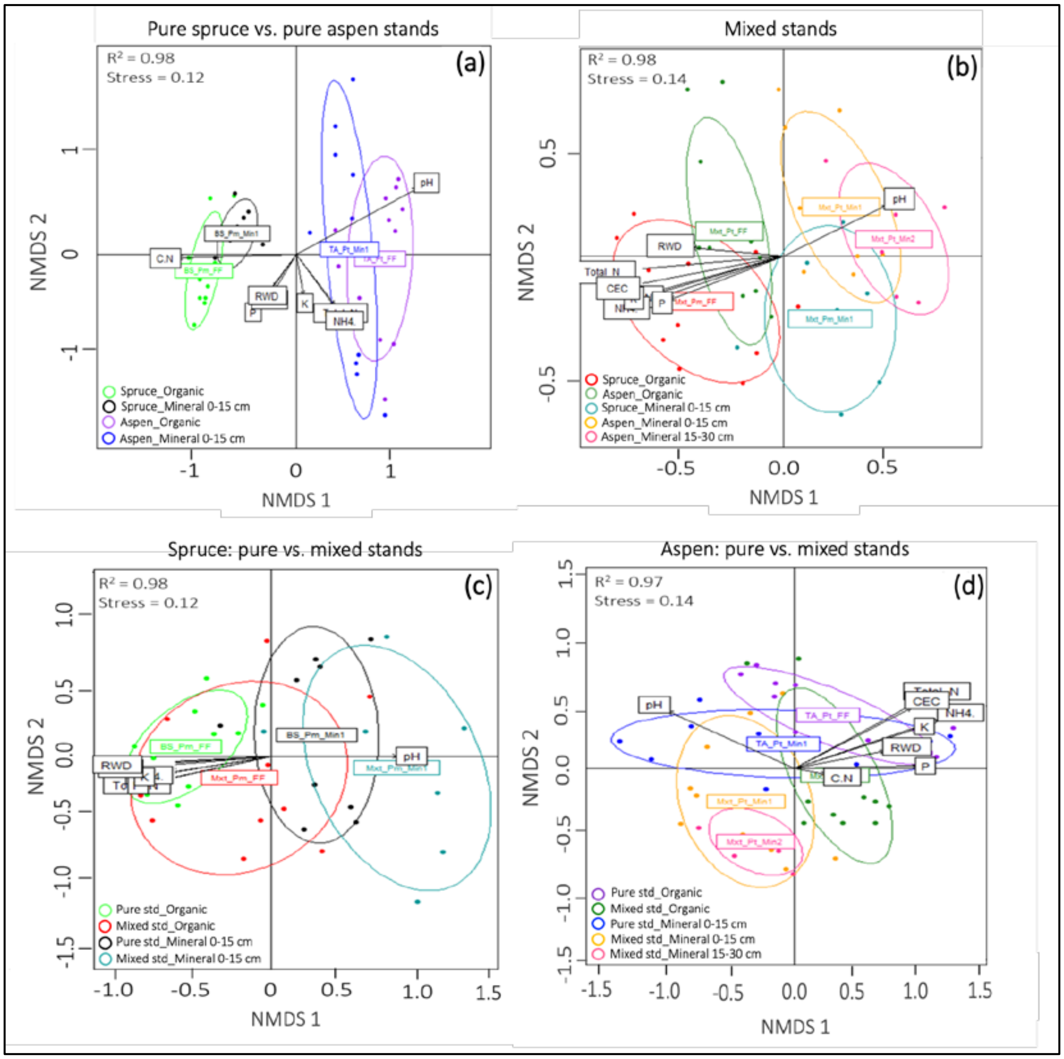

Figure 3.1 Non-metric multidimensional scaling (NMDS) of a Bray-Curtis distance matrix describing the structure of root-associated mycorrhizal communities of spruce and aspen along the soil profile (a) between pure spruce and pure aspen stands, (b) within mixed stands, (c) of spruce between pure spruce and mixed stands, and (d) aspen between pure aspen and mixed stands. Each point symbolizes a single mycorrhizal community taken per transect whereas point and ellipse colors indicate communities affected by stand type and soil layer. Ellipses represent 95% confidence intervals around groups' centroids. Non-overlapping centroids are considered significantly different at $p < 0.05$. The stress value given is a measure of the disagreement between the rank order in the original data set and that in the NMDS (lower numbers indicate better agreement).

Table 3.2 Results of the PERMANOVA performed on the NMDS showing the significance of different factors of mycorrhizal communities' composition of spruce and aspen within and between pure and mixed stands.

Factor	Aspen vs Spruce				Spruce		Aspen	
	Pure stands		Mixed stands		Pure vs Mixed stands		Pure vs Mixed stands	
	R^2	*p.value*	R^2	*p.value*	R^2	*p.value*	R^2	*p.value*
C:N ratio	**0.536**	**<0.001**	**0.51**	**<0.001**	**0.55**	**<0.001**	0.01	0.687
NH_4^+	0.2	0.016	**0.64**	**<0.001**	0.32	0.002	0.34	<0.001
N_{total}	0.148	0.042	**0.71**	**<0.001**	0.35	<0.001	0.34	<0.001
K	0.06	0.313	**0.67**	**<0.001**	0.45	<0.001	0.24	0.003
P	0.141	0.041	0.45	<0.001	**0.52**	**<0.001**	0.21	0.003
pH	**0.717**	**<0.001**	0.40	<0.001	**0.50**	**<0.001**	**0.55**	**<0.001**
CEC	0.066	0.275	**0.69**	**<0.001**	**0.53**	**<0.001**	0.27	<0.001
RWD	0.06	0.30	0.26	<0.001	**0.54**	**<0.001**	0.12	0.046
Host tree			**0.59**	**<0.001**				
Stand type	**0.513**	**<0.001**			0.07	0.038	0.18	<0.001
Soil layer	0.01	0.652	0.40	<0.001	0.29	<0.001	0.22	<0.001

The R^2 (cut-off 0.5) and the *p.value* of the most relevant explanatory factor for each comparison are in bold. RWD refers to the fine root density.

The *β*-diversity indices of communities associated with spruce roots in the organic soil were more variable in mixed than in pure stands (Figure 3.2a). In contrast, in the mineral soil both communities were significantly dissimilar (Appendix B Table S3.2) with a higher and nonsignificant intra-stand variability of the *β*-diversity indices (Figure 3.2a) between the two types of stands.

Unlike spruce, the root-associated mycorrhizal communities of aspen were significantly dissimilar between pure and mixed stands in both the organic and the mineral soil layers (Appendix B Table S3.2). In both pure and mixed stands, the α-diversity indices of the mycorrhizal communities of aspen were more variable than in spruce (Figures 3.2a, 3.2b and 3.2c). The two species had significantly dissimilar root-associated mycorrhizal communities in their respective pure stands (Figure 3.2d; Appendix B Table S3.2). Despite an overlap between the mycorrhizal communities of the two tree species in mixed stands, the distance between the two community centroids showed two significantly dissimilar communities (Appendix B Table S3.2). This difference in community composition between the two tree species in mixed stands was more pronounced in the mineral than in the organic soil layer.

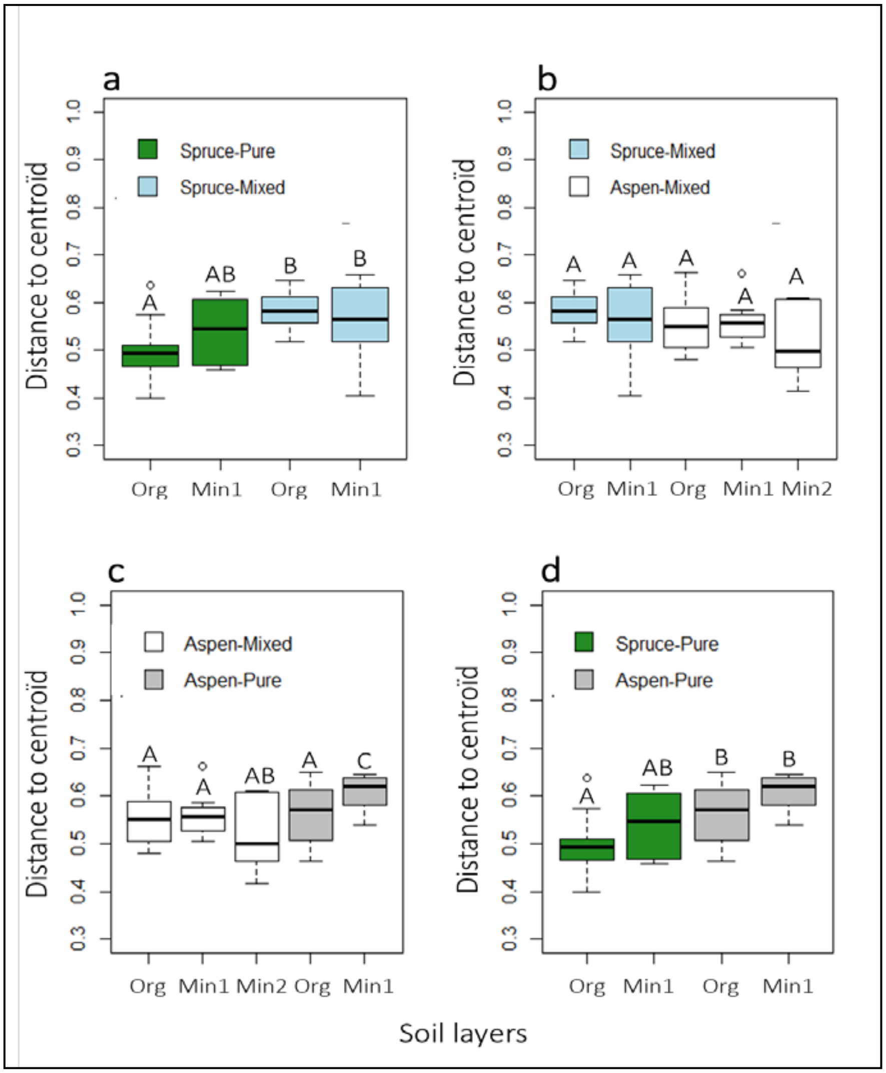

Figure 3.2 Boxplots comparing the variance of Bray-Curtis distances (computed as the distance to the centroid) within each soil layer for (a) spruce between pure and mixed stands, (b) spruce and aspen in mixed stands, (c) aspen between pure and mixed stands, and (d) aspen and spruce between their respective pure stands. Org, Min1 and Min2 refer to the organic, the top 0-15 cm and bottom 15-30 cm mineral soil layers, respectively. Box and whiskers plots represent the first and third quartiles (hinges), the median (bold line), and 1.5 times the interquartile range (error bars). Outlier points are plotted individually. Within each of four panels, groups labeled A are significantly different from groups labeled B at *p* = 0.05 (Tukey's HSD).

3.5.4 Host preference

A total of 307 OTUs was found on aspen roots in the organic layer of both pure and mixed stands. From these, 40% (122 OTUs) and 14% (43 OTUs) preferred aspen when grown in mixed stands and pure stands, respectively. The remaining 46% were habitat generalists (11%, 35 OTUs; i.e. commonly found on aspen roots in both stand types) and rare OTUs (35%, 107 OTUs) (Figure 3.3a). A similar pattern was found within the mineral soil with the only difference that the proportion of rare OTUs decreased by half compared to the organic soil (Figure 3.3b).

The classification analysis revealed a high host specificity in mixed stands. In the organic layer of mixed stands, the richness of aspen specialists was approximately 2-fold (35%, 107 OTUs) of spruce specialists (19%, 61 OTUs) (Figure 3.3a). Only 9% (28 OTUs) were generalists and 36% (112 OTUs) were too rare to be classified with confidence. Despite their lower OTUs richness, spruce specialists were more abundant than aspen specialists (50% vs. 23% of the total number of sequences in the organic layer).

The most abundant OTUs in the organic layer belonged to families *Russsulaceae* (9% aspen specialist, 16% spruce specialists and 14% generalist), *Atheliaceae* (0.5% aspen specialists, 15% spruce specialists), *Thelephoraceae* (3% aspen specialists, 8% spruce specialists), *Cortinariaceae* (2.2% aspen specialists, 2.2% spruce specialists, 2% generalist), *Sebacinaceae* (5% spruce specialists <1% aspen specialist and 2.5% generalist), *Pyronemataceae* (1.5% aspen specialist, 2.5% spruce specialists, <1% generalist), *Hymenogasteraceae* (2% strict aspen specialist) and *Hygrophoraceae* (2% aspen specialists, <1% spruce specialist) (Figure 3.4a). Generalist OTUs represented 21% of the total number of sequences in the organic layer in mixed stands. From the 20 families identified, only *Gloniaceae* were strict generalists. Rare OTUs represented <1% of the total abundance of the community in each soil layer.

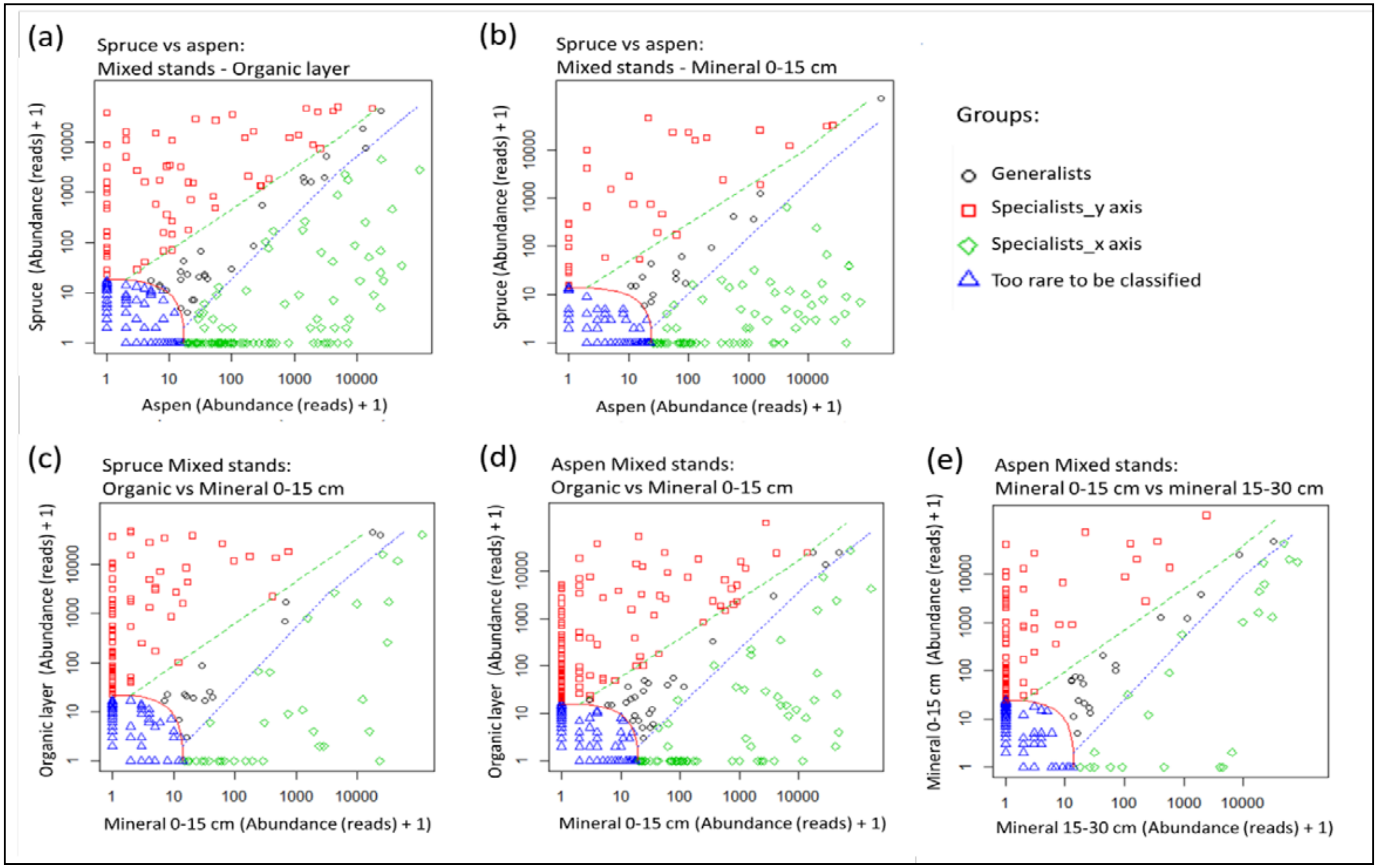

Figure 3.3. CLAM test results showing mycorrhizal host preference based on OTUs rank and their abundance (number of reads) in the organic and the mineral soil layers of mixed stands.

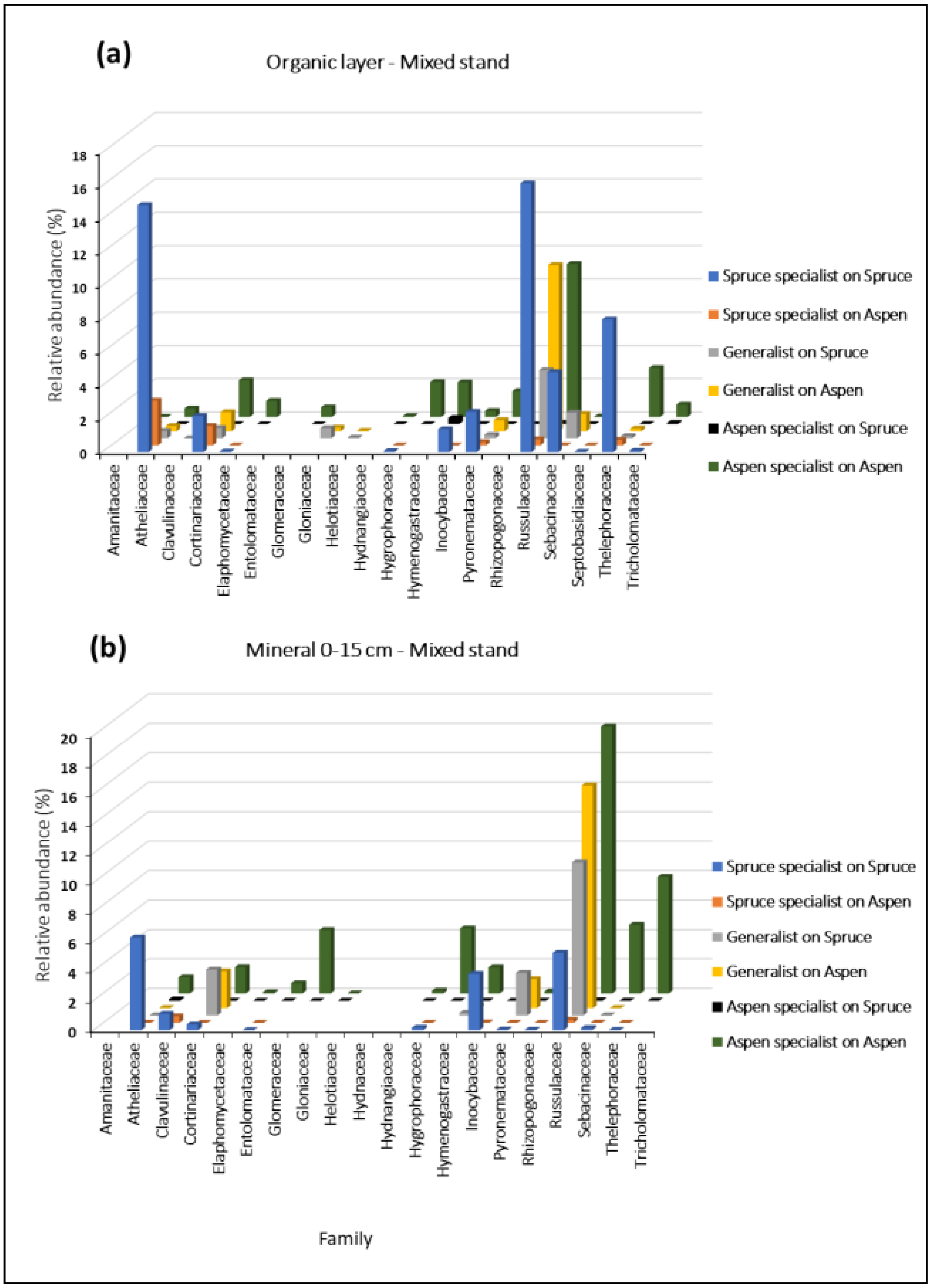

Figure 3.4. Relative abundance of mycorrhizal fungal taxa associated preferentially (specialists) and commonly found (generalists) on spruce and aspen roots in (a) the organic and (b) the top 0-15 cm mineral soil layers of mixed stands.

