AIX MARSEILLE UNIVERSITÉ
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SYLVICULTURE INTENSIVE EN RÉGION BORÉALE : IMPACT DE LA MIXITÉ DES ESSENCES SUR LE PROCESSUS DE DÉCOMPOSITION DES LITIÈRES ET LE STOCKAGE DE CARBONE

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À tous mes amis et ma famille

pour m'avoir encouragée et épaulée durant

ces 4 ans de double vie…

AVANT-PROPOS

Le document est composé de six sections : la première partie est consacrée à introduire les thématiques de recherche à travers une revue de littérature et à définir les objectifs de recherche et la méthodologie générale de ce travail. Les chapitres II à V forment le corps de cette thèse et ont été dédiés à la vérification et la discussion des hypothèses de travail. Ils ont été rédigés en langue anglaise sous la forme d'articles scientifiques. Le chapitre III a été subdivisé en 2 articles, car ces deux parties concernent la même thématique, mais l'une traitant de l'étude *in situ* (IIIa) et l'autre traitant de l'étude en laboratoire (IIIb). Le chapitre V a été publié, le chapitre II est en révision chez un éditeur et les autres chapitres seront soumis prochainement à des revues avec comité de lecture. Dans la dernière section, nous avons discuté des principaux résultats et ouvert des perspectives sur des avenues de recherche.

Chapitre II: Chomel M., Larchevêque M., DesRochers A., Baldy V. Home field advantage of litter decomposition in pure and mixed plantations under boreal climate. Révisions majeures dans Ecosystems (Facteur d'impact : 3.531).

Chapitre IIIa: Chomel M., Baldy V., Larchevêque M., DesRochers A. Litter quality and mixing effect on brown food web under intensive silvicultural system in the boreal region of eastern Canada (à soumettre à soil biology and biochemistry).

Chapitre IIIb: Chomel M., Baldy V., DesRochers A., Larchevêque M. Impact of litter mixtures and leachates on *Folsomia candida* fitness in microcosms (à soumettre à Pedobiologia).

Chapitre IV: Chomel M., Larchevêque M., DesRochers A., Baldy V. Effect of the mixing of herbaceous litter with tree litters on decomposition and N release in intensive silvicultural system (à soumettre à Plant and Soil).

Chapitre V: Chomel M, DesRochers A, Baldy V, Larchevêque M, Gauquelin T. 2014. Non-additive effects of mixing hybrid poplar and white spruce on aboveground and soil carbon storage in boreal plantations. Forest Ecology and Management 328: 292-299 (Facteur d'impact : 2.667).

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TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RESUME

Depuis quelques années, la sylviculture intensive prend de l'ampleur au Canada afin de rapprocher la source de fibres des usines, d'accroître la productivité des plantations, et de diminuer la pression de coupe sur les forêts naturelles. Toutefois, un débat sur le type d'aménagement optimal des plantations oppose l'aménagement mono- et plurispécifique. Malgré des effets antagonistes possibles sur la productivité des arbres, il semblerait que les plantations mixtes procureraient des avantages au niveau des propriétés du sol, de la stabilité environnementale, mais aussi du maintien de la biodiversité et de la valeur esthétique. Les espèces végétales et leur mélange sont susceptibles d'influencer le processus de décomposition selon deux mécanismes qui opèrent à différentes échelles : l'effet ressource par la production de litière possédant des caractéristiques physiques et chimiques propres qui constituent la ressource nutritive pour les décomposeurs, et l'effet habitat qui correspond à l'effet à plus long terme de l'arbre sur son environnement en influençant les microconditions climatiques et édaphiques, et donc les communautés d'organismes présents dans le sol. Le mélange de diverses espèces engendrerait à la fois une plus grande diversité d'habitats et de ressources favorisant une plus grande diversité et abondance des organismes décomposeurs, ce qui accélérerait le processus de décomposition et la remise à disposition des nutriments dans le sol. Il est important de mieux comprendre le fonctionnement de ces écosystèmes pour en effectuer une bonne gestion et pour optimiser les services écosystémiques que ces plantations fournissent. Ainsi cette thèse visait à mieux comprendre l'influence de la mixité de deux essences forestières, à savoir l'épinette blanche et le peuplier hybride, en comparaison à des plantations pures sur le processus de décomposition des litières en séparant l'effet ressource de l'effet habitat. Cette étude a été menée sur des plantations intensivement aménagées qui étaient largement colonisées par des herbacées. Ainsi une autre partie de cette thèse consistait à déterminer si la présence d'herbacées était bénéfique au processus de décomposition des litières et à la libération des éléments nutritifs dans les différentes plantations mono- ou pluri-spécifiques. Finalement, dans l'optique de relier ces données avec le fonctionnement global de l'écosystème, le stockage de carbone de la phytomasse aérienne et dans le sol (excepté les racines) a été étudié dans les deux types de plantations. La qualité des ressources et l'effet du mélange des arbres et des litières sur les décomposeurs ont été étudiés dans une expérimentation de décomposition *in-situ* avec des litter bags de chaque type de litière (peuplier, épinette, herbacées, ainsi que leur mélange) dans chaque type de plantations. Cette étude a été appuyée par une expérimentation *ex-situ* utilisant une espèce cible d'organisme du sol, *Folsomia candida* (collembola). Un intérêt particulier a été porté sur le rôle et l'impact des métabolites secondaires contenus dans les espèces végétales concernées sur le processus de décomposition mais aussi sur leurs interactions avec les organismes décomposeurs.

Concernant l'effet habitat, la plantation monospécifique de peuplier semblait être défavorable à la colonisation de la litière par la mésofaune, probablement dû à l'effet négatif des lixiviats de feuilles de peuplier mais également à la faible accumulation des litières. À l'inverse, la plantation pure d'épinette favorisait la décomposition de sa propre litière par la sélection d'organismes plus spécialisés. Les résultats de cette étude ne montraient pas d'amélioration du processus de décomposition avec le mélange du peuplier et de l'épinette (effet habitat) ou de leurs litières (effet ressource). En revanche, le mélange de ces deux espèces en plantation a tamponné les effets contrastés du peuplier et de l'épinette sur les organismes et le taux de décomposition observés dans les plantations monospécifiques. Le stockage de carbone et la productivité du peuplier étaient supérieurs dans les plantations mixtes par rapport aux plantations monospécifiques. Finalement, la litière d'herbacées semblait être bénéfique pour l'abondance d'organismes décomposeurs et favorisait la libération d'azote des litières d'arbres. Cet aspect pourrait contrebalancer l'effet négatif de la présence d'herbacées qui entrent en compétition avec les arbres pour les ressources. Ces résultats nous indiquent qu'après 10 ans, les plantations mixtes optimiseraient la productivité et le stockage de carbone, double avantage généralement recherché dans les systèmes sylvicoles.

ABSTRACT

The use of intensively managed plantations is of particular interest in Canada for rapid fiber production and to reduce harvesting pressure on natural forests in boreal regions. However, a debate on the best management scenarios opposes monocultures and mixed plantations management. Despite the possible antagonistic effects on tree productivity, it seems that mixed plantations could have benefits on soil properties, environmental stability, but also to maintain biodiversity and aesthetic value. Tree species and their mixture affect decomposition processes through two mechanisms that operate at different levels: the resource effect, with the nutritional quality of each litter type for decomposers and the habitat effect, with longer-term effects of trees on the environment by the influence of their presence on soil micro-climatic conditions and communities. Mixture of various species leads to greater diversity of habitats and resources that could induce greater diversity and abundance of decomposers, increasing decomposition rates and the release of nutrients in the soil. It is important to better understand the functioning of these ecosystems in order to choose the best management scenarios to optimize ecosystem services of these plantations. The main goal of this thesis was to understand the influence of mixed plantations of two tree species, namely white spruce and hybrid poplar, on litter decomposition process and communities of decomposers, compared to monospecific plantations by dissociating the resource and habitat effects. This study was conducted on intensively managed plantations that were largely colonized by grasses. Therefore another part of this thesis was to determine if the presence of herbaceous species was beneficial for litter decomposition process and nutrient release in mono- or pluri-specific plantations. Finally carbon storage on aboveground and belowground (excluding roots) compartments was studied in the three types of plantation (pure poplar or spruce, mixed) in order to link these data with the overall functioning of these ecosystems. The quality of resources and the effect of mixing trees and their litters on decomposer organisms were studied in a decomposition field experiment with litter bags of each litter type (poplar, spruce, herbaceous, and their mixture) in each plantation type. This study was supported by a laboratory experiment using a target soil organism, collembola. Particular interest was given to the role and the impact of plant secondary metabolites on decomposition process but also on the activity of decomposers.

Concerning the habitat effect, poplar monospecific plantations seemed to inhibit the colonization of litter by mesofauna, probably due to the negative impact of leachates from poplar leaves but also to the low accumulation of litter in this environment. Spruce monospecific plantations increased the decomposition of its own litter by selecting more specialized organisms. The results of this study showed no improvement in the decomposition process and decomposer diversity or abundance with the mixture of poplar and spruce (habitat effect) or their litters (resource effect). However, mixing these two species in plantation buffered the contrasting effects of poplar and spruce on organisms and decomposition rates observed in monospecific plantations. Carbon storage and poplar productivity were greater in mixed compared to monospecific plantations. Herbaceous litter increased the abundance of decomposer organisms and promoted the release of nitrogen from tree litter. This could offset the negative effect of the presence of herbaceous species that compete with trees for resources. These results indicate that after 10 years, mixed plantations could optimize productivity and carbon storage, a double advantage usually sought for by plantation managers.

CHAPITRE I

INTRODUCTION GÉNÉRALE

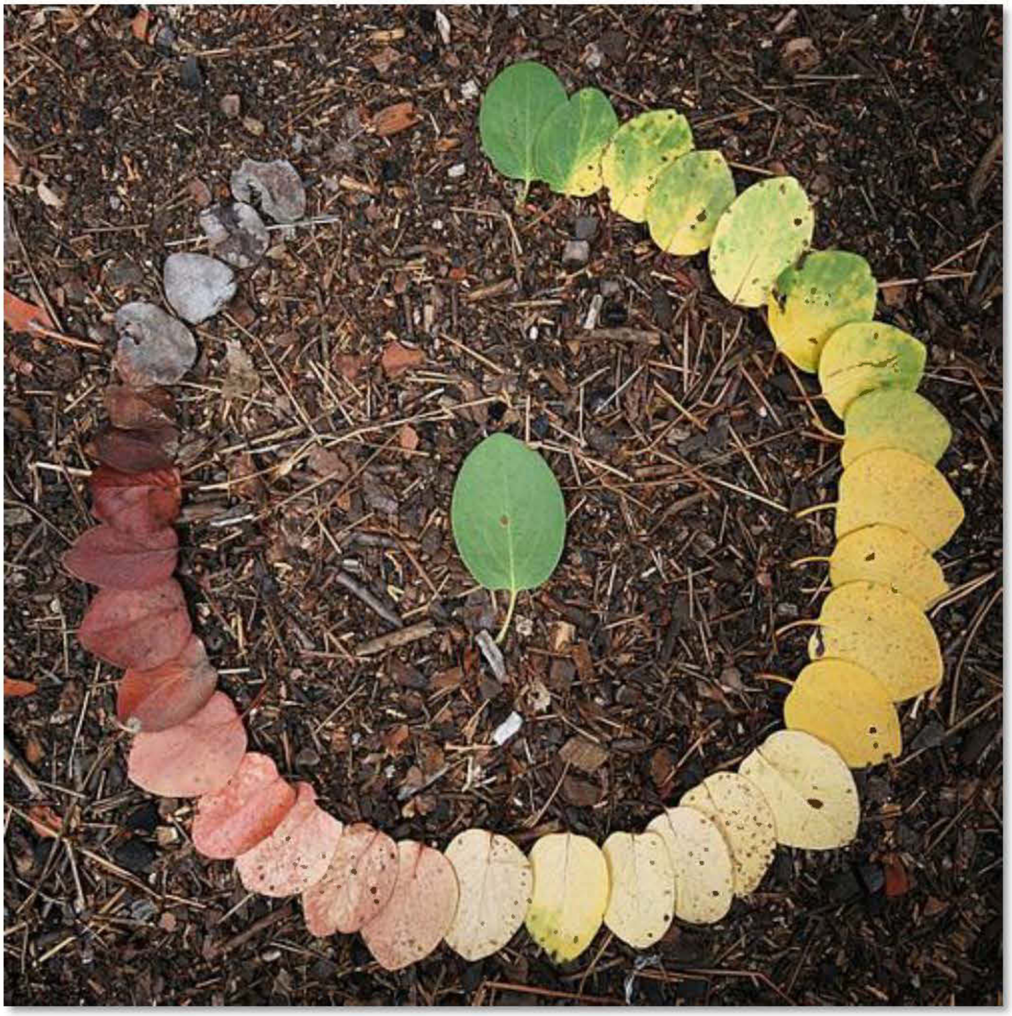

Figure 1.1 Le "cycle de vie d'une feuille" de Manzanita (© RobHerr)

1.1 Contexte et problématique

L'économie de la plupart des régions boréales du Canada est basée sur la récolte de bois. Mais depuis quelques années, on observe une diminution des ressources forestières due à la surexploitation des forêts naturelles. La pression sociale grandissante a alimenté une réflexion autour de la gestion durable et écologique de ces forêts. En 2010, la commission Coulombe a recommandé au gouvernement du Québec un aménagement forestier durable des forêts, comprenant des zones d'aménagement écosystémique des forêts naturelles, des zones de protection et des zones d'aménagement intensif[1]. Ce contexte a suscité un intérêt pour des systèmes sylvicoles intensifs afin de rapprocher la source de fibre des usines et d'accroître la productivité des plantations, notamment avec l'utilisation du peuplier hybride (*Populus*). Ces plantations permettent également de diminuer la pression de coupe sur les forêts naturelles en produisant du bois plus rapidement (temps de rotation plus court) sur de petites superficies. Parallèlement, depuis quelques années, de vastes étendues de terres agricoles ont été abandonnées dans l'Est de l'Amérique du Nord (McLauchlan, 2006) principalement à cause de l'exode rural, de l'industrialisation ou de la mauvaise gestion des terres agricoles. Dans la Province de Québec, 100 000 ha de terres agricoles abandonnées ont été recensés entre 1997 et 2007 (Vouligny and Gariépy, 2008). Ainsi, l'utilisation de ces terres fertiles abandonnées pour implanter des systèmes de sylviculture intensive paraît opportune.

Les plantations d'arbres à croissance rapide sont depuis longtemps basées sur le système de culture monospécifique. Mais depuis la "prise de conscience écologique", ces monocultures sont décriées, car elles sont considérées comme étant des déserts biologiques, alors que des plantations mixtes permettraient de préserver une certaine

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[1] On parle d'aménagement intensif pour des plantations qui sont régulièrement entretenues avec généralement des apports de fertilisants, des labours et de l'élagage. Ce type de plantations concerne généralement des variétés d'arbres améliorées ou à croissance rapide.

biodiversité. L'idée véhiculée depuis longtemps par les forestiers, selon laquelle les mélanges d'espèces favoriseraient la croissance des arbres, ne se vérifie pas forcément pour tous les systèmes forestiers (Gartner and Cardon, 2004; Jonsson and Wardle, 2008; Wardle et al., 1997).

Dans ce contexte nous voulions apporter des connaissances scientifiques sur le fonctionnement des plantations monospécifiques ou mixtes afin d'optimiser leur gestion et leur productivité en région boréale. Notre étude s'est focalisée sur le processus de décomposition, car il est à la base du fonctionnement des écosystèmes, et gouverne les cycles biogéochimiques des nutriments essentiels à la croissance des plantes.

1.2 Les plantations

1.2.1 Les enjeux de la sylviculture intensive

Les systèmes de sylviculture intensive connaissent un essor, car ils permettent d'obtenir un bois de qualité tout en ayant une durée de croissance courte et une grande productivité. De plus, dans le contexte boréal canadien, les plantations peuvent constituer un bon moyen pour lutter contre la surexploitation des forêts naturelles en diminuant la pression de coupe sur celles-ci tout en augmentant la production de fibre sur une plus petite surface du territoire (Hartley, 2002). Ces plantations peuvent également être intéressantes dans un contexte d'accroissement du CO_2 atmosphérique, car elles semblent favoriser le stockage du carbone (Laganière et al., 2010c).

Depuis le début de la sylviculture, un débat sur le type d'aménagement optimal des plantations oppose l'aménagement mono — et plurispécifique (Knoke et al., 2008). Malgré des effets antagonistes possibles sur la productivité, les plantations mixtes garderaient des avantages pour des questions de propriétés du sol, de stabilité environnementale et financière, mais aussi de maintien de la biodiversité et de la valeur esthétique (Hartley, 2002; Knoke et al., 2008). En effet, une forêt mixte serait plus résistante aux dommages causés par les insectes ou les catastrophes naturelles, tout en permettant une meilleure diversité d'habitats et d'organismes et une optimisation de l'utilisation des ressources (Hartley, 2002; Knoke et al., 2008). Mais, au-delà de ces aspects quel est l'effet d'un aménagement mixte sur les processus et la biodiversité du sol et la croissance des espèces?

Des plantations expérimentales à croissance rapide ont été mises en place afin d'étudier plus en détail les mécanismes sous-jacents à la mixité des espèces (Benomar et al., 2013). Les premiers résultats montrent en général que la croissance initiale du peuplier hybride et de l'épinette blanche est plus importante dans les plantations mixtes. En effet, durant les six premières années de croissance, le diamètre basal et la hauteur des épinettes blanches (*Picea glauca* (Moench) Voss) et des peupliers hybrides (clone 915319 : *Populus maximowiczii* x *P. balsamifera*) étaient plus élevés dans les parcelles plantées en mélange en comparaison des parcelles monospécifiques (Benomar et al., 2013). Il devient donc intéressant de se pencher sur le fonctionnement de ces écosystèmes pour mieux comprendre ces résultats.

1.2.2 Les essences concernées

Le peuplier hybride (*Populus sp*) montre généralement des taux de croissance très élevés (Taylor, 2002), et donc, en contrepartie, a une forte demande en nutriments (Steckler, 2007). Ainsi, une plantation de peuplier hybride peut immobiliser jusqu'à 20-25 kg ha^{-1} an^{-1} d'azote et 5-6 kg ha^{-1} an^{-1} de phosphore (Berthelot et al., 2000). La culture des espèces de *Populus*, incluant les peupliers hybrides, a été très étudiée en vue de réaliser des plantations à haut rendement, car elles sont connues pour avoir des temps de rotation courts (environ 20 ans) (Ceulemans et al., 1992; Eckenwalder, 1996).

Figure 1.2 Peuplier hybride

Le contenu en nutriments dans les feuilles d'un peuplier hybride avec une nutrition optimale peut atteindre jusqu'à 3 % d'azote, 0.4 % de phosphore, 2 % de potassium, 1,7 % de calcium et 0,4 % de magnésium (Steckler, 2007). Les peupliers hybrides participent donc de manière très importante au cycle des nutriments dans les plantations en raison de leur fort taux d'absorption des nutriments et de leur remise à disposition après la chute des litières et leur décomposition (Steckler, 2007).

<u>L'épinette blanche</u> (*Picea glauca* (Moench) Voss) est une espèce à forte valeur commerciale, mais elle présente un faible taux de croissance. Le temps de rotation d'une plantation d'épinette est beaucoup plus élevé que celui du peuplier hybride, avec un temps de résidence compris entre 40 et 60 ans (Steckler, 2007). Les concentrations en nutriments dans les aiguilles d'épinette blanche sont aussi plus faibles que dans les feuilles de peuplier, avec 1,38 % d'azote, 0,13 % de phosphore, 0,71% de potassium, 0,66 % de calcium et 0,10 % de magnésium (Gordon et al., 2000).

Figure 1.3 Épinette blanche

En forêt naturelle mixte, la litière de peuplier semble améliorer les différentes composantes du processus de décomposition (abondance des organismes décomposeurs, qualité de la litière, conditions physico-chimiques du sol) comparativement aux forêts de conifères pures (Laganière et al., 2009; Légaré et al., 2005). Une augmentation de la croissance de l'épinette est observée lorsque cette espèce est en mélange avec moins de 41% de peuplier (Légaré et al., 2004), en raison d'une amélioration des propriétés physico-chimiques de la litière et du sol, et de la diversification des communautés de macrofaune favorisées par le peuplier (Laganière et al., 2009). En revanche, on observe une diminution de la productivité du peuplier faux-tremble en forêt naturelle mixte par rapport aux forêts pures de peuplier (MacPherson et al., 2001). En effet, la litière d'épinette est plus difficilement dégradable et contient plus de composés récalcitrants, expliquant les stocks de carbone plus importants dans les sols de peuplements purs d'épinette en comparaison des peuplements mixtes ou purs de peuplier (Cavard et al., 2010; Laganière et al., 2010c).

Malgré cette tendance à l'amélioration de la productivité dans les forêts naturelles, il semble que les effets soient différents dans les plantations. En effet, Kabzems et ses collaborateurs (2007) ont montré que la présence du peuplier diminuait de moitié la productivité de l'épinette. Les plantations sont des systèmes fortement modifiés, ainsi les différences observées pourraient être dues à la vocation antérieurement agricole de ces sites qui change fondamentalement la nature des sols, ainsi qu'à la nature de la végétation de sous-bois. En effet, le passage d'une végétation de type arbustif en milieu naturel à un sous-bois d'herbacées en plantation (Gachet et al., 2007) pourrait améliorer la décomposition en générant une litière plus riche en azote et moins riche en lignine (Hoorens et al., 2002). Ainsi, on pourrait voir dans ces plantations une plus grande disponibilité des nutriments, notamment de l'azote, favorisant la croissance des plantes (Hättenschwiler et al., 2005). Les sous-bois d'herbacées pourraient également créer des conditions microclimatiques favorables associées à leur structure (i.e. haut tapis denses) (Standish et al., 2004), ce qui expliquerait l'absence d'accumulation de matière organique généralement observée dans ces sites.

1.3 Le processus de décomposition des litières

1.3.1 Un processus écosystémique clé

La litière représente l'ensemble des débris végétaux qui vont s'accumuler au niveau de l'interface lithosphère — atmosphère. Cette matière organique morte possède une place importante dans l'écosystème, car elle est la source énergétique et nutritive de nombreux organismes décomposeurs du sol (Hättenschwiler et al., 2005). Ces organismes vont assimiler les composés contenus dans la litière et libérer dans le milieu des nutriments et des éléments minéraux nécessaires à la survie et à la croissance des végétaux (Lévêque, 2001). La décomposition de la litière contrôle donc les flux de nutriments (Gobat et al., 2010), la structure des communautés de microorganismes et de la faune du sol, la productivité (Koukoura et al., 2003) et le fonctionnement global des écosystèmes (Hättenschwiler et al., 2005). Ces propriétés font de ce mécanisme un processus fondamental dans le fonctionnement des écosystèmes forestiers.

Mais l'étude de ce processus fondamental révèle rapidement sa grande complexité. En premier lieu, la matière végétale qui entre en décomposition contient une gamme de composés très divers, allant de sucres simples aux molécules beaucoup plus complexes tels que les composés structuraux et les métabolites secondaires. En second lieu, une large gamme d'organismes décomposeurs va être attirée par cette matière végétale tombée au sol, et l'utilisera comme source nutritive attirant ensuite d'autres types d'organismes, constituant ainsi les chaînes trophiques. Enfin, divers facteurs vont influencer ce processus directement par des actions physiques ou chimiques, ou indirectement en jouant sur la composition de la matière végétale et sur l'activité des décomposeurs. À cela s'ajoute une complexité supplémentaire : tous ces compartiments sont interconnectés et des boucles de rétroactions agissent simultanément.

1.3.2 Les constituants de la litière

Le contenu du matériel végétal est divisé en deux groupes de constituants, bien que cette dénomination soit remise en question (Karlovsky, 2008) : i) Les métabolites primaires d'une part, correspondant aux molécules qui constituent les tissus de la plante et qui sont essentielles à la vie de la plante. Ils intègrent le matériel intracellulaire et de stockage (e.g. protéines, glucides) facilement dégradable, et les composés structuraux (e.g. cellulose, holocellulose,) plus récalcitrants à la décomposition (Guggenberger, 2005). ii) D'autre part, les métabolites secondaires qui, contrairement aux métabolites primaires, ne participent pas directement au développement de la plante, mais sont nécessaires à la survie de la plante dans son environnement (Hopkins, 2003).