In the mineral soil layer of mixed stands, the relative abundance of aspen specialists was higher than that of spruce (Figure 3.4b). As compared to the pattern observed in the organic layer, the relative abundance of spruce specialist decreased by 17% while that of aspen specialists increased by 46% and was approximately 3-fold of spruce specialists. Members of *Russulaceae* constituted 50% (19% aspen specialist, 26% generalists and 5% spruce specialists) of the total community abundance (total number of sequences). In the mineral layer, compared to the organic layer, the *Sebacinaceae* shifted from spruce specialists to aspen specialist whereas the *Atheliaceae* and *Inocybaceae* remained spruce specialist. The abundance of aspen specialists (*Glomeraceae*, *Hygrophoraceae*, *Hymenogasteraceae* and *Thelephoraceae*) increased in the mineral layer compared to their abundance in the organic layer (Figure 3.4a and 3.4b). The *Cortinariaceae* and *Pyronemataceae* became generalist.

3.5.5 Stand type preference

The relative abundance of OTUs preferring spruce and aspen between the two types of stands was higher in mixed than in pure stands of respective species. For spruce, the OTUs commonly found in both types of stands (generalist) had the lowest richness (Appendix B Figure S3.2). Despite their lower OTU richness, the organic layer featured higher abundance of the habitat generalists than pure spruce stands specialists (21%) and spruce-mixed stand specialists (35%) (Appendix B Figure S3.3). Spruce habitat generalists mainly belonged to families *Atheliaceae*, *Russulaceae* and *Pyronemataceae*. The generalists were higher in pure spruce than in mixed stands in the organic layer with a reverse pattern observed in the mineral layer. In the mineral layer, however, the abundances of pure spruce stand specialists (25%) and spruce-mixed stand specialists (27%) were approximately equal.

Aspen had opposite patterns to spruce in both the organic and the mineral soil layers between the two types of stands. In the organic layer, pure aspen stand specialists were more abundant than aspen-mixed stand specialists. The opposite pattern was observed in the mineral soil. As for the generalists, their abundance was almost doubled in the mixed than in the pure stands in both soil layers.

3.6 Discussion

Our results revealed a high mycorrhizal richness and diversity in boreal forests. Aspen exhibited generally higher and more unevenly distributed mycorrhizal diversity than spruce (Table 3.1, Figure 3.2). These results are consistent with previous studies comparing the fungi diversity of hardwood and conifer tree species in boreal forests in eastern Canada (Nagati *et al.*, 2018; Reithmeier et Kernaghan, 2013), Alaska (Bent *et al.*, 2011) and Sweden (Kyaschenko *et al.*, 2017). The ectomycorrhizal species identified on spruce in our study were similar to those identified on spruce in the Mealy Mountains in eastern Labrador-Canada, at 1350 km from our study site (Reithmeier et Kernaghan, 2013).

The richness and the abundance of mycorrhizal OTUs were higher in our study than reported elsewhere. These differences in richness and abundance might result from differences in methodological approaches (sampling, sequencing and bioinformatics analysis). For instance, Nagati et al. (2018) sampling the same study sites did not include mixed stands. They refined their taxonomic identification by combining the UNITE and GENBANK databases while we only used GENBANK. In addition, the sampling in our study was conducted at a finer scale (root tips) while other studies used soil samples and tended to focus on the organic layer of the soil. Considering a high variability in the exploration types (the functional trait that connects the morphology and differentiation of ECM hyphae to differences in nutrient acquisition strategies) of mycorrhizal taxa (Agerer, 2001) existing sampling methods might not be able to identify many species of mycorrhiza. Removal of roots potentially hosting mycorrhiza of contact exploration type prior to DNA extractions could be an example of such a sampling bias. The diversity of AM fungi might also have been underestimated. Although the ECM metagenome was correctly analyzed using primers ITS1 (Gardes et Bruns, 1993) and ITS5 (White *et al.*, 1990) commonly used to amplify ectomycorrhizal fungi ITS regions, these primers may not be suitable for studying AM metagenome. Not surprisingly, only *Glomus* genus was identified. Therefore, there is a need to use AM-specific primers (Senés-Guerrero *et al.*, 2020; Suzuki *et al.*, 2020; Xu *et al.*, 2017) for improved AMF detection rates.

3.6.1 Role of soil chemical properties

The richness and composition of mycorrhizal communities strongly depend on soil chemical properties. The separation of communities on the first NMDS-axis by pH and C:N ratio, and on the second NMDS-axis by soil nutrient content indicated that pH is the main factor controlling the composition of mycorrhizal communities whereas the nutrient content mainly controls the mycorrhizal richness and diversity. This pattern has already been emphasized in previous studies (Siciliano *et al.*, 2014; Wubet *et al.*, 2012). The strong similarity between the ECM communities associated with spruce roots in the organic soil of mixed and pure spruce stands, observed in this study, suggests that the relationship between the composition of mycorrhizal communities and the chemical properties of the soil is host specific. Therefore, a non-significant relationship may be observed in spruce and a significant relationship in aspen. In aspen, the higher the fertility and the pH in pure stands compared to mixed stands, the lower the species richness and the more different the mycorrhizal community's composition associated with roots is. This soil pH - mycorrhizal community's composition relationship observed in aspen may be common among broadleaf trees: a similar pattern to that has been reported in European beech forests (Wubet *et al.*, 2012).

Competitive interactions among mycorrhizal species may add another layer of complexity in soil effects on mycorrhizal communities. The distinct community composition of the pure stands of both species (this study and Nagati et al. (2018)) indicate that the soil pH - mycorrhizal richness relationship may be more pronounced in forests composed of phylogenetically distinct tree species. This may explain why some studies have found a relationship between pH and mycorrhizal richness (Wubet *et al.*, 2012) while others have not (Rousk *et al.*, 2010). Host specificity (significant effect of dominant tree species, sensus Nagati et al. (2018)) can therefore play an important role in shaping variation of fungal community composition across the boreal forest landscape. Observed differences in the composition of mycorrhizal communities between spruce and aspen on the soils with the broadly similar pH and nutrient concentrations (mixed stands) support this interpretation (Figure 3.1b; Appendix B Table S3.1 and S3.2). We therefore speculate that it is host specificity effects rather than differences in soil physicochemical properties that define differences in mycorrhizal community composition two forest types in our study.

3.6.2 Shift in mycorrhizal communities' composition and potential impact on host species growth in pure and mixed stands

3.6.2.1 Black spruce

Our study revealed the typical features of stressful (limiting) versus improved (non-limiting) growth conditions for spruce in pure spruce and mixed stands, respectively. Although a significant proportion of spruce root-associated OTUs was common to both types of stands, the combined abundance of spruce specialists and generalists on spruce roots was higher in mixed than in pure spruce stands (Appendix B Figure S3.3). The *Atheliaceae* and the *Russulaceae* were the most abundant taxa in pure spruce stands. The better adaptation of these two families to acidic and stressful conditions makes them the main ectomycorrhizal taxa dominating the mycorrhizal network of trees in nutrient limited sites in the boreal forest (Hedh *et al.*, 2008; Kalliokoski *et al.*, 2010; Peter *et al.*, 2008). Some *Atheliaceae* species such as *Tylospora fibrillosa* (abundant in pure spruce stands) were previously reported to represent up to 70% of the total abundance of the mycorrhizal network of roots of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) growing in pure stand under anoxic soil conditions in Northern England (Palfner *et al.*, 2005). Palfner et al. (2005) showed that their abundance was associated with higher fine root biomass and a high C concentration in the soil. These conditions prevailed in pure spruce stands (Ghotsa Mekontchou *et al.*, 2020). Under such conditions, medium-fringe exploration type and the hydrophobic property of their emanating hyphae favor a rapid immobilization of N in *Atheliaceae* mycelium, intensifying the N-limiting conditions of the medium (Näsholm *et al.*, 2013). In addition, under these conditions, ericoid mycorrhizae (associated with *Ericaceae*, abundant in the understory of pure spruce stands) hamper the decomposition process by a competitive suppression of saprotroph fungi *Atheliaceae* (Bending, 2003; Gadgil et Gadgil, 1975; Lindahl *et al.*, 2001) leading to the accumulation of organic matter in the soil (Averill et Hawkes, 2016). These processes may negatively affect the nutrition of spruce and, ultimately, its growth.

The increased total nitrogen and ammonium concentrations as well as the decreased abundance of *Atheliaceae* generalists and the higher abundance of *Atheliaceae* specialists in mixed stands might favor spruce growth and persistence in mixed compared to pure spruce stands. The higher abundance of *Cortinariaceae*, *Gloniaceae*, *Thelephoraceae* and *Russulaceae* in mixed stands as compared to pure spruce stands is in line with this interpretation. These families, besides being excellent decomposers (Bödeker *et al.*, 2014; Kuiters, 1990; Tedersoo et Smith, 2013), also have a significant enzymatic activity and are hydrophilic which facilitates the mobilization of nitrogen and phosphorus from complex organic matter in the immediate vicinity of fungal mycelium (Agerer, 2001; Kyaschenko *et al.*, 2017; Lindahl et Tunlid, 2015). This would allow spruce to take up a varied range of nutrients (organic and mineral forms) from soil. The presence of *Thelephoraceae* exclusively on spruce roots in mixed stands (and not in pure spruce stands, Figure 3.4b) might point to an increased nutrient demand of spruce as this fungus is effective in absorbing nutrients (phosphorus, nitrogen and potassium) from the soil, the soil solution, and from the fermenting organic matter (Bending et Read, 1997). Their medium-smooth exploration type also allows for exploring a greater volume of soil (Agerer, 2001). The *Inocybaceae*, another abundant fungal taxa in the mineral horizon of the studied mixed stands (Figure 3.4b), is known to dominate in stressful environments (Nara, 2006; Tedersoo *et al.*, 2006). Their high abundance in the mineral horizon has been reported to improve the resilience of the host tree to harsh environmental conditions such as water stress (Reverchon *et al.*, 2012).

3.6.2.2 Trembling aspen

The spatial (along soil profile) and the functional (within each soil layer) niche differentiation of root-associated mycorrhizal communities may be the key driver of differences in tree nutrition between spruce and aspen in mixed stands. The spatial niche differentiation exhibited itself through the stronger separation of root-associated mycorrhizal communities of spruce and aspen in mixed as compared to their respective pure stands (Figure 3.1). This pattern is generally interpreted as the result of nutrients mobilization by mycorrhizal fungi along the soil profile (Lindahl *et al.*, 2007). However, it is likely not the case in mixed stands since most of the abundant mycorrhizae associated with spruce and aspen within the both organic and the mineral layers were of contact and short-distance exploration types (Appendix B Table S3.3). This observation suggests the absence of a common mycelial network along the soil profile (Kennedy *et al.*, 2003), supporting the idea of a spatial segregation between mycorrhizal communities in mixed stands. The functional niche differentiation between root-associated mycorrhizal communities exhibited itself through the differences in the richness and abundance of spruce specialists (abundant in the organic layer) and aspen specialists (abundant in the mineral layer) in mixed stands. In the absence of a common mycorrhizal network, such pattern most often results in the competitive dominance of the most abundant community over the less abundant one (Kennedy *et al.*, 2011). This might be the case between the mycorrhizal communities of spruce and aspen within each soil layer in mixed stands. The higher relative abundance of *Atheliaceae*, *Russulaceae*, *Thelephoraceae*, *Sebacinaceae* and *Pyronemataceae* that are all spruce specialists as well as the significant effect of the interaction between host tree and nitrogen content in mixed stands support this possibility and suggest a competitive dominance of spruce mycorrhizal communities over that of aspen in the organic layer of mixed stands.

Aspen likely avoids the competitive pressure of spruce in the organic soil by developing a denser mycorrhizal network made up of highly competitive mycorrhizal species in the mineral horizon. Compared to the organic layer, the abundance of aspen specialists increased in the mineral soil of mixed stands. Two main reasons for this could be (1) an increased fine root biomass in the mineral layer (Ghotsa Mekontchou *et al.*, 2020) and (2) a competitive exclusion of aspen-associated mycorrhizae by that of spruce in the organic layer.

A lower richness and abundance of the *Glomeraceae* in the organic than in the mineral soil layer support the idea of competitive exclusion. On one hand, the increasing richness and abundance of *Glomeraceae* along the profile could be the result of a negative association between ECM and AM in the organic layer of the soil (Aguillon et Garbaye, 1990; Lodge et Wentworth, 1990; Neville *et al.*, 2002). In these studies, the negative association between ECM and AM fungi was reported to be the main cause of a decreasing ECM:AM ratio along the soil profile on aspen roots. On the other hand, the increasing abundance of *Glomeraceae* with soil depth might be the result of a reciprocal reward mechanism known to ensure fair trade in *Glomus* symbiosis (Kiers *et al.*, 2011). Unlike ECM fungi, AM fungi are obligate biotroph and depend exclusively on host derived C to complete their life-cycle (Wright *et al.*, 1998). *Glomus* symbiosis (the only AM genus identified in this study) has been reported to be controlled by the nutrient demand of the host tree (Benedetto *et al.*, 2005). Both the host and the *Glomus* fungi can detect variation in the resources supplied by the relationship, allowing them to adjust their own resource allocation accordingly, a pattern known as *reciprocal reward mechanism* (Kiers *et al.*, 2011). The increased richness and abundance of AM fungi along the soil profile depth could therefore be interpreted as a strategy used by aspen to maximize the nutritional benefit from the mycorrhizal symbiosis.

Interestingly, a higher relative abundance of the *Russulaceae*, *Thelephoraceae*, *Glomeraceae*, *Hygrophoraceae*, *Sebacinaceae* and *Hymenogasteraceae* on aspen roots as compared to spruce roots in the mineral layer pointed to a competitive dominance of aspen-associated mycorrhizal community over that of the spruce in this soil layer. Members of these fungi families are known to form contact, short- or medium-smooth exploration-type ECM that are hydrophilic and lack rhizomorphs (Agerer, 2001). Most of them and, particularly, members of the *Hygrophoraceae*, are considered nitrophilic as they respond positively to high N inputs (Lilleskov *et al.*, 2001, 2002), and possess therefore a competitive advantage over other mycorrhizal species in their close vicinity (Lodge *et al.*, 2014). The *Hygrophoraceae* are more adapted to calcareous ground in the Nordic countries (Kovalenko, 1999, 2012; Tedersoo *et al.*, 2010). As a result, they are frequently detected as ECM specialists on the roots of deep-rooted trees such as *Pinus* species in the mineral soil (Larsson *et al.*, 2018). Thus, root-associated mycorrhizal communities of spruce and aspen may compete along the soil profile, resulting in a strong partitioning of the nutrient uptake of the two species at different soil horizon in mixed stands.

It is unclear whether aspen growth is enhanced in mixed as compared to pure aspen stands. Plants can acquire nutrients via two uptake pathways: (a) the direct pathway by nutrient uptake from soil-root interface by root hairs and (b) the mycorrhizal pathway involving extraradical mycelium (Smith et al. 2013).

A possible reciprocal reward mechanism has been reported to generally result in a higher mycorrhizal dependency of the host plant on fungi-mediated uptake of P and N. The observation of such pattern has led many authors to suggest that a higher dependence on the mycorrhizal pathway for nutrient uptake stimulate the C allocation to roots than to the aboveground biomass (Jakobsen *et al.*, 2003; Nielsen *et al.*, 1998; Postma et Lynch, 2011). The higher fine root biomass of aspen in mixed stands as compared to pure stands (Ghotsa Mekontchou *et al.*, 2020) support this statement. In-depth studies of the two nutrient uptake pathways and examination of nutrient content of leaves are therefore warranted to conclude on the potential impact of the changes in richness and abundance of root-associated mycorrhizal communities on aspen growth.

3.7 Conclusion

Differences in diversity, abundance and composition of ectomycorrhizal communities of tree species growing in pure and mixed stands are strongly influenced by soil chemical properties and host species identity. We found that the root-associated mycorrhizal community of spruce differed significantly from that of aspen when both species were in their respective pure stands, supporting Hypothesis 1. Hypothesis 2 was partially supported for spruce roots as an increased diversity and changes in the composition of mycorrhizal communities associated with spruce was a result of increased soil fertility in mixed stands as compared to pure spruce stands. In contrast, for aspen it was the competitive interactions that structured the mycorrhizal community in mixed stands as compared to pure stands. Despite a small overlap between the communities of the two species in mixed stands, the higher relative abundance of spruce specialists than aspen specialists suggested a competitive dominance of communities associated with spruce over that of aspen in the organic horizon. This pattern was reversed in the mineral horizon, supporting our Hypothesis 3. The competitive dominance of root-associated specialist mycorrhizal communities of spruce and aspen in different sections of soil profile suggests a strong partitioning of resources in different soil layers between the two species in the mixed stands. The higher richness and abundance of mycorrhizal communities of spruce in mixed than in pure stands may support better growth of spruce in mixed stands (Légaré *et al.*, 2004) as a result of increased spruce nutrient uptake.

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CHAPTER IV

THE PARTITIONING OF NITROGEN USE OF BLACK SPRUCE AND TREMBLING ASPEN IN BOREAL MIXEDWOODS OF EASTERN CANADA SUPPORTS COMPLEMENTARITY HYPOTHESIS

(PARTITIONNEMENT DES ABSORPTIONS D'AZOTE DE L'ÉPINETTE NOIRE ET LE PEUPLIER FAUX-TREMBLE DANS LES FORÊTS BORÉALES MIXTES DE L'EST DU CANADA SUPPORTE L'HYPOTHÈSE DE COMPLÉMENTARITÉ)

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4.1 Résumé

Afin de quantifier les mécanismes favorisant la coexistence de l'épinette noire et du peuplier faux-tremble dans les forêts boréales nord-américaines, nous avons exploré leur absorption d'azote (N) dans les peuplements purs et mixtes de l'ouest du Québec. Nous avons d'abord analysé la teneur totale en N et l'abondance isotopique naturelle ($\delta^{15}N$) des feuilles, et le $\delta^{15}N$ des sols prélevés à différentes profondeurs du sol (organique, couches supérieure 0-15 cm et inférieure 15-30 cm du sol minéral). Dans un deuxième temps, nous avons réalisé une expérience *in situ* d'ajouts d'ammonium ($^{15}N\text{-}NH_4\text{-}NO_3$) et de nitrate ($NH_4\text{-}^{15}N\text{-}NO_3$) marqués dans des mini-parcelles de sol. La teneur totale en N des feuilles du tremble était 3,5 fois plus élevée que celle des aiguilles d'épinette dans les peuplements purs. Dans les peuplements mixtes, la teneur totale en N des feuilles d'épinette et de tremble augmentait et diminuait respectivement et de manière significative comparé à leurs peuplements purs. Les résultats de l'abondance isotopique naturelle ont révélé que le $\delta^{15}N$ des aiguilles d'épinette était fortement corrélé avec le $\delta^{15}N$ des sols organiques tandis que le $\delta^{15}N$ des feuilles du tremble était fortement corrélé avec le $\delta^{15}N$ de la couche supérieure du sol minéral dans les peuplements purs et mixtes. L'expérience d'ajout du ^{15}N a montré une nette préférence pour le $^{15}N\text{-}NO_3^-$ et le $^{15}N\text{-}NH_4^+$ par le tremble et l'épinette, respectivement, dans des peuplements purs. Ces préférences n'ont pas été observées dans les peuplements mixtes où les deux espèces prélevaient les deux formes de ^{15}N ajoutées dans des proportions similaires. Cependant, l'absorption de $^{15}N\text{-}NO_3^-$ du tremble diminuait de 3 fois tandis que celle de $^{15}N\text{-}NH_4^+$ augmentait de 2 fois dans les peuplements mixtes par rapport aux peuplements purs. Chez l'épinette en revanche, l'absorption de $^{15}N\text{-}NO_3^-$ était multipliée par 2 dans les peuplements mixtes par rapport aux peuplements purs, tandis que l'absorption de $^{15}N\text{-}NH_4^+$ était similaire entre les deux types de peuplements. Nos résultats montrent que le mélange d'épinette et de tremble profite principalement à la nutrition de l'épinette qu'à la nutrition du tremble tel que le suggère la teneur totale en N des feuilles. Dans les peuplements mixtes, l'épinette et le tremble partitionnent leur absorption d'azote à différentes profondeurs du sol, tout en ayant la même demande pour les deux formes de N. Ces résultats sont cohérents avec l'hypothèse de complémentarité postulant que l'augmentation de la diversité compositionnelle des peuplements augmente la productivité des peuplements grâce une compétition limitée et une utilisation plus efficace des ressources par les espèces cooccurrentes.

Mots-clés: ^{15}N, abondance isotopique naturelle, partitionnement de l'azote, forêts boréales, relation diversité-productivité

4.2 Abstract

To quantify the mechanism supporting coexistence of black spruce and trembling aspen in North American boreal mixedwoods we explored their nitrogen (N) uptake in pure and mixed stands of western Quebec. We first analyzed the total N content and the natural isotopic abundance ($\delta^{15}N$) of leaves, and the $\delta^{15}N$ of soils taken at different soil depth (organic, top 0-15 cm and bottom 15-30 cm mineral soils). In a second step, we did an experiment *in situ* by adding labelled ammonium ($^{15}N\text{-}NH_4\text{-}NO_3$) and nitrate ($NH_4\text{-}^{15}N\text{-}NO_3$) on soil plots. The total N content of aspen leaves was 3.5 times higher than spruce needles in pure stands. In mixed stands, the N total content of spruce and aspen leaves significantly increased and decreased respectively as compared to their pure stands. The results of natural isotopic abundance revealed that spruce needle $\delta^{15}N$ was strongly correlated with $\delta^{15}N$ of the organic soils while aspen leaves ^{15}N was more strongly correlated with the ^{15}N of the top mineral soil in both pure and mixed stands revealing that spruce and aspen partition their N uptake over different soil depths. The ^{15}N addition experiment showed a clear preference for $^{15}N\text{-}NO_3^-$ and $^{15}N\text{-}NH_4^+$ for aspen and spruce respectively, in pure stands. These preferences were not observed in mixed stands where the two species took up the two added ^{15}N forms in the same proportions. However, the $^{15}N\text{-}NO_3^-$ uptake of aspen decreased by 3-fold while that of $^{15}N\text{-}NH_4^+$ increased by 2-fold in mixed as compared to pure stands. In spruce by contrast, the $^{15}N\text{-}NO_3^-$ uptake increased by 2-fold in mixed as compared to pure stands whereas the $^{15}N\text{-}NH_4^+$ uptake was similar between the two types of stands. Our results show that mixed stand benefit mostly to spruce nutrition as suggested by the total N content of leaves. Overall, our findings are consistent with the complementarity hypothesis postulating that increasing stand compositional diversity increased stand productivity through limited competition and more efficient use of resources by co-occurring species.

Keywords: ^{15}N, natural isotopic abundance, nitrogen partitioning, boreal forests, diversity-productivity relationship

4.3 Introduction

Resource partitioning support species coexistence within ecosystems (Houle *et al.*, 2014; Turner, 2008) through reduced competition among species (Neufeld *et al.*, 2014). This mechanism has been hypothesized to lead to a more efficient acquisition of limiting resources and, therefore, a positive effect on productivity (Loreau et de Mazancourt, 2013; Loreau et Hector, 2001; Tilman, 1999). Resource partitioning is traditionally assessed through analysis of spatial distribution of fine roots (Brassard *et al.*, 2009; de Kroon *et al.*, 2012), and by analysing the relationship between nutrient content in soil and plant tissues (Craine *et al.*, 2009), which reflects the use of soil nutrients by a species.

Nitrogen (N) is considered the most limiting nutrient for plant growth in temperate and boreal forests (Tamm, 1991). N dynamics has been shown to be controlled by climate variability (McLauchlan et Craine, 2012; Ouimet *et al.*, 2015), natural disturbances

(Beghin *et al.*, 2011; Choi *et al.*, 2007), stand age and composition (Côté *et al.*, 2000; Pörtl *et al.*, 2007), and microbial activity (Knops *et al.*, 2002; Paul et Clark, 1996). The presence of multiple factors controlling biological availability of N forms constrains the generalization of N cycle (Galloway *et al.*, 2004, 2008; Schimel et Bennett, 2004) and challenge the understanding of N partitioning in the boreal forests.

N isotopic ratios ($\delta^{15}N$) of plant tissues (e.g., roots and leaves) and soil have been proven useful to elucidate patterns of N utilization. The use of tree leaves as an index of whole-plant $\delta^{15}N$ has revealed partitioning for soil nitrogen, mycorrhizal dependence and utilization of depositional N (Vallano et Sparks, 2013) which are likely to occur widely in nature (Craine *et al.*, 2015). N partitioning generally involves (a) variation in the uptake rate of N from different soil horizons and (b) variation in the use of different N bio-available forms by the co-occurring species (Kronzucker *et al.*, 1997, 2003; Shenoy *et al.*, 2013; Van den Driessche, 1971). Empirical and experimental evidences of N's spatial partitioning have been widely reported in temperate grasslands (Weigelt *et al.* 2005; Kahmen *et al.* 2006) while evidences are very scarce for trees growing in mature stands apart from the study of Houle et al. (2014) in mixed black spruce – jack pine boreal forests of Quebec. Concerning partitioning of N through tree preference for different chemical N forms, *ex-situ* ^{15}N addition experiments with seedlings have shown a high preference of conifers for ammonium than for nitrate (Kronzucker *et al.*, 1997; Van den Driessche, 1971). An *in-situ* experiment confirmed a strong preference of white spruce seedling (*Picea glauca* (Moench) Voss) for ammonium while a preference for nitrate was observed for seedlings of aspen (Shenoy *et al.*, 2013). Spatial and chemical partitioning of N species may exist in mixed stands of black spruce (BS; *Picea mariana* [Mill.] B.S.P.) and trembling aspen (TA; *Populus tremuloides* Michx.), supporting coexistence of these species. This may be particularly the case in the spruce feathermoss domain of Eastern Canada, where competitive exclusion of aspen by spruce has been earlier proposed as the main successional pathway (Bergeron, 2000; Bergeron et Dubuc, 1988).

This study aimed to determine the existence of two forms of N partitioning, spatial and N-form related, between black spruce and trembling aspen in boreal mixedwood stands. First, to test for the N spatial partitioning, we compared the ^{15}N natural abundance in the soils and in the foliage of spruce and aspen in pure and mixed stands. We hypothesized (H1) that the two species takes up the N at different soil depth (shallower N-uptake in spruce and deeper in aspen) in both pure and mixed stands. Second, to test for partitioning of N-inorganic forms, we performed a 30 day *in-situ* ^{15}N-labeling experiment in pure and mixed stands. We hypothesized (H2) that in their respective pure stands, black spruce would prefer ammonium and aspen would prefer nitrate. In mixed stands, we expected (H3) the N-forms preference of both species to be more pronounced as the two species will seek to distance themselves to avoid competition. Finally, since the nutrient content increases mostly in the organic layer of mixed stands, as compared to pure spruce stands (Légaré *et al.*, 2005), we hypothesized (H4) that spruce will benefit from a better N nutrition in mixed than in pure stands while the net effect will be neutral for aspen.

4.4 Material and methods

4.4.1 Study area

The study sites (three in total) were located in the black spruce-feathermoss bioclimatic domain in North-Western Quebec. The three sites were 2 to 15 km away from each other. Site characteristics including mean annual temperature, total annual precipitation, soil type and the age of stands are described in Ghotsa Mekontchou et al. (2020). Each site each feature three stand types: black spruce dominated (BS), trembling aspen dominated (TA), and mixed black spruce – trembling aspen (MXT) stands. These stands were 20 x 50 m^2 (0.1 ha) rectangular plots, each of them being uniform in terms of topography and vegetation, and representing a particular stand type. We defined pure stands as those with the proportion of stems and basal area of the most abundant tree species exceeding respectively 75 % and 60 % of the total count of individuals with a diameter at 1.3 m above 10 cm. Mixed stands were those with the number of trees of individual species representing 30 % to 50 % of the total number of stems in the stand (see Ghotsa Mekontchou *et al.*, 2020).

4.4.2 Sampling

4.4.2.1 Leaves

Leaf samples were collected in triplicate from dominant healthy trees of each species, randomly selected in each plot on the 28th of August 2016. For spruce, the needles older than two years were discarded from twigs before drying (Houle *et al.*, 2014). The leaves were air-dried for one month and ground at the Laboratory of Organic and Inorganic Chemistry of the Ministry of Forests, Wildlife and Parks (MFFP) of Quebec.

4.4.2.2 Soil

At each plot, five soil cores were extracted at regular intervals within a distance 7 m around each selected tree (one at the foot of the tree and the other four at 1m, 3m, 5m and 7m) using a 7 cm diameter manual auger. The 7 m space set around the tree represented the distance at which the effect of aspen on soil physical and chemical properties persists (Légaré *et al.*, 2005). We collected soil samples from the organic horizon (F and H layer combined) and from the top (0-15 cm) and the bottom (15-30 cm) of the mineral soil. The samples (n = 135) were placed in plastic bags, transported to the laboratory in an ice-filled cooler and stored at -20°C temperature prior to analyses. Thawed samples were pooled per tree and soil horizon to form a set of three composite samples corresponding to the three selected trees in each plot. An aliquot was taken from each soil sample and air-dried to constant weight for a week (Carter et Gregorich, 2008), ground and sieved (< 2 mm) for further analyses.

4.4.3 N labelling experiment

4.4.3.1 Experimental design

We implemented an *in situ* ^{15}N addition experiment between June 12 and July 12, 2016. The experiment was carried out in two of the three sites selected for this study (sites 1 and 2, Figure 2.1 in Chapter II). It consisted of an addition of two 98% ^{15}N-enriched N forms of ammonium nitrate i.e. ^{15}N-NH^4-NO^3 and NH^4-^{15}N-NO^3, later referred to ^{15}N-NH_4^+ and ^{15}N-NO^3 for ammonium and nitrate, respectively. Each N form was applied in two 30 x 30 cm^2 quadrates established around three replicates of dominant healthy trees per stand type, under the criteria of a free-standing canopy and representing the spatial variability of the plot (Hayashi *et al.*, 2018). 39 mg of each ^{15}N-enriched N forms was diluted with 900 ml of deionised water and applied in each quadrate. These estimates were computed based on the ^{15}N addition experiment described in Houle et al. (2014).

4.4.3.2 Soil and root samples collection

One soil core was extracted in each quadrate after 30 days using a 7 cm diameter auger and separated into three sections as described in the section above. The samples were placed in plastic bags, transported to the laboratory in an ice-filled cooler and stored at -20°C temperature prior to analyses. Soil samples were let to thaw over six hours and then soaked in water for at least one hour. The mixture was then stirred carefully to separate roots from the soil particles and poured through a 750 µm mesh round sieve. The sieve was suspended under a distilled water bath and shaken continuously until the roots were free from any soil particle. The roots were collected and separated between live and dead roots (Brassard *et al.*, 2013). We discarded dead roots from further analyses. Live fine roots were sorted by species using a combination of morphological characteristics established from prior root reference samples collected on known younger and older trees of each studied species in the study stands. Used morphological criteria were colour, size, ramifications and presence/absence of root hairs (Brassard *et al.*, 2013). Aspen roots were less ramified with colors ranging between white and pale, whereas roots of coniferous trees were ramified, finer in structure, and of the color ranging between red and brown. Compared to others coniferous trees, spruce roots were more reddish in color with a black bark. The presence of root hairs was mostly used to separate non-tree roots (commonly with root hairs) from tree roots. We discarded roots larger than 2 mm in diameter using a calliper. The separated fine roots were gently dried between two filter papers under room temperature to remove water. Roots samples were oven-dried at 60 °C for 48 hours, ground, and sent to GEOTOP to analyze their total $\delta^{15}N$ content.

4.4.4 Analytical procedure

4.4.4.1 Chemical analysis

Soil, root and foliage ^{15}N natural isotopic abundance were analyzed using an elemental analyzer in continuous flow mode, coupled to an isotope ratio mass spectrometer (EA-IRMS) at the Centre de recherche en géochimie et géodynamique (GEOTOP) in Montreal. The isotope ratio was expressed using the δ notation:

$$\delta^{15}N\ (‰) = (R_{sample}/R_{standard} - 1) \times 1000 \quad \text{(Eq 1)}$$

where R_{sample} is the isotope ratio ($^{15}N/^{14}N$) of a sample, and R standard is the isotope ratio ($^{15}N/^{14}N$) of atmospheric N_2 ($\delta^{15}N$ = 0 ‰) (Coplen, 2011). The $\delta^{15}N$ values (expressed in ‰ vs air-N_2 (±0.1 ‰ à 1σ)) were corrected with a calibration line obtained from two reference materials (urea ($\delta^{15}N$ = –0.1 ‰) & dogfish tissue ($\delta^{15}N$ = +14.95 ‰)). Furthermore, leucine ($\delta^{15}N$ = –0.1 ‰) was used as a third internal reference material to verify the calibration skill. All these internal reference materials were normalized to IAEA-N1, N-2, and N-3 scales for $\delta^{15}N$.

Foliage total N concentrations were measured with an automatic elemental analyzer in continuous flow mode at the GEOTOP in Montreal. For soil, samples were extracted with 2M KCl (10:1 solution soil ratio, 30 minutes). Soil total N concentration was measured with an elemental analyzer (Carlo Erba, Milan, Italy) at the MFFP in Quebec. Nitrate (NO_3) and ammonium (NH_4) concentrations were measured respectively by ion chromatography (Dionex2120i, Thermo Fisher Scientific Inc., Sunnyvale, USA) and colorimetrically with a Technicon Autoanalyzer (Technicon AA2, Seal Analytical Inc., Mequon, USA). Since observed nitrate concentrations were below or close to the detection limit (limit of < 1 mg kg^{-1} for extractable NO_3), we only report NH_4 results.

4.4.4.2 Statistical analysis

To test H1, we assessed the correlation between leaf $\delta^{15}N$ and soil $\delta^{15}N$ using *Spearman*'s rank correlation coefficient at $p < 0.05$.

Several approaches were used to test H2. First, we calculated the ^{15}N enrichment in soil and roots. The enrichment represented the influx of the ^{15}N-labeled isotopes in soil and roots. It was expressed in $\delta^{15}N$ notation and calculated as follows:

$$\delta^{15}N_{enrichment} = \delta^{15}N_{experiment} - \delta^{15}N_{reference} \quad \text{(Eq 2)}$$

where $\delta^{15}N_{experiment}$ is the isotope ratio ($^{15}N/^{14}N$) of the sample at the end of the experiment, and $\delta^{15}N_{reference}$ the natural isotopic abundance ($^{15}N/^{14}N$) of the sample. Temporal changes in ^{15}N natural isotopic abundance of roots and soil were considered negligible during the experiment (Craine *et al.*, 2015; Koba *et al.*, 2003). Secondly, we calculated the isotopic fractionation factor, so-called enrichment factor (Coplen, 2011), expressed in ε notation and calculated as follows:

$$\varepsilon_{R/S} \approx \Delta^{i}\delta^{15}N_{R/S} = \delta^{15}N_{R,enrichment} - \delta^{15}N_{S,enrichment} \quad \text{(Eq 3)}$$

where $\varepsilon_{R/S}$ represented the discrimination of the added ^{15}N-labeled isotope between roots and soil (Coplen, 2011). Since several chemical and biogeochemical reactions (e.g. assimilation, mineralization, diffusion and nitrification) generally occur downstream of the N-uptake, the $\varepsilon_{R/S}$, as computed in equation 3, assessed uptake of the ^{15}N-labeled isotopes in relation to the retention of the ^{15}N-labeled in soil. $\varepsilon_{R/S}$ was used to assess the preference of tree species for the two added ^{15}N-forms in the mineral layer where $\delta^{15}N_{experiment}$ values of soil samples were closer to the natural isotopic abundance ^{15}N (Craine *et al.*, 2015). Positive values of $\varepsilon_{R/S}$ indicated root N-uptake above N-retention in soil, whereas negative values of $\varepsilon_{R/S}$ indicated that retention of N in the soil dominates over its uptake by tree roots. Finally, we calculated the correction factor *k* (*k-factor*) which represents the isotopic discrimination effect of the ^{15}N-labeled sources of nitrogen between roots and soil (Coplen, 2011). This procedure was only applied in the organic soil layer since the N-labeling was effective in both roots and soils in that soil layer. The *k-factor* was calculated as the ratio of ^{15}N-labeled influx between root and soil. As computed, *k* defines the rate constant of roots' reaction in response to the ^{15}N-labeled addition (Kendall et Caldwell, 1998).Values of *k* greater than 1 indicated that roots react more readily to N addition than soil reactions (N uptake being above the N retention in the soil). We referred to this pattern as *normal*. Values of *k* below 1 indicated a higher N retention in soil than its root uptake. We referred to such pattern as *inverse* (Kendall et Caldwell, 1998).

To test hypothesis 3, we compared *k-factor*'s values for ^{15}N-form preferences of each of the two species between pure and mixed stands. We used the analysis of variance (ANOVA) followed with the Tukey HSD post hoc tests to evaluate the significance of differences between variables among stand types.