Certains de ces métabolites secondaires, notamment les terpènes et les composés phénoliques, participent à la lutte contre l'herbivorie, le parasitisme et interviennent dans la compétition inter et intraspécifique au travers des processus d'allélopathie (Fernandez et al., 2006; Ormeño et al., 2007). Mais ce sont également des composés difficilement dégradables et nuisibles à la croissance et l'activité des organismes décomposeurs, des symbiotes et des microorganismes (Hättenschwiler and Vitousek, 2000; Kuiters, 1990). Ainsi, ils vont être d'importants régulateurs du cycle du carbone et de l'azote en ralentissant le taux de décomposition des litières (Kainulainen and Holopainen, 2002; Kainulainen et al., 2003; Ormeño et al., 2006; Poinsot-Balaguer, 1996; Souto et al., 1994). On peut les diviser en trois principaux groupes :

i) les composés phénoliques qui se caractérisent par au moins un cycle aromatique hydroxylé. Ces composés sont très diversifiés, ils vont des simples acides phénoliques aux grands polymères plus complexes tels que les tanins et la lignine (Hopkins, 2003). Les tanins ont une capacité importante à retarder le processus de décomposition en formant des complexes récalcitrants avec les protéines (Hättenschwiler and Vitousek, 2000; Kuiters, 1990). Le peuplier faux-tremble (*Populus tremuloides*) (Erwin et al., 2001) et l'épinette blanche (*Picea glauca*) (Bauce et al., 2006) possèdent beaucoup de ces composés, notamment des tanins condensés (environ 8% du poids sec de la feuille).

ii) Les terpènes sont des substances en général lipophiles qui dérivent d'une entité simple à cinq atomes de carbone. La famille des terpènes comprend des hormones, des pigments caroténoïdes, le latex, et la plupart des huiles essentielles (Hopkins, 2003). Les terpènes ont des rôles variés, ils peuvent servir d'attraction pour les pollinisateurs grâce à des formes volatils, de protection contre les herbivores (Langenheim, 1994), de toxines, et de répulsifs contre les insectes (Hopkins, 2003).

iii) Les alcaloïdes sont des composés solubles qui contiennent tous au moins un atome d'azote et qui ont une forte activité biologique, comme des propriétés analgésiques ou toxiques (Hopkins, 2003). À plus forte dose, la plupart des alcaloïdes sont très toxiques (morphine, nicotine, caféine, quinine etc.).

1.3.3 La dynamique du processus de décomposition

Le processus de décomposition se déroule grâce à l'action de différents acteurs :

i) L'eau, qui permet le lessivage, c'est-à-dire l'entraînement par l'eau des composés solubles, engendrant une importante perte de masse au début du processus de décomposition.

ii) Les macrodétritivores, qui vont avoir un rôle de fragmentation primaire de la litière; de plus les boulettes fécales qu'ils déposent dans la litière possèdent une meilleure qualité chimique et une meilleure rétention en eau que la litière non transformée, ce qui améliore le développement microbien (Coûteaux et al., 2002; Garcia-Pausas et al., 2004).

iii) Les microarthropodes, organismes appartenant à la mésofaune, tels que les collemboles et les acariens, vont réaliser une fragmentation plus fine de la matière végétale (Gobat et al., 2010). Ils sont d'importants régulateurs des populations microbiennes en les consommant directement et, par leur déplacement dans la litière, permettent un microbrassage de la matière végétale.

iiii) Les microorganismes effectuent la majeure partie des transformations élémentaires à l'origine des flux de matière et d'énergie dans les écosystèmes. C'est donc un des compartiments essentiels dans le fonctionnement de l'écosystème. On distingue les mycètes, qui, en général, peuvent assimiler les composés végétaux les plus récalcitrants tels que la lignine, les pectines et les tanins (Criquet, 1999) ou les transformer en composés plus simples, et les bactéries qui assimilent les composés déjà plus ou moins oxydés. Les microorganismes ont également un rôle important dans la détoxification des litières par la dégradation des métabolites secondaires (Bonanomi et al., 2005).

Il n'existe pas réellement de séparation dans le temps de ces différents acteurs au cours du processus de décomposition, au contraire tous ces acteurs interagissent ensemble. Malgré tout, le lessivage domine généralement la première phase de décomposition (Figure 1.4). La composition du substrat évolue avec le processus de décomposition, car les composés labiles sont plus rapidement lessivés ou dégradés que les composés récalcitrants. Les glucides simples sont alors les premiers à disparaître, sous l'action des microorganismes ou par lessivage. L'hémicellulose et la cellulose sont ensuite minéralisées. La matière organique va peu à peu se concentrer en composés récalcitrants à la décomposition, tels que la lignine et les polyphénols (Figure 1.4). Ces composés organiques restants vont s'agglomérer en macromolécules, de plus en plus complexes, de nature colloïdale et de couleur foncée, dont l'ensemble constitue l'humus, on parle alors du processus d'humification de la matière organique (Duchaufour, 1997).

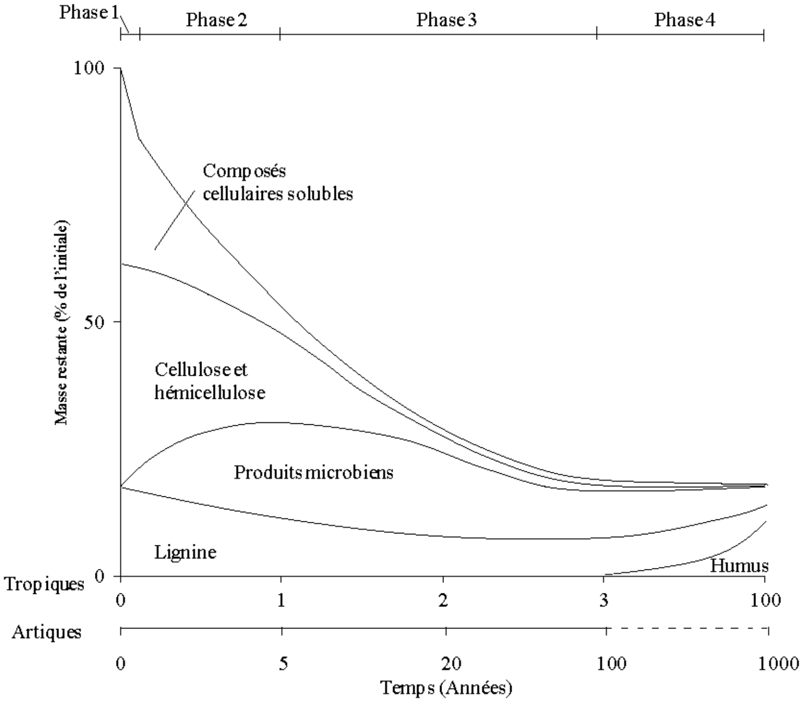

Figure 1.4 : Représentation des 4 phases majeures du processus de décomposition, et échelle temporelle communément observée dans des environnements chauds (les tropiques) et froids (la toundra). D'après Chapin *et al*, 2002.

1.3.4 Les facteurs influençant le processus

Différents facteurs influencent le processus de décomposition, mais ils ne peuvent pas réellement être dissociés, car des boucles de rétroactions les relient et influencent le processus de décomposition par l'intermédiaire de l'activité des décomposeurs.

Les facteurs environnementaux

Un des déterminants essentiels du processus de décomposition est le climat, i.e. la température et l'humidité (Aerts, 1997; Meentemeyer, 1978). Il explique une portion importante du taux de décomposition d'une part, car il détermine la composition des communautés végétales, et donc la qualité de la matière organique. D'autre part, le climat influence la disponibilité en eau déterminante pour l'activité des décomposeurs par le biais de l'humidité et de la température (Poinsot-Balaguer, 1996). On peut également citer les caractéristiques pédologiques (e.g. type de sol, topographie) qui peuvent également influencer la composition des communautés végétales ainsi que la disponibilité en eau du sol et donc agir sur l'activité des organismes et le processus de décomposition (Jonsson and Wardle, 2008).

La qualité de la litière

La notion de qualité fait référence aux caractéristiques physiques (i.e. capacité de rétention en eau, dureté de la feuille) ou chimiques de la litière, et la notion de "bonne" ou de "mauvaise" qualité n'est qu'arbitraire et correspond à la difficulté de dégradation de la litière par les organismes décomposeurs. Le processus de décomposition est fortement dépendant de la composition biochimique de la litière. Les débris végétaux peuvent contenir des composés labiles (e.g. sucres), des composés réfractaires à la décomposition (e.g. lignine) et des composés inhibiteurs des décomposeurs (e.g. composés phénoliques). La proportion relative de ces composés dans la litière influence sa vitesse de décomposition, car les organismes décomposeurs ont des capacités différentes à dégrader chaque type de composés (Cortez et al., 1996). Les litières de "bonne" qualité ont généralement une teneur en nutriments élevée avec une importante teneur en azote, identifiées par un faible ratio C/N. Au contraire, un C/N élevé dénote une forte proportion de composés difficiles à dégrader et pauvres en azote tels que les composés structuraux et les métabolites secondaires, caractéristiques d'une litière de "mauvaise" qualité.

La mixité des litières

De nombreux chercheurs se sont intéressés à la décomposition de litières monospécifiques et à l'impact de différents facteurs tels que l'humidité, la température, le pH sur celle-ci. Cependant, dans le milieu naturel, la litière d'une espèce ne se décompose pas de façon isolée, mais en mélange avec les débris végétaux de l'ensemble de la communauté végétale. Dans les années 90, certains chercheurs se sont donc intéressés à l'effet de la mixité des litières sur le processus de décomposition. Les résultats ont montré plusieurs types de réponses (Blair et al., 1990; Jonsson and Wardle, 2008; Wardle et al., 1997), synthétisées par Gartner et Cardon en 2004 (synthèse de 30 études) :

Un effet additif : chaque espèce se décompose à la même allure en situation monospécifique et en mélange plurispécifique. Cette réponse a été observée dans 30 % des mélanges étudiés.

Un effet non-additif : on observe une amélioration (*synergie*) ou une diminution (*antagonisme)* du processus par rapport à la moyenne des résultats des litières monospécifiques. Environ 50 % des mélanges de litières se sont décomposés de manière non-additive synergique, et 20 % des mélanges se sont quant à eux décomposés de manière non-additive antagoniste.

Les mécanismes de ces interactions peuvent être multiples, dans une synthèse bibliographique Hättenschwiler et ses collaborateurs (2005) distinguent quatre principaux types de mécanismes :

i) Le transfert de nutriments d'une litière plus riche en nutriments à une litière plus pauvre impliquant des interactions synergiques. Ce transfert s'effectue probablement par diffusion dans les films d'eau ou par transport actif par les hyphes des champignons (McTiernan et al., 1997). Les organismes décomposeurs exploitent préférentiellement la litière de meilleure qualité, impliquant une disponibilité des nutriments qui vont être transférés à la litière de moins bonne qualité, ce qui induit une décomposition plus rapide du mélange de litière, c'est le "priming effect" (Hättenschwiler et al., 2005).

ii) Les effets de composés spécifiques qui peuvent générer des interactions synergiques ou antagonistes. Par exemple, les polyphénols peuvent complexer des nutriments et les rendre inaccessibles ou non-disponibles à la dégradation par les décomposeurs (Hättenschwiler and Vitousek, 2000).

iii) L'amélioration des conditions micro-environnementales conduisant à des effets synergiques induits par les structures d'habitats et les microclimats des litières. Ainsi, des litières de différentes structures, couleurs et formes contribuent à des capacités de rétention en eau différentes, et des habitats diversifiés pour les organismes, ce qui peut augmenter les effets synergiques.

iv) Les interactions entre niveaux trophiques, tels que les actions mécaniques et la production de fèces par la macrofaune, ou encore la régulation des populations de champignons et bactéries par broutage des fongivores (cf. revue de littérature de Hättenschwiler et al 2005).

1.4 Interactions entre les compartiments aérien et souterrain

Comme nous l'avons vu précédemment, les facteurs environnementaux et la qualité de la litière influencent le processus de décomposition. Cet effet est principalement mis en avant par des corrélations avec le taux de décomposition, paramètre global influencé par les relations entre divers organismes acteurs de la décomposition, et n'est pas forcément révélateur d'une relation de cause à effet (Prescott, 2005). Ainsi pour mieux comprendre ces relations et le processus de décomposition, il est important de comprendre les interactions entre les communautés végétales et les organismes du sol.

1.4.1 Le réseau trophique du sol ("brown food chain")

La chaîne alimentaire du sol est exceptionnellement complexe et repose presque entièrement sur les nutriments d'origine végétale. La complexité des relations entre organismes du sol a pendant longtemps constitué un verrou à la compréhension du processus de décomposition, et les organismes du sol ont longtemps été traités comme une « boîte noire » dans la modélisation des écosystèmes (Allison and Martiny, 2008). La préférence alimentaire exacte de la plupart des organismes du sol n'est pas connue et la plupart des organismes sont flexibles dans leur régime alimentaire (Maraun et al., 2003; Scheu, 2002; Scheu and Setälä, 2002). Néanmoins, deux canaux de transfert d'énergie émergent passant soit par les décomposeurs primaires soit par les secondaires (Figure 1.5, Scheu 2002). Les décomposeurs primaires se nourrissent principalement d'un mélange de feuilles et de racines, mais peuvent également se nourrir des exsudats racinaires (Ruf et al., 2006); on y retrouve par exemple les collemboles (Collembola), les diplopodes (myriapoda), les oribates (arachnida), les lombrics (Oligochaeta) etc. Les décomposeurs secondaires se nourrissent d'un mélange de ressources incluant notamment les bactéries et les champignons (on parle généralement de microbivores) et directement de la litière déjà fragmentée; on y retrouve les collemboles, les oribates, les isopodes etc. Enfin, il y a les prédateurs, généralement divisés en deux niveaux : les prédateurs des décomposeurs (comme les gamasides, les araignées, les staphylins), et les prédateurs des prédateurs (comme les pseudoscorpions) (Scheu, 2002).

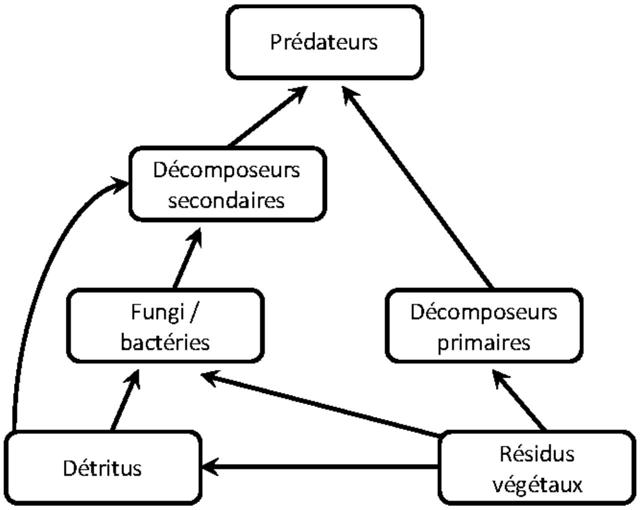

Figure 1.5 Modèle conceptuel de la chaîne alimentaire du sol inspiré de Scheu (2002).

1.4.2 Rétro-action : le home field advantage

Nous avons vu que les espèces végétales influençaient le processus de décomposition notamment par les propriétés physiques et chimiques de leur litière. Cette qualité de la matière organique influence à son tour les communautés d'organismes du sol. Les conditions microclimatiques créées par un arbre dans son aire d'influence peuvent aussi avoir un effet sur les organismes et le processus de décomposition (Laganière et al., 2009), indépendamment de la composition biochimique des litières (Prescott et al., 2000). Ces relations impliquent que les communautés d'organismes présents dans la litière et le sol se sont adaptées aux conditions créées par les communautés végétales présentes dans l'écosystème. Ainsi, une théorie a récemment émergé, le « home field advantage », qui suggère que la litière d'une espèce végétale a tendance à se décomposer plus rapidement dans l'habitat d'où elle provient grâce à une adaptation des organismes à la décomposer (Ayres et al., 2006; Ayres et al., 2009a; Ayres et al., 2009b; Gholz et al., 2000; Strickland et al., 2009; Vivanco and Austin, 2008).

1.4.3 Remise à disposition des nutriments

Nous avons vu que le processus de décomposition avait un rôle majeur dans le fonctionnement des écosystèmes, notamment car il permet de "boucler" les cycles biogéochimiques. Nous parlerons ici des deux principaux éléments, le carbone et l'azote. À leur sénescence, les tissus végétaux sont en partie dégradés et assimilés par les microorganismes qui permettent de transformer la matière organique en éléments minéraux. La majorité du carbone dégradé (environ 60%) est minéralisé en CO_2 par la respiration des microorganismes hétérotrophes, et donc est remis à disposition dans l'atmosphère, et utilisable par les plantes (Gobat et al., 2010). Concernant le deuxième élément, le principal réservoir d'azote est l'atmosphère qui en contient 78% en volume, sous forme gazeuse (diazote, N_2). Cette forme est inutilisable par les végétaux (exception faite de l'association symbiotique entre les bactéries du genre *Rhizobium* et les racines des légumineuses), car ils ont besoin d'une autre forme inorganique comme l'ion ammonium (NH_4^+) ou les nitrates (NO_3^-). Les bactéries hétérotrophes et les champignons dégradent les matières organiques azotées (notamment les protéines et les acides aminés), une part de cet azote est stockée dans leur biomasse (i.e. immobilisation), une autre part est totalement minéralisée (Gobat et al., 2010). L'azote se retrouve alors sous la forme d'ion ammonium, assimilable par les végétaux. Mais la croissance des microorganismes et donc la disponibilité en azote dépend essentiellement de la décomposition de la matière organique et de la capacité des microorganismes à l'immobiliser, c'est pour cette raison que l'azote est généralement considéré comme un des principaux facteurs limitant la croissance des végétaux.

1.4.4 Le stockage de carbone

Une grande part du carbone des écosystèmes forestiers est séquestrée dans la végétation, constituant en moyenne 50% de la biomasse végétale. Une autre partie du carbone est également séquestrée dans le sol, pouvant représenter de 50% dans les forêts tropicales à 98% du stockage de carbone total dans les terres cultivées (Bolin et al., 2000). Les forêts boréales ont un niveau intermédiaire, avec des concentrations de carbone organique du sol correspondant à 84% de stockage total de carbone au niveau de l'écosystème (Bolin et al., 2000). Après les premières phases de lessivage et d'assimilation des composés labiles, la matière organique va peu à peu s'humifier (Duchaufour, 1997). Ainsi, le stockage du carbone dans les sols dépend de l'équilibre entre les gains de carbone provenant des débris végétaux, et les pertes de carbone au cours de la minéralisation de la matière organique. Si la décomposition de la litière est rapide, le stock d'humus incorporé au sol est faible, et à l'inverse si la décomposition est lente, le stock d'humus et donc de carbone est important dans le sol. Dans le contexte des changements globaux, l'intérêt pour le stockage de carbone a pris une grande ampleur ces dernières années, car il permettrait de compenser les émissions de CO_2 (IPCC, 2007). Au Canada, l'installation de peuplements de peupliers faux tremble (*Populus tremuloides* Michx.) en Saskatchewan centrale sur des champs ou des pâtures permettrait sur 50 ans de séquestrer 30 à 70 tonnes de carbone supplémentaires par hectare (Fitzsimmons et al. 2004).

Figure 1.6 Photos des trois types de plantations sur le site d'Amos

1.5 Objectifs de l'étude

Ce projet de recherche se situe au croisement entre la recherche fondamentale et la recherche appliquée car il vise à améliorer les connaissances fondamentales sur le processus de décomposition pour la communauté scientifique, mais aussi pour aider à l'amélioration des systèmes de sylviculture intensifs.

Dans ce travail de thèse, nous avons choisi d'adopter une approche fonctionnelle intégrative pour comprendre l'effet de la mixité des espèces sur le fonctionnement des plantations sous aménagement intensif en climat boréal. Le processus de décomposition des litières est au cœur de cette thèse, car il intègre de nombreux paramètres de l'écosystème. Ainsi, nous déterminerons s'il y a un bénéfice en terme de diversité des organismes, de relargage des éléments nutritifs et de microconditions favorables dans les plantations mixtes en comparaison aux plantations monospécifiques. La qualité des ressources et l'effet du mélange des litières sur les décomposeurs ont été étudiés dans une expérimentation de décomposition *in situ* et appuyés par une expérimentation *ex situ* utilisant une espèce cible d'organisme du sol. Un intérêt particulier a été porté sur le rôle et l'impact des métabolites secondaires contenus dans les espèces végétales concernées sur le processus de décomposition, mais aussi sur leurs interactions avec les organismes décomposeurs.

Nous avons également choisi de nous intéresser aux herbacées qui colonisent naturellement ces plantations et dont l'effet sur le fonctionnement des plantations sous système intensif est encore méconnu. Finalement, dans l'optique de relier ces données avec le fonctionnement global de l'écosystème, la productivité des arbres, le stockage de carbone aérien et dans le sol ont été étudiés dans les plantations monospécifiques ou mixtes. Les objectifs spécifiques étaient les suivants :

1) Déterminer l'influence de la mixité des espèces dans des plantations soumises à des systèmes de sylviculture intensifs sur le processus de décomposition des litières, en comparaison avec les plantations pures de peuplier hybride et d'épinette (chapitres 2 et 3a).

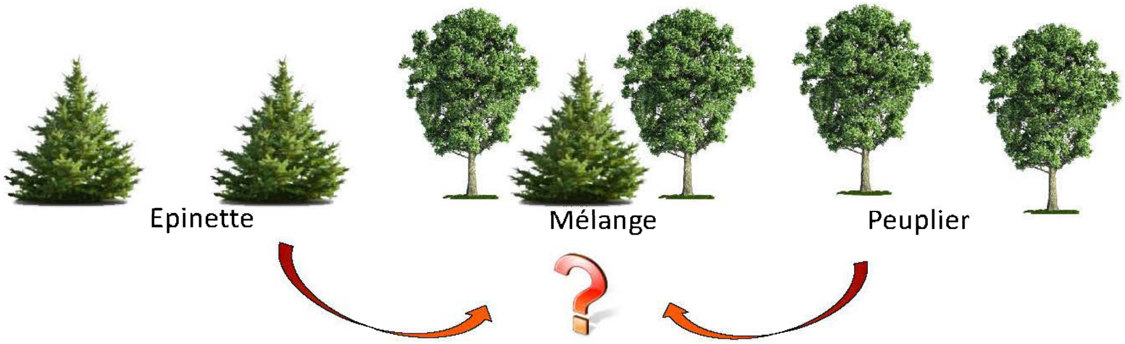

Figure 1.7 Schéma synthétisant la première problématique

En forêt naturelle, la litière de peuplier faux-tremble améliore les conditions de décomposition de la litière d'épinette. Des études antérieures ont en effet reporté des améliorations à un niveau physico-chimique de la litière, au niveau de la colonisation et de la diversification des communautés de macrofaune, ainsi qu'au niveau des vitesses des processus des sols (Laganière et al., 2009, 2010 b; Légaré et al., 2005). Cette différence entre peuplements purs et mixtes pourrait être due à la diversification ou l'amélioration des microconditions environnementales, au mélange des composés chimiques des litières, au transfert de nutriments entre les deux types de litières, créant des habitats plus variés favorisant la diversité des organismes présents dans le sol. Malgré une très grande différence entre les systèmes cultivés et naturels, on peut supposer que les plantations mixtes ou pures pourraient démontrer des différences similaires : on peut s'attendre à voir une plus grande abondance des organismes décomposeurs ainsi qu'une diversification des communautés dans les plantations mixtes en comparaison avec les plantations pures. On peut également s'attendre à un transfert de nutriments entre la litière de peuplier, qui contient de plus grandes teneurs en nutriments (NPK) et en composés facilement dégradables, et celle d'épinette, entraînant donc un taux de décomposition plus rapide de l'épinette lorsqu'elle est en mélange. Pour dissocier deux mécanismes distincts de l'influence du mélange de deux espèces végétales, nous avons séparé dans ce travail l'effet habitat (Chapitre 1) de l'effet ressource (Chapitre 3a).

2) Déterminer les effets des métabolites secondaires sur l'activité des organismes décomposeurs et sur le processus de décomposition de la litière de peuplier et d'épinette. Déterminer notamment la potentialité allélopathique des pluviolixiviats sur l'activité des communautés de décomposeurs (Chapitre 3b).