To test hypothesis 4, we compared the total N content and the δ^{15}N of the leaves of the two species among stand types using the Kruskal-Wallis and Dunn tests of R package *dunn.test*, since the normality and the homoscedasticity was not met, even after log10 transformation.

All statistical analyses were conducted with R, version 3.4.4 (R Core Team, 2016). The homogeneity of variances and the normality of distributions of all data sets were checked prior to the analysis.

4.5 Results

4.5.1 Leaf total N content and $\delta^{15}N$

In respective pure stands, the total N content of aspen leaves was 3.5 times higher than that of spruce needles (Figure 4.1a). In mixed stands, the N total content of spruce needles significantly increased as compared to pure spruce stands while the opposite was observed for aspen in mixed and pure stands. For both species, the $\delta^{15}N$ and total N content of leaves were positively correlated in the pure and mixed stands (Appendix C Figure S4.1).

Overall, the foliage $\delta^{15}N$ values of spruce were more ^{15}N-depleted in pure than in mixed stands while the opposite pattern was observed for aspen (Figure 4.1b). The differences between pure and mixed stands were higher in spruce than in aspen. The lowest and the highest foliage ^{15}N natural isotopic abundance were recorded in spruce-pure stands and spruce-mixed stands, respectively (Figure 4.1b).

In pure stands, the average $\delta^{15}N$ of needles of spruce (-3.12±2.52 ‰) was significantly lower than for aspen leaves (0.31 ± 1.56 ‰). Aspen had significantly higher foliage $\delta^{15}N$ values in pure than in mixed stands (Figure 4.2b). The foliage $\delta^{15}N$ of the two species growing in close proximity in mixed stands was significantly higher in spruce (1.25 ± 1.66 ‰) than in aspen (-0.64 ± 0.65 ‰).

4.5.2 Soil $\delta^{15}N$

The soil $\delta^{15}N$ increased with increasing soil depth in the three stand types (Figure 4.1c, 4.1d and 4.1e). In pure spruce stands, the $\delta^{15}N$ values ranged from 3.14±0.58 ‰ to 8.5±0.6 ‰ in the organic and mineral soil, respectively (Figure 4.1c). The increase in soil $\delta^{15}N$ with soil depth was more pronounced in pure spruce stands than in mixed stands where the $\delta^{15}N$ values ranged between 4.93±0.81 ‰ to 7.7±0.78 ‰ in the two soil horizons (Figure 4.1d). The gradient observed in mixed stands was similar to that of pure aspen stands ($\delta^{15}N$ values ranging from 4.93±1.01 ‰ to 7.82±0.73 ‰ between the organic and mineral soil layers, Figure 4.1e). Among all stand types and depth combinations, pure spruce stands had the most ^{15}N enriched part of soil profile (the top mineral soil) and the most ^{15}N depleted parts (the organic layer).

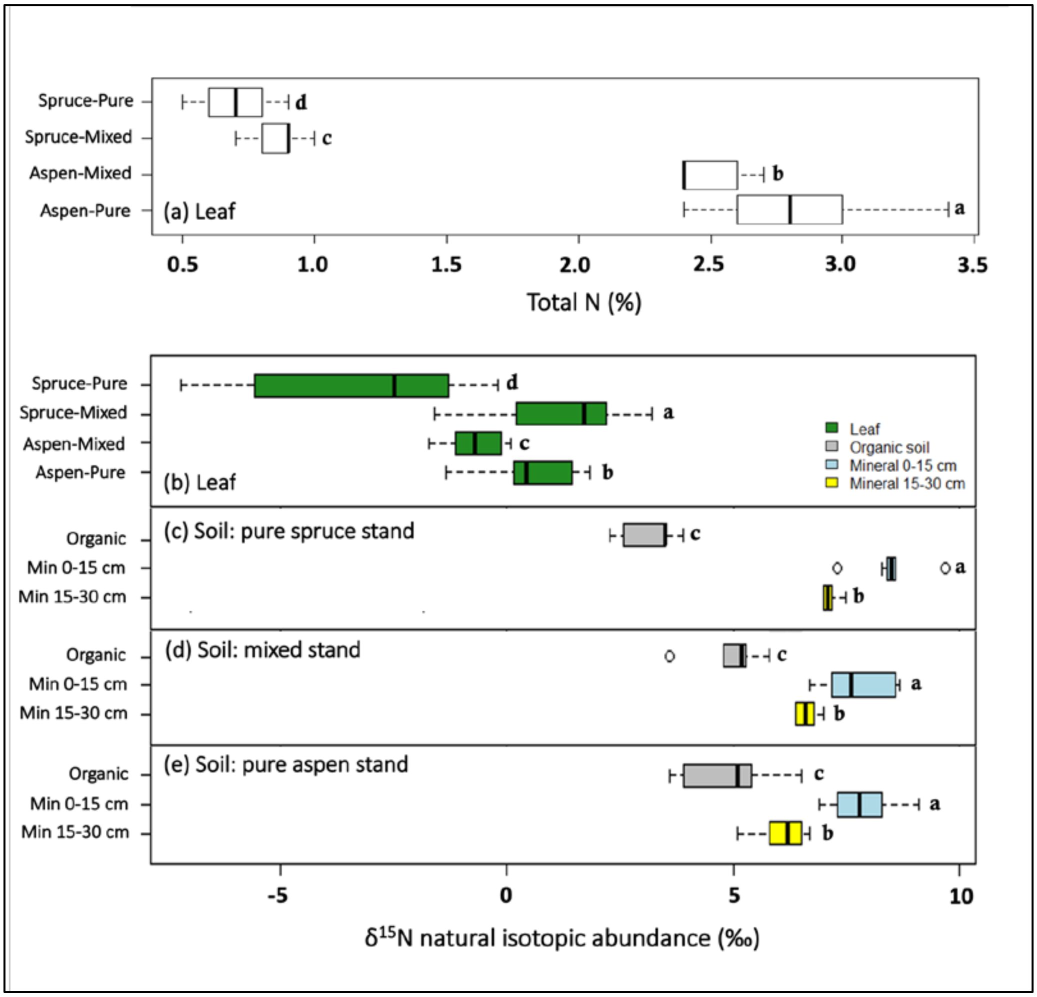

Figure 4.1 Variation of leaf (a) total N content and (b) δ^{15}N, and (c,e) soil δ^{15}N natural isotopic abundance in pure and mixed stands of spruce and aspen. The letters indicate significant differences at $p < 0.05$.

4.5.3 Relationships between soil δ^{15}N and leaf δ^{15}N

The relationships between soil δ^{15}N and foliage δ^{15}N are shown in Figure 4.2. In spruce, the δ^{15}N of needles showed a positive correlation with the δ^{15}N of the organic soil in both pure and mixed stands (Figure 4.2a and 4.2b). The correlation was lower in pure spruce (Figure 4.2a) than in mixed stands (Figure 4.2b).

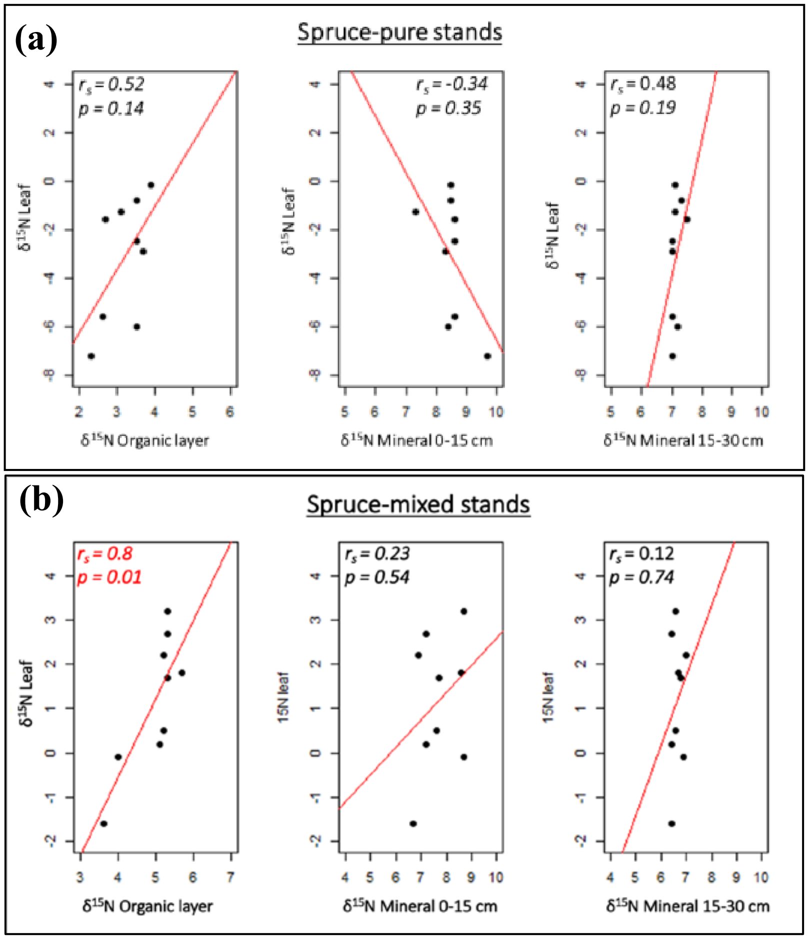

Figure 4.2 Simple linear regression analysis of soil $\delta^{15}N$ and leaf $\delta^{15}N$ for spruce and aspen in pure and mixed stands. *Spearman*'s correlation coefficient (r_s) and p values in red indicates significant relationships.

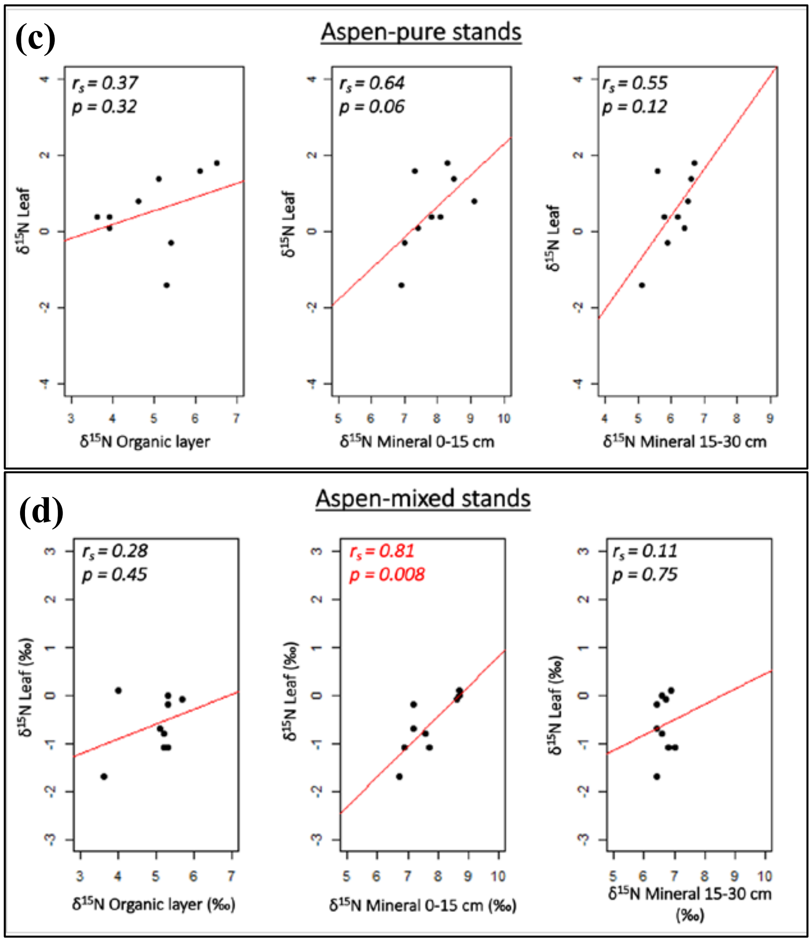

Figure 4.2 Continued.

In aspen, in contrast, the $\delta^{15}N$ of foliage showed a significant positive correlation with the $\delta^{15}N$ of the top mineral layer in mixed stands (Figure 4.2d) whereas no significant correlation was detected in pure aspen stands (Figure 4.2c). Although no significant correlation was observed between leaf $\delta^{15}N$ and the $\delta^{15}N$ in different soil N pools in pure aspen stands, the correlations tended to be higher in the top and the bottom mineral layers than in the organic layer (Figure 4.2c).

4.5.4 ^{15}N labelling experiment

Overall, the results of the labelling experiment (absolute δ^{15}N values) showed a decrease in ^{15}N-enrichment for both forms of ^{15}N-labeled with soil depth (Table 4.1). This pattern was observed in both soil and roots. Following the ^{15}N-NH_4^+ addition, the roots were more ^{15}N-enriched than soils in the three types of stands (Table 4.1). The same pattern was observed for ^{15}N-NO_3^- addition, except in pure spruce stands where the average ^{15}N enrichment was significantly higher in soil than in roots following the ^{15}N-NO_3^- addition.

Table 4.1. The δ^{15}N (mean and SEM) of roots and soils along the soil profile following the addition of the two ^{15}N-labelled forms in pure and mixed stands of spruce and aspen.

		Pure spruce		Mixed (Spruce + Aspen)		Pure Aspen	
		δ^{15}N NO_3^-	δ^{15}N NH_4^+	δ^{15}N NO_3^-	δ^{15}N NH_4^+	δ^{15}N NO_3^-	δ^{15}N NH_4^+
Soil	Org	163.18±66.9	100.2±27.2	70.96±20.2	61.33±31.8	48.41±30.75	125.03±54.2
	Min1	0.86±0.84	4.88±4.90	3.13±3.40	11.06±14.48	5.93±2.35	25.53±17.36
	Min2	1.15±0.87	3.34±3.54	3.58±2.40	4.23±6.96	1.675±1.63	1.56±1.47
Aspen Roots	Org			240.5±119.1	155.2±55.9	275.91±67.27	224.8±74.2
	Min1			43.46±37.68	46.23±80.13	150.5±121.4	127.7±139.6
	Min2					41.63±67.58	17.71±9.4
Spruce Roots	Org	147.46±70.7	220.3±89.9	181.6±64.2	198.4±105.7		
	Min1	73.25±47.78	98.43±31.3	37.16±41.43	51.18±60.23		
	Min2						

Org, Min1 and Min2 refer to organic, mineral soil at 0-15 cm and mineral soil at 15-30 cm, respectively.

4.5.4.1 Patterns of root ^{15}N enrichment in the organic soil

The values of the *k-factor* in both spruce and aspen revealed substantial variability within and between pure and mixed stands (Figure 4.3a). Overall, roots of both species reacted more readily to ^{15}N addition than the reactions leading to the retention of added ^{15}N in the soil medium ($k > 1$).

In pure aspen stands, the enrichment of aspen roots in $^{15}N\text{-}NO_3^-$ was approximately 6-fold that of $^{15}N\text{-}NH_4^+$. In mixed stands, aspen maintained the same enrichment level for $^{15}N\text{-}NO_3^-$ and $^{15}N\text{-}NH_4^+$. However, the $^{15}N\text{-}NO_3^-$ enrichment of roots of aspen was just one third of that in mixed stands as compared to pure stands. Instead, the $^{15}N\text{-}NH_4^+$ enrichment in the mixed stands was approximately 2-fold that of pure stands.

In pure spruce stands, in contrast, the enrichment of roots by $^{15}N\text{-}NH_4^+$ was approximately 3-fold of that by $^{15}N\text{-}NO_3^-$. In mixed stands, spruce retained the same level of enrichment for $^{15}N\text{-}NH_4^+$ and $^{15}N\text{-}NO_3^-$. While spruce retained the same level of $^{15}N\text{-}NH_4^+$ enrichment in pure and mixed stands, the $^{15}N\text{-}NO_3^-$ enrichment two times higher in mixed than in pure stands.

4.5.4.2 Patterns of root ^{15}N enrichment in the mineral soil

The soil ^{15}N-labeled enrichment was lower in the mineral horizon than in the organic horizon in the three types of stands. The $\delta^{15}N$ values recorded in mineral soil were closer to the ^{15}N natural isotopic abundance of soil (Figure 4.3b). In contrast, roots were significantly more enriched than soils.

In aspen and spruce, the enrichment of roots was higher in pure than in mixed stands for both ^{15}N-labeled forms (Figure 4.3b), with the highest values found in aspen (Table 4.1). The values of the isotopic fractionation ($\varepsilon^{15}N$) were not significantly different between the two N-labeled forms within each stand type for aspen (Figure 4.3b). In spruce, however, while the values of the isotopic fractionation were significantly higher for $^{15}N\text{-}NH_4^+$ than for $^{15}N\text{-}NO_3^-$ in mixed stands, that of pure stands did not show significant differences.

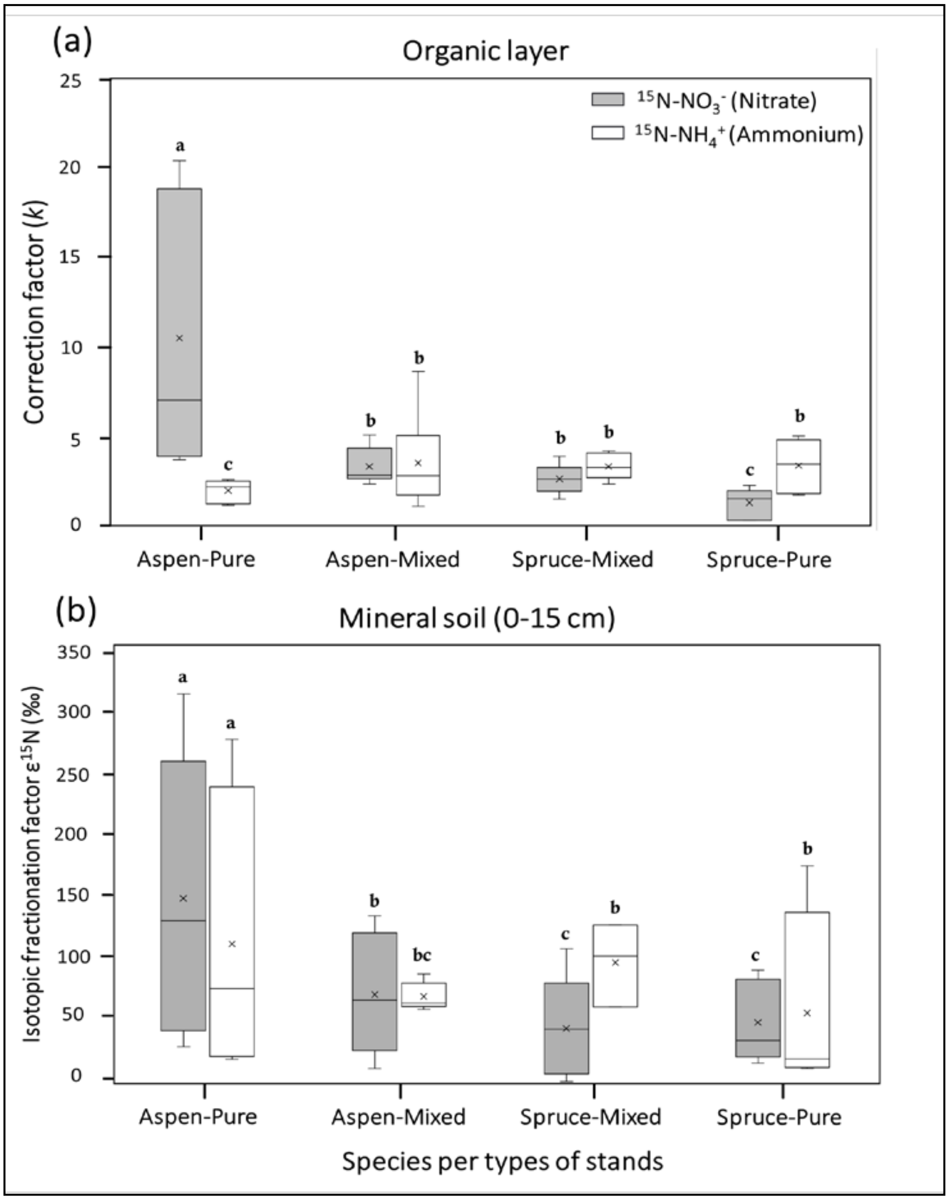

Figure 4.3 Variation of the correction factor (*k*) and the isotopic fractionation factor (ε) describing the preference of spruce and aspen for the two ^{15}N-labeled forms in (a) the organic soil layer and (b) the mineral soil layers within and between stand types. The letters indicate significant differences among stand types (Tukey multiple means test, $p < 0.05$). The x in the box represents the mean (n = 6). The median divides the box into the interquartile range. The box represents 50% of the data set, distributed between the 2nd and 3rd quartiles. The lower and upper whiskers represent the minimum and maximum quartiles.

4.6 Discussion

4.6.1 Soil and foliage ^{15}N natural abundance

We found an increasing gradient in ^{15}N natural isotopic abundance from the organic to the mineral soils in the three type of stands (Figure 4.1). This result is consistent with previous studies in the boreal forest (Fujiyoshi *et al.*, 2019; Hayashi *et al.*, 2018; Houle *et al.*, 2014; Marty *et al.*, 2011; Nadelhoffer *et al.*, 1996). The natural variation of soil ^{15}N reflect both soil N sources in the organic layer and fractionation of the soil N pool during N transformation, i.e. increasing of ^{15}N natural isotopic abundance in the residual soil fraction due to mineralization of the organic matter. The fractionation associated with the organic matter decomposition alter natural soil ^{15}N, resulting in a strong enrichment of ^{15}N in the top mineral soil or in more thoroughly decomposed soil organic matter over time (Handley *et al.*, 1999; Nadelhoffer et Fry, 1988; Xu *et al.*, 2010). The fact that this pattern was more pronounced in pure spruce stands (especially due to low ^{15}N values in the organic horizon) may be attributed to the contribution of ^{15}N-depleted needles of spruce onto the soil surface by litter-fall and their lower organic matter decomposition rate (Boström *et al.*, 2007; Emmett *et al.*, 1998; Nadelhoffer et Fry, 1994).

In agreement with previous studies, foliage $\delta^{15}N$ values of both species were lower than the $\delta^{15}N$ of bulk soil total-N (Craine *et al.*, 2015; Fujiyoshi *et al.*, 2019; Hayashi *et al.*, 2018; Houle *et al.*, 2014) in the pure and mixed stands. The foliage $\delta^{15}N$ is generally ^{15}N-depleted relative to atmospheric N_2 and to putative soil N source (Austin et Vitousek, 1998; Chang et Handley, 2000; Marty *et al.*, 2019) in wet and/or cold sites. In pure stands, the $\delta^{15}N$ values of spruce needles were lower than aspen leaves. These observations are consistent with those of previous studies in boreal forest (Choi *et al.*, 2005; Min *et al.*, 1999, 2000; Siemens *et al.*, 2011). Unexpectedly, aspen leaves had lower $\delta^{15}N$ values than spruce needles in mixed stands than in pure stands. These results may suggest changes in the N requirements of the two species between the two stand types.

4.6.2 Correlation between leaves and soils $\delta^{15}N$

We found a positive correlation between the $\delta^{15}N$ of spruce needles and $\delta^{15}N$ of the bulk organic soil in both pure and mixed stands supporting hypothesis 1 stating that spruce takes up N in the shallow soil horizon of soil. Our data did not yield conclusive result in respect to H1 for aspen: in mixed stands we observed a significant positive correlation between the $\delta^{15}N$ of aspen leaves and the $\delta^{15}N$ of the top mineral soil. However, this pattern was absent in pure aspen stands. Aspen in the mixed stands takes up its N in the top mineral soil layer, suggesting that aspen and spruce partition their N uptake between different soil depths there. These observations corroborate with previous finding that the shallower rooting of spruce and the deeper rooting of aspen likely contribute to a stronger partition of their nutrient uptake in mixed stands (Ghotsa Mekontchou *et al.*, 2020).

The lack of significant correlation between leaf and soil $\delta^{15}N$ in pure aspen stands may suggest the aspen uptake of N is driven by the soil inorganic N pool. The dominant role of inorganic N as a N source in plants appears to be associated with $\delta^{15}N$ of the plant being more closely correlated with the $\delta^{15}N$ of the inorganic N than with that of the total N content of the medium (Cheng *et al.*, 2010). A strong preference of aspen for $^{15}N\text{-}NO_3^-$ in pure stands, following the ^{15}N addition experiment, supported this idea (see below). Consistent with earlier studies (Kronzucker *et al.*, 2003; Min *et al.*, 2000; Shenoy *et al.*, 2013), the strong preference for NO_3^- over NH_4^+ by aspen may result from the less acidic soils in pure aspen stands (Hawkins et Robbins, 2010). These interpretations are also consistent with findings of previous studies, which showed very low isotopic fractionation when NO_3^- is the major N source of the plant (Mariotti *et al.*, 1981; Yoshida, 1988; Yoshida *et al.*, 1989). Moreover, the thin organic layer of pure aspen stands may help maintain high temperature of the soil during the growing season, which favors NO_3^- uptake (Clarkson *et al.*, 1986) in pure aspen than in mixed and pure spruce stands.

Surprisingly, the $\delta^{15}N$ values of spruce needles were significantly higher in mixed than in pure stands. The large isotopic difference recorded between the $\delta^{15}N$ of spruce needles of both pure and mixed stands result from difference in root distribution within the organic soil horizon. Field observation revealed that spruce roots were much more abundant in the H layer (at the limit with the mineral soil) in the organic horizon of mixed stands while roots were mostly distributed in the F layer in pure stands. Although we measured only the $\delta^{15}N$ value of the bulk organic layer, other studies reported a strong increasing $\delta^{15}N$ gradient from the L to the F and further down to the H layers in boreal forests (Houle *et al.*, 2014; Marty *et al.*, 2011). In fact, the isotopic difference (4‰) recorded between the $\delta^{15}N$ of spruce needles of pure and mixed stands is close to the 3‰ isotopic difference recorded by Houle et al. (2014) between the F and H layers of the organic horizon of spruce stands in Quebec.

On the other hand, we observed a higher soil N availability and a higher N foliar content of spruce in mixed stands, and the lower isotopic difference between the $\delta^{15}N$ of spruce needles and the soil N source (organic layer). This pattern suggested a smaller dependence of spruce on mycorrhizally derived N in mixed stands as compared to pure stands (Hobbie *et al.*, 2000, 2005). The lower $\delta^{15}N$ values of spruce needles in pure stands might therefore indicate a higher N input through ectomycorrhizae (ECM), consistent with observation that the ^{15}N fractionation is greater compared to the source when the ECM are involved in the N uptake (Hobbie *et al.*, 2005, 2009). This pattern is common to N-limiting ecosystems and has been reported to result from high dependence of the species on ECMs for N uptake (Hobbie *et al.*, 1999; Hogberg, 1997). Indeed, spruce mostly link with ECM fungi (see Chapter III; Robertson et al., 2006).

In aspen, the ^{15}N isotopic difference of leaves between pure and mixed stands was smaller than in spruce. Unlike spruce where the large isotopic difference suggested both change in N cycling and the differences in the composition of ECM communities between the two stand types, the lower $\delta^{15}N$ of aspen leaves in mixed than in pure stands may result from a strong dependence of aspen upon mycorrhizae or from preference for different N-inorganic forms. Indeed, the total N nutrient concentrations did not differ significantly between the two stand types (Ghotsa Mekontchou *et al.*, 2020) and the richness and abundance of mycorrhizae species were found to be higher on aspen roots in mixed than in pure stands (see Chapter III).

4.6.3 N inorganic forms preference

The ^{15}N labelling experiment revealed a clear preference of spruce for $^{15}N\text{-}NH_4^+$ and aspen - for $^{15}N\text{-}NO_3^-$ in respective pure stands, supporting hypothesis 2. These results demonstrate that the preference of black spruce for $N\text{-}NH_4^+$ (Shenoy *et al.*, 2013) and that of trembling aspen for $N\text{-}NO_3^-$ (DesRochers *et al.*, 2003; Shenoy *et al.*, 2013) as previously reported for seedling, are also observable for adult trees. The preference for different forms of inorganic N may result from adaptations to the availability of N in the habitat of these species (Min *et al.*, 1999, 2000) and could be dependent on the contrasting pH and soil temperature between the two stand types (Britto et Kronzucker, 2013). Indeed, a previous study in the studied stands had shown a higher rate of nitrification than ammonification in pure aspen stands and the opposite pattern has been reported in pure spruce stands (Légaré *et al.*, 2005).

In mixed stands, both tree species had similar preference for $^{15}N\text{-}NO_3^-$ and $^{15}N\text{-}NH_4^+$ that rejects hypothesis 3 stating that the inorganic N-form preferences of both species observed in pure stands will be more pronounced in mixed stands. Spruce appears to be more efficient in using the two inorganic N-forms in mixed than in pure stands. Spruce preference for $^{15}N\text{-}NO_3^-$ increased by 2-fold whereas that for $^{15}N\text{-}NH_4^+$ was similar in mixed compared to pure stands. However, the fact that spruce and aspen showed similar preference for both forms of inorganic N may indicate an increased competition for the two inorganic N forms in the organic soil layer. As spruce uses an intensive nutrient uptake strategy (Ghotsa Mekontchou *et al.*, 2020) and has a higher richness and abundance of mycorrhizae than aspen in organic soil layer (see Chapter III), spruce likely overcompetes aspen in the organic soil horizon of mixed stands. The richest and the most abundant ECM taxa on spruce roots in the organic soil layer of mixed stands were *Cortinariaceae*, *Gloniaceae*, *Thelephoraceae* and *Russulaceae* (see Chapter III). These families have a significant enzymatic activity, which facilitates the mobilization of varied forms of nitrogen (organic and inorganic) in their immediate vicinity (Agerer, 2001; Kyaschenko *et al.*, 2017; Lindahl et Tunlid, 2015).

4.6.4 The impact of species mixture on N nutrition

Overall, aspen leaves had remarkably higher total N content than spruce even in mixed stands where they grow in similar soil conditions. The higher N content of spruce needles in mixed than in pure stands demonstrates a better N nutrition in mixed stands supporting hypothesis 4. We speculate that the observed pattern probably reflects the facilitative effect of aspen litter on soil N availability (Cavard *et al.*, 2011; Légaré *et al.*, 2001, 2005; McClaugherty *et al.*, 1982; Vogt *et al.*, 1991), due to its litter high N content and decomposition rate (Brassard *et al.*, 2013; Steele *et al.*, 1997). The total N content of aspen leaves were lower in mixed stands although it remained relatively high, suggesting a neutral or slightly negative effect of species mixture on aspen nutrition. These results support previous findings that in the mixtures favors nutrition of spruce more than that of aspen (Ghotsa Mekontchou *et al.*, 2020) and growth (Légaré *et al.*, 2005a, 2004).

4.7 Conclusion

Providing accurate mechanistic interpretation of $\delta^{15}N$ variations of natural samples (leaves and soils) is a challenging task as these are the result of many biogeochemical and physiological processes causing ^{15}N-depletion or -enrichment of N pools. Aspen and spruce are more likely to partition their N uptake among different soil horizons rather than between forms of N within mixed stands of boreal mixedwoods. Specifically, the strong correlation between the $\delta^{15}N$ values of aspen leaves and that of the upper mineral layer in mixed stands indicated that it is the N uptake from the mineral layer which drives the N dynamics of aspen in mixed stands. In contrast, spruce N dynamics was driven by the N uptake from the organic soil layer. This pattern appears to be common to mixed stands of deep- and shallow-rooted competitive species in boreal forests (e.g., mixed jack pine and black spruce stands, Houle et al., 2014), suggesting a harmonious coexistence between spruce and aspen because of reduced competition for resources. The ^{15}N-labeling experiment and the total N content of leaves suggested an improvement in the N uptake capacity of spruce than that of aspen in mixed stands as compared to pure stands. The results are consistent with the niche complementarity hypothesis proposing that limited competition between species and a more efficient use of resources diversified make communities containing species with different functional traits more productive (Loreau et de Mazancourt, 2013; Loreau et Hector, 2001; Tilman, 1999). These results therefore support previous findings of Légaré et al. (2004) that mixed spruce–aspen stands have a higher volume of spruce merchantable biomass, compared to pure spruce stands.

4.8 Acknowledgments

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CHAPTER V

GENERAL CONCLUSION

The three articles presented in this thesis examined the belowground interactions between black spruce and trembling aspen in the boreal mixedwoods of eastern Canada. The spatial distribution of fine roots and mycorrhizae within the soil profile as well as the ^{15}N of leaves and soils were analyzed and compared between pure and mixed stands of the two species to understand how these species partition their use of resources. The comparative approach was used to test whether the patterns observed in mixed stands result from the effect of species mixing on species-specific resource use strategy or from the fact that they maintain the same strategy as observed in their respective pure stands.

The study results add another layer to the hypothesized competitive exclusion of aspen by spruce with regard to competition for light in mixed stands, suggesting that aspen could also be competitively excluded by aspen regarding soil resources usage. The observed competitive exclusion mainly occurs in the organic horizon of mixed stands where spruce benefits from a facilitative effect of aspen on the soil chemical properties to adopt an intensive nutrient uptake strategy. This strategy provides spruce a competitive advantage over aspen in the organic layer. The higher diversity and abundance of root-associated mycorrhizal communities of spruce compared to those of aspen in the organic horizon of mixed stands also suggested a competitive dominance of spruce communities over that of aspen; supporting the hypothesis of competitive exclusion in the organic horizon. The organic horizon was further proven to be the major source of spruce nutrition as revealed by the positive correlations between the

^{15}N of spruce needles and the ^{15}N of the organic layer of the soil in both pure and mixed stands.

The mixture of spruce and aspen is not as negative to aspen nutrition as suggested by previous studies. Aspen maintained the same fine root biomass in the organic horizon and increases it by 25% in the mineral horizon of mixed stands as compared to pure aspen stands. We interpreted this pattern as competition avoidance mechanism since the increased fine root biomass in the mineral soil was not correlated with the variations and changes in the soil chemical properties within the soil profile of mixed stands and between the two stand types, respectively. Such mechanism generally leads to the specialization of the part of the root system free from interspecific competition in the uptake of locally abundant resources (Hutchings et Wijesinghe, 1997; Stuefer, 1998; Stueffer *et al.*, 1996). The higher nutrient content of the mineral soil in mixed than in pure aspen stands and their correlation with aspen fine root biomass indicated that aspen nutrient uptake mainly takes place in the mineral horizon in mixed stands. Additionally, the higher diversity and abundance of root-associated mycorrhizal communities of aspen than that of spruce in the mineral horizon of mixed stands suggested a competitive dominance of aspen over spruce in the mineral soil of mixed stands. These finding corroborated the significant correlation observed between the natural isotopic abundance of N in aspen leaves and that of the top mineral soil in mixed stands.

This thesis shows that spruce nutrition improved in mixed stands as suggested by the total N content of leaves than in pure spruce stands. The results also demonstrated that spruce and aspen partition their N uptake at different soil depths in both stand types. The ^{15}N addition experiment showed a clear preference of spruce and aspen for ammonium and nitrate, respectively. These preferences were not observed in mixed stand were both species taken up the two forms of inorganic N in similar proportions. Specifically, the results indicated that spruce N dynamics is driven by the N uptake from the organic soil layer whereas aspen N dynamics is driven by uptake from the mineral N pool. This pattern is common to mixed stands of deep- and shallow-rooted competitive species in boreal forests (e.g., mixed jack pine and black spruce stands, Houle *et al.*, 2014), suggesting a harmonious coexistence between spruce and aspen because of reduced competition for soil resources. This could therefore justify why an earlier study (Kemperman et Barnes, 1976) that investigated aspen root system suggested that aspen can persist in mixed stands, refuting the hypothesized competitive exclusion of aspen by conifers in the intermediate stages of forest succession.

Regarding the implications for tree growth, the contrasting root foraging strategies of spruce between the two stand types suggested a better spruce growth in mixed stands than in pure stands. The intensive nutrient uptake strategy (lower FRB and higher RDMC) used by spruce in mixed stands are generally associated with low C cost for root production to the plant, and the reverse for the extensive strategy (higher C cost to the plant) (Addo-Danso *et al.*, 2018; Lõhmus *et al.*, 1989). This indicates a reduced carbon allocation into root biomass (Bauhus et Messier, 1999; Eissenstat *et al.*, 2015). In pure stands, the extensive strategy was exhibited through higher spruce FRB, its strong and negative correlation with nutrient content (N, NH_4, K, CEC), and higher RDMC in both the organic and the top mineral layers of soil (Craine, 2005; Tilman, 1982, 2007). Spruce would therefore allocate more C to its aboveground growth in mixed than in pure stands where the C is mostly allocated underground for nutrients foraging. These results are consistent with the previous observation (Légaré *et al.*, 2004) that mixed spruce–aspen stands have a higher merchantable volume with a similar spruce biomass whose individual stems size are larger than pure spruce stands.

Aspen, unlike spruce, may have a better growth in pure than in mixed stands, although it has the same root foraging strategy in the two stand types. Compared to the total root biomass of aspen in pure stands, the increased root biomass of aspen in mixed stands suggests that aspen allocate more biomass to fine roots compared to aboveground biomass in mixed than in pure stands. Its double symbiosis (linkage with both ECM and AM) as well as the decrease of its ECM:AM ratio likely contribute to increasing the underground allocations of C in mixed than in pure stands. Unlike ECM fungi, AM fungi are obligate biotroph and depend exclusively on host-derived C to complete their life cycle (Wright *et al.*, 1998). This explains the smaller size (DBH) of aspen stems in mixed than in pure stands.

The main limitation of this study was the limited number of sites. Indeed, the inter-site variability observed in the rooting patterns of spruce in mixed stands suggests that the interspecific competition may increase with a higher aspen basal area. However, the limited number of sites in our study did not allow us to test such hypothesis. To do so, it would be necessary to increase the sampling size to ensure adequate coverage of a range of canopy compositions. Nevertheless, we speculate from the study results that the negative impact of aspen on spruce nutrient uptake would be minimal, due to the facilitative effect of aspen on soil nutrient availability compared to multiple competitive mechanisms (intraspecific competition, interference with *Ericaceae* and nutrient immobilization by moss layer) which are at play in pure spruce stands.

At a practical level, we recommend forest managers to diversify silvicultural practices across the forest landscape according to the types of stands.