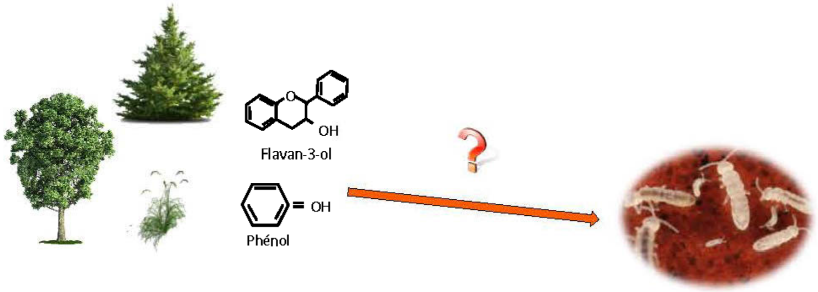

Figure 1.8 Schéma synthétisant la deuxième problématique

Les métabolites secondaires peuvent jouer un rôle important dans le processus de décomposition, en affectant d'une manière radicale les différents organismes impliqués dans le processus. L'épinette et le peuplier semblent contenir beaucoup de composés phénoliques et notamment des tanins, qui rendent la matière organique indisponible en se complexant avec elle. On peut donc supposer une diminution de l'activité des organismes décomposeurs lorsque ces composés sont présents en grande quantité, notamment au début du processus de décomposition, et lorsqu'il y a un apport important de pluviolixiviats.

3) Comprendre le rôle de la végétation herbacée de sous-bois dans l'accumulation et la décomposition de la litière dans les plantations sous système intensif (Chapitre 4)

Une densité importante d'herbacées est souvent observée en plantations sur d'anciennes terres agricoles (Gachet et al., 2007; Guillemette and DesRochers, 2008) remplaçant le sous-bois des forêts naturelles. Ce matériel végétal étant plus appétant pour les décomposeurs, on suppose une amélioration du processus de décomposition en leur présence. De plus, la végétation herbacée retiendrait plus d'humidité que la litière d'épinette et de peuplier, ce qui pourrait être bénéfique pour le processus de décomposition et l'activité des décomposeurs (Xiong et al., 2008). On s'attend donc à ce que la présence d'herbacées augmente l'humidité et l'abondance des décomposeurs dans la litière de peuplier et d'épinette impliquant donc une amélioration du processus de décomposition.

4) Étudier l'effet de la mixité sur les stocks de carbone aériens et des différents horizons de sol dans les plantations étudiées (Chapitre 5).

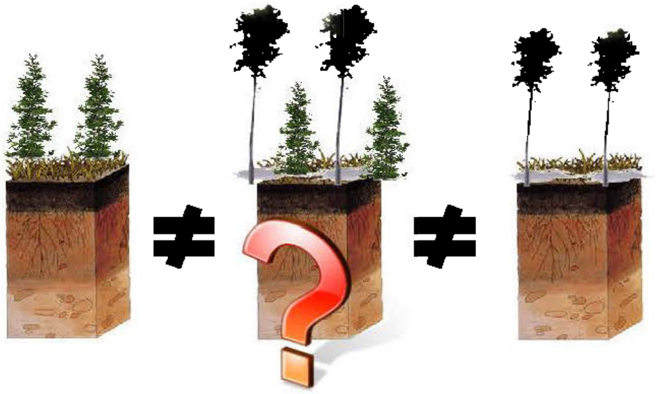

Figure 1.9 Schéma synthétisant la quatrième problématique

On peut s'attendre, tout comme dans les forêts naturelles, à avoir un stock de carbone souterrain plus important dans les plantations pures d'épinette, suivi des plantations mixtes et enfin des plantations de peuplier. Cette différence serait due à une litière plus récalcitrante et des organismes décomposeurs moins abondants, et donc à une plus grande immobilisation de la matière organique par un processus de décomposition moins efficace dans les plantations d'épinette.

1.6 Méthodologie

1.6.1 Présentation de l'écosystème étudié

Trois sites d´études ont été sélectionnés dans la région boréale de l´Abitibi-Témiscamingue, Québec, Canada : Amos (48°36'N, 78°04'O), Rivière-Héva (48°11'N, 78°16'O), et Nédelec (47°45'N, 79°22'O). Le site d´Amos était une ancienne friche agricole composée d´un sol argileux, qui était dominée par des herbacées et des patchs d´aulnes (*Alnus incana* ssp. *rugosa*), de saules (*Salix* spp.) et de peuplier faux-tremble. Le site de Rivière Héva était plus ou moins similaire, mais avec un sol argilo-sableux et un sous-bois plutôt arbustif qu'herbacé. Le site de Nédelec était un terrain forestier, composé d´un sol limoneux, dont le bois commercialisable avait été récolté en 2000. Il a été recolonisé de manière éparse par du peuplier faux-tremble, du bouleau blanc (*Betula papyrifera* Marsh.), et du cerisier rouge sauvage (*Prunus pensylvanica* L.f).

Les sites ont tout d'abord été préparés en 2002 pour enlever la végétation et les souches. Les sols ont ensuite été labourés jusqu´à 30 cm de profondeur en automne 2002 et nivelés au printemps 2003, puis les arbres ont été plantés durant l´été 2003. Durant les cinq premières années, les herbacées ont été enlevées par hersage. Ces sites comprennent des blocs de plantations pures et mixtes de peuplier hybride (clone 915319 : *P. maximowiczii* x *P. balsamifera*) et d'épinette blanche (*Picea glauca* (Moench) Voss) avec une densité de plantation de 1 × 1 m et de 3 x 3 m. Les aspects physiologiques ainsi que la croissance ont été suivis.

1.6.2 Expérimentation de décomposition

Pour effectuer un suivi du processus de décomposition, nous avons utilisé la méthode des « litter bags » (sacs de litière), laquelle consiste à placer des litières de feuilles de différentes espèces végétales dans des filets de polypropylène dont le vide de maille est variable en fonction des organismes que l'on veut prendre en compte. Ces filets ont été déposés sur les sites expérimentaux, puis récoltés à des intervalles de temps rapprochés durant deux années complètes.

Pour cette étude, des feuilles sénescentes de peuplier hybride et d'épinette blanche ont été récoltées durant l'automne 2010, pour avoir un matériel en cours d'abscission tout en empêchant le contact avec le sol afin d'éviter la colonisation des feuilles par les organismes avant le début de l'étude de décomposition. Une petite proportion de cette litière a été séchée à 40°C pour en déterminer le taux d'humidité. Cette valeur nous a permis de calculer des poids frais en équivalent poids sec afin de ne pas sécher la litière utilisée dans les litter bags pour éviter toutes modifications physico-chimiques. Sept grammes de feuilles de chaque espèce (équivalent environ à 6,5 g sec) ont été placés dans les litter bags. Ces sacs avaient une dimension de 10 x 15 cm pour les sacs ne contenant que des aiguilles d'épinette pour limiter les pertes dues à la faible taille des aiguilles, et 15 x 15 cm pour les autres, avec un vide de maille de 1 mm pour permettre à la mésofaune de coloniser la litière tout en excluant la macrofaune. Malgré le rôle important de la macrofaune dans le processus de décomposition et son influence possible sur les effets d'interaction entre les deux espèces végétales, nous avons choisi de l'exclure pour nous intéresser plus particulièrement aux effets de la mixité des litières sur les aspects physico-chimiques et microbiologiques. De plus, la macrofaune réalise un brassage de la litière entraînant d'importantes pertes de matière végétale du litter bag, limitant l'étude du processus de décomposition à plus fine échelle sur le long terme. Pour étudier les différences dans le processus de décomposition entre les plantations pures ou mixtes, plusieurs types de sacs ont été réalisés : des litter bags contenant 100% de peuplier, 100% d'épinette ou 100% d'herbacées, ainsi que des litter bags avec le mélange peuplier / épinette (50-50 % du poids). Pour déterminer comment les herbacées colonisant ces plantations influencent le processus de décomposition, des litter bags contenant 50% d'herbacées et 50% d'épinette ou de peuplier ont été rajoutés dans les plantations pures correspondant à l´espèce, et enfin des litter bags contenant les trois sortes de litière à proportions égales (33,3%) ont été rajoutés dans les plantations mixtes. Ces litter bags ont été déposés dans les plantations selon la disposition schématisée dans la Figure 1.10.

Pour compléter l'étude sur l'effet de l'habitat, des litter bags supplémentaires contenant de la cellulose ont été fabriqués. Ils ont été déposés dans les plantations pures et mixtes sous les épinettes et les peupliers, et entre deux arbres (à 1.50 m des arbres) pour déterminer l'influence de l'arbre dans les plantations 3 m x 3m.

Nous avons utilisé un total de 19 combinaisons de types de litter bags et de plantations pour l'expérimentation principale. Deux litter bags (un pour les analyses et un pour la mésofaune mis côte à côte) x 19 modalités x 3 pseudoréplicats x 3 sites (réplicats) x 4 prélèvements = 1368 litter bags ont été réalisés au total. Finalement, 63 litter bags additionnels contenant la cellulose ont été utilisés.

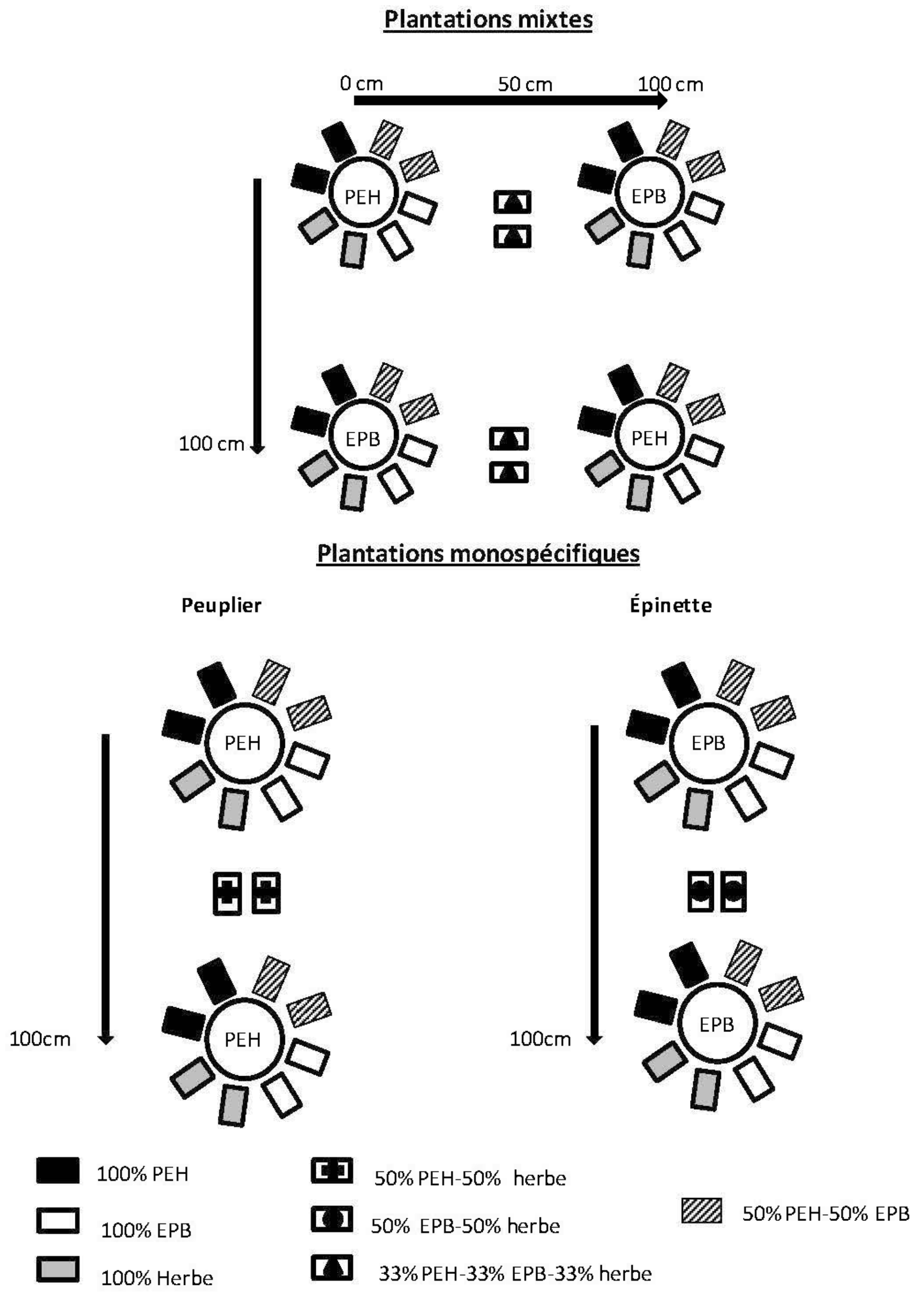

Figure 1.10 Schéma du dispositif expérimental pour la mise en place des litter bags. EPB = épinette blanche, PEH = peuplier hybride

Méthodes : Le suivi de la décomposition s'est déroulé sur deux ans, au printemps (à la fonte des neiges, mi-mai), et en automne (fin octobre). Six sacs de litières ont été prélevés pour chacune des modalités dans chacun des réplicats sites, ce qui fait un total de 114 sacs prélevés pour chaque site et chaque date. La litière des mélanges a d'abord été séparée pour peser la masse fraiche puis sèche restante, par la suite les litières ont été à nouveau mélangées afin de disposer de suffisamment de matériel pour les analyses. Des analyses chimiques (carbone, azote et métabolites secondaires) ainsi qu'un suivi de la mésofaune et des microorganismes ont été effectuées sur le contenu de ces sacs. Des mesures identiques ont été réalisées sur les aiguilles et les feuilles à la date initiale, c'est-à-dire le jour du dépôt des sacs de litière. Sur le terrain, des mesures de température et d'humidité du sol ont été effectuées à l'aide de sondes (Oakton® Acorn series et Spectrum® FieldScout TDR100 respectivement) aux alentours de 5 arbres choisis aléatoirement dans chacune des parcelles, lors de la mise en place du dispositif et lors de chaque prélèvement. Les conditions climatiques ont également été suivies (données de températures et de pluviométries mensuelles). Des bacs à litière ont été installés sur les sites au début de la deuxième année pour caractériser la nature et la quantité des apports en litière pour chaque type de plantation. Quatre bacs dans les plantations pures, et huit bacs (4 sous chaque espèce) ont été installés dans chaque type de plantations de chaque site (16x3 = 48 au total).

1.6.3 Expérimentation en laboratoire

Pour évaluer l'effet des différentes litières sur le processus de décomposition et notamment sur les communautés de décomposeurs via les métabolites secondaires libérés dans le milieu, une expérimentation en microcosmes a été effectuée afin de mesurer le degré d'écotoxicité des litières et des pluviolixiviats d'épinette, de peuplier et d'herbacées sur une espèce cible du sol, *Folsomia sp.* (Collembole).

1.6.4 Stockage de carbone.

Au cours de l'été 2011, des prélèvements de chaque horizon holorganique OL, OF et OH ont été effectués. Des analyses de carbone ont été réalisées grâce à un analyseur CHN (FlashEA® 1112 elemental analyser, Thermofisher Scientific). La hauteur et le diamètre des arbres ont été mesurés chaque année pour pouvoir estimer la biomasse grâce à des équations allométriques.

CHAPITRE II

PLANTATION MONOSPÉCIFIQUE OU MIXTE DU PEUPLIER ET DE L'ÉPINETTE : EFFET DE L'HABITAT SUR LE PROCESSUS DE DÉCOMPOSITION

Figure 2.1 Plantation monospécifique de peuplier hybride avec un espacement de 3 x 3m

Ce chapitre correspond à un article soumis à Ecosystems

"Home field advantage of litter decomposition in pure and mixed plantations under boreal climate "

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Keywords: litter decomposition, white spruce, hybrid poplar, cellulose, home field advantage, fungi, mites, collembola, microorganisms, reciprocal transplant, mixed plantation

Résumé

Les espèces végétales influencent le processus de décomposition par la qualité de leur litière et par leurs effets sur les conditions microclimatiques du sol. Des études ont montré que la litière d'une espèce se décompose plus rapidement lorsqu'elle est placée dans l'habitat d'où elle provient plutôt que dans un habitat composé d'autres espèces, c'est ce qu'on appelle le "home field advantage" (HFA). Quelques études ont testé cette hypothèse dans des plantations mixtes avec un mélange de plusieurs litières placées à équidistance des différentes espèces forestières. Mais dans des plantations mixtes, chaque espèce d'arbre peut avoir des effets distincts sur la décomposition de chaque type de litière. Nous avons testé si l'épinette blanche et le peuplier hybride montrent un HFA dans des plantations monospécifiques ou mixtes sous chaque espèce d'arbre en transplantant réciproquement les litières sous chacune des espèces dans les deux types de plantations. Le taux de décomposition et les communautés de décomposeurs ont été suivis pendant deux ans pour comparer l'influence de chaque espèce d'arbre dans chaque type de plantation. De plus, pour mesurer la capacité de dégradation des communautés du sol, des litter bags de cellulose ont également été placés au-dessous de chaque espèce et dans les différents types de plantations. Seules les plantations pures d'épinette ont montré un "home field advantage", *i.e.* sa propre litière se décomposait plus vite dans sa plantation. Ce résultat peut être expliqué par le fait que l'abondance des champignons, et donc par rétroaction celle des acariens détritivores, était plus importante dans les plantations pures d'épinette. En outre, la cellulose était moins décomposée dans cet environnement, suggérant que les communautés de décomposeurs présentes dans les plantations d'épinettes pures étaient capables de décomposer des litières relativement récalcitrantes, mais elles étaient moins efficaces dans la décomposition de substrats "plus simples". Dans les plantations mixtes aucun HFA n'a été observé, mais cet "environnement mixte" présentait des effets non-additifs sur le taux de décomposition (comparé aux taux prédit par la moyenne des deux plantations pures), mais seulement

sous les peupliers. Ces résultats confirment que dans des plantations mixtes, une espèce d'arbre affecte le sol d'une façon localisée par la distribution spatiale de sa litière. L'influence de la capacité de dispersion de la litière pourrait être prise en compte dans des études futures pour étudier l'effet du mélange d'espèces sur le processus de décomposition.

Abstract

Tree species affect decomposition processes through litter quality and their influence on soil microclimatic conditions. Plant litter could decompose faster when placed in the habitat from which it was derived than in a foreign habitat, which has been termed home field advantage (HFA) of litter decomposition. Some studies have tested this hypothesis in mixed plantations with a mixture of different litters placed equidistantly to the different tree species. In mixed plantations, however, each tree species can have different effect on the decomposition of each litter. We tested if spruce and poplar litter show HFA in mono-specific and in mixed species plantations under each tree species by reciprocally transplanting litter "at home" and "away" in the two plantation types. The decomposition rate and decomposer communities were monitored during two years to compare the influence of each tree species on each plantation type. Furthermore, to measure the degradation ability of soil communities, cellulose was also placed beneath each tree species in each plantation type. Only coniferous litter exhibited a faster decomposition rate at home. This HFA can be explained by higher abundance of fungi and detritivorous mites, with a reciprocal positive feedback. Furthermore, cellulose was less decomposed in this environment, suggesting that soil communities of mono-specific spruce plantations were more able to decompose relatively recalcitrant litter, but they were less efficient at decomposing more "simple" substrates. In mixed plantations, there was no HFA, but this "mixed environment" had non-additive effects on decomposition rates (compared to what was predicted from the two mono-specific plantations), but only under poplar trees. These 'tree environment-specific' results confirm that within mixed stands, a tree species affects the forest floor, but only in a localized way through spatial distribution of its litter. The influence of litter dispersal on the effect of mixing tree species on decomposition rate must thus be taken into account in future studies.

2.1 Introduction

Tree species partially determine litter decomposition processes by controlling litter chemical composition. The main litter chemical components can be divided into three categories, ranging from those that are most easily to those that are most difficult to decompose: labile compounds (sugars and amino acids), labile structural compounds (cellulose and hemicellulose), and secondary metabolites (phenolics, terpenoids) (Chapin et al., 2002). Quality and decomposability of litter depend upon the proportions of these compounds (Cortez et al., 1996) and can vary greatly among plant species. Tree species can also influence decomposition rates indirectly through their effects on environmental conditions. For example, trees can induce changes in soil pH or microclimatic conditions of the forest floor (Aussenac, 2000). Therefore, the composition of soil decomposer communities should differ among areas that are dominated by different plant species due to adaptations, to both local microenvironments and the chemical composition of litters that are produced by plant species that are present in their own ecosystems (Ayres et al., 2009b; Wang et al., 2013; Wardle and van der Putten, 2002). This mechanism implies that litter tends to decompose more rapidly in the habitat from which it was derived (i.e., home) than in other habitats (i.e., away), which has been termed the “home field advantage” (HFA) of litter decomposition (Ayres et al., 2006; Ayres et al., 2009a; Ayres et al., 2009b; Gholz et al., 2000; Strickland et al., 2009; Vivanco and Austin, 2008).

At the ecosystem level, climatic conditions are important factors controlling decomposition processes (Chapin et al., 2002; Swift et al., 1979). Temperature and soil moisture availability indirectly govern decomposition by selecting communities of plants with traits that confer adaptations to specific micro-environmental ranges (Moles et al., 2014), but they can also directly influence decay processes by driving the activity of soil organisms (Coûteaux et al., 2002). In boreal ecosystems, winter is typically long and cold with a short summer season, which leads to slow nutrient cycling (McMillan et al., 2007) and to the dominance of evergreen species that are adapted to low nutrient availability (Aerts, 1995). The boreal forest is dominated by coniferous species with litters that tend to decompose slowly in comparison to broadleaf species such as poplars (*Populus* spp.), due to the low nutrient and high secondary metabolite content, and the toughness of their needles (Cornwell et al., 2008; Perez-Harguindeguy et al., 2000). Furthermore, low-quality litter, which often contains highly recalcitrant or toxic compounds, might generate a larger HFA since fewer soil communities would include biota that are capable of degrading these compounds, in contrast to higher quality litter (Ayres et al 2009a and references therein). For example, Strickland et al. (2009) found greater carbon mineralization rates of microbial communities in contact with their "home litter" and this effect was greater for the lower quality litter.

Although litter decomposition processes from single plant species are relatively well known, decomposition of litter from mixed species requires further investigation. It is generally agreed that litter diversity enhances decomposition due to complementary effects that are caused by diversification of microhabitats and resources for decomposer organisms (Ettema and Wardle, 2002; Vos et al., 2013). However, the effects of litter diversity on decomposition rates vary greatly, are often context-dependent, and can be positive (50% of the studies), negative (20% of the studies) or null (Cardinale et al., 2006; Gartner and Cardon, 2004; Hättenschwiler et al., 2005). These contrasting results could be attributed to the influence of litter diversity on soil organism communities, but only few studies have addressed whether mixing plant species influences soil communities and then decomposition (Vivanco and Austin, 2008). Moreover, most studies addressing the effect of mixed species forests on soil communities and litter decomposition have used litter bags that are placed equidistantly to the different tree species, overlooking the spatial influence of each species that is present in the mixture (Berger and Berger, 2014; Chapman and Koch, 2007; Vivanco and Austin, 2008; Wang et al., 2009). Spatial scale is particularly important for understanding the nature of the relationships between plant and soil communities (De Deyn and van der Putten, 2005; Ettema and Wardle, 2002). In a mixed forest, litter quality differences among tree species can lead to the spatial patterning of soil organisms and processes (Ettema and Wardle, 2002; Saetre and Baath, 2000). There is a need for improved understanding of the home field advantage in mixed species ecosystems by accounting for the influence of each species in the mixture. It is difficult to study HFA in natural forests due to the variability in microclimate and soil parameters between two sites with different plant cover (Prescott and Grayston, 2013). Therefore, this study deals with reciprocal litter transplantation between pure and mixed plantations (poplar and spruce) that were established in the same site, thereby minimizing differences in climate and soil parameters. The aim of this study was to compare the effects that poplar and spruce trees exert on soil communities (microorganisms and mesofauna) and litter decomposition processes in monospecific compared to mixed plantations. In home field advantage studies, it is difficult to know whether soil communities are really adapted to decompose a "home" litter or they just may simply be more capable of decomposing all litters (Keiser et al., 2014). To measure this 'ability' of soil communities and the influence of trees on decomposition processes, cellulose was also placed under and between trees in each plantation type. For the first time, we calculated a non-additive effect (NAE) of mixing tree species on decomposition (i.e., NAE of mixed habitats), rather than NAE of mixing litters.

The following hypotheses were addressed: i) There is a HFA for litter decomposition of the tree species in spruce and poplar mono-specific plantations due to the specialization of soil communities that decompose their litter; ii) HFA is more pronounced for the low-quality spruce litter compared to poplar litter (Ayres et al., 2009b); iii) HFA is maintained in mixed plantations for litter placed under its corresponding tree species; iiii) Spruce and poplar litter, and a standard substrate (cellulose) decompose more rapidly in the mixed plantations since their decomposer communities are potentially more diverse.