- In spruce-dominated stands, we recommend maintaining the hardwood component during pre-commercial thinning. Spruce-dominated stands are generally strewn with small clumps of aspen stems. The pre-commercial thinning traditionally used in the spruce-feathermoss domain are often oriented to eliminate the hardwood component during the intermediate stage of the forest succession in order to confirm the main vocation of these stands i.e. the production of softwood. This practice should be considered obsolete. Precommercial thinning should rather be redirected towards the conifers component to reduce the competition (intraspecific, moss and ericaceous) for resources while keeping an open canopy with low proportion of aspen. The presence of aspen would provide some stability to spruce-dominated stands and will reduce their susceptibility to productivity losses. The aspen kept in the stands will play the role of shelter for regeneration and favor the decomposition process while limiting the risk of paludification; phenomenon which is likely to dominate in the study area if the frequency of fires decreases with changing climatic conditions.

- In pure aspen and mixed stands, we recommend promoting the mixing of spruce and aspen. We found that beside their coexistence, spruce and aspen also efficiently used the available resources. Thus, to encourage mixing, pre-commercial and commercial thinning or regular progressive and variable retention cuts should be prescribed in pure aspen stands. In contrast, irregular progressive cuts or selective cuttings should be prescribed in mixed stands. The spatial stratification observed in the root system of the two species is similar to that of the structure of their crowns. Aspen are generally taller than spruce. Their crown hierarchy was reported to benefit spruce which prefers diffuse light for its photosynthesis since the aspen in the upper strata effectively capture direct light. These mixed silvicultural practices will therefore create and maintain stands with complex and varied internal structures (Grenon *et al.*, 2010; Grondin *et al.*, 2003; Patry *et al.*, 2013). They will also allow, in mixed stands, to maintain ecological attributes associated with older forests (Grenon *et al.*, 2010; Jetté *et al.*, 2013). However, the proportion of species that should be extracted still have to be determined.

At the theoretical level, the study results are consistent with the niche complementarity hypothesis in the context of biodiversity-productivity relationship studies. Specifically, the accentuation of the spatial differences in the root structure and in the distribution of root-associated mycorrhizal community of spruce and aspen along the soil profile, as well as the shift from the preference for one form of inorganic in pure stands to the uptake of both N-inorganic forms in mixed stands support the premise (Loreau et de Mazancourt, 2013; Loreau et Hector, 2001; Tilman, 1999) that diversified communities containing species with different functional traits are the most productive because of limited competition between species and more efficient use of resources. The variations in root biomass observed in spruce in response to the change in soil chemical properties and not to interspecific competition add another dimension to Philip Grime's CSR theory (Grime, 1977) on the importance of competition. Indeed, Grime (1977) suggests that in response to competition for resources, stress tolerant species like spruce will generally exhibit slow and small amplitude change in the root:shoot ratio. However, we recorded large amplitude of root biomass variations (23 to 45%) between mixed and pure spruce stands. This confirms Tilman's theory (Tilman, 1980, 1982) which, unlike Grime, suggests that competition is always present and variations in species attributes could simply depend on the concentration of the limiting resource in the ecosystem. Thus, future diversity-productivity studies should combine these two theories as suggested by Craine (2005) to investigate how interactions between species influence the productivity of ecosystems.

The results revealed the complexity of providing accurate mechanistic interpretation of $\delta^{15}N$ variations of natural samples (leaves and soils) which are the result of many biogeochemical and physiological processes causing ^{15}N-depletion or -enrichment of N pools. We therefore suggest that, first, to use the rooting depth in DPR models to assess the potential impact of the vertical partitioning of resources between species on stand productivity. Second, the diversity and abundance of mycorrhizal symbiosis should be used to deduce competitive interactions within the soil profile. Information on mycorrhizae was found to provide results similar to those obtained by combining the root biomass and root tissue density (nutrient uptake strategy). The quantification of their diversity and abundance is also less susceptible to measurement bias as is the case for the measurement for the root tissue density. Such an approach has been successfully used by Paquette and Messier (2011), which so far represents the only DPR study whose model used explains a greater part of productivity variation in the boreal forest.

APPENDIX A

SUPPLEMENTARY INFORMATION CHAPTER II

Table S2.1 Summary of soil chemical properties (mean and SEM). Each stand type was replicated three times. FF, Min1 and Min2 refer to organic horizon, mineral soil at 0-15 cm and mineral soil at 15-30 cm, respectively.

Properties	Soil layer	Stand type		
		Pure spruce	Mixed (spruce + aspen)	Pure aspen
Total C (g kg^{-1})	FF	341.66 ± 32.8 ^{aA}	323.83 ± 23.83 ^{aA}	263.33 ± 60.76 ^{bA}
	Min1	23.5 ± 8.03 ^{aB}	24.33 ± 5.78 ^{aB}	20.41 ± 5.86 ^{bB}
	Min2	5.58 ± 02.96 ^{aC}	7.16 ± 3.12 ^{aC}	5.91 ± 1.66 ^{aC}
Total N (g kg^{-1})	FF	8.73 ± 1.68 ^{aA}	12.21 ± 1.41 ^{bA}	13.14 ± 3.63 ^{bA}
	Min1	1.09 ± 0.55 ^{aB}	1.25 ± 0.28 ^{aB}	1.20 ± 0.38 ^{aB}
	Min2	0.3 ± 0.17 ^{aC}	0.4 ±0.11 ^{aC}	0.35 ± 0.06 ^{aC}
C:N ratio	FF	40.13 ± 8.62 ^{aA}	26.91 ± 4.94 ^{bA}	20.54 ± 5.35 ^{cA}
	Min1	22.65 ± 3.18 ^{aB}	19.42 ± 0.43 ^{bB}	17.36 ± 1.64 ^{cA}
	Min2	19 ± 1.01 ^{aB}	17.18 ± 3.34 ^{aB}	16.91. ± 1.93 ^{aA}
pH (H_2O)	FF	3.93 ± 0.27 ^{aA}	4.68 ± 0.23 ^{bA}	5.15 ± 0.25 ^{cA}
	Min1	4.74 ± 0.13 ^{aB}	5.02 ± 0.23 ^{bB}	5.43 ± 0.51 ^{cA}
	Min2	5.42 ± 0.36 ^{aC}	5.44 ± 0.3 ^{aC}	6.11 ± 0.8 ^{bB}
NH_4 (mg kg^{-1})	FF	28.66 ± 5.9 ^{aA}	35.58 ± 7.4 ^{bA}	49.08 ± 20.69 ^{cA}
	Min1	2.66 ± 0.28 ^{aB}	4 ± 1.25 ^{bB}	3.58 ± 1.01 ^{bB}
	Min2	2.08 ± 0.14 ^{aB}	2 ± 0.75 ^{aC}	2.5 ± 0.5 ^{aC}
Exchangeable P (mg kg^{-1})	FF	93.58 ± 31.9 ^{aA}	94.16 ± 58.10 ^{aA}	68.58 ± 28.58 ^{aA}
	Min1	7.33 ± 1.75 ^{aB}	6.08 ± 1.01 ^{aB}	5.66 ± 0.57 ^{aB}
	Min2	12.33 ± 4.88 ^{aC}	9.66 ± 6.13 ^{aB}	8.08 ± 7.3 ^{aB}
Exchangeable K (mg kg^{-1})	FF	473.33 ± 73.43 ^{aA}	520.41 ± 101.5 ^{aA}	480.33 ± 132.93 ^{aA}
	Min1	76.75 ± 28.36 ^{aB}	118.16 ± 41.64 ^{bB}	144.58 ± 58.13 ^{bB}
	Min2	99.5 ± 24.6 ^{aC}	93.83 ± 18 ^{aB}	121.75 ± 27.94 ^{bB}
CEC (meq 100g^{-1} soil)	FF	127.95 ± 3.32 ^{aA}	114.65 ± 3.6 ^{bA}	107.61 ± 6.86 ^{cA}
	Min1	28.64 ± 5.36 ^{aB}	26.22 ± 4.9 ^{aB}	25.88 ± 3.38 ^{aB}
	Min2	19.10 ± 2.75 ^{aC}	19.5 ± 2.9 ^{aC}	20.13 ± 1.9 ^{aC}
Organic layer depth (cm)		10.75 ± 2.19 ^{a}	9.13 ± 0.99 ^{a}	6.78 ± 2.11 ^{b}

Differences among stand types for each soil layer and differences among soil layers within each stand type were tested using a one-way analysis of variance. Statistical differences among pairwise comparisons at $p = 0.05$ are denoted by lowercase letters for significant differences among stand types, and capital letters for significant differences among soil layers. pH, total carbon (C), total nitrogen (N), ammonium (NH_4) and C to N ratio were determined as in Carter & Gregorich (Carter et Gregorich, 2008) whereas exchangeable phosphorus (P), exchangeable potassium (K) and cation exchange capacity (CEC) were determined by Mehlich 3 extraction technique (Mehlich, 1984).

Table S2.2. Effect *p.values* of the analysis of covariance for spruce. *p. values* for the effect of stand type test the similarity of the linear relationship between the FRB and the variation of each soil property between pure and mixed stands, and similarly for the RDMC. *p.values* for mixed effect (interaction between stand type and soil property) test the homogeneity of the response of FRB and RDMC to the variation of each soil property in different soil horizon between pure and mixed stands. Significant *p.values* are in bold. FF, Min1 and Min2 refer to organic, mineral soil at 0-15 cm and mineral soil at 15-30 cm, respectively. In sources of variations, ST and ST x SP refers to stand type and interaction between stand type and soil property, respectively.

	Black Spruce							
	Root weight density				Root dry matter content			
	FRB FF		FRB Min1		RDMC FF		RDMC Min1	
Sources	ST (Similarity)	ST x SP (Mixed effect)	ST (Similarity)	ST x SP (Mixed effect)	ST (Similarity)	ST x SP (Mixed effect)	ST (similarity)	ST x SP (Mixed effect)
Total carbon								
FF	**0.029**	0.206	**0.001**	0.709	**0.035**	**0.036**	**<0.001**	0.345
Min1	**0.006**	0.257	**<0.001**	**0.006**	**0.032**	0.343	**<0.001**	0.397
Total nitrogen								
FF	0.959	0.418	0.376	**<0.001**	0.64	0.199	**0.003**	0.543
Min1	**0.015**	0.444	**<0.001**	**0.03**	**0.042**	0.377	**<0.001**	0.354
C:N ratio								
FF	0.291	0.445	0.344	0.116	0.253	**0.032**	**0.001**	0.887
Min1	0.209	0.335	**0.046**	**0.025**	**0.065**	0.579	**0.001**	0.637
Ammonium								
FF	**0.022**	**<0.001**	**0.003**	**0.011**	**0.002**	0.409	**<0.001**	0.726
Min1	**0.011**	0.425	**0.003**	0.441	**0.018**	0.832	**0.005**	0.812
Phosphorus								
FF	**<0.001**	**<0.001**	**<0.001**	0.128	0.027	0.210	**<0.001**	0.494
Min1	**0.018**	0.510	**0.003**	0.503	0.053	0.315	**<0.001**	0.333
pH (H_2O)								
FF	0.242	0.251	0.625	**0.018**	0.641	0.103	**0.005**	0.717
Min1	0.153	0.888	**0.005**	**<0.001**	0.548	0.456	**0.001**	0.428
Potassium								
FF	**0.008**	0.422	**<0.001**	**0.002**	0.018	0.280	**0.001**	0.964
Min1	**0.042**	**0.003**	**0.007**	**0.006**	0.009	0.774	**0.002**	0.718
CEC								
FF	**0.007**	**0.046**	**0.004**	**0.034**	0.113	0.960	**0.004**	0.906
Min1	**0.002**	0.122	**<0.001**	**0.006**	0.052	0.924	**<0.001**	0.552
Organic layer depth	**0.003**	0.589	**<0.001**	0.082	0.071	0.158	**0.001**	0.965

Table S2.3. Effect *p.values* of the analysis of covariance for aspen.

Sources	Trembling aspen											
	Root weight density						Root dry matter conten					
	FRB FF		FRB Min1		FRB Min2		RDMC FF		RDMC Min1		RDMC Min2	
	ST (Similarity)	ST x SP (Mx effect)	ST (Similarity)	ST x SP (Mx effect)	ST Similarity	ST x SP (Mx effect)	ST (Similarity)	ST x SP (Mx effect)	ST (Similarity)	ST x SP (Mx effect)	ST (Similarity)	ST x SP (Mx effect)
Total carbon												
FF	0.362	0.989	0.336	0.246	0.498	0.107	**0.03**	0.919	0.956	0.609	0.275	0.317
Min1	0.631	0.579	**0.005**	**<0.001**	0.058	**0.008**	0.491	0.233	0.480	0.118	0.32	0.446
Min2	0.5	0.973	**0.007**	0.708	**0.023**	0.44	0.898	0.541	0.546	0.604	0.242	0.895
Total nitrogen												
FF	0.456	0.418	**0.006**	0.106	0.065	0.175	0.85	0.1	0.626	0.245	0.225	0.08
Min1	0.015	0.477	**0.002**	**0.002**	**0.043**	**0.009**	0.653	0.283	0.655	0.072	0.191	0.304
Min2	0.441	0.36	**0.009**	0.818	**0.035**	0.195	0.936	0.22	0.497	0.56	0.284	0.91
C:N ratio												
FF	0.598	0.147	0.193	0.396	0.473	0.218	0.145	0.89	0.659	0.747	0.643	0.215
Min1	0.461	0.093	**0.003**	0.396	**0.043**	0.848	0.626	0.837	0.9	0.884	0.203	0.582
Min2	0.435	0.164	**0.007**	0.255	**0.026**	0.466	0.764	0.212	0.737	0.393	0.173	0.9
Ammonium												
FF	0.256	0.167	0.005	0.533	**0.038**	0.89	0.7	0.63	0.968	**0.017**	0.064	**0.001**
Min1	0.58	0.529	**0.01**	**0.03**	0.091	0.11	0.557	0.929	0.481	**0.048**	0.213	**0.014**
Min2	0.19	0.277	**0.003**	**0.036**	**0.026**	0.06	0.657	0.141	0.791	0.384	**0.023**	0.334
Phosphorus												
FF	0.643	0.186	**0.034**	0.407	0.213	0.65	0.302	**0.041**	0.982	0.97	0.246	0.528
Min1	0.547	0.13	**0.017**	**0.049**	0.186	0.476	0.327	**0.027**	0.836	0.797	0.282	0.68
Min2	0.423	0.703	**0.013**	0.423	0.075	0.097	0.605	0.855	0.85	0.724	0.195	0.433
pH (H_2O)												
FF	0.6	0.194	0.467	0.819	0.534	0.454	**0.013**	0.374	0.907	0.714	0.674	0.241
Min1	0.775	0.775	0.235	0.984	0.54	0.428	0.07	0.691	0.686	0.218	0.512	**0.016**
Min2	0.459	0.134	0.078	0.562	0.218	0.945	0.266	0.653	0.519	0.064	0.472	**0.006**
Potassium												
FF	0.626	0.192	**0.014**	0.818	0.115	0.312	0.294	0.4	0.793	0.98	0.231	0.336
Min1	0.144	0.846	**<0.001**	0.12	**0.025**	0.167	0.608	0.543	0.917	**0.041**	**0.037**	0.058
Min2	0.056	0.852	**<0.001**	0.41	**0.01**	0.804	0.32	0.872	0.956	0.367	**0.02**	0.186
CEC												
FF	0.731	0.865	0.168	0.895	0.238	0.675	0.113	0.185	0.731	0.857	0.255	0.374
Min1	0.453	0.868	**0.002**	**0.003**	**0.046**	0.192	0.715	0.463	0.645	0.081	0.142	0.14
Min2	0.34	0.683	**0.011**	0.858	**0.08**	0.584	0.831	0.742	0.878	0.586	0.09	0.9
Organic layer depth	0.642	0.654	0.174	0.881	0.453	0.98	0.337	0.277	0.926	0.145	0.196	0.92

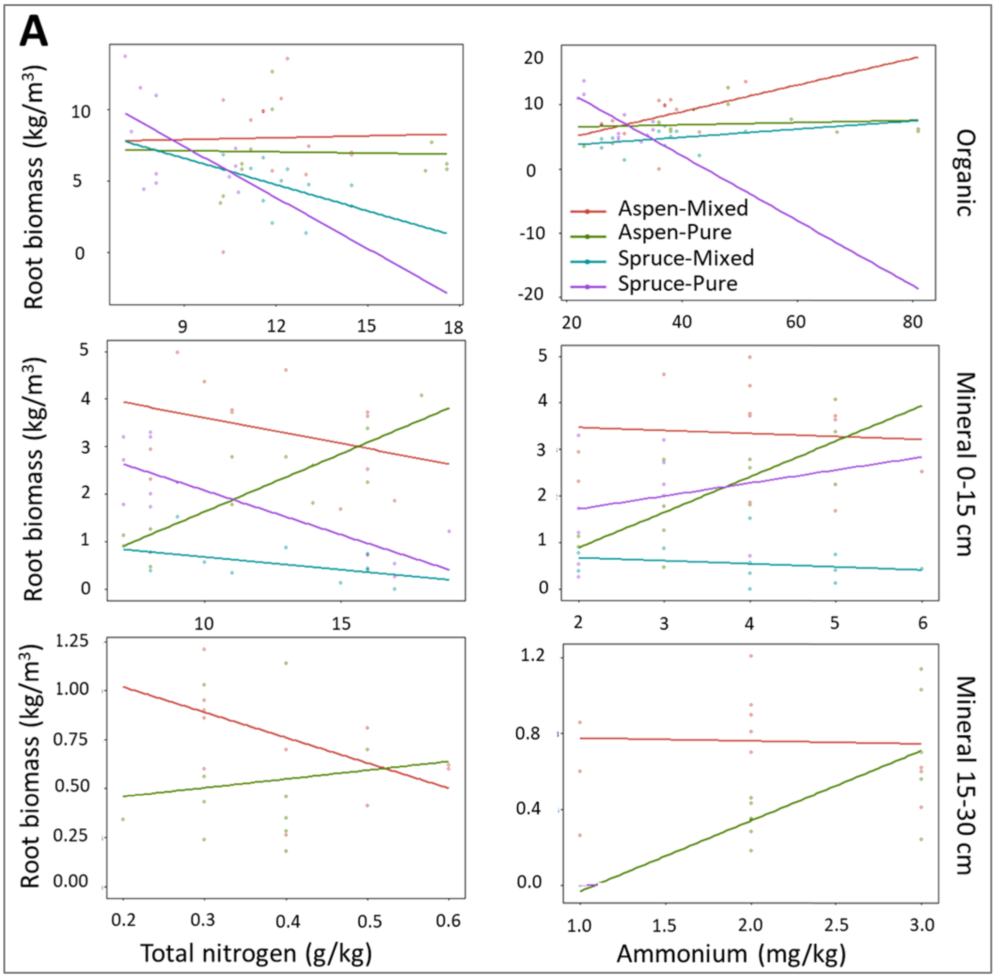


Figure S2.1 ANCOVA results comparing the variation in (A) fine root biomass (kg m^{-3}) and (B) root dry matter content (g g^{-1}) of black spruce and trembling aspen with soil C:N ratio, total N, ammonium, exchangeable phosphorus and potassium and the sum of exchangeable cations (CEC) concentration within the three soil horizon layers for both species among the three types stands. Each line represent the relationship between the two variables for each species per each stand type (Aspen-Mixed, Aspen-Pure, Spruce-Mixed and Spruce-Pure). For each species, the lines with the same direction indicate the same root allocation strategy between pure and mixed stands whereas lines with opposite directions indicate different strategies. The stronger the correlation between a given nutrient and FRB, the more competitive the species is in one type of stand compared to the other.

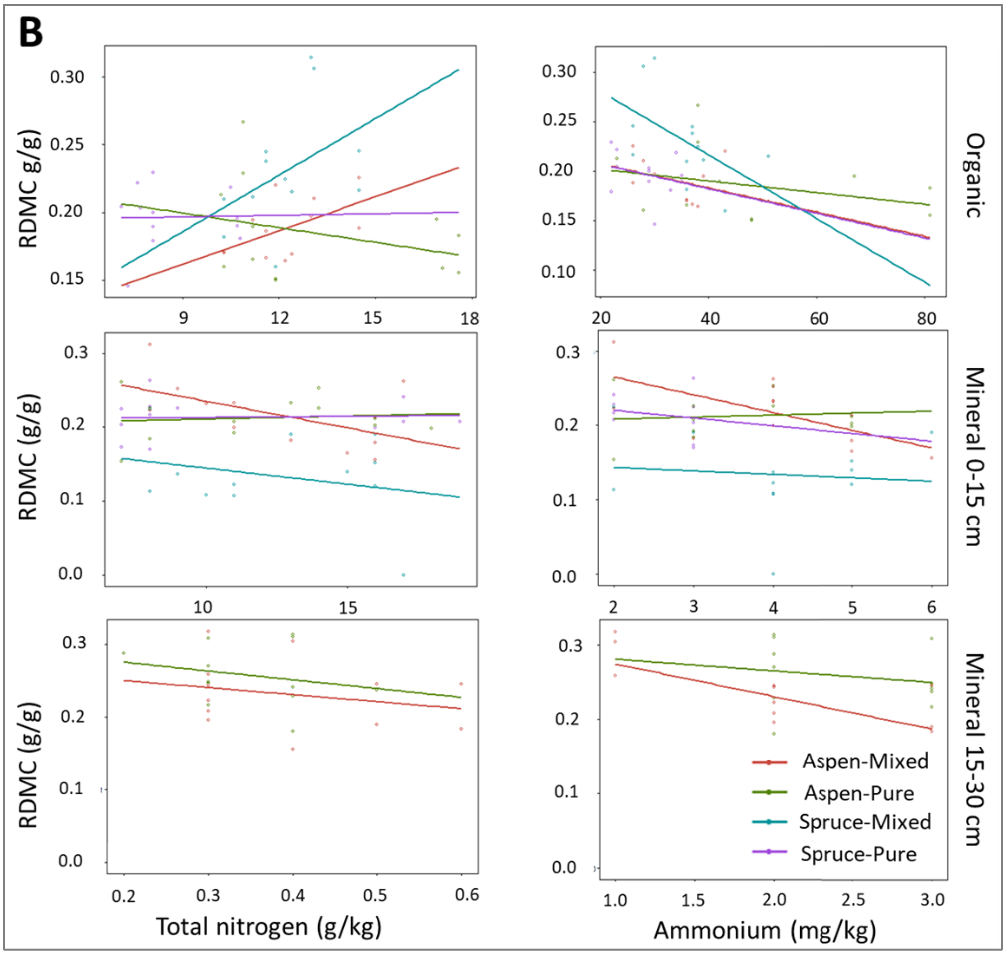
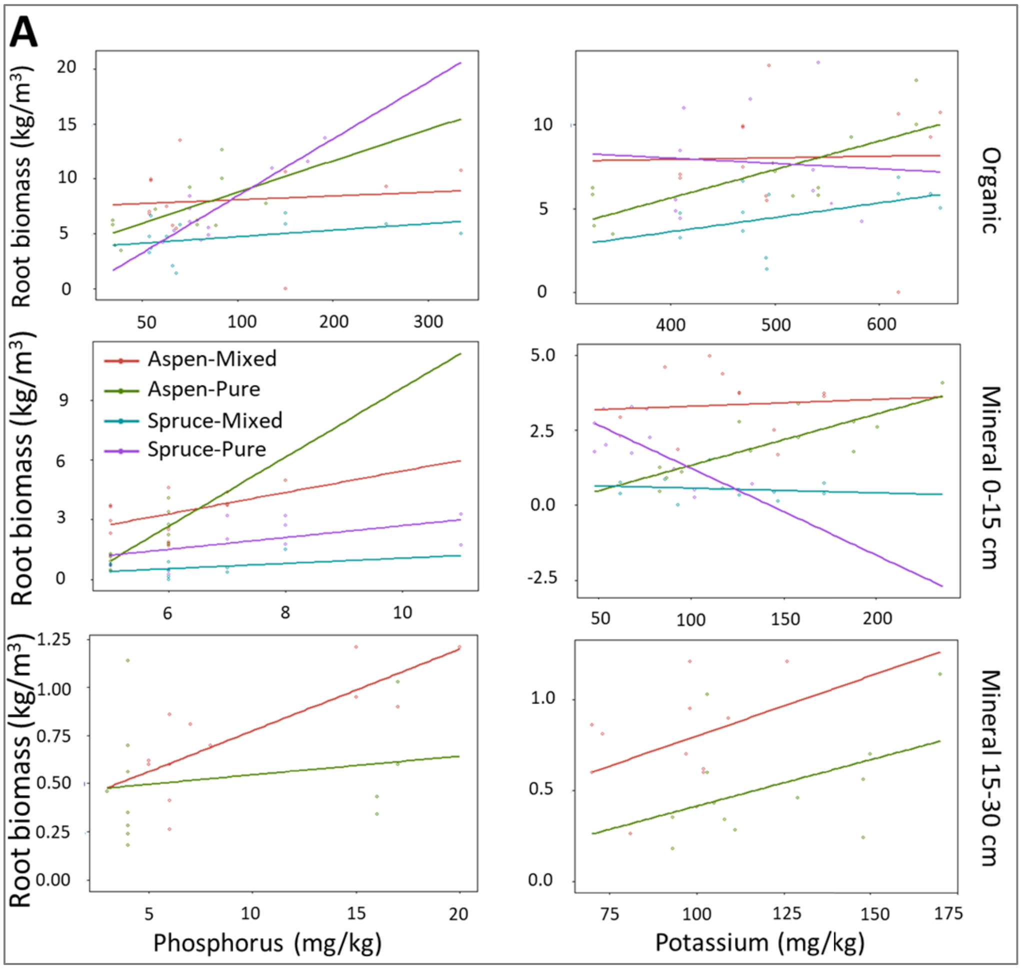


Figure S2.1 Continued.



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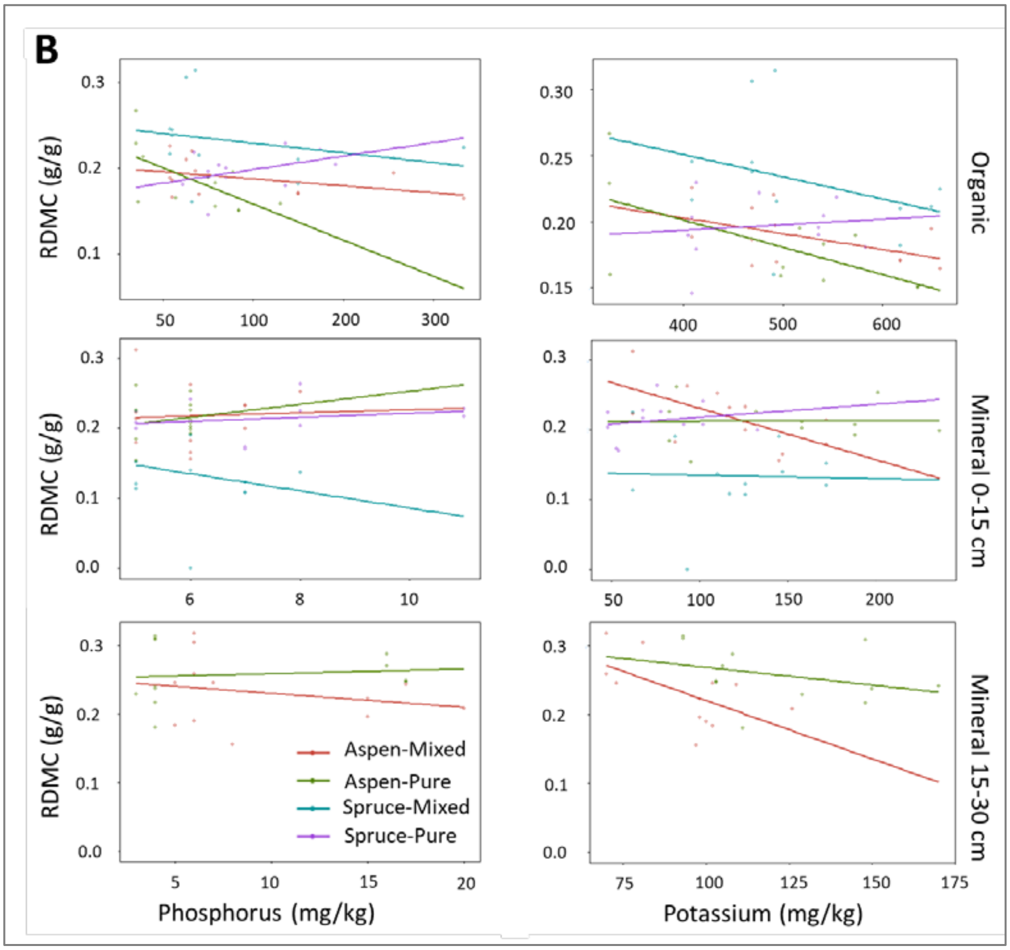

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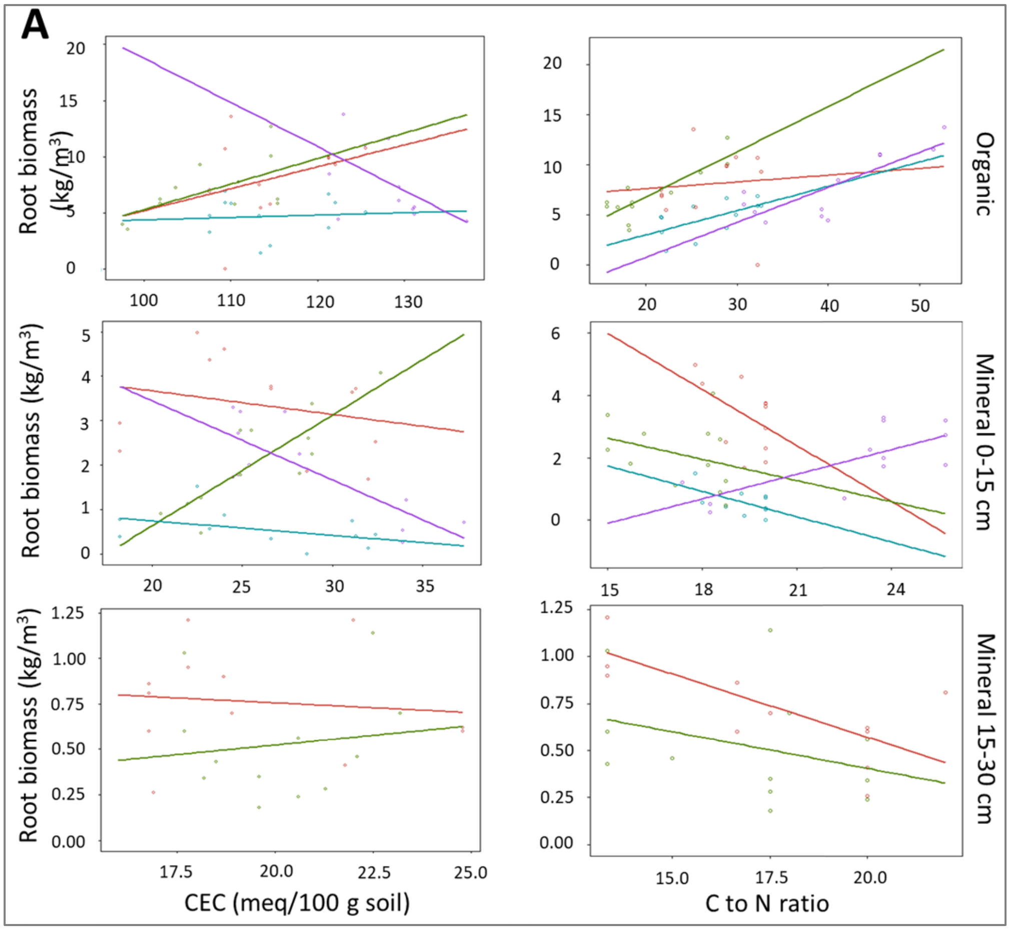

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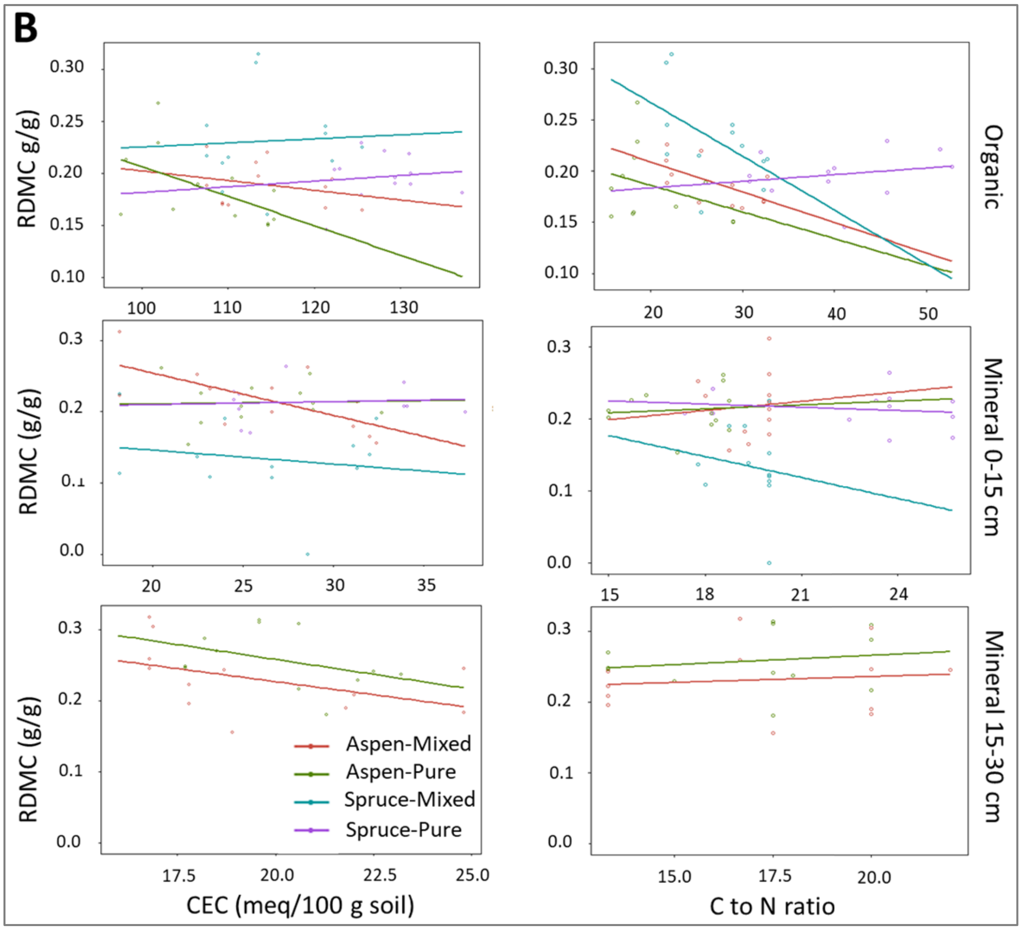

Figure S2.1 Continued.

APPENDIX B

SUPLLEMENTARY INFORMATION CHAPTER III

Table S2.1 Summary of soil chemical properties (mean and SEM). Each stand type was replicated three times. FF, Min1 and Min2 refer to organic horizon, mineral soil at 0-15 cm and mineral soil at 15-30 cm, respectively.

Properties	Soil layer	Stand type		
		Pure spruce	Mixed (spruce + aspen)	Pure aspen
Total C (g kg^{-1})	FF	341.66 ± 32.8 ^{aA}	323.83 ± 23.83 ^{aA}	263.33 ± 60.76 ^{bA}
	Min1	23.5 ± 8.03 ^{aB}	24.33 ± 5.78 ^{aB}	20.41 ± 5.86 ^{bB}
	Min2	5.58 ± 02.96 ^{aC}	7.16 ± 3.12 ^{aC}	5.91 ± 1.66 ^{aC}
Total N (g kg^{-1})	FF	8.73 ± 1.68 ^{aA}	12.21 ± 1.41 ^{bA}	13.14 ± 3.63 ^{bA}
	Min1	1.09 ± 0.55 ^{aB}	1.25 ± 0.28 ^{aB}	1.20 ± 0.38 ^{aB}
	Min2	0.3 ± 0.17 ^{aC}	0.4 ±0.11 ^{aC}	0.35 ± 0.06 ^{aC}
C:N ratio	FF	40.13 ± 8.62 ^{aA}	26.91 ± 4.94 ^{bA}	20.54 ± 5.35 ^{cA}
	Min1	22.65 ± 3.18 ^{aB}	19.42 ± 0.43 ^{bB}	17.36 ± 1.64 ^{cA}
	Min2	19 ± 1.01 ^{aB}	17.18 ± 3.34 ^{aB}	16.91. ± 1.93 ^{aA}
pH (H_2O)	FF	3.93 ± 0.27 ^{aA}	4.68 ± 0.23 ^{bA}	5.15 ± 0.25 ^{cA}
	Min1	4.74 ± 0.13 ^{aB}	5.02 ± 0.23 ^{bB}	5.43 ± 0.51 ^{cA}
	Min2	5.42 ± 0.36 ^{aC}	5.44 ± 0.3 ^{aC}	6.11 ± 0.8 ^{bB}
NH_4 (mg kg^{-1})	FF	28.66 ± 5.9 ^{aA}	35.58 ± 7.4 ^{bA}	49.08 ± 20.69 ^{cA}
	Min1	2.66 ± 0.28 ^{aB}	4 ± 1.25 ^{bB}	3.58 ± 1.01 ^{bB}
	Min2	2.08 ± 0.14 ^{aB}	2 ± 0.75 ^{aC}	2.5 ± 0.5 ^{aC}
Exchangeable P (mg kg^{-1})	FF	93.58 ± 31.9 ^{aA}	94.16 ± 58.10 ^{aA}	68.58 ± 28.58 ^{aA}
	Min1	7.33 ± 1.75 ^{aB}	6.08 ± 1.01 ^{aB}	5.66 ± 0.57 ^{aB}
	Min2	12.33 ± 4.88 ^{aC}	9.66 ± 6.13 ^{aB}	8.08 ± 7.3 ^{aB}
Exchangeable K (mg kg^{-1})	FF	473.33 ± 73.43 ^{aA}	520.41 ± 101.5 ^{aA}	480.33 ± 132.93 ^{aA}
	Min1	76.75 ± 28.36 ^{aB}	118.16 ± 41.64 ^{bB}	144.58 ± 58.13 ^{bB}
	Min2	99.5 ± 24.6 ^{aC}	93.83 ± 18 ^{aB}	121.75 ± 27.94 ^{bB}
CEC (meq 100g^{-1} soil)	FF	127.95 ± 3.32 ^{aA}	114.65 ± 3.6 ^{bA}	107.61 ± 6.86 ^{cA}
	Min1	28.64 ± 5.36 ^{aB}	26.22 ± 4.9 ^{aB}	25.88 ± 3.38 ^{aB}
	Min2	19.10 ± 2.75 ^{aC}	19.5 ± 2.9 ^{aC}	20.13 ± 1.9 ^{aC}
Organic layer depth (cm)		10.75 ± 2.19 ^{a}	9.13 ± 0.99 ^{a}	6.78 ± 2.11 ^{b}

Differences among stand types for each soil layer and differences among soil layers within each stand type were tested using a one-way analysis of variance. Statistical differences among pairwise comparisons at $p = 0.05$ are denoted by lowercase letters for significant differences among stand types, and capital letters for significant differences among soil layers. pH, total carbon (C), total nitrogen (N), ammonium (NH_4) and C to N ratio were determined as in Carter & Gregorich (Carter et Gregorich, 2008) whereas exchangeable phosphorus (P), exchangeable potassium (K) and cation exchange capacity (CEC) were determined by Mehlich 3 extraction technique (Mehlich, 1984).