2.2 Materials and Methods

2.2.1 Site description

The study was located in the boreal region of Abitibi-Temiscamingue, Quebec, Canada. Three sites were selected for the study : Amos (48°36’N, 78°04’W), Rivière Héva (48°11’N, 78°16’W), and Nédelec (47°45’N, 79°22’W). The Amos site was abandoned farmland with a heavy clay soil that was dominated by grasses and sparse patches of alder (*Alnus incana* [L.] Moench ssp. *rugosa* [Du Roi] R.T. Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was an abandoned farmland site with heavy clay soil, which was also dominated by shrubs, including patches of alder, willow, and trembling aspen. Nédelec had been previously dominated by trembling aspen forest, which was commercially harvested in 2000. This last site was characterized by soils with a sandy loam texture. Based on the 30-year running climate average (1970-2000), Amos and Rivière Héva receive an annual mean 918 mm of precipitation (Amos station) and have a mean temperature of 1.2 °C, while Nédelec has mean precipitation of 916 mm year^{-1} and a mean temperature of 1.9 °C (Remigny station, Environment Canada 2014). Site preparation was conducted in 2002, where tree stumps were removed and soils were ploughed to a depth of about 30 cm. The plantations were established in 2003, using one hybrid poplar clone (*Populus maximowiczii* A.Henry x P. *balsamifera* L., clone MB915319), and an improved white spruce family (*Picea glauca* [Moench] Voss). These two species were planted in both mono-specific and mixed species plots under two spacings, i.e., 1 × 1 m and 3 × 3 m. For the mixed plantation, each row consisted of spruce alternating with poplar. Each experimental unit contained 36 trees (6 × 6 trees). The experiment was designed as a randomized block design with three blocks (replicates = sites), three plantation types (pure poplar, pure spruce and mixed), and two spacings (1 × 1 m and 3 × 3 m). Through this paper, we have divided mixed plantations into mixed-spruce (under spruce trees) and mixed-poplar (under poplar trees).

2.2.2 Litter decomposition experiment

In late September 2010, spruce needles and hybrid poplar leaves were collected from plantations that were close to the Amos study site. Abscission of needles or leaves in which senescence was complete was aided by shaking the trees, and the fallen needles/leaves were collected on a plastic sheet that was placed on the ground beneath the trees to prevent soil contamination. Collected leaf material was homogenized and stored at room temperature prior to the experiment. A subsample of each species was oven-dried at 60 °C to establish the relationships between air-dried and oven-dried mass. Seven grams (air-dried) of either poplar or spruce litter were placed in 1-mm mesh litter bags (15 x 15 cm for poplar litter; 10 × 15 cm for spruce litter) to allow colonization by soil mesofauna and microbes, while excluding macrofauna (Swift et al., 1979). We used pairs of litter bags with one bag being used for chemical and microbial measurements and the other for mesofauna extraction.

To prevent losses of spruce needles through the net mesh during handling, a sheet of paper was inserted into each litter bag with spruce needles. These sheets of paper were removed and the litter bags were finally closed just before they were placed on the soil. The dimensions of the litter bags containing spruce needles was smaller than those for poplar leaves, to create the same litter incubation conditions among litter types and to prevent needle losses.

To optimize the influence of trees on the decomposition process, this experiment was performed in the 1 x 1 m spacing plantations. In November 2010, 12 pairs of litter bags that were filled with poplar litter and 12 pairs of litter bags that were filled with spruce litter were randomly deposited around 12 trees in each mono-specific plantation (pure poplar and pure spruce). In mixed plantations, 24 pairs of litter bags of each litter were placed, half under poplar trees and half under spruce trees. This was repeated at the 3 sites (replicates), resulting in a total of 576 litter bags (12 pairs x 2 litter bags x 2 litter species x 4 plantations types x 3 sites = 576). The litter bags were placed on the experimental sites on 9–10 November 2010. Freshly fallen litter was removed from the surface of the forest floor prior to placing the litter bags on the ground surface, and then replaced over the litter bags. Litter bags were fixed with one galvanized nail to prevent movement by animals or by the wind. After 7, 11, 18 and 24 months, 3 pairs (pseudo-replicates) of litter bags were retrieved from around three randomly chosen trees at each site. Sampling dates corresponded to snowmelt and anticipated snowpack development, generally mid-May and early or mid-October, respectively.

2.2.3 Litter bag processing

The first litter bag of each pair was used for mesofauna extraction, after which it was oven-dried at 60°C for 3 days. An aliquot of fresh material from the second litter bag was used for microbial analysis and the remainder of the sample were freeze-dried (Lyovac GT2®) for chemical analysis. To prevent soil contamination of litter, we wiped needles/leaves thoroughly before analysis. At t_0, 26 samples of each litter type (7 g air-dried) were used to determine initial litter quality.

Mass loss

Litter decomposition rates were determined from the full set of litter bags. Mass loss was expressed as the percentage of total initial dry mass.

Mesofauna extraction

Mesofauna were extracted from fresh litter using the dry funnel method (Berlese, 1905). Organisms were stored in 90 % alcohol, counted using a binocular scope, and identified to family for Collembola (Gisin, 1960) and to order for Acari (Gamasida, Acaridida, Actinedida, Oribatida; (Coineau, 1974). Other invertebrates were separated according to taxa (e.g., Arachnida, Diplopoda, Chilopoda, Araneae, Hymenoptera, etc.).

Fungal biomass

Fungal biomass was determined by quantifying ergosterol, a fungal membrane constituent and good indicator of living fungal biomass (Gessner and Chauvet, 1993; Ruzicka et al., 2000). Samples were frozen and lyophilized to enable more efficient extraction of ergosterol (Gessner and Schmitt, 1996). Ergosterol was extracted from 50 mg of needles/leaves with 5 mL of an alcohol base (KOH/methanol 8 g L^{-1}) for 30 min, and purified by solid-phase extraction on a Waters® (Milford, MA, USA) Oasis HLB cartridge (Gessner and Schmitt, 1996). The extract that was produced was purified and quantified by high-performance liquid chromatography (HPLC) on a Hewlett Packard series 1050 system running with HPLC-grade methanol at a flow rate of 1.5 mL min^{-1}. Detection was performed at 282 nm, and the ergosterol peak was identified based on the retention time of an ergosterol standard.

Catabolic profiles of microorganisms

Microbial (fungal and bacterial) catabolic profiles were assessed using Biolog® EcoPlates (Biolog Inc., Hayward, CA, USA) for all sampling dates using a procedure adapted from (Garland and Mills, 1991). To have enough fresh material, the three pseudo-replicates in each plantation were pooled, with the three sites remaining as replicates. Briefly, 2 g (dry mass equiv.) of ground litter were stirred in 100 mL of a sterile 0.1% tetra-sodium pyrophosphate solution for 1 h to suspend microbial communities. Each 96-well plate contained 3 replicate blocks of a water blank and 31 of the most useful carbon sources for soil community analysis, nine of which are considered as constituents of plant root exudates (Preston-Mafham et al., 2002). A 125 µL aliquot of extract solution, diluted 1:110, was added to all 96 wells in each EcoPlate. The plates were incubated at 30 °C for 7 days, and absorbance was measured at 595 nm on a microplate spectrophotometer (Multiskan GO, Thermo Fisher Scientific). Different microbial communities can exhibit different patterns of substrate use, as revealed by the ensuing colorimetric reactions.

2.2.4 Soil temperature and moisture content

At each litter bag sampling date, soil temperature and volumetric water content (VWC) under 6 randomly chosen trees per plantation type and at each site were measured respectively with an Acorn series meter with K probe (Oakton Instruments, Vernon Hills, IL, USA), and a Field Scout TDR 100 with 12 cm-long probe (Spectrum Technologies Inc., Plainfield, IL, USA).

2.2.5 Standard substrate decomposition

Cellulose decay rates were measured on each plot using Whatman no. 5 filter papers as standard substrates. Two filters (corresponding to 2.44 g dry mass) were enclosed in the same size of litter bags that were used for poplar litter (15 x 15 cm, 1mm mesh). To study the area of tree influence on decomposition processes, these litter bags were placed in 3 x 3m plantations. In October 2011, 4 litter bags were randomly placed beneath 4 trees, and 4 more litter bags were placed between the trees in the mono-specific plantations (poplar and spruce plantations). For mixed plantations, 8 litter bags were placed, half under poplar trees and half under spruce trees, and 4 more litter bags were placed equidistantly from spruce and poplar. Since there were 3 replicate sites, this resulted in a total of 84 litter bags (3 sites x 28 litter bags = 84). Freshly fallen litter was removed from the forest floor surface prior to placing the litter bags on the ground. Litter bags were fixed with one galvanized nail to prevent movement by animals or by the wind. All litter bags were removed after one year. Remaining dry mass was determined after oven-drying the litter at 60 °C for 3 days. Mass loss was expressed as the percentage of total initial dry mass.

2.2.6 Data analyses

To compare needle decomposition rates between plantation types and litter types, needle/leaf mass loss data were fitted to a simple negative exponential model $m_t = m_0.e^{-kt}$, where m_t is needle mass remaining (g) at time t (years), m_0 is initial needle mass (g), and k ($year^{-1}$) is the exponential decomposition rate coefficient (Olson, 1963). A multiple slope comparison was made to test for differences between decomposition rates of the different litter and plantation types after log-transformation of mass remaining (Statgraphics Plus 5.1). All other statistical analyses were performed using R version 3.1.0 (R Development Core Team 2008). To determine bacterial catabolic diversity and mesofauna community diversity, Shannon indices were calculated. Mean values (soil temperature and humidity, ergosterol, mesofauna abundance, mesofauna diversity and catabolic diversity) were compared among decomposition times and plantation types for each litter type using hierarchical linear mixed-effects models using the *lme* function in the *nlme* package (Pinheiro et al., 2014). Site replicates were treated as random effects, and plantation type was nested within site replicates to reflect the structure of our data set. If the effect of treatment was significant, the different treatments were compared with pre-planned linear contrasts (differences are noted in the manuscript as a < b < c). To compare catabolic profiles of microbial communities among samples, non-metric multidimensional scaling (NMDS) was performed to find the best low-dimensional representation of the distance matrix (function *metaMDS* of R *Vegan* package, (Oksanen et al., 2012). For catabolic profiles of microorganisms, the data were first normalized. A data matrix of pairwise comparisons among samples was then calculated using Euclidean distance. To evaluate how well (or poorly) the particular configuration produced the observed distance matrix, the stress value was given. The best solution to the dimensional reduction of the data set minimized the stress value associated with the NMDS solution, the smaller the stress value, the better the fit of the reproduced distance matrix to the observed distance matrix. Permutation-based

Multivariate Analysis of Variance (PERMANOVA) was used to test differences in patterns of the catabolic profiles and those of the mesofaunal community composition among plantations and between litter types, based on 999 permutations of the data (function *adonis* of R package *vegan*). For mesofaunal abundances, the data were subjected to Wisconsin double standardization, with pairwise dissimilarities calculated among samples using Bray-Curtis indices (Bray and Curtis, 1957). When plantation types were significantly different, SIMPER (similarity percentage) was used to identify the species/compounds that were responsible for dissimilarities between plantations. For all statistical analyses, the significance threshold was set at $\alpha = 0.05$.

To determine whether interactions occurred in the mixed compared to pure plantations, predicted mass loss in mixed plantation was calculated based on observed mass losses of the component species in monoculture, which assumes that there are no diversity effects, i.e., the decomposition in mixed species plantation are the additive sums of mass loss in the two mono-specific plantations. According to (Wardle et al., 1997), the relative mixture effect can be calculated as the ratio: [(observed — predicted) / predicted]*100. If this ratio differs from zero, it would indicate non-additive effects of mixing tree species on decomposition rate. To test if the observed vs predicted ratios of litter decomposition in mixed plantations differed significantly from zero, we used one-sample Student's *t*-tests, and associated 95 % confidence intervals.

2.3 Results

2.3.1 Soil temperature and humidity

Across all sampling dates, soil temperature was greater in poplar mono-specific plantations and lower in spruce mono-specific plantations with differences of 1.5, 0.6, 1.9, 0.5 °C at each respective sampling date (Table 2.1, linear contrasts, $P < 0.05$). In mixed plantations, temperature had intermediate values, regardless of tree species.

Soil volumetric water content was not significantly different between plantation types (*lme*, $F_{3,6} = 1.38$, $P = 0.34$).

Table 2.1 Soil moisture expressed as volumetric water content (VWC, %) and soil temperature (Temp, °C). Mean ± SE from May 2011 to October 2012 for each plantation type. Significant differences (pairwise contrasts) between plantation types within each row are presented with different letter.

Sampling dates	Variables	Plantation types			
		Poplar	Spruce	mixP	mixS
May 2011	Temp	11.6 ± 0.1 (c)	10.1 ± 0.1 (a)	10.4 ± 0.1 (b)	10.8 ± 0.2 (b)
	VWC	15.1 ± 0.6 (ns)	13.0 ± 0.4 (ns)	15.3 ± 0.9 (ns)	15.5 ± 0.9 (ns)
October 2011	Temp	11.9 ± 0.1 (b)	11.3 ± 0.1 (a)	11.5 ± 0.1 (a)	11.8 ± 0.2 (b)
	VWC	9.7 ± 0.5 (ns)	7.7 ± 0.3 (ns)	9.2 ± 0.6 (ns)	8.0 ± 0.8 (ns)
May 2012	Temp	8.9 ± 0.2 (c)	7.0 ± 0.2 (a)	8.2 ± 0.1 (b)	8.0 ± 0.1 (b)
	VWC	18.8 ± 1.1 (ns)	14.1 ± 0.7 (ns)	17.6 ± 0.5 (ns)	17.4 ± 1.1 (ns)
October 2012	Temp	8.1 ± 0.1 (b)	7.7 ± 0.1 (a)	8.0 ± 0.1 (ab)	7.8 ± 0.1 (ab)
	VWC	18.7 ± 1.0 (ns)	16.2 ± 1.3 (ns)	18.8 ± 0.7 (ns)	15.7 ± 0.8 (ns)

Note : mixP= mixed-poplar plantation, mixS= mixed-spruce plantation

2.3.2 Decomposition rate and home field advantage

On average, 53 % of poplar and 40 % spruce litter was lost after 2 years. Decomposition rates of spruce litter were significantly greater in mono-specific spruce plantations (0.29 year^{-1}) compared to rates that were measured in mono-specific poplar (0.21 year^{-1}), mixed-spruce (0.22 year^{-1}), and mixed-poplar plantations

(0.23 year^{-1}; ANOVA for slopes, $F_3 = 12$. $P < 0.001$). Poplar litter decomposition rates were similar among the four plantation types (Fig. 1), with 0.35 year^{-1} in spruce, 0.33 year^{-1} in poplar, 0.34 year^{-1} in mixed-spruce and 0.36 year^{-1} in mixed-poplar plantations, respectively.

2.3.3 Ergosterol

Regardless of plantation type, ergosterol concentrations were greater in poplar litter than in spruce litter at 11 (330 vs 269 $\mu g\ g^{-1}$, respectively; *lme*, $F_{1,57} = 13.2$ $P < 0.001$) and 18 months (417 *vs* 348 $\mu g\ g^{-1}$, respectively; *lme*, $F_{1,56} = 11.2$ $P < 0.01$) of decomposition (Fig. 2.2). Before 18 months of decomposition had elapsed for spruce litter and 11 months for poplar litter, ergosterol concentrations were the same under each plantation type. For spruce litter, fungal biomass was greater at home than in poplar plantations after 18 and 24 months of decomposition (Fig. 2.2, linear contrasts, $P < 0.05$). For poplar litter, after 24 months of decomposition, fungal biomass was greater away than at home (Fig. 2.2, linear contrasts, $P < 0.05$). Fungal biomass in mixed-spruce and mixed-poplar plantations attained similar values during the experiment, except at 18 months of decomposition for spruce litter and at 11 months of decomposition for poplar litter, where values were higher under poplar than under spruce in mixed plantations. After 24 months of decomposition, ergosterol concentrations in mixed plantation were intermediate between poplar and spruce mono-specific plantation values (Fig. 2.2, linear contrasts, $P < 0.05$). Ergosterol dynamics in the different plantation types suggested that fungal biomass was still increasing in mono-specific spruce plantations for the two litter types after 24 months of decomposition, whereas fungal biomass reached a plateau from 11 months of decomposition onward in mono-specific poplar plantations. In mixed plantations, a decrease of fungal biomass was observed between 18 and 24 months of decomposition (except for spruce litter under spruce trees) (Fig. 2.2, linear contrasts, $P < 0.05$).

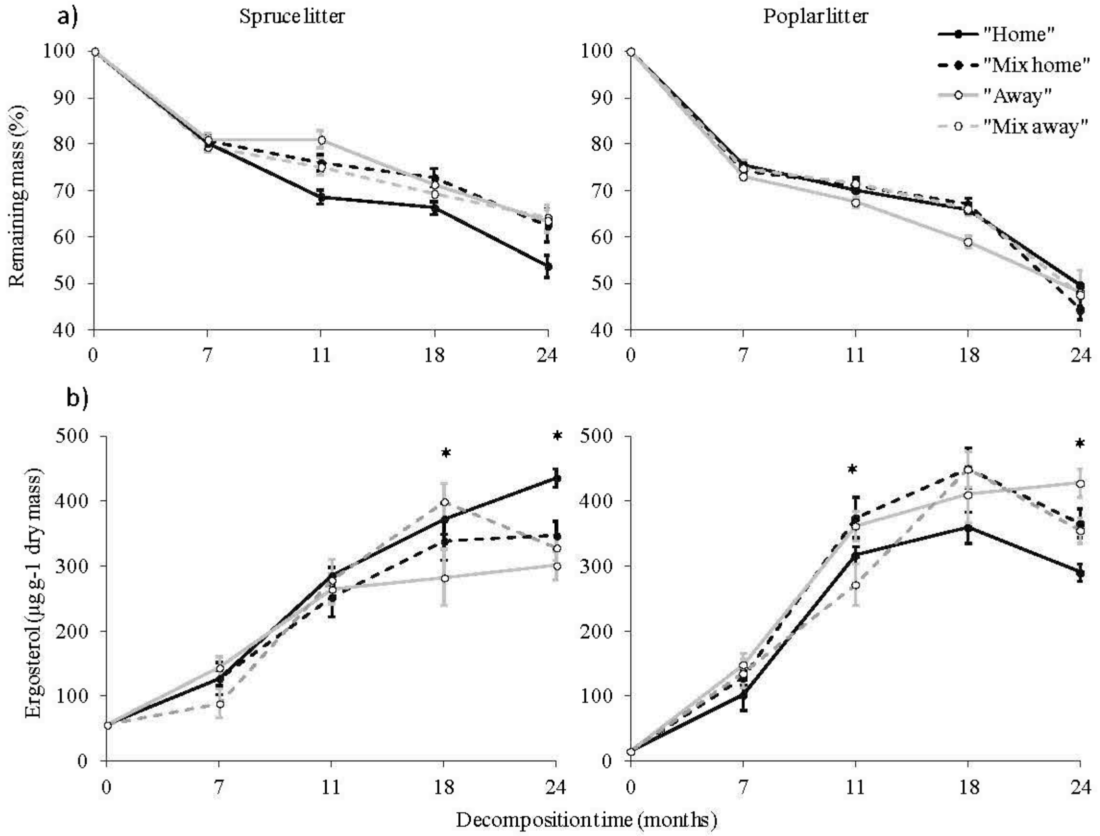

Figure 2.2 a) Litter mass remaining expressed as a relative fraction of initial mass, and b) ergosterol content for spruce litter (left side) and poplar litter (right side) incubated in litter bags at "home" (black line) or "away" (gray line) in mono-specific plantations (solid line) or mixed-species plantations (dashed line) during decomposition. Means and SD. Significant differences between plantation type according to linear contrasts are indicated by *.

2.3.4 Biologs

Ordination (NMDS) of the different catabolic profiles that was based on Euclidean distance is presented in Fig. 2.3. At 7, 11 and 18 months, NMDS globally showed that catabolic profiles of poplar litter communities were more similar than communities associated with spruce litter. NMDS revealed temporal differences among plantation types, as confirmed by PERMANOVA, which was performed on the spruce and poplar litter datasets separately. Catabolic profiles of microbial communities that were present in spruce litter significantly varied among plantation types at 7 and 11 months of decomposition (Permanova on spruce litter data among plantation type at 7 and 11 months, $F_3 = 2.2$, $P = 0.037$, and $F_3 = 1.33$, $P = 0.015$, respectively), but catabolic profiles for poplar litter remained different among plantation types throughout the experiment (Permanova on poplar litter data among plantation type, $F_3 = 1.68$, $P = 0.014$).

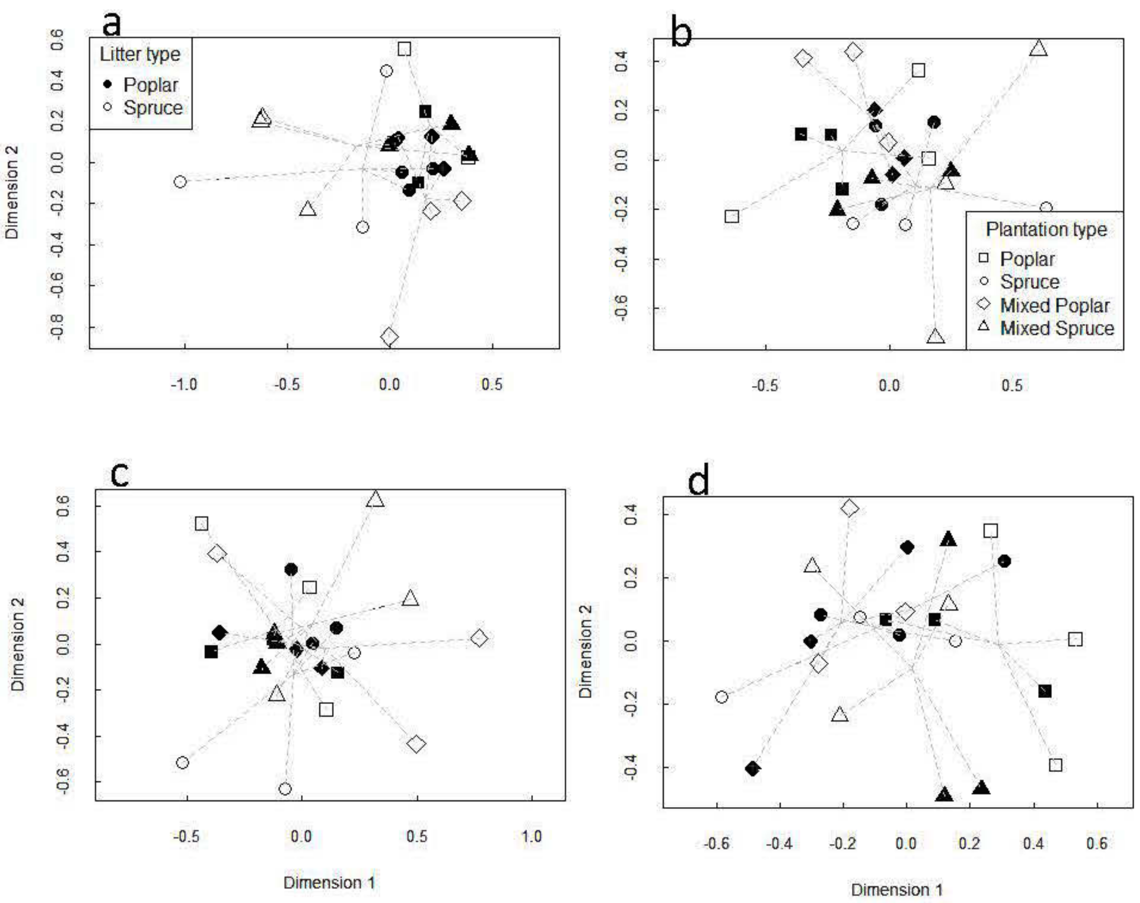

Figure 2.3 Non-metric multidimensional scaling (NMDS) ordination of catabolic profiles of microbial communities of both litter type and plantation type based on

Euclidean distance at 7 (a), 11 (b), 18 (c) and 24 (d) months of decomposition (a, b, c and d, respectively). Stress = 0.15, 0.21, 0.21 and 0.19, respectively. Samples are grouped (dashed lines) by plantation type and the centroid of each group is indicated.