Table S3.2 Matrix of dissimilarity (permuted *p-value*) of mycorrhizal communities associated with spruce and aspen roots along the soil profile within and between pure and mixed stands.

Species			Spruce				Aspen				
	Stand type		Pure stand		Mixed stand		Mixed stand			Pure stand	
		Soil layer	Org	Min1	Org	Min1	Org	Min1	Min2	Org	Min1
Spruce	Pure stand	Org		0.14	**0.002**	0.11				0.23	0.58
		Min1			0.15	0.68					0.44
	Mixed stand	Org				0.47	0.26	0.171	0.33		
		Min1					0.89	0.895	0.37		
Aspen	Mixed stand	Org						0.989	0.25	0.86	**0.03**
		Min1							0.17	0.87	**0.01**
		Min2								0.19	**0.005**
	Pure stand	Org									**0.041**
		Min1									

The *p.values* were computed using the permutational analysis for the multivariate homogeneity of dispersion which compare the Bray-Curtis distance from the NMDS. Significant *p.value* (in bold) indicate a similarity in the composition of mycorrhizal communities. For soil layers, the abbreviations Org, Min1 and Min2 refers to the organic, the top 0-15 cm and bottom 15-30 cm mineral layers, respectively.

Table S3.3 Exploration types and hydrophobicity of identified mycorrhizal fungi ranked at family and genus level. Hi and Ho refers to hydrophilic and hydrophobic, respectively. nd stands for undetermined.

Family	**Genus**	**Exploration types**	**Hydrophobicity**
Amanitaceae	*Amanita*	Medium-distance (Smooth subtype)	Hi
Atheliaceae	*Amphinema*	Medium-distance (Fringe subtype)	Ho
	Piloderma	Medium-distance (Fringe subtype)	
	Tylospora	Medium-distance (Fringe subtype)	
Clavulinaceae	*Clavulina*	Contact	Hi (Nitrophobic)
Cortinariaceae	*Alnicola*	Medium-distance (Fringe subtype)	Ho
	Cortinarius		
	Leucocortinarius		
Elaphomycetaceae	*Elaphomyces*	Short-distance	Hi
Entolomataceae	*Entoloma*	Medium-distance (Fringe subtype)	Ho
Glomeraceae	*Glomus*	nd (nitrophilic fungi)	Nitrophilic
Gloniaceae	*Cenococcum*	Short-distance	Hi
Helotiaceae	*Meliniomyces*	Short-distance	Hi
Hydnangiaceae	*Laccaria*	Medium-distance (Fringe subtype)	Ho
Hygrophoraceae	*Gliophorus*	Contact	Hi
	Hygrophorus		
Hymenogastraceae	*Hebeloma*	Short-distance	Hi
Inocybaceae	*Inocybe*	Short-distance	Hi
Pyronemataceae	*Genea*	Short-distance	Hi
	Humaria		
	Sphaerosporella		
	Tricharina		
Rhizopogonaceae	*Rhizopogon*	Long distance	Ho
Russulaceae	*Lactarius*	Contact	Hi (Nitrophobic)
	Russula	Contact	Hi (Nitrophobic)
Sebacinaceae	*Sebacina*	Short-distance	Hi
Septobasidiaceae	*Auriculoscypha*	nd	nd
Thelephoraceae	*Pseudotomentella*	Medium-distance (Smooth subtype)	Ho
	Tomentella / Thelephora		Ho (Nitrophilic)
Tricholomataceae	*Fayodia*	Medium-distance (Fringe subtype) / Long-distance	Ho
	Tricholoma		

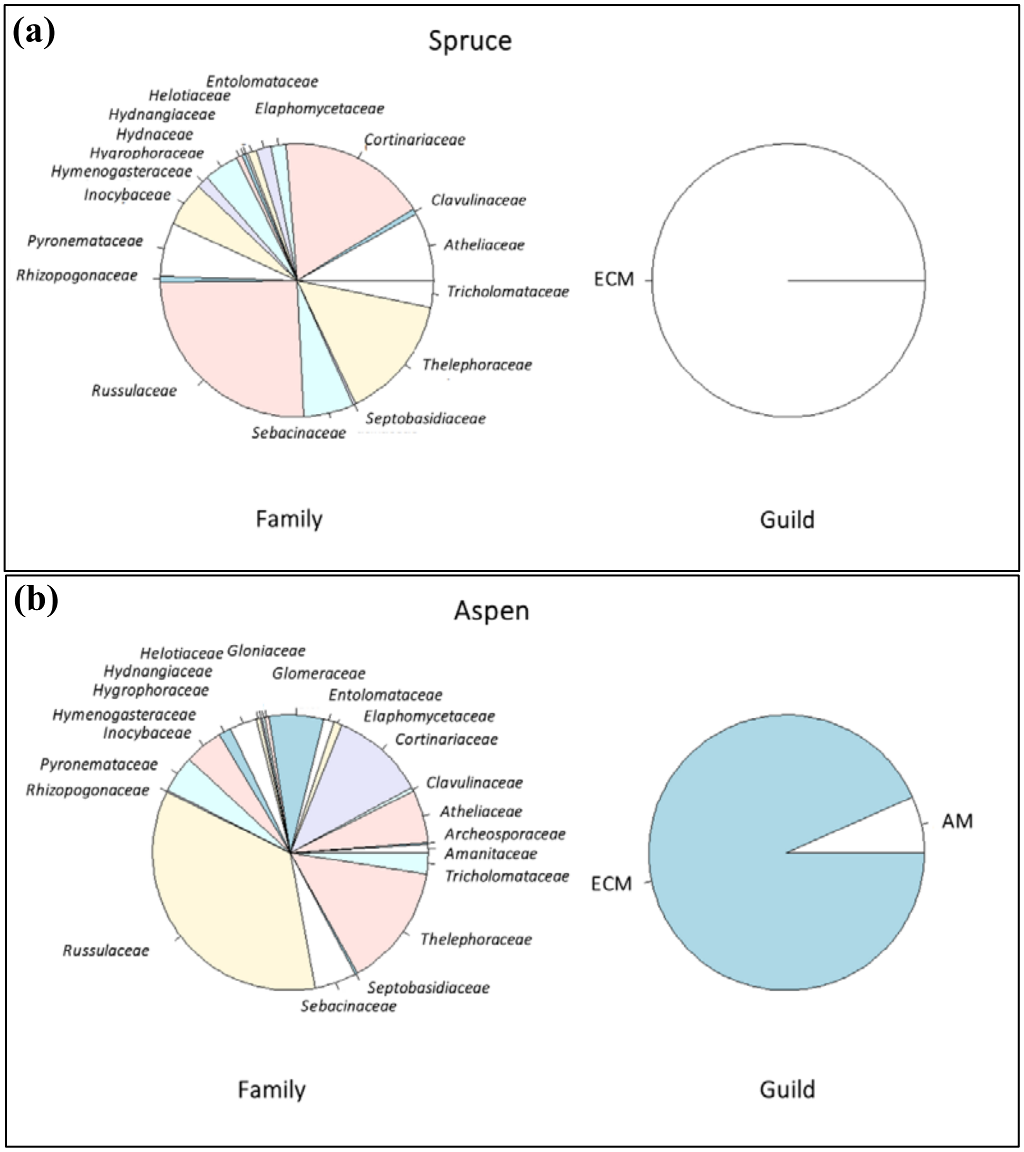

Figure S3.1 Distribution of mycorrhizal communities of (a) spruce and (b) aspen affected by family and guild for combined data of pure and mixed stands.

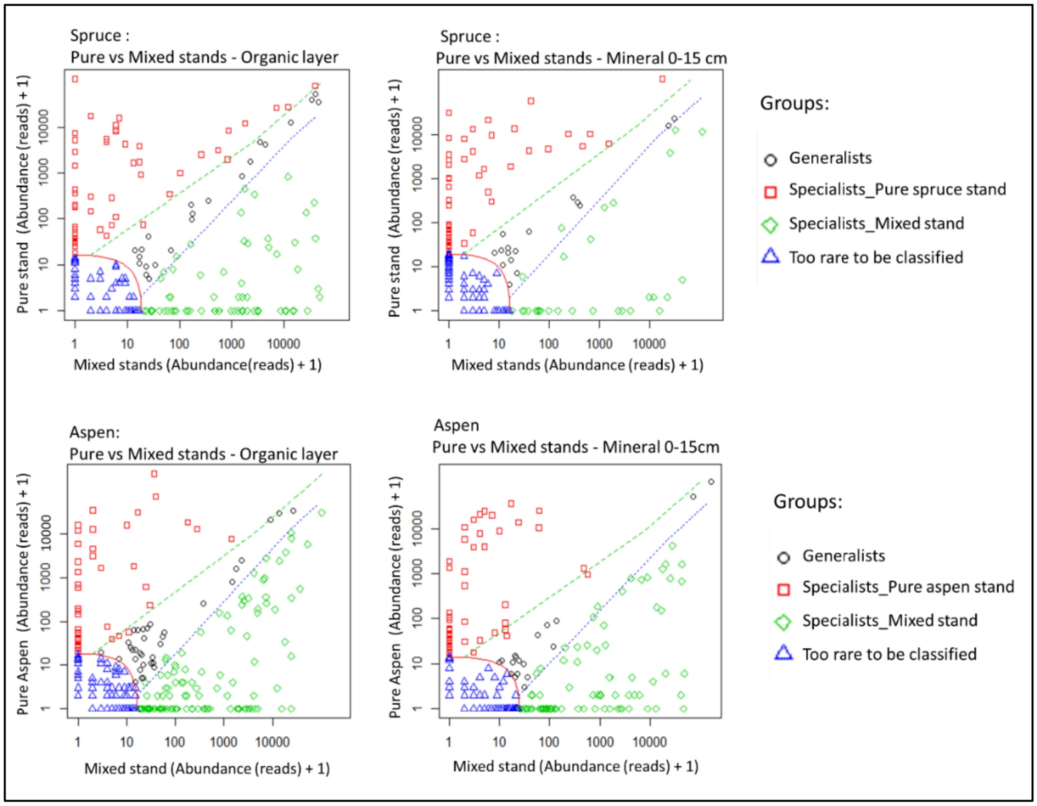

Figure S3.2 CLAM test results showing stand type preference of root-associated mycorrhizal communities of spruce and aspen based on OTUs rank and their abundance (number of reads) in the organic and the mineral soil layers.

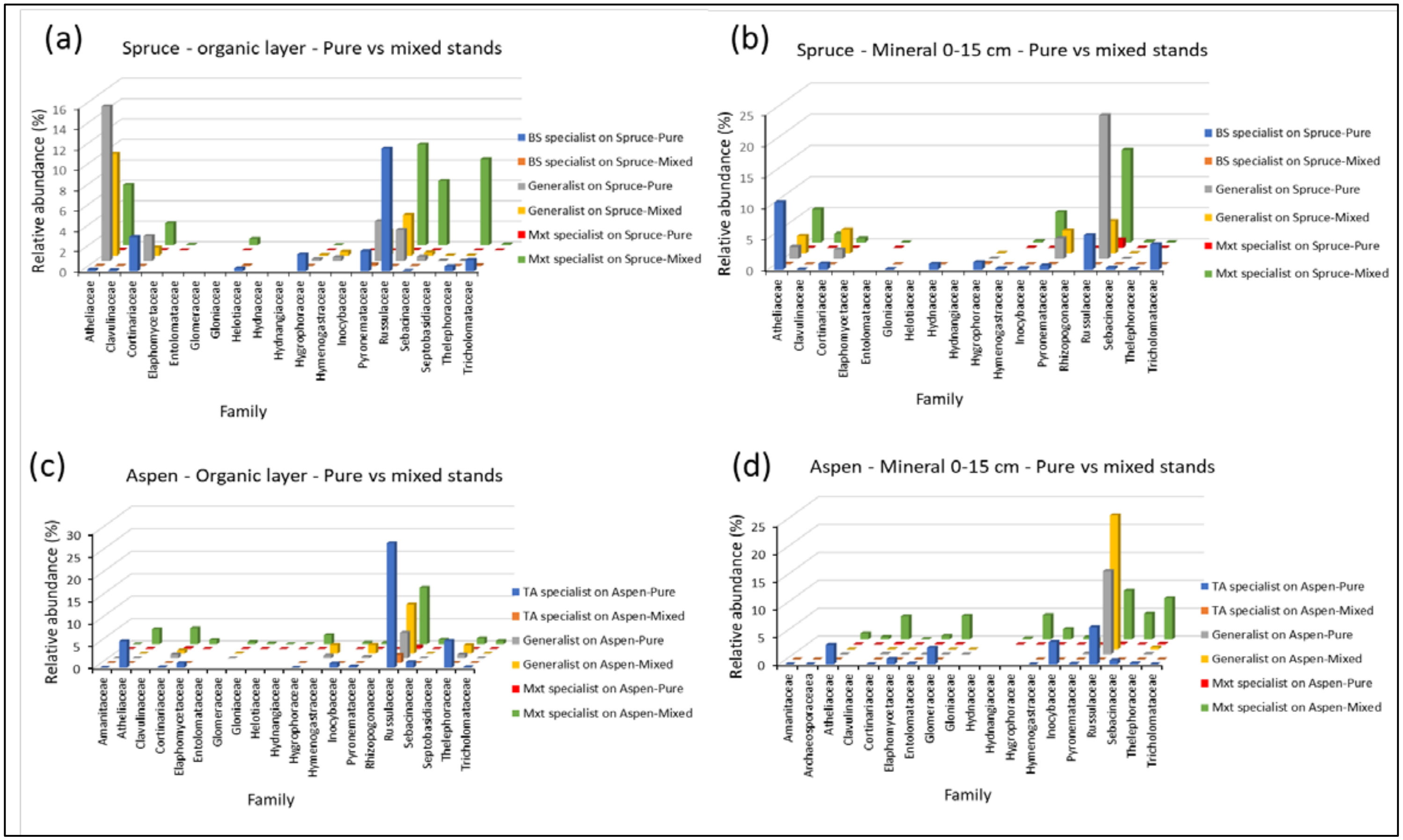

Figure S3.3 Relative abundance of mycorrhizal fungal taxa associated preferentially (specialists) and commonly found (generalists) on (a,b) spruce and (c,d) aspen roots in pure compared to mixed stands. BS, TA, and Mxt refers to pure spruce, pure aspen and mixed stands, respectively.

APPENDIX C

SUPPLEMENTARY INFORMATION CHAPTER IV

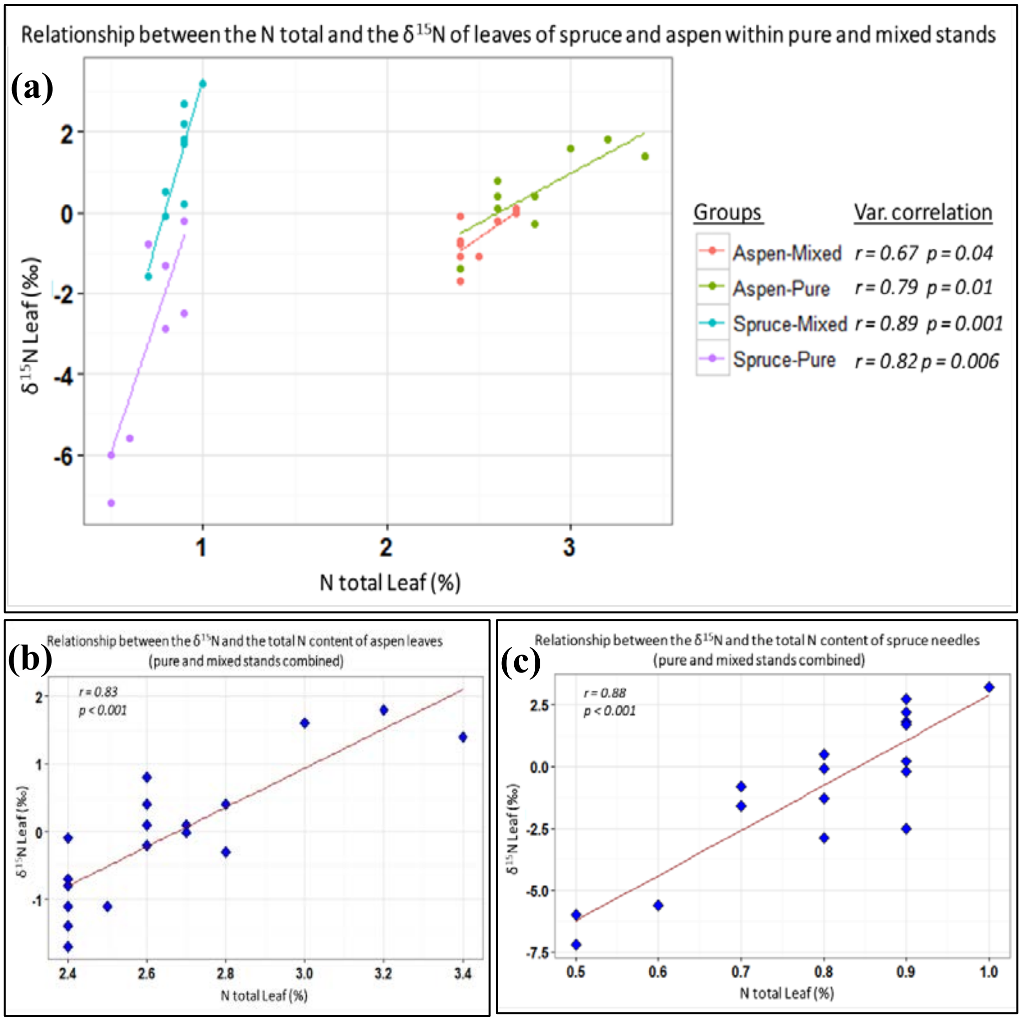

Figure S4.1 Simple linear regression analysis of total N content and δ^{15}N of leaves of spruce and aspen (a) within pure and mixed stands, and (b,c) for the combined data of pure and mixed stands. *r* is the Pearson's correlation coefficient and *p* indicates the significance of the relationship at $p = 0.05$.

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