Catabolic diversity of microbial communities, as measured by the Shannon index, was similar in all plantation types (Table 2.2, *lme*, $F = 2.01$, $P = 0.21$). After 7, 11 and 18 months of decomposition, catabolic diversity was lower in spruce litter than in poplar litter (linear contrast, $P < 0.001$). Whereas microbial catabolic diversity was constant among dates for poplar litter (mean of 27 compounds used), diversity shifted with time during spruce litter decay (Table 2.2, *lme*, $F = 12$, $P = 0.0015$). Lower catabolic diversity in spruce litter was found after 7 and 18 months of decomposition (mean of 17 compounds used), and higher values, similar to poplar litter values, were reached after 24 months of decomposition (28 compounds used).

Table 2.2 Mean (± SE) catabolic diversity (Shannon index) of microorganisms colonizing different litter and plantation types along decomposition time.

Litter type	Plantation type	Decomposition time (months)			
		7	11	18	24
Spruce	Spruce	1.47 ± 0.25	2.36 ± 0.31	1.64 ± 0.55	2.88 ± 0.06
	Mixed-spruce	0.90 ± 0.17	1.68 ± 0.60	1.58 ± 0.41	2.73 0.08
	Mixed-poplar	1.59 ± 0.68	2.50 ± 0.17	1.76 ± 0.28	2.73 ± 0.12
	Poplar	2.45 ± 0.26	2.45 ± 0.33	1.72 ± 0.23	2.69 ± 0.05
Poplar	Spruce	2.8 ± 0.02	2.95 ± 0.05	2.58 ± 0.27	2.89 ± 0.08
	Mixed-spruce	2.61 ± 0.08	2.77 ± 0.01	2.58 ± 0.10	2.72 ± 0.01
	Mixed-poplar	2.64 ± 0.04	2.79 ± 0.07	2.57 ± 0.05	2.80 ± 0.05
	Poplar	2.75 ± 0.07	2.84 ± 0.06	2.56 ± 0.09	2.83 ± 0.02

2.3.5 Mesofauna

During two years of litter decomposition, the composition of mesofauna communities differed among plantation types for spruce and poplar litters (Permanova on spruce and poplar litter data among plantation type, $F_3 = 0.03$, $P = 0.02$; and $F_3 = 1.76$, $P =$

0.001, respectively). These differences were mainly due to a greater abundance of oribatids in spruce plantations, Coleoptera larvae in poplar plantations, and Symphypleona and Araneae in mixed plantations. As mesofaunal diversity was not different among plantation types, the results are not shown. Abundance of main groups (detritivorous mites, springtails and predators) of mesofauna are summarized in Fig. 2.4. Statistical analysis (*Lme)* showed no significant interactions between the three factors, i.e., time, litter and plantation for mites and predators. Of the two litter types, mites were significantly more abundant in spruce than in poplar and mixed-spruce plantations throughout the experiment, with mixed-poplar plantations having intermediate abundances relative to the 3 other plantation types (lme, $F = 20.1$, $P = 0.002$). Springtails abundance were significantly different between plantation type only at 24 months of decomposition, with greater abundance under spruce in each plantation type compared to poplar mono-specific plantation (lme, $F_{3,6} = 6.02$, $P = 0.03$). Predator abundances were similar among the plantation types (lme, $F_{3,6} = 0.68$, $P = 0.6$, respectively). For these three groups, abundances varied with decomposition time, reaching maxima of 34, 17, and 3 individuals per g of litter after 24 months of decomposition for detritivorous mites, springtails and predators, respectively (linear contrast, $P < 0.05$).

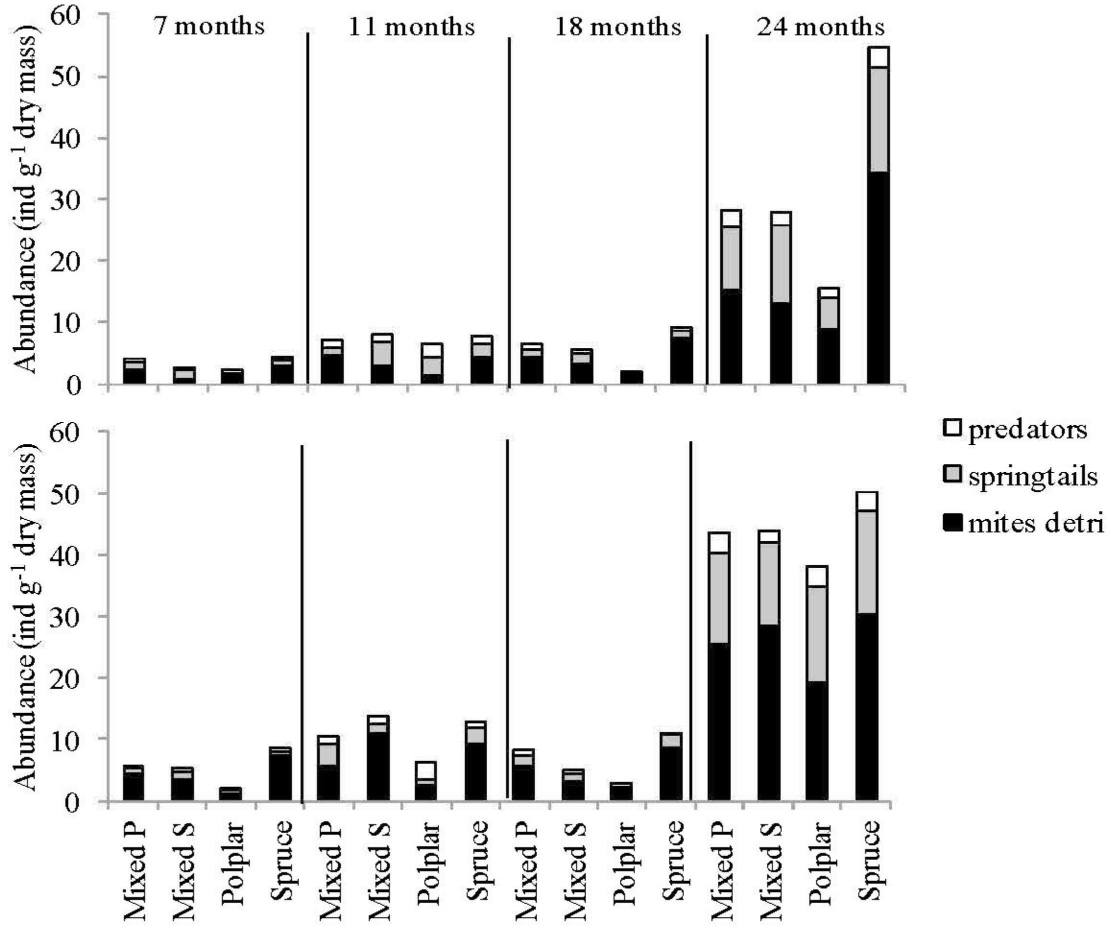

Figure 2.4 Dynamics of abundance of different functional groups of mesofauna in spruce litter (a) and poplar litter (b) in the different plantations.

2.3.6 Decomposition rate of a standard substrate and litter bag positioning

When the litter bags were placed beneath the trees, the lowest cellulose decomposition rate was measured under spruce in mono-specific plantations (mean of 20 % of mass loss), while the highest decay rate was found under poplar trees, regardless of plantation type (mean 55 % mass loss, lme, $P < 0.01$, Table 2.3). When litter bags were placed between the trees, in contrast, plantation type influenced cellulose decomposition rates; decomposition rates decreased from pure poplar to mixed plantation (linear mixed model, $P < 0.05$), reaching minimum values similar to those found under spruce in mixed plantations. In pure plantations, cellulose was more rapidly decomposed between than beneath trees (lme, $F_{1,42} = 5.17$, $P = 0.028$).

Table 2.3 Mass loss of cellulose (%) beneath or between the trees (poplar or spruce) in pure or mixed plantations. Mean ± SE. Across litter bag positioning, different letters within each plantation type represent a significant difference between means according to linear contrast.

Plantation	Species	Under	Between
Pure	Poplar	55.2 ± 9.1 b	62.6 ± 8.3 b
	Spruce	19.7 ± 3.5 a	44.7 ± 8.3 ab
Mixed	Poplar	54.1 ± 7.5 b	35.2 ± 7.6 a
	Spruce	35.9 ± 10.4 ab	

2.3.7 Non-additive effect of mixed plantations

Non-additive effects (NAE) of habitat on litter decomposition represent the difference between litter decomposition rates that were expected (mean of the decomposition rates measured in the two mono-specific plantations) and the litter decomposition rate that was measured in mixed plantations, under each tree species. We observed significant synergistic NAE for poplar litter and cellulose decomposition under poplar trees in mixed plantations (12 %, $t = 2.15$, $df = 17$, $P = 0.046$, and 53 %, and $t = 2.21$, $df = 11$, $P = 0.049$, respectively). However, antagonistic NAE was significant for spruce litter decomposition under poplar in mixed plantations (-16%, $t = -2.78$, $df = 16$, $P = 0.013$). Mean NAE for cellulose decomposition between trees represented a decrease of 36 % in mixed plantations compared to predicted values ($t = -2.66$, $df = 11$, $P = 0.022$) (Figure 2.5).

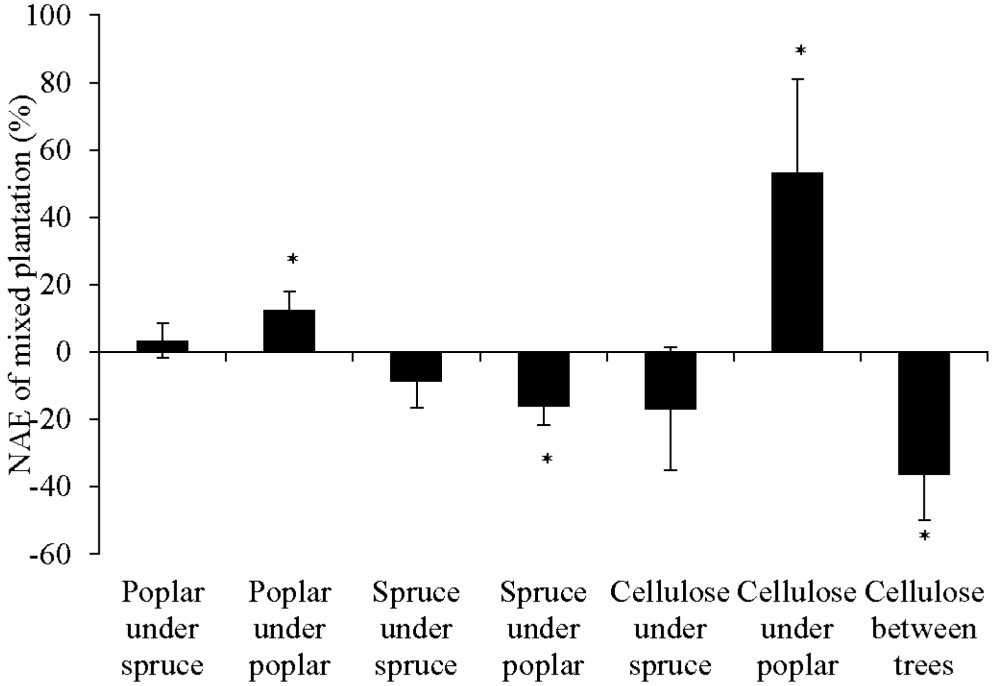

Figure 2.5 Non-additive effects of mixed plantations on decomposition of cellulose, poplar and spruce litter under spruce or poplar trees (Mean ± SE). NAE (Non-additive effect) that are significantly different from zero, according to one-sample Student's *t*-tests, are indicated by * ($P < 0.05$).

2.4 Discussion

There is an increasing awareness that the feedbacks between above- and below-ground biota are major ecological drivers in terrestrial ecosystems (Wardle and van der Putten, 2002). Our study is among the first to observe the home field advantage (HFA) of two tree species in mono-specific and pluri-specific "environments," while separating the influence of tree species in the mixed plantations. By performing litter transplants, we were able to tease apart the mechanisms that contribute to HFA among three distinct levels of the soil food web (microorganisms, detritivores and predators), and the influence of each tree species on litter decomposition processes in the mixture.

2.4.1 Home field advantage depending on litter type: biological drivers

Our first two hypotheses were partly supported, as home field advantage was only found for spruce litter. Coniferous species are recognized as having lower quality litter compared to broadleaf species (Cornwell et al., 2008; Perez-Harguindeguy et al., 2000). Spruce litter was more rapidly decomposed under spruce mono-specific plantations, with 10 % increase in mass loss compared to the poplar mono-specific environment. Poplar litter did not exhibit HFA, as it decomposed in the same way under the two tree species. As only spruce litter decomposed more rapidly in the spruce environment, this study confirms that HFA was more pronounced for low-quality litter (Ayres et al., 2009b; Strickland et al., 2009). Cellulose decomposition was measured under the different plantation types to observe the ‘ability’ (Keiser et al., 2014) of organisms to decompose litter in the different plantations in this experiment. Interestingly, when cellulose (least recalcitrant litter) was placed in spruce plantations, its decomposition was 35 % lower than in poplar plantations. The low rate of cellulose decomposition in spruce plantations confirmed that HFA found for spruce litter in its environment was really due to an adaptation of litter organisms, rather than an overall ability of spruce soil communities to decompose litter (Keiser et al., 2014). This result suggests that soil communities of spruce mono-specific plantations are able to decompose relatively recalcitrant litter, but they are less efficient in decomposing more “simple” substrates. However, these communities decomposed poplar litter, which have an intermediate quality, at the same rate as the ‘poplar-environment adapted’ communities. In this situation, litter quality is thus not sufficient to explain the ability of organisms to decompose it. Rather, their ability could be linked to the frequency of contact between decomposer organisms and litter, depending upon litter type. Poplar has high litter dispersal capacity; given that it is tall and its leaves have high specific leaf area (SLA), in contrast to spruce height and

SLA of needles. During the experiment, poplar litter was collected in litter traps that were placed beneath spruces in mono-specific plantations, whereas the opposite was not observed (Chomel et al., 2014a). Under our experimental conditions, decomposer communities that were present under spruce in mono-specific plantations were consequently more likely to have been in contact with poplar litter than the reverse. Spruce decomposer communities could have "learned" to decompose poplar litter. We could pose the hypothesis that the intensity of home field advantage would be partially controlled by litter dispersal capacity: the greater the litter dispersal, the less intense home field advantage would be. The dispersability of litter would thus be an important trait to consider in decomposition studies of mixed species.

This study also showed that fungal biomass was more important in spruce plantations compared to poplar plantations after 18 and 24 months in spruce litter, and after 24 months of decomposition for poplar litter. Further, fungal biomass was still increasing after 24 months of decomposition in spruce plantations, while it reached a plateau or decreased in all other plantations. Fungi are recognized to assimilate organic matter more efficiently than bacteria because of their higher biomass C:N ratio and, consequently, their lower N demand per C unit (Killham, 1994). Furthermore, fungi are better adapted to decomposing recalcitrant materials through their enzymatic activities and given their hyphal growth form (Meidute et al., 2008; Paterson et al., 2008). Therefore, the greater fungal biomass that was found in spruce plantations could partially explain HFA for spruce litter in its environment. Further, these results confirm that low litter quality promotes fungal-based energy channels in contrast to high litter quality, which promotes bacterial ones (Wardle et al., 2004).

Although there were shifts in microbial community composition during decomposition, the different plantation types were also drivers of microbial catabolic profiles, but only at the initial stage of decomposition (after 7 and 11 months) for spruce litter and throughout the whole experiment for poplar litter. Catabolic diversity did not differ among plantation types, indicating that these differences were due to different combinations of substrates that were used by microorganisms. In all plantation types, microorganisms colonizing spruce litter had lower catabolic diversity (mean of 19 compounds used) compared to those colonizing poplar litter (mean of 28 compounds used), until 24 months of decomposition had elapsed. This result means that microbial communities colonizing poplar litter were able to decompose a greater number of compounds, and would be more opportunistic than microbes that were colonizing spruce litter, and which were more specialized until 24 months of decomposition.

Concerning the mesofauna, mites (especially oribatids) and springtails (only at 24 months of decomposition) were more abundant under mono-specific spruce cover, regardless of litter type. Fungivores and microbivores (such as mites and springtails) have important indirect regulatory controls on microorganisms through their grazing activities and often stimulate hyphal growth if the grazing is at low intensity (Crowther et al., 2011). Among the litter mesofauna taxa, oribatid mites and springtails were typically among the most important fungal feeders (Scheu, 2002; Schneider et al., 2005). Mites, springtails and fungal abundances in mono-specific spruce plantations could be reciprocally linked by a positive feedback. Similar results were found in natural forests, with a higher abundance of microbes and mesofauna found under spruce than under aspen in mixed forests (Laganière et al., 2009). According to (Wardle, 2002), broadleaved species should favor soil communities that are based on bacteria and earthworms, while conifers should lead to communities that are dominated by fungi and fungivorous microarthropods.

As suggested by Prescott and Grayston (2013), the change in communities with different tree species could be attributed to changes in temperature and moisture conditions. In our study, moisture conditions were similar among plantation types and temperatures were higher in poplar compared to spruce plantations, with mean differences of 1.7 °C in May and 0.6 °C in October, respectively. Higher soil temperatures in the boreal region should promote greater abundance and activity of soil organisms. However, in poplar plantations, where soil temperature was greater than spruce plantation, the lowest abundance of fungi and mites suggested that the differences observed in soil communities were mainly due to the effects of tree species and litter chemistry.

2.4.2 Distinct effects of tree species in mixed plantations

Contrary to what we hypothesized, the home field advantage of spruce litter disappeared in mixed plantations, which could indicate that HFA also depends upon the accompanying plant communities. According to NAE calculations of mixed *vs* mono-specific environments, a "mixed environment" showed non-additive effect on litter and cellulose decomposition only under poplar trees, with an increase of 16 % (poplar litter) and 53 % (cellulose) in mass loss, and a decrease of 16 % in spruce litter mass loss. In contrast, mixing species had an additive effect on litter decomposition under spruce trees (cellulose, poplar and spruce litter). This result indicates that decomposition rates in mixed plantation under spruce correspond to the mean decomposition rate in the two mono-specific plantations, whereas decomposition rates under poplar were different from this mean. In mixed plantations, litter cover is not homogenous, with spruce litter being restricted to being under spruce whereas poplar litter is more widely spread. Both litters may be present under the spruce canopy, which could explain the intermediate results between what was observed in the two mono-specific plantations, whereas the lack of spruce litter under poplar trees induced decomposition rates similar to what was observed in poplar mono-specific plantations. These 'tree environment-specific' results confirm that within mixed stands, a tree species has an effect on the forest floor only in a localized way through the spatial distribution of its litter (Aubert et al., 2006; Saetre and Baath, 2000; Saetre et al., 1999).

Concerning the area of influence, there was a net effect of cellulose litter bag positioning both under and between the trees. Cellulose was decomposed rapidly in poplar mono-specific plantations, under and between the trees. However, in spruce mono-specific plantations, cellulose was poorly decomposed under spruce trees (20 % mass loss), but rapidly decomposed between the spruce trees (45 % mass loss), showing an important negative effect of spruce canopy on decomposition rates. In mixed plantations, a high decomposition rate was maintained beneath the poplar trees (53 % mass loss), but between the trees cellulose was less decomposed (19 % less mass loss). These results show that the tree canopy has an important effect on decomposition processes. For example, Saetre and Baath (2000) found ranges of 1–3 m for changes in microbial communities in a *Picea abies–Betula pubescens* forest. Therefore, the positioning of litter bags appears to be rather important when studying the effects of diversity of plant communities on soil processes and should be carefully considered regarding the research objectives.

We did not find support for our hypothesis that litter would decompose more rapidly in mixed compared to pure plantations, as decomposition rates of the three litter types was not greater in mixed plantations. Therefore, our study does not support the hypothesis that activity and diversity of decomposer communities are stimulated by mixing tree species (Ettema and Wardle, 2002; Hansen, 2000; McTiernan et al., 1997; Wardle, 2006). In another way, mixing tree species with different canopy covers promotes spatial separation of specific resources, and associated spatial separation of diverse organisms (Ettema and Wardle, 2002).

2.5 Conclusion

Our study showed a home field advantage only for spruce litter in spruce mono-specific plantations, whereas poplar litter was decomposed to a similar degree under all tree species and plantation types. This HFA could be partially explained by greater abundance of fungi, detritivorous mites and springtails, with a reciprocal positive feedback. Furthermore, cellulose was less decomposed in spruce plantations, indicating that soil communities of spruce mono-specific plantations were more capable of decomposing relatively recalcitrant litter, but they were less efficient in decomposing more "simple" substrates. We posit that the intensity of the home field advantage would be partially controlled by litter dispersal capacity: the greater the litter dispersal, the less intense home field advantage would be. In mixed plantations the activity and diversity of decomposer communities and thus, the litter decomposition rates, were not stimulated compared to mono-specific plantations. However, a "mixed environment" had a synergistic effect on decomposition rates (compared to what was predicted from the two mono-specific plantations), but only under poplar trees. These 'tree environment-specific' results signify that within mixed stands, spruce trees affected the forest floor, but only in a localized way through the limited spatial distribution of their needle litter. This knowledge could contribute to understand how mixing tree species influences soil processes, and how differences in litter dispersal must be taken into account in future studies.

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CHAPITRE IIIa

EFFETS DE LA QUALITÉ DE LA LITIÈRE ET DE LEUR MÉLANGE SUR LE PROCESSUS DE DÉCOMPOSITION

Figure 3.1 Photos de l'expérimentation des litter bags dans une plantation mixte de peuplier hybride et d'épinette blanche

Ce chapitre correspond à un article qui sera soumis à Soil biology and biochemistry

"Litter quality and mixing effect on brown food web under intensive silvicultural system in the boreal region of eastern Canada "

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Résumé

La sylviculture intensive a pris de l'ampleur ces dernières années au Canada, mais nous ne savons toujours pas si le mélange de diverses espèces améliore le fonctionnement des écosystèmes forestiers. Des plantations plurispécifiques utilisant des espèces forestières qui ont des qualités de litières différentes, comme le peuplier hybride et l'épinette blanche, pourraient potentiellement induire une communauté de décomposeurs plus diverse en comparaison avec une plantation monospécifique produisant une litière seule, en diversifiant les microhabitats et les ressources. Cette plus grande diversité de décomposeurs pourrait améliorer l'efficacité de décomposition de la matière organique grâce à des complémentarités parmi les décomposeurs pour utiliser divers types de ressources. Pour comprendre l'importance relative de la qualité des litières d'épinette blanche et de peuplier hybride et de leur mélange sur le processus de décomposition et les organismes décomposeurs, le réseau trophique du sol et la libération des éléments nutritifs ont été étudiés dans une plantation mixte à croissance rapide avec des sacs de litière (litter bags) de chaque espèce et de leur mélange pendant deux ans.

Les composés phénoliques dans la litière de peuplier ont été plus rapidement lessivés ou dégradés que dans la litière d'épinette. La concentration en phénol étant plus faible dans la litière de peuplier, cela pourrait partiellement expliquer la biomasse fongique plus grande à 11 et 18 mois de décomposition et par répercussion dans le réseau alimentaire du sol la plus grande abondance d'oribates et d'acariens prostigmates. Ces différences induisent un relargage plus rapide de carbone et d'azote dans la litière de peuplier. La litière d'épinette était majoritairement colonisée par des microorganismes à croissance lente (stratégie k) qui sont plus capables de dégrader les polymères, tandis que la litière de peuplier était colonisée par des microorganismes opportunistes à croissance rapide (stratégie r) possédant une diversité catabolique plus grande. Le mélange de ces deux types de litière a montré une dynamique semblable à ce qui a été observé dans la litière d'épinette, excepté

l'activité microbienne qui était différente. Les microorganismes à croissance rapide attirés par la litière de peuplier ont supplanté les microorganismes plus spécialisés à dégrader les composés de l'épinette, ce qui pourrait expliquer la plus faible dégradation de la litière d'épinette dans le mélange. Ainsi la litière d'épinette et le mélange peuplier / épinette ont un relargage de C et de N similaire et plus faible que la litière de peuplier.

Abstract

Intensive silvicultural systems have been rapidly expanding in Canada, but we still do not know if mixing species enhance forest ecosystem functioning. Plurispecific plantations using tree species that have different litter qualities, such as hybrid poplar (*P. maximowiczii* x *P. balsamifera*) and white spruce (*Picea glauca*) can potentially support a more diverse community of decomposers than a single litter composition, by diversifying microhabitats and resources. This greater diversity of decomposers could improve the efficiency of organic matter recycling due to complementarities among decomposers taxa for using resources.

In order to understand the relative importance of litter quality of white spruce and hybrid poplar and their mixing on decomposition process and decomposer organisms, decomposer food web and nutrient release were investigated in a mixed fast-growing plantation with litterbags of each species and their mixing during two years.

Phenolic compounds in poplar litter were more rapidly leached or degraded than spruce litter. This lower phenol content could partially explain the greater fungal biomass at 11 and 18 months of decomposition, and by bottom up in the brown food web, greater oribatids and prostigmatid mites abundance. These differences lead to a greater C and N release in the soil. Slow-growing microorganisms, better at degrading polymers, colonized spruce litter, whereas fast-growing opportunistic microorganisms with greater catabolic diversity colonized poplar litter. The mixture of these two litter types showed a similar dynamics to what was observed in spruce litter, except for microbial activity. The fast-growing microorganisms attracted by poplar litter in the mixture outcompeted the more specialized microorganisms able to degrade spruce compounds, which induced a slower decomposition rate of spruce litter in the mixture. Therefore, spruce and mixed litter had similar C and N release, and both were lower than poplar litter alone.

3.1 Introduction

To meet the ever-growing demand for wood fiber while avoiding excessive harvesting of natural forests, intensive silvicultural systems have been rapidly expanding in Canada, where growth rates of natural forests are relatively low (Pothier and Savard, 1998). Forests, besides offering wood for the industry, provide other fundamental ecosystem services such as nutrient availability, tree productivity, carbon storage and biodiversity of organisms. However impacts of the intensification of silvicultural systems on ecosystem functioning remain unknown, and could reduce, as agricultural systems, soil organic matter content and the biomass and diversity of soil biota (Postma-Blaauw et al., 2010).

Litter decomposition is a central process in ecosystem functioning, as it drives the return of nutrients from leaf litter to soil, where it gradually becomes available for plant uptake, and then for all ecosystem biota. Many studies have shown a strong relationship between the chemical composition of litter, which varies considerably between plant species, and their decomposition rate (Meentemeyer 1978; Aerts 1997). This strong relationship is first and foremost determined by interactions between resource quality and soil communities (Crotty et al., 2014; Makkonen et al., 2012; Wardle et al., 2004). This suggests that the effects of plant chemical composition on decomposition rate may be indirect and result from direct effects on decomposer organisms (Wardle, 2002). However, the mechanisms and importance of interactions between litter quality and the structure of soil communities remains poorly understood, and soil communities is often treated as a “black box” when modelling ecosystem processes (Allison and Martiny, 2008). The huge diversity of soil organisms, from bacteria and fungi able to mineralize organic matter, to macropredators form the “brown food web” (Kaspari and Yanoviak, 2009). Structure of this food web, which could greatly vary according to the plant cover (Crotty et al., 2014), is important to understand when trying to determine effects of litter quality on decomposition processes. Generally, microbiota (fungi and bacteria) show the best relative contribution to the litter decomposition and are responsible for chemical degradation of molecules, whereas soil fauna mostly act in the fragmentation of organic matter, increasing the contact surface of the litter with microflora (Berg and Laskowski, 2005; Filser, 2002; Seastedt, 1984). Faunal biota also have indirect regulatory controls through a top-down effect on soil microbial decomposers by grazing activity, showing strong positive impact on fungal growth and respiration, thus stimulating fungal activity (Filser, 2002).

Mixing species in silvicultural systems could favor ecosystem services such as productivity and carbon storage (Chomel et al., 2014a), and litter mixture was also shown to support a more diverse community of decomposers than a single species litter by diversifying microhabitats and resources (Ettema and Wardle, 2002; Kaneko and Salamanca, 1999; Wardle, 2006). This greater diversity of decomposers could improve the efficiency of organic matter recycling due to complementarities among decomposer taxa for using resources (Gessner et al., 2010). Conversely, mixing litters could have negative effects on leaf litter decay by the release of inhibitory compounds such as phenolic compounds by some species in the mixture (Fyles and Fyles, 1993; Prescott et al., 2000). The effect of litter mixing on decomposition rate still remains unknown because it is always site or species dependent, and contradictory results were reported, with additive, non-additive negative or positive effects of mixing (Gartner and Cardon, 2004). Gessner et al (2010) recently pointed out that the lack of comprehensive studies indicates the need for experiments manipulating decomposer communities and litter quality to properly assess the influence of the decomposer community on decomposition of litter mixtures. Understanding the mechanisms linking plant diversity in plantations to soil processes must go through studying relationships between above and belowground diversity, and this knowledge is essential in order to optimize the functioning and the ecosystem services of plantations in a longer term perspective (de Vries et al., 2013).

In this study, we compared decomposition rates of two litter types (poplar and spruce) when they decompose separately or in a mixture, in a mixed-species plantation. The objective was to quantify if there was change in soil food web structure, decomposition rate and nutrient release depending on the quality of each litter and if their mixing influenced soil fertility and diversity of microorganisms and mesofauna communities. We hypothesized that i) decomposition of spruce litter would be slower compared to poplar litter and that decomposers associated with spruce litter are more specialist ii) non-additive positive effect of mixing poplar and spruce litter will occur due to an increase of microbial activity and mesofauna diversity by increasing resource complementarities by the mixture of two litter types.

3.2 Materials and methods

3.2.1 Site description

The study was located in the boreal region of Abitibi-Temiscamingue, Quebec, Canada. Three sites were selected for study : Amos (48°36'N, 78°04'W), Rivière-Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was abandoned farmland with a heavy clay soil that was dominated by grasses and sparse patches of alder (*Alnus incana* [L.] Moench ssp. *rugosa* [Du Roi] R.T. Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière-Héva was an abandoned farmland site with heavy clay soil, which was also dominated by shrubs, including patches of alder, willow, and trembling aspen. Nédelec had been previously dominated by trembling aspen forest, which was commercially harvested in 2000. This last site was characterized by soils with a sandy loam texture. Based on the 30-year running climate average (1970-2000), Amos and Rivière-Héva receive an annual mean 918 mm of precipitation (Amos station) and a mean temperature of 1.2 °C, while Nédelec has mean precipitation of 916 mm year^{-1} and a mean temperature of 1.9 °C (Remigny station, Environment Canada 2014). Site preparation was conducted in 2002, where tree stumps were removed, and soils were ploughed to a depth of about 30 cm. The plantations were established in 2003, using one hybrid poplar clone (*Populus maximowiczii* A. Henry x P. *balsamifera* L., clone MB915319), and an improved white spruce family (*Picea glauca* [Moench] Voss). These two species were planted in mixed-species plots under a spacing of 1 × 1 m, each row consisting of spruce alternated with poplar. Each experimental unit contained 36 trees (6 × 6 trees).

3.2.2 Litter decomposition experiment

In late September 2010, spruce needles and hybrid poplar leaves were collected from plantations that were close to the Amos study site. Abscission of needles or leaves in which senescence was complete was aided by shaking the trees, and the fallen needles/leaves were collected on a plastic sheet that was placed on the ground beneath the trees to prevent soil contamination. Collected material was homogenized and stored at room temperature prior to the experiment. A subsample of each species was oven-dried at 60°C to establish the relationships between air-dried and oven-dried mass. Seven gram (air-dried) of either poplar, spruce and a mixing of these two litter types were placed in 1 mm mesh litter bags (15 x 15 cm for poplar; 10 × 15 cm for spruce litter) to allow colonization by soil mesofauna and microbes, while excluding macrofauna (Swift et al., 1979). We used pairs of litterbags with one bag being used for chemical and microbial measurements and the other for mesofauna extraction. To prevent losses of spruce needles through the net mesh during handling, a sheet of paper was inserted into each litterbag with spruce needles. These sheets of paper were removed and the litterbags were finally closed just before they were placed on the soil. The dimensions of the litter bags containing spruce needles was smaller than those for poplar leaves, to create the same litter incubation conditions among litter type, and to prevent needle loss.

In November 2010, 12 pairs of litterbags of each litter were placed in the plantation at each replicate site, under poplar trees and 12 other pairs under spruce trees. Through this paper, we have further divided mixed plantations into mixed-spruce (under spruce trees) and mixed-poplar (under poplar trees) as they can have different influence on soil communities and decomposition process (Chomel et al., 2014c). This experiment resulted in a total of 432 litterbags (12 pairs x 2 litterbags x 3 litter species x 2 positioning x 3 sites = 432). Freshly fallen litter was removed from the surface of the forest floor prior to placing the litterbags on the ground, and handed over after placing. Litterbags were fixed with one galvanized nail to prevent movement by animals or by the wind. After 7, 11, 18 and 24 months, 3 pairs (pseudo-replicates) of litterbags were retrieved from around three randomly chosen trees at each site. Sampling dates corresponded to snowmelt and anticipated snowpack development, generally mid-May and early or mid-October, respectively.

3.2.3 Litter bag processing

The first litterbag of each pair was used for mesofauna extraction for ten days, after which it was oven-dried at 60°C for 3 days. An aliquot of the second litterbag was used for microbial analysis and the remainder of the sample were freeze-dried (Lyovac GT2®) for chemical analysis. To prevent soil contamination of litter, we wiped each needle/leaf thoroughly before analysis. At t_0, 26 samples of each litter type (equivalent to 5 g dry mass) were used to determine initial litter quality.

Litter mass remaining

Decay rates were determined from the full set of litter bags. Mass loss was expressed as the percentage of total initial dry mass.

Chemical analysis

C and N

Litter samples were finely ground with a ball mill (MM301, Retsch Inc., Newtown, PA), and carbon and nitrogen concentrations were determined with a C/N elemental analyzer (Flash EA 1112 series, ThermoScientific, U.S.A.).

Phenolic compounds

The method used to extract total phenolic contents was based on the work of (Peñuelas et al., 1996): 0.25 mL of filtered aqueous extract was mixed with 0.25 mL of Folin-Ciocalteu reagent (Folin and Denis, 1915) and 0.5 mL of saturated aqueous Na_2CO_3 to stabilize the colour reaction, after which 4 mL of distilled water was added to dilute the extract. After 1 hour, the reaction was completed and measured at 765 nm on a UV/Vis spectrophotometer (Thermoscientific, U.S.A.). Quantitative results were expressed with reference to gallic acid.

Mesofauna extraction

Invertebrates were extracted from fresh litter using the dry funnel method (Berlese, 1905), and were stored in 90% alcohol. Invertebrate groups were identified and counted under a binocular scope. Invertebrates were separated into the four main Collembola orders – Entomobryomorpha, Poduromorpha, Neelipleona, and Symphypleona; and the Acari – Mesostigmata, Prostigmata, Oribatida, and Astigmata. Other invertebrates were separated to the family. Invertebrate fauna was assigned to each of the following feeding guilds according to Crotty et al, (2013): microbivores, detritivores, omnivores, herbivores and predators.

Fungal biomass

Fungal biomass was determined by quantifying ergosterol, a fungal membrane constituent and a good indicator of living fungal biomass (Gessner and Chauvet, 1993; Ruzicka et al., 2000). Samples were frozen and lyophilized to enable more efficient extraction of ergosterol (Gessner and Schmitt, 1996). Ergosterol was extracted from 50 mg of needles/leaves with 5 mL of an alcohol base (KOH/methanol 8 g L^{-1}) for 30 min, and purified by solid-phase extraction on a Waters® (Milford, MA, U.S.A.) Oasis HLB cartridge (Gessner and Schmitt, 1996). The extract that was produced was purified and quantified by high-performance liquid chromatography (HPLC) on a Hewlett Packard series 1050 system running with HPLC-grade methanol at a flow rate of 1.5 mL min^{-1}. Detection was performed at 282 nm, and the ergosterol peak was identified based on the retention time of an ergosterol standard. For conversion into fungal biomass we used the conversion rate of ergosterol * 250 = fungal biomass (Montgomery et al., 2000).

Catabolic profiles of microorganisms

Microbial (fungal and bacterial) catabolic profiles were assessed using Biolog® EcoPlates (Biolog Inc., Hayward, CA, USA) for all sampling dates using a procedure adapted from (Garland and Mills, 1991). We purposely did not adjust inoculum concentration because we considered total microbial number to be an inherent characteristic of microbial communities in each sample. To have enough fresh material, the three pseudo-replicates in each plantation were pooled, remaining only the three sites as replicates. Briefly, 2 g (dry mass equiv.) of ground litter were stirred in 100 mL of a sterile 0.1% tetrasodium pyrophosphate solution for 1 h to suspend microbial communities. Each 96-well plate contained 3 replicate blocks of a water blank and 31 of the most useful carbon sources for soil community analysis (Preston-Mafham et al., 2002). A 125 µL aliquot of extract solution, diluted 1:110, was added to all 96 wells in each EcoPlate. The plates were incubated at 30 C for 7 days, and absorbance was measured at 595 nm on a microplate spectrophotometer (Multiskan GO, Thermo Fisher Scientific). Different microbial communities can exhibit different patterns of substrate use, as revealed the ensuing by colorimetric reactions.

3.2.4 Data analyses

All statistical analyses were performed using R version 3.1.0 (R Development Core Team, 2008). To determine differences among litter types at initial time, data were analyzed using ANOVA (one factor: litter species). To determine differences among litter types for measured responses during decomposition time, data were analyzed using hierarchical linear mixed-effect model using the *lme* function in the nlme package (Pinheiro et al., 2014). Litter type, decomposition time and positioning (under spruce or under poplar) were treated as main effects, the random effects structure of the model positioning within site replicates. If the effect of the different factors was significant, the different treatments were compared with pre-planned linear contrasts (differences are noted in the manuscript as a<b<c).

3.3 Results

3.3.1 Initial litter quality

Poplar litter had a significantly lower C content and C/N ratio than the spruce litter, while mixed litter had intermediate values (Table 3.1). There was no significant difference in phenolic compounds concentration between the three litter types (Table 3.1).

Table 3.1 Initial C, N and phenolics concentrations, and C/N ratio of the two different litter types and their mixing (mean ± SE). Results of Anova are reported in the left side, with significant differences indicated with *0.05, **0.01, ***0.001. Different letters denote significant differences according to Tukey tests.

Initial litter quality	Litter species			N	F value
	Poplar	Spruce	Mixed		
C (% DM)	38.01 ± 1.15 (a)	42.35 ± 1.51 (b	38.61 ± 1.45 (ab)	72	3.9*
N (% DM)	0.53 ± 0.03	0.50 ± 0.02	0.50 ± 0.01	72	0.01^{ns}
C/N	76.65 ± 3.98 (a)	86.73 ± 3.47 (b	77.33 ± 2.33 (ab)	72	4.5*
Phenolics (mg.g^{-1} DM)	52.2 ± 3.5	44.2 ± 2.6	46.3 ± 1.9	21	2.29^{ns}

3.3.2 Litter mass loss

Litter mass loss was compared for the two litter types taken separately and mixed at the last sampling date after 2 years of decomposition. Mass loss of spruce litter alone was 36% on average and was significantly lower than mass loss of poplar litter (mean of 54%) (lme, F = 188.4, $P < 0.001$, Figure 3.2). In the mixture, spruce litter had a significant lower mass loss than alone (mean of 26%), whereas poplar mass loss in mixture (57%) was equivalent to mass loss alone (linear contrasts, $P < 0.001$, Fig.3.2). When the decomposition rate was compared between the three litter types, mass loss of mixed litter was 42%, and was similar to mass loss of spruce, and lower than poplar alone mass loss (lme, $F_{2,96} = 29.8, P < 0.001$).

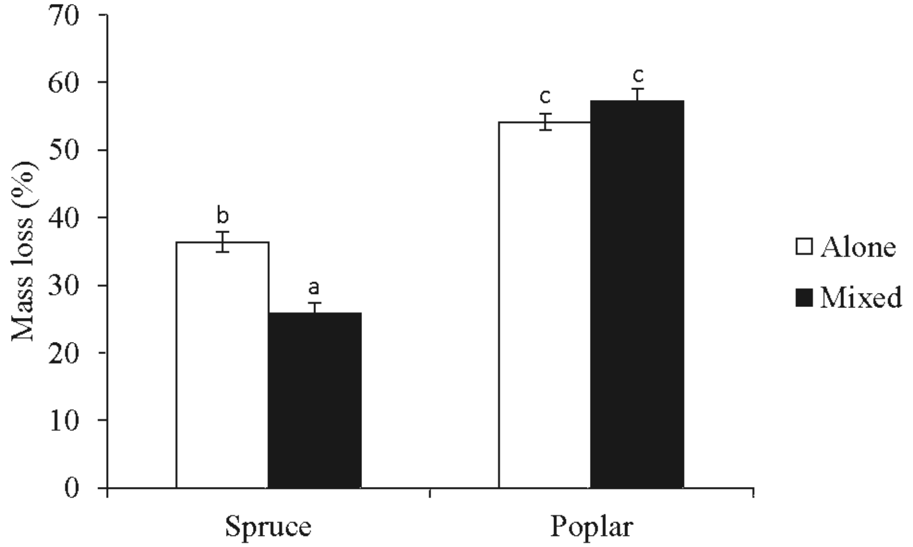

Figure 3.2 Mass loss after 24 months of decomposition (Mean and SE) of the single litter types (white bars) or in mixture (grey bars). Bars with different letters represent a significant difference between means according to linear contrast.

3.3.3 Litter component release

For remaining C and N, we observed significant interactions between litter type and time of decomposition (lme, $p<0.01$). During the two years of decomposition, C remaining was greater in spruce than poplar litter (linear contrasts, $P < 0.05$, Figure 3.3a). Mixed litter had intermediate values but was only significantly different from poplar at 7 and 24 months of decomposition (linear contrasts, $P < 0.05$, Figure 3.3a). After two years of decomposition, C release was 35% for spruce, 37% for mixed and 56% for poplar.

At 7 and 24 months of decomposition poplar litter had lower N remaining than mixed and spruce litter (linear contrast, $P < 0.05$, Figure 3.3b), and at 11 months of decomposition mixed litter had greater value than spruce and poplar (linear contrast, $P < 0.05$). In spruce and mixed litter, N was still immobilized after 24 months of decomposition (increase of 15 and 11% of initial N content), and in poplar there was a release of 5% of initial N (Figure 3.3b).

Phenolic compounds remaining was different between litter types at all sampling dates, with spruce > mixed > poplar litter (linear contrasts, $P < 0.005$, Figure 3.3c), corresponding to phenolics release of 97% for poplar, 91% for mixed and 84% for spruce litter.

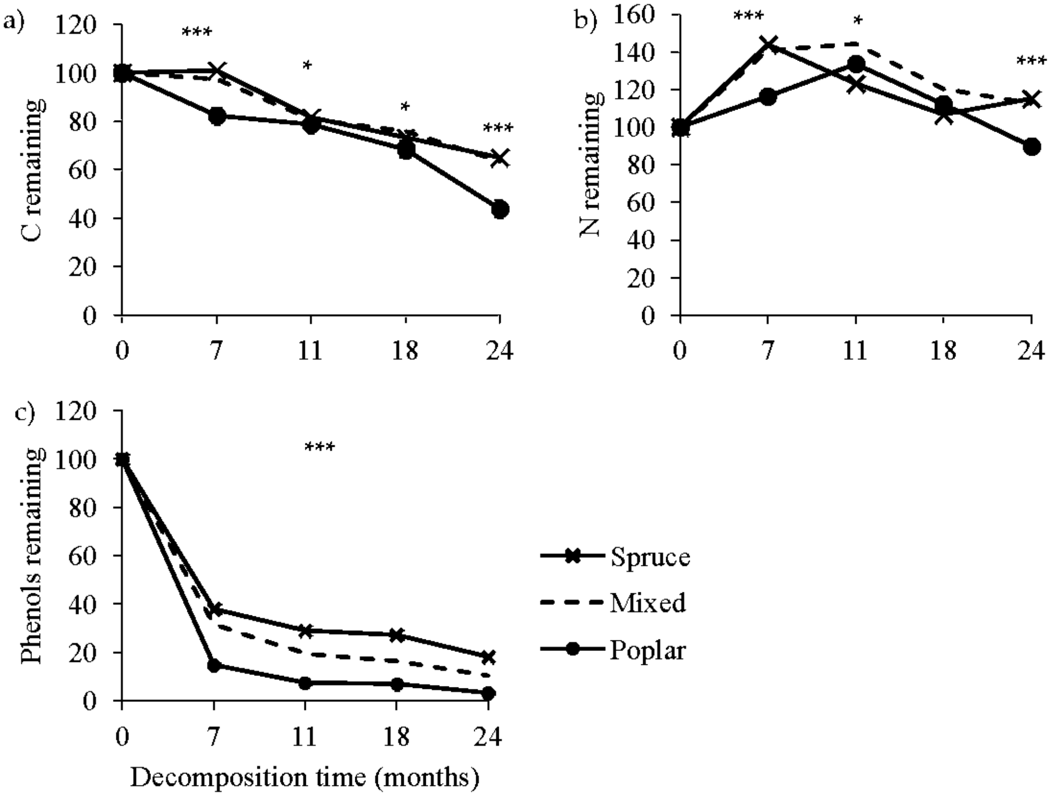

Figure 3.3 Mean of C (a), N (b) and phenolics compounds (c) remaining (% of initial litter content) in the different litter types along decomposition time. Significant

differences among litter type, according to linear contrast, are indicated by * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$).

3.3.4 Catabolic activity of microorganisms

Microbial activity was greater in poplar and mixed litters than in spruce litter at 7 months of decomposition for the majority of substrate family present in the Biolog Ecoplate except Amines (Table 3.2). At 11 months of decomposition, microorganisms associated to spruce litter were still less active to decompose carbohydrates, carboxilic acid and amino acids (Table 3.2) than microorganisms associated to the two other litter types. At 18 months of decomposition, microbial activity was lower in spruce litter for the majority of substrates. Finally, at 24 months of decomposition, there no longer was a difference in microbial activity between litter types (Table 3.2). Along the two years of the experiment, microbial catabolic capacity mainly was the decomposition of amino acids, carbohydrates and carboxylic acids (accounted for more than 60% of total substrate use), except for spruce litter for which polymers were more decomposed than carbohydrates at 7 months (24 and 16% respectively), whereas in poplar and mixed litters the reverse was observed (15 and 12% respectively for carboxylic acid, and 19% for polymers for the poplar and mixed litters).

Table 3.2 Mean microbial utilization per substrate type of each litter type (Litter, S = Spruce, M = Mixed, P = Poplar) along decomposition time (months). Results of Anova are indicated as “F-value***” with post-hoc Tukey test for litter type differences among sampling dates.

Time	Litter	Amine	Amino acid	Carbohydrate	Carboxylic acid	Phosphorylated	Polymer
7	S	0.06	0.28 (a)	0.14 (a)	0.18 (a)	0.03 (a)	0.22 (a)
7	M	0.18	0.82 (b)	0.57 (b)	0.65 (b)	0.27 (ab)	0.44 (b)
7	P	0.19	0.76 (b)	0.54 (b)	0.66 (b)	0.40 (b)	0.35 (ab)
ANOVA		**ns**	**14.6*****	**7.4****	**39.45*****	**5.9****	**7.53****
11	S	0.23	0.57 (a)	0.39 (a)	0.41 (a)	0.40	0.42
11	M	0.27	0.86 (b)	0.70 (b)	0.65 (b)	0.48	0.50
11	P	0.31	0.81 (b)	0.85 (b)	0.68 (b)	0.62	0.55
ANOVA		**n.s**	**6.1****	**11.7*****	**16.6*****	**n.s**	**n.s**
18	S	0.09 (a)	0.27 (a)	0.18 (a)	0.19 (a)	0.02	0.08 (a)
18	M	0.22 (b)	0.56 (b)	0.30 (ab)	0.47 (b)	0.22	0.32 (b)
18	P	0.24 (b)	0.58 (b)	0.35 (b)	0.48 (b)	0.25	0.40 (b)
ANOVA		**3.3***	**12.1*****	**4.1***	**16.5*****	**n.s**	**25.85*****
24	S	0.80	1.37	1.20	1.00	0.91	0.75
24	M	0.83	1.47	1.26	0.98	0.58	0.84
24	P	0.92	1.48	1.26	0.97	0.99	0.85
ANOVA		**n.s**	**n.s**	**n.s**	**n.s**	**n.s**	**n.s**

3.3.5 Brown food web

An interaction between litter types and decomposition time was observed for fungal biomass (lme, *P* < 0.05), showing that fungal biomass was lower in mixed litter compared to poplar and spruce litters at 7 months of decomposition (linear contrast, *P* < 0.05, Figure 3.4). At 18 months of decomposition, poplar litter had greater fungal biomass than spruce and mixed litters (linear contrasts, *P* < 0.05, Figure 3.4). For spruce litter, fungal biomass increased until 18 months of decomposition, and remained stable until 24 months of decomposition. For mixed litter, fungal biomass increased between 7 and 11 months of decomposition and then reached a plateau until the end of the experiment. For poplar litter, fungal biomass increased until 18 months of decomposition, and finally decreased between 18 and 24 months (linear contrasts, $P < 0.01$, Figure 3.4).

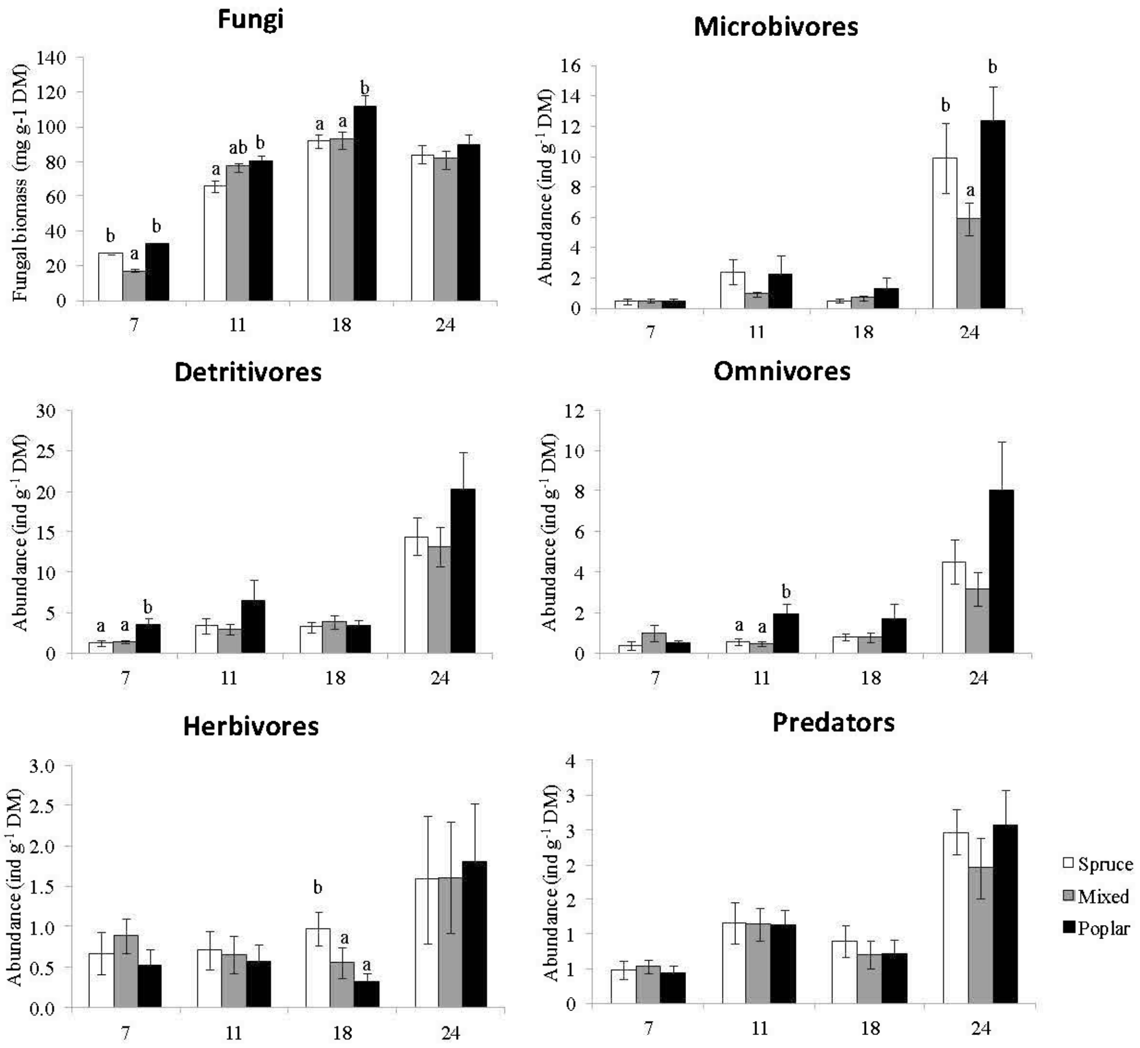

Figure 3.4 Mean ± SE of fungal biomass and abundance of different guilds of organisms in the different litter types during time of decomposition.

A total of 31 different soil fauna orders were recorded in the litterbags all along the experiment (Table 3.4). Oribates and entomobryomorpha (collembola) dominated litter fauna in abundance for the two types of litter and all the sampling dates, representing meanly 42 % and 17 % of total abundance, respectively (Table 3.4). Oribates were more abundant relative to springtails in poplar litter compared to spruce litter as we found significant greater oribates/collembola ratio in poplar litter along the decomposition time (lme, $F_{2,183} = 6.47$, $P = 0.002$, Fig. 3.5). This ratio was lower at 7 and 24 months of decomposition, and greater at 18 months of decomposition (lme, $F_{2,183} = 7.74$, $P < 0.001$, Fig. 3.5).

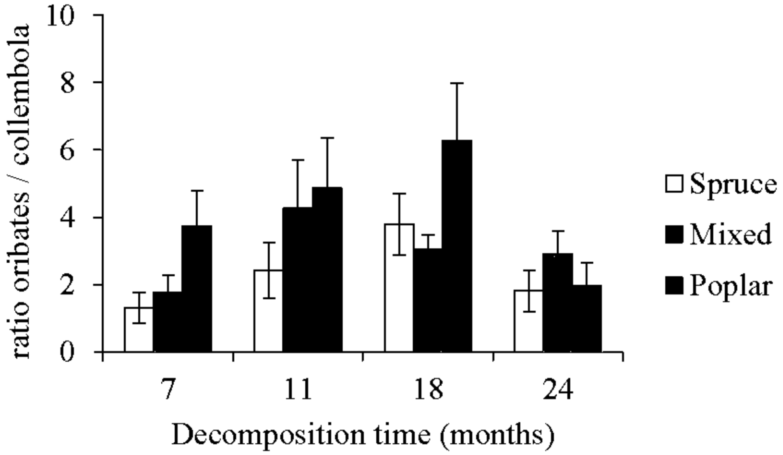

Figure 3.5 Mean ratio of oribates to collembola (± SE) of each litter type during decomposition time.

The three litter types differed in abundance of detritivores, omnivores, herbivores and microbivores at different decomposition sampling dates. Only predator's abundance was similar across the three litter types all along the two years of decomposition (Fig 3.4). At 7 months of decomposition, detritivores were more abundant in poplar litter than in spruce and mixed litter (lme, $F_{2,45} = 9.3$, $P < 0.001$), and represented 56% of the total abundance compared to 29% for the two other litter types (Table 3.4). At 11 months of decomposition, omnivores were more abundant in poplar litter than in spruce and mixed litters (lme, $F_{2,45} = 9.3$, $P < 0.001$, Fig. 3.4) and represented 17% of the total abundance, compared to 8 and 7% for spruce and mixed litters, respectively (Table 3.4). Whereas the abundance of microbivores and predator were not significantly different between litter types, the proportion of these trophic groups was different between litter types (Table 3.4); Omnivores had a greater proportion in spruce litter (25%) than poplar litter (15%), and predators had a greater proportion of the community in mixed litter (23%) compared to spruce (15%) and poplar (19%)

litters. At 18 months of decomposition, herbivores were more abundant in spruce litter than in poplar and mixed litters (lme, $F_{2,44} = 3.4$, $P < 0.05$) and represented 14% of the community compared to 7% for the two other litter types (Table 3.4). And finally, at 24 months of decomposition, microbivores were more abundant in poplar and spruce litters than in mixed litter (lme, $F_{2,44} = 3.7$, $P < 0.05$) (Fig 3.4). Total abundance was significantly greater in poplar litter than spruce litter at 7 months of decomposition and greater than mixed litter at 24 months of decomposition (lme, Table 3.4).

Table 3.4 Mean trophic groups proportion (%) and total abundance of mesofauna from three litter types (spruce, poplar and mixed) along decomposition time (months). Significant difference between plantation types within each row and date are presented with different letter.

Trophic group	Organism	7			lme ($F_{2,44}$)	11			lme ($F_{2,44}$)	18			lme ($F_{2,44}$)	24			lme ($F_{2,44}$)
		Spruce	Mixed	Poplar		Spruce	Mixed	Poplar		Spruce	Mixed	Poplar		Spruce	Mixed	Poplar	
Microbivore	Entomobryomorpha	16.00	14.20	7.79		25.22	17.59	14.76		6.97	12.06	15.35		24.71	21.09	25.38	
	Poduromorpha	1.63	0.18	1.60		0.10	0.15	0.04		0.45	0.15	0.13		3.50	2.78	3.44	
	Total	**17.62**	**14.38**	**9.38**	**ns**	**25.32 (b)**	**17.74 (ab)**	**14.79 (b)**	**2.52***	**7.43**	**12.21**	**15.49**	**ns**	**28.21**	**23.88**	**28.82**	**ns**
Detritivores	Oribatida	28.57	28.62	53.30		37.23	40.49	46.27		46.79	56.54	51.08		34.38	42.12	37.81	
	Isopoda	0.00	0.00	0.00		0.00	0.00	0.00		0.00	0.00	0.00		0.04	0.00	0.00	
	Annelida	0.00	0.00	0.00		0.00	0.00	0.07		0.00	0.00	0.07		1.24	2.28	0.59	
	Myriapoda:	0.37	0.23	0.62		0.00	0.00	0.04		0.00	0.00	0.00		0.47	0.27	0.22	
	Psocoptera	0.00	0.21	0.00		0.00	0.00	0.00		0.00	0.00	0.46		0.00	0.00	0.00	
	Diptera larvae	0.00	0.00	0.00		1.25	0.83	1.12		1.70	0.14	0.00		10.03	5.09	2.85	
	Total	**28.94 (a)**	**29.06 (a)**	**53.92 (b)**	**8.1*****	**38.49**	**41.32**	**47.51**	**ns**	**48.50**	**56.68**	**51.61**	**ns**	**46.15**	**49.76**	**41.47**	**ns**
Omnivore	Prostigmata	4.81	13.96	6.73		5.57	5.99	14.37		11.61	9.03	9.51		11.99	9.76	15.24	
	Astigmata	0.56	2.80	1.05		0.00	0.00	0.00		0.00	0.00	0.00		0.00	0.00	0.00	
	Diptera	0.00	0.26	5.26		0.00	0.00	0.00		0.11	0.15	0.00		0.00	0.07	0.03	
	Hymenoptera	0.15	2.96	0.11		0.82	0.78	1.19		1.83	1.32	5.42		0.17	0.26	0.03	
	Coloeptera	0.87	1.92	0.55		1.82	0.44	0.78		0.82	0.00	0.00		0.30	0.31	0.61	
	Other larvae	0.00	0.00	0.00		0.00	0.00	0.18		0.00	0.00	0.00		0.00	0.00	0.00	
	Total	**6.39 (a)**	**21.91 (b)**	**13.70 (a)**	**11.6*****	**8.21 (a)**	**7.21 (a)**	**16.52 (b)**	**5.0***	**14.37**	**10.50**	**14.93**	**ns**	**12.46**	**10.40**	**15.91**	**ns**
Herbivores	Symphypleona	29.67	18.13	11.74		6.87	5.07	5.13		12.08	6.35	6.19		4.37	5.38	5.67	
	Hemiptera larvae	0.00	0.00	0.00		0.79	0.64	0.20		0.00	0.00	0.00		0.00	1.33	0.00	
	Larvae lepidoptera	0.00	0.00	0.00		0.00	0.00	0.00		0.00	0.00	0.00		0.00	0.07	0.00	
	Hemiptera	0.00	1.05	1.00		3.00	2.63	1.39		1.97	0.31	0.00		0.04	0.00	0.08	
	Gasteropoda	0.79	0.08	0.81		1.54	1.73	0.96		0.00	0.15	0.33		0.16	0.12	0.08	
	Thrips	0.00	0.00	0.00		0.88	0.28	0.16		0.31	0.00	0.00		0.16	0.06	0.00	
	Total	**30.46**	**19.26**	**13.55**	**ns**	**13.09**	**10.35**	**7.84**	**ns**	**14.36 (b)**	**6.81 (a)**	**6.51 (a)**	**3.7***	**4.73**	**6.96**	**5.83**	**ns**
Predator	Prostigmata: Rhaghidiidae /	2.60	0.56	0.26		0.10	0.13	0.10		2.03	4.75	1.80		0.00	0.09	0.00	
	Ixodida	0.56	0.15	0.00		0.98	0.82	0.00		0.31	2.28	0.00		0.00	0.00	0.00	
	Gamaside	8.79	9.77	4.64		13.90	18.98	12.10		11.05	6.16	8.30		7.87	8.24	6.99	
	Coleoptera larvae	4.05	3.13	2.86		0.00	0.00	0.00		0.31	0.00	0.00		0.00	0.00	0.00	
	Pseudoscorpions	0.00	0.00	0.23		0.00	0.00	0.00		0.00	0.00	0.00		0.13	0.47	0.32	
	Aranae	0.10	1.28	1.23		0.41	3.12	0.86		1.53	0.56	1.35		0.36	0.14	0.31	
	Opilion	0.00	0.00	0.00		0.00	0.00	0.00		0.13	0.06	0.00		0.00	0.00	0.00	
	Myriapoda: chilipoda	0.00	0.00	0.00		0.00	0.32	0.00		0.00	0.00	0.00		0.00	0.03	0.27	
	Total	**16.09**	**14.89**	**9.21**	**ns**	**15.39 (a)**	**23.37 (b)**	**13.07 (a)**	**3.8***	**15.35**	**13.80**	**11.46**	**ns**	**8.36**	**8.97**	**7.89**	**ns**
Total abundance per gram litter		3.3 ± 0.7 (a)	4.2 ± 0.7 (ab)	5.5 ± 0.7 (b)	3.2*	8.2 ± 1.3	6.1 ± 0.8	12.4 ± 3.3	ns	6.4 ± 0.8	6.7 ± 1.3	7.5 ± 1.3	ns	32.9 ± 4.0 (ab)	25.7 ± 3.4 (a)	42.8 ± 5.9 (b)	3.6*

3.4 Discussion

Our experiment showed empirical differences in microbial and mesofaunal communities colonizing two litters of different quality and their mixing. These differences lead to a greater C and N release in poplar litter than spruce and mixed litters.

3.4.1 Micro food web

Microbial activity in spruce litter was lower than in poplar or mixed litters until 18 months of decomposition. This difference was probably due to the observed lower fungal biomass and a potential lower bacterial density in spruce litter until it was well fragmented (18 months). Furthermore, we previously observed that microorganisms colonizing spruce litter were more specialists, and that they were able to degrade a lower diversity of compounds compared to poplar (Chomel et al., 2014c). Microbial degradation of polymeric substrates in spruce litter represented 23% of the total activity in the biolog ecoplate, and was proportionally more degraded than carbohydrates (simpler substrates) at 7 months of decomposition, whereas in poplar and mixed litter the opposite was observed. Lignin and cellulose are the most abundant biopolymers on earth, and Norway spruce leaves, for example, contain 32% of lignin and 29% of cellulose (Johansson, 1995), contrary to hybrid aspens which contain 9% of lignin and 15% of cellulose (Mandre et al., 2011). The decay of lignin in the early stages of decomposition has been reported to occur in boreal and temperate forests when its content in the litter was higher than 30% of the initial organic matter (McClaugherty and Berg, 1987). Therefore, greater amounts of lignin and cellulose in spruce needles could have selected microorganisms able to degrade polymers at the initial stage of decomposition. Lignin is known to limit microbial enzyme accessibility to more labile cell-wall polysaccharides (Austin and Ballaé, 2010) and could slow down the colonization of more opportunist and fast-growing microorganisms. For the mixed litter, the presence of poplar litter induced an addition of labile compounds, attracting these fast-growing microorganisms in early stages of decomposition (Swift et al., 1979). These organisms typically degrade more diverse simple resources but they are less able to degrade recalcitrant compounds. Slow-growing microorganisms probably present in spruce litter were unable to compete with fast-growing microbes and could have been eliminated from the community of decomposers in mixed litter (Couteaux et al., 1991).

Elevated microbial activity was observed at 24 months of decomposition in the three litter types compared to the three other sampling dates. During two years, numerous soil organisms came into the litterbags, promoting physical and chemical degradation of organic matter, and faeces deposition. These products increase the surface exchange of organic matter with microorganisms and promote their colonization and activity (Carrillo et al., 2011; Chamberlain et al., 2006).

The most common organisms for the three types of litter were oribatida (Acari), entomobryomorpha, and symphypleona (Collembola) mainly at the initial stages of decomposition (42, 17 and 10 % of mean relative abundance all along the experiment, respectively) which is in line with several other studies (Chomel et al., 2014b; Petersen and Luxton, 1982). The ratio oribatid mites/springtails was greater in poplar than spruce litter, while mixed litter had intermediate values. Oribates are considered as detritivores, as they have different food preferences and can be fungivores, herbivores, or omnivores (Zaitsev et al, 2014). With poplar litter, an increase in litter quality could induce a shift of oribatid communities to specialized fungivorous (Salamon et al., 2008), attracted by a greater fungal biomass in this litter.

High amounts of living plant material in the upper soil surface lead to a greater proportion of herbivorous, mainly symphypleona (collembolan), in the three litter types at the initial stages of decomposition, and decreased with decomposition time. Interestingly, herbivorous were proportionally greater at 18 months of decomposition in spruce litter, probably due to the fact that needles were not yet entirely fragmented.

Although the abundance of predators was not different between litter types, in mixed litter the proportion of gamasid mites (predators) and aranae was greater than in the two other litter types at 11 months of decomposition. This greater predation pressure could partially explain the lower abundance of mesofauna associated to mixed litter compared to poplar litter.

3.4.2 Decomposition and release

Decomposition rate of spruce litter was significantly lower than poplar litter, as we expected. Spruce litter had initially greater C/N ratios than poplar litter, which is widely recognized to restrain microbial decomposition activities and then decomposition rate (Aber et al., 1990; Aerts, 1997). Furthermore, phenolic compounds were more rapidly released in poplar litter (97%) than in spruce litter (82%), and mixed litter had intermediate values (89%). Another experiment (Chomel et al, in prep (chapter 3b)) showed that leachates of poplar contained 36% of phenolic compounds present in the litter, whereas leachates of spruce needles only contained 7% of the compounds present in the needles. Poplar litter could contain greater hydrosoluble compounds and/or phenolics of poplar litter could be more rapidly leached and then degraded than spruce litter compounds. Moreover, this lower content of phenolic compounds in poplar could explain the greater fungal biomass associated to this litter (Chomel et al., 2014b), which could have enhanced its decomposition rate.

The activity of fauna is recognized to induce greater availability to soil microbes of litter-derived substrates by faeces deposition, enhancing the decomposition of organic matter (Carrillo et al., 2011). The greater oribatid mites abundance in poplar litter at 7 months of decomposition could thus explain the lower C and N remaining in poplar litter compared to spruce and mixed litters. During decomposition processes, amounts of litter elements (such as phosphorus or nitrogen) increase due to microbial immobilization. Faunal grazing allows these nutrients to be released leading to higher overall efficiency of the mineralization process (Petersen and Luxton, 1982; Seastedt, 1984). Nitrogen was highly immobilized along decomposition time, and a release was observed only in poplar litter after 24 months of decomposition. In this litter, a decrease of fungal biomass was observed between 18 and 24 months of decomposition, and a greater litter mass loss than spruce and mixed litter was observed, which induced this greater N release.

Contrary to what we expected, the mixture of the two litter types didn't increase microbial activity and mesofauna diversity, and the mass loss of the mixture was similar than spruce litter alone. The litter of each species in mixed litter bags was separated throughout the experiment to evaluate mass loss of each litter type. Our results indicate that mixing spruce and poplar litter had a negative effect on spruce litter decomposition with a decrease of 10% of mass loss, while it had no effect on poplar litter decomposition. Microbial activity in mixed litter was comparable to the activity found in poplar litter, but all other components (fungal biomass, abundance of mesofauna) were similar to spruce litter. Despite the presence of poplar litter in the mixture, C and N releases were similar to that of spruce litter. Furthermore, at the final stage of decomposition, there was proportionally more spruce litter than poplar litter in the mixture; the fast-growing microorganisms present in the initial stage of decomposition could have delayed the degradation of lignin and cellulose, which limit the accessibility of more labile compounds.

3.5 Conclusion

Phenolic compounds in poplar litter were more rapidly leached or degraded than spruce litter. This lower phenol content could partially explain the greater fungal biomass at 11 and 18 months of decomposition, and by bottom up in the brown food web, greater oribatids and prostigmatid mites abundance. These differences lead to a greater C and N release in the soil. Slow-growing microorganisms better at degrading polymers colonized spruce litter, whereas fast-growing opportunistic microorganisms with greater catabolic diversity colonized poplar litter. The mixture of these two litter types showed a similar dynamic to what was observed in spruce litter, except for microbial activity. The fast-growing microorganisms attracted by poplar litter in the mixture outcompeted the more specialized microorganisms able to degrade spruce compounds, which induced a lower decomposition rate of spruce litter in the mixture. Therefore, spruce and mixed litter had similar C and N release, and both were lower than poplar litter alone.

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CHAPITRE IIIb

EFFETS DE LA QUALITÉ DE LA LITIÈRE SUR LES COLLEMBOLES EN MICROCOSMES

Figure 3.6 Folsomia candida. © Murray, A.

Ce chapitre correspond à un article qui sera soumis à Pedobiologia

"Impact of litter mixtures and leachates on *Folsomia candida* fitness in microcosms"

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Key words : Leachate, Phenolic compounds, Collembola, hybrid poplar, white spruce, herbaceous, mortality, reproduction

Résumé

Dans les régions boréales, l'exode rural induit de vastes étendues de terres agricoles abandonnées. Ces terrains, généralement colonisés par le foin, sont souvent utilisés pour développer les plantations monospécifiques de peuplier hybride ou d'épinette blanche. Le peuplier, l'épinette et les herbacées ont des qualités de litières différentes, et particulièrement dans leur contenu en métabolites secondaires. Ainsi leur co-occurrence dans des plantations mixtes pourrait avoir un impact sur les communautés du sol et le fonctionnement de l'écosystème. Les collemboles jouent un rôle essentiel dans le processus de décomposition, principalement par des effets indirects de stimulation ou de régulation des microorganismes colonisant les litières. Même s'il est largement reconnu que la qualité de la matière organique influence l'activité des collemboles, les mécanismes par lequel la structure des communautés est influencée par la qualité de la litière et leur mélange demeurent inconnus. Le lessivage des litières est une importante voie de libération des composés chimiques des feuilles, et des métabolites secondaires. Pour connaitre comment la qualité des litières pourraient influencer l'activité des collemboles, des essais en laboratoire ont été réalisés avec quatre types de litière (peuplier hybride, épinette blanche, le mélange peuplier / épinette et les herbacées) et une espèce cible de collemboles, *Folsomia candida*, selon une adaptation de la norme ISO 11267 (organisme international de normalisation). Dix individus de *F. candida* ont été déposés dans des microcosmes contenant un substrat standardisé auquel nous avons ajouté séparément de la litière de peuplier, d'épinette et d'herbacées, ainsi que du mélange épinette / peuplier. Pour prendre en compte la variabilité de la biodisponibilité des composés chimiques des litières sur *F. candida*, d'autres microcosmes ont été réalisés en mélangeant des lixiviats des différentes litières au substrat (concentration à 5 ou 10 %). Après 30 jours d'incubation, nous avons déterminé la reproduction et les taux de mortalité des collemboles. Les résultats ont montré que les lixiviats avaient un impact plus important sur la fitness des collemboles comparé à la litière elle-même avec une

réduction des taux de reproduction et de survie. Entre 94 et 100 % des collemboles sont morts dans les microcosmes qui ont reçu les lixiviats de peuplier ou du mélange peuplier/épinette, ce qui indique l'importante influence négative des composés contenus dans les feuilles de peuplier sur les collemboles. Nos résultats ont également montré un important effet positif de la litière et des lixiviats à 10% d'herbacées sur la reproduction comparé au témoin.

Abstract

In boreal regions, rural depopulation in recent year induced extensive areas of abandoned agricultural land. These lands colonized by hay are often used to develop monospecific plantations of hybrid poplar (*Populus*) or white spruce (*Picea*). Since poplar, spruce and herbaceous species have different litter qualities, especially in their content of secondary metabolites, co-occurrence of these species in mixed plantations could impact soil communities and ecosystem functioning. Springtails (Collembola) play an essential role on decomposition processes, mainly by the indirect effect of stimulating or regulating microorganisms colonizing the litter by grazing. Even if the effects of soil conditions and the nature of organic matter on collembola are demonstrated, mechanisms by which structure of springtails communities is influenced by chemical quality of litters and their mixing, in particular allelochemicals, remain unclear. Leaching of litter is an important way of the liberation of allelochemicals. In order to know how litter quality can influence the decomposition process through its effect on springtails, laboratory tests were conducted with four litter types (hybrid poplar, white spruce, mixture of poplar / spruce and herbaceous hay species) on standard arthropods, *F. candida*, according to an adaptation of the standard ISO 11267. Ten individuals of *Folsomia candida* were bread in microcosms containing a standardized substratum to which we added separately poplar, spruce and herbaceous litter or a mixture of poplar and spruce litter. In order to take into account the availability variability of litter chemicals on Folsomia, other microcosms were set up by mixing litter leachates (at 5 % and 10 % concentration) to the substratum. After 30 days of incubation, reproduction and mortality rates of Collembola were determined. Results showed that leachates had stronger impacts on springtails fitness compared to the litter itself with a reduction of survival and reproduction rates. Between 94 and 100% springtail mortality was observed in microcosms that received leachates of poplar or mixed poplar/spruce litters, indicating a strong influence of the compounds contained in the poplar leaves

on springtails. However there was a positive effect of litter or the 10% leachates of herbaceous species on the reproduction rate compared to control.

3.1 Introduction

For the last two decades, short rotation forestry using fast-growing species has gained interest in response to worldwide increases in wood demand. In boreal regions, extensive areas of agricultural land have been abandoned in recent years due to rural depopulation (Vouligny and Gariépy, 2008). These lands colonized by hay are often used to develop monospecific plantations of hybrid poplar or white spruce. But the ecological suitability of tree species in silvicultural systems is a recurrent question, mainly regarding the effects of monocultures on the biodiversity of soil organisms. Mixing tree species in plantations has often been targeted to optimize ecosystem services such as ecosystem biodiversity and functioning all the while maintaining wood production (Hartley, 2002; Knoke et al., 2008). We previously showed that mixing spruce and poplar in plantations could be valuable to ecosystem services, such as tree productivity and soil carbon storage (Chomel et al., 2014a). Since poplar, spruce and herbaceous species have different litter qualities, especially in their content of secondary metabolites, co-occurrence of these species in mixed plantations could impact soil communities and ecosystem functioning. Physical and chemical characteristics of organic matter exert an important control on litter decomposition, mostly through the composition of soil fauna and decomposers communities. Soil microarthropods are dominated by groups like Acari and Collembola (Chomel et al., 2014b; Petersen and Luxton, 1982) that have important direct or indirect roles on decomposition processes. Some are microbivores and stimulate or regulate fungal colonization by grazing, while others are detritivores and participate directly to organic matter transformation by fragmenting and ingesting the litter. Decomposers are sensitive to the litter quality as shown by preference and colonization in choice experiments (Hättenschwiler and Bretscher, 2001; Joy and Joy, 1991; Rief et al., 2012). Collembola feed mainly on soil fungi and bacteria, but are considered to be detritivores because they derive nutritional benefits from the decomposing litter source (Das and Joy, 2009). Collembola can perceive chemical cues of fungi at a distance of 1 cm - 2.5 cm (Auclerc et al., 2010; Salmon and Ponge, 2001), prefer some fungal species over others (Hedĕnec et al., 2013; Scheu and Simmerling, 2004), and can suffer from reduced fitness from ingestion of specific fungal species (Klironomos et al., 1999; Scheu and Simmerling, 2004). Furthermore, collembolan raised on fungal-colonized litter show grazing preferences and reproduction rates that are more affected by litter type than by fungal species (Hedĕnec et al., 2013), demonstrating the strong influence of litter quality on springtails activity. Some plant species produce a great quantity of secondary metabolites against herbivory or parasitism (i.e. terpenes and phenolic compounds) or to resist against inter- and intraspecific competition in allelopathic mechanisms (Fernandez et al., 2006; Fernandez et al., 2013; Ormeño et al., 2007). Allelochemicals are released into the ecosystem through four ways: volatilization, foliar leaching, litter decomposition, and root exudation (Rice, 1984). They are considered to be recalcitrant to degradation and can limit the growth and activity of decomposer organisms, from macro-arthropods to micro-organisms (Hättenschwiler and Vitousek, 2000; Kuiters, 1990). Few studies have addressed the direct impact of chemical composition of litter, including secondary metabolites content, on the abundance and diversity of soil mesofauna. Das and Joy (2009) reported that a springtail (*Cyphoderus javanus* Börner) tended to avoid litter with greater amounts of secondary metabolites, and that those that did, exhibited lower fecundity and moulting rates (Das and Joy, 2009). Poinsot-Balaguer et al (1993) found that condensed and hydrolysable tanins extracted from oak leaves were toxic to Collembola (Poinsot-balaguer et al., 1993). However, these studies did not take into account the bioavailability of secondary compounds to organisms since total compound concentrations in litters are generally used. As some authors have shown that water-soluble compounds were probably most involved in allelophathy (Vyvyan, 2002), perhaps these soluble compounds are also most important for soil organisms.

Collembola communities are often used as soil quality indicators, due to their sensitivity to pollutant and environmental change, and are increasingly used as model organisms for soil arthropods (Fountain and Hopkin, 2005) and can be indicators of the nutritional quality of resources (Das and Joy, 2009). It has also been shown that mixed diets could significantly increase collembolan fitness, or at least at levels similar to the food with the greatest quality present in the mixture (Scheu and Simmerling, 2004). This finding could be explained by a balance in nutrient intake when there is a mixture of food resources (Scheu and Simmerling, 2004).

In this study, we compared the effect of four litter types and their leachates (hybrid poplar, white spruce, mixture of poplar/spruce and herbaceous) on standard arthropods, *F. candida* by using the modified ecotoxicological test proposed by the International Standards Organization (ISO) on effects of pollutants on reproduction of *Folsomia candida*. Previous in-situ studies showed i) a lower springtail abundance under poplar trees than spruce trees (Chomel et al., 2014c), and ii) that herbaceous species increased springtail abundance compared to poplar or spruce litter (Chapter 3), and iii) that the addition of herbaceous in poplar or spruce litterbags increased mesofauna abundance (Chapter 3). Based on this field experiment results, we sought to test the following hypotheses: (i) owing to the chemical properties of the different litter types studied, we expected to observe an effect of litter and leachates on fitness of *F. candida* in the followed order: herbaceous > poplar > mixed > spruce, with a positive impact of herbaceous litter and negative impact of spruce litter; (ii) litter leachates have a more pronounced impact on *F. candida* since nutrients and secondary compounds could be directly bioavailable for the Collembola.

3.2 Materials and methods

3.2.1 Litter and leachates

In late September 2010, three litter types (poplar, spruce and herbaceous) were collected from an experimental monospecific plantation of hybrid poplar (*Populus* *maximowiczii* A.Henry x *P. balsamifera* L.) and white spruce (*Picea glauca* [Moench] Voss) located in Amos (48°36'N, 78°04'W) in the boreal region of Abitibi-Temiscamingue, Quebec, Canada. Abscission of spruce needles and hybrid poplar leaves in which senescence was complete was aided by shaking the trees, and the fallen needles/leaves were collected on a plastic sheet that was placed on the ground beneath the trees to prevent soil contamination. Aerial parts of herbaceous species (mainly grasses, *i.e. Poa sp.*) naturally present were cut at ground level at the same period in the experimental plantation. Collected leaf material was homogenized and stored at room temperature prior to the experiment. Leachates of each litter (poplar, spruce and herbaceous) and a mixture of poplar and spruce (50:50) were prepared by soaking 100 g litter (air-dry weight) in 1 liter of deionized water (10 % dry weight) for 24 h in darkness. This concentration is the most commonly used in vitro allelopathy bioassays (Chen et al., 2013; Fernandez et al., 2013). Although they are higher than what is found in natural conditions, it allows studying the potential effect of a species (Bong-Seop 1992). Diluted solution at 5% was also prepared and used.

3.2.2 Chemical composition of litter and leachates

Litter initial content of major nutrients (C, N) and secondary metabolites (phenolic compounds) were estimated by standard methods; For C and N analysis, litter samples were finely ground with a ball mill (MM301, Retsch Inc., Newtown, PA), and carbon and nitrogen concentrations determined with a CHN elemental analyzer (Flash EA 1112 series, ThermoScientific, U.S.A.). Phenolics content was measured by the method of Folin-Ciocalteu (Folin and Denis, 1915) : 0.25 mL of filtered aqueous extract was mixed with 0.25 mL of Folin-Ciocalteu reagent and 0.5 mL of saturated aqueous Na_2CO_3 to stabilize the colour reaction, after which 4 mL of distilled water was added to dilute the extract. After 1 hour, the reaction was completed and measured at 765 nm on a UV/Vis spectrophotometer

(Thermoscientific, U.S.A.). Quantitative results were expressed with reference to gallic acid.

3.2.3 Breeding of Folsomia candida

Populations were composed of a single clone of the parthenogenetic collembolan species *Folsomia candida* (Willem) and were kept at 95–100% humidity and 20°C with food (dry yeast pellets) available *ad libitum*. Under these conditions, eggs hatched 10 days after laying and individuals became sexually mature 16 days after hatching. Populations were reared in plastic boxes containing a mixture of plaster of Paris and activated charcoal in a ratio 9:1 permanently water saturated flat. To synchronize age of the organisms, oviposition was stimulated by placing adult Collembola on a new breeding substrate (Fountain and Hopkin, 2005). After oviposition, adults were removed; the eggs hatched 3-4 days later. To ensure that juveniles were as homogeneous as possible, they were placed in a large container and were fed for the first time altogether.

3.2.4 Reproduction test

The *F. candida* reproduction test was carried out according to an adaptation of the ISO standard 11267 (ISO 11267, 1999). For each treatment of the assays (leachates at 5, 10% and poplar, spruce, mixture of poplar/spruce and herbaceous litter), ten 10–12-day-old juveniles were introduced into 120-mL plastic bottles with screw caps containing 32 g of wet artificial soil. The artificial soil consisted of 70% quartz sand, 20% kaolinite, and 10% peat ground, dried, and sieved to 0.5 mm with the pH adjusted to 6 ± 0.5 by the addition of $CaCO_3$. It was moistened to 50% of water holding capacity with distilled water (about 7 mL). Chemicals to be tested in this ISO norm are generally pollutants dissolved in water at the range of concentrations that will give appropriate reproduction of reduction levels (LOEC, CE 50). Here, 7 mL of leachate was directly mixed into the soil, and for the litter treatments, distilled water was added to the substrate, and 1g (corresponding to the amount of litterfall per surface area in natural plantations, Chomel et al, 2014) of coarsely chopped litter were rehumidified and placed above the substrate. Five replicates per treatment were made, with 5 controls humidified with deionised water and without litter, for a total of 65 pots. The pots were placed within a room giving a controlled temperature of 20°C and continuous darkness. They were opened twice a week for aeration and fed with baker's yeast (about 2 mg) at the initial time and after 2 weeks. The assay was stopped after 28 days as recommended in the ISO guidelines. The pots were flooded with tap water and gently stirred before the floating animals were counted. Mortality rate was estimated by the ratio: number of adults at the end of the test over the initial number of adults, while the reproduction rate was estimated as the number of juveniles at the end of the test.

3.2.5 Statistical analysis

A Negative Binomial GLM (*i.e.*, a specific version of a Poisson model that uses an additional parameter to correct for data over-dispersion) with a log link function was used to compare the number of offsprings in the different litter types (poplar, spruce, mixture poplar/spruce and herbaceous litters) and modalities (litter, leachates at 5 or 10%, control). Negative Binomial GLMs are designed to fit count data (data that usually lacks normality), as it is generally the case when sampling invertebrate taxa. Chi-Square test (X^2) was used to test the general hypothesis that our treatments (litter and modality) had a significant explanatory power. A binomial GLM was used to compare the mortality rate in the different litter types and the control and the different modalities. Binomial GLMs are designed to fit proportions or percentages. For chemical data, ANOVAS were performed to test differences between litter types. After these analyses, multiple comparisons (Tukey contrasts) were done. All statistical analyses were done with R v.3.1.0 (R Development Core Team, 2011).

3.3 Results

3.3.1 Chemical composition of litter

Spruce litter presented greater C concentrations, while herbaceous litter had greater N concentrations compared to the three other litter types (ANOVA, $P < 0.001$, Table 3.5). Consequently, herbaceous litter had the lower and spruce litter the greater C/N ratios, while poplar and mixed litters had intermediate values ($P < 0.001$).

Table 3.5 Initial concentrations of C and N and C / N ratio of the different litter types. Results of Anova are indicated in the last column.

Initial litter quality	Litter species				N	F value
	Herbs	Poplar	Spruce	Mixed		
C (% DM)	36.9 ± 1.1 (a)	38.1 ± 1.2 (a)	44.0 ± 1.4 (b)	38.6 ± 1.5 (a)	97	6.04***
N (% DM)	0.65 ± 0.03 (b)	0.49 ± 0.02 (a)	0.50 ± 0.02 (a)	0.50 ± 0.01 (a	97	13.9***
C/N	58.5 ± 2.1 (a)	78.8 ± 3.4 (b)	89.4 ± 3.6 (c)	77.3 ± 2.3 (b)	97	22.7***

Note : *** indicate significant differences among litter species ($P < 0.001$)

Concerning secondary metabolites, litter phenolic content was lower for herbaceous compared to the three other litter types (ANOVA, $P < 0.001$, Figure 3.7). Phenolic content of leachates corresponded to 36, 7, 31, and 38% of the contents found in litters, respectively for herbaceous, spruce, mixed and poplar litters (Figure 3.7). Herbaceous and spruce litter leachates contained lower amounts of phenolic compounds compared to poplar and mixed litters (ANOVA, $p < 0.005$, Figure 3.7).

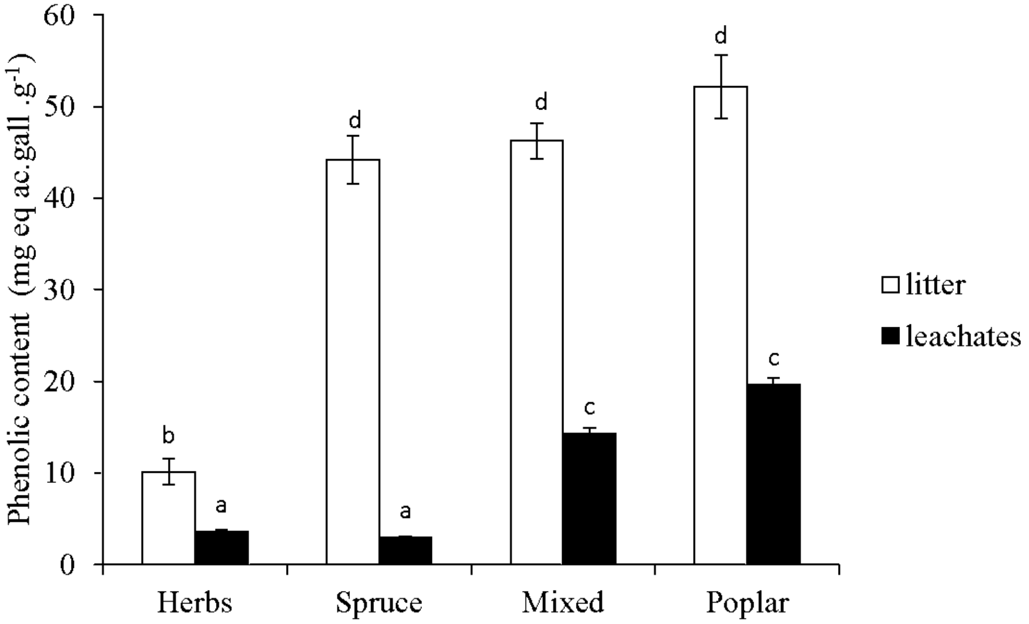

Figure 3.7 Mean (± SE) phenolic content of litters (white bars) and leachates at 10% concentration (black bars).

3.3.2 Effects on survival

Survival of *F. candida* differed across combinations of litter types (X^2 = 63.1, *P* <0.001) and modalities (X^2 = 259.7, *P* < 0.001) with a significant interaction term (X^2 = 57.5, *P* <0.001). Only herbaceous and mixed litters had no effect on springtail survival compared to control; Spruce and poplar litter reduced survival by 42 and 48% compared to control, respectively (Tukey contrasts, P<0.05, Figure 3.8a). Only 10% herbaceous litter leachates had no effect on springtail survival compared to the control; all other leachates had a significant negative effect on springtail survival. Mortality reached 98 and 100% for mixed and poplar 10% leachates, respectively (linear contrasts, P<0.05, Figure 3.8a).

3.3.3 Effects on reproduction

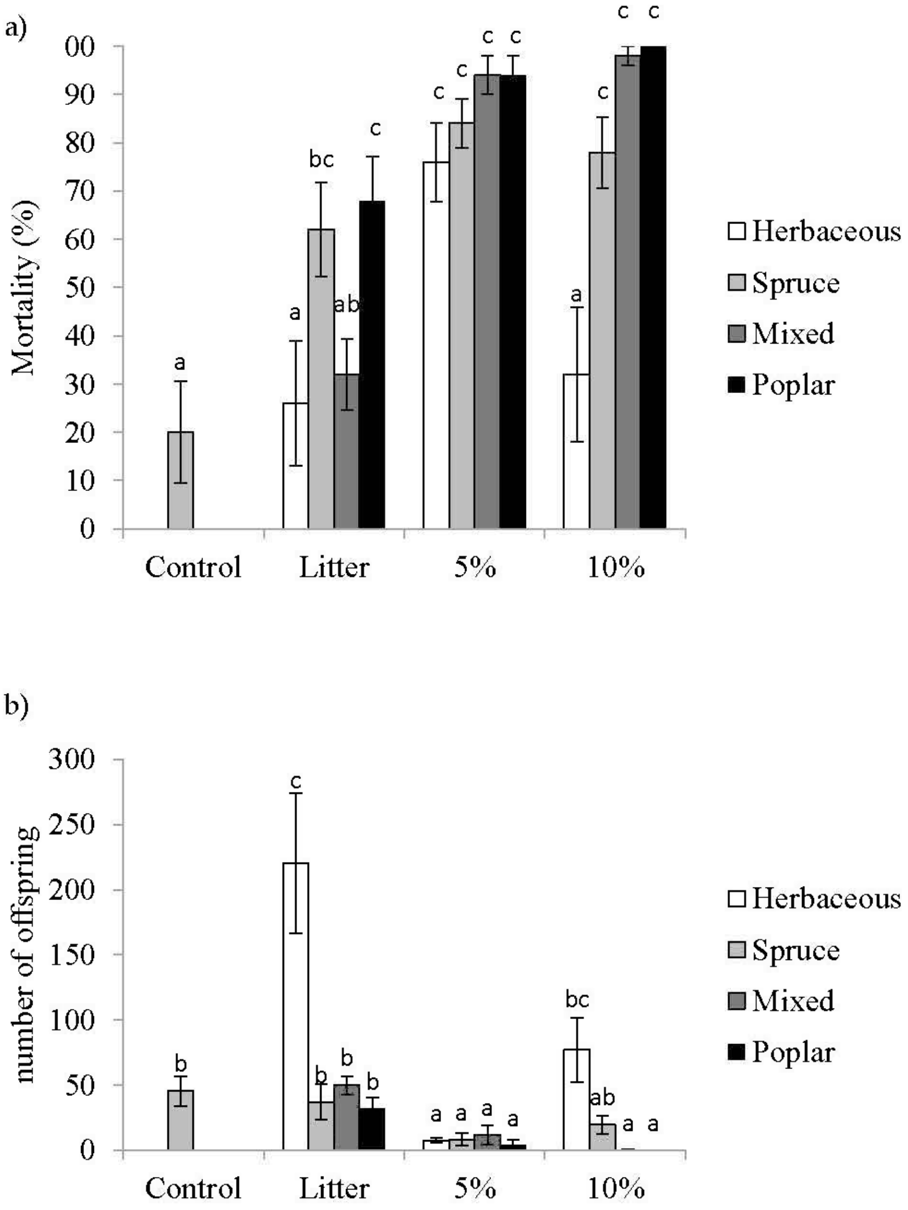

Figure 3.8 Mean (± SE) percent mortality (a) and reproduction (b) of *F. candida* growing in mesocosms with the different litter types and modalities. Different letters denote significant differences according to linear contrasts.

Reproduction of *F. candida* differed across combinations of litter types (negative Binomial GLM, $X^2 = 39.4$, $P < 0.001$) and modalities (Binomial GLM, $X^2 = 70.5$, $P < 0.001$) with a significant interaction term (Binomial GLM, $X^2 = 75.7$, $P < 0.001$. Reproduction of *F. candida* was greater on herbaceous litter compared to the control, while all other litter types had no effect on springtail reproduction (Figure 3.8b). Five percent leachate of all litter types reduced reproduction, while only poplar and mixed litter 10% leachates lowered reproduction. However, reproduction was greater with 10% leachates of herbaceous than poplar and mixed litters, while spruce litter leachates showed intermediate value (Figure 3.8b).

3.4 Discussion

The main finding of the study was that leachates had a stronger impact on *F. candida* fitness compared to litters themselves, but this effect depended on each litter type. Furthermore, herbaceous litter had a positive effect on the fitness of *F. Candida* and this result is in line with *in-situ* litter decomposition studies where we observed greater abundance of organisms associated with spruce and poplar litters in mixture with herbaceous litter (Chomel et al, in prep).

3.4.1 Effects of litters

Herbaceous litter improved survival and reproduction of springtails, as expected; Nutritional quality of decomposing litter depends on the chemical constituents of leaf tissues (Das and Joy, 2009; Hedĕnec et al., 2013). Herbaceous litter had relatively low C/N ratios and phenolics contents, indicating greater concentrations of carbohydrates and proteins. This labile organic matter of herbaceous species provides a readily available energy source to decomposers (Aber et al., 1990; Aerts, 1997), and induced better conditions for feeding and reproduction of springtails (Das and Joy, 2009), which most likely explains why herbaceous litter improved survival and reproduction of *F. candida*. Mixed litter produced similar survival rates than herbaceous litter, but lower reproduction. This result confirms the benefit of the "high" litter quality on enhanced fecundity of *F. candida* (Booth and Anderson, 1979; Scheu and Simmerling, 2004). Feeding on high quality food generally shortens the period until oviposition starts (Scheu and Simmerling, 2004).

Poplar litter had lower C/N ratios and similar phenolic concentrations than spruce litter, and both litter types negatively affected survival similarly. With this result we can hypothesize that secondary metabolic content could have a greater impact than nutrient content. Whereas spruce and poplar litters had negative effect on the survival of *F. candida* compared to control, when these two litter types were mixed, survival was similar to the control or herbaceous litter; Mixed diets may significantly increase collembolan fitness, by a balance in nutrient intake from the different litters present in the mixture or by a dilution of toxic compounds (Scheu and Simmerling, 2004). Since the two litter types had high contents of secondary metabolites and have relatively high C/N ratio, a "dilution" was not possible, however the lower mortality observed in mixed litter could indicate a positive effect of resources diversity surpassing the negative effect of toxic compounds. Although mixing the two litters increased survival compared to single species litter, it had no effect on reproduction.

3.4.2 Effects of leachates

According to our second hypothesis, leachates had a greater impact on our springtails compared to the effects of litters. Compounds present in the leachates, as well as secondary metabolites, can act as carbon and other nutrient sources for decomposer organisms and are directly bioavailable, contrarily to compounds present in the litter itself. However, other secondary metabolites, that can act as allelochemicals, could also become more available and so have a greater impact than when these compounds are trapped in the litter. It appears that phenolic compounds were more watersoluble in poplar litter, since 38% of phenolic compounds of poplar litter were found in the leachates, against 7% for spruce leachates. Microcosms that received 10% leachates of poplar or mixed poplar/spruce showed 100 and 94 % of mortality, respectively, whereas spruce leachates only induced 78% of mortality, indicating a strong influence of the compounds contained in the poplar leaves on springtails. The greater bioavailability of poplar compounds could explain why this litter induced stronger effects compared to spruce litter. Whereas we observed a negative effect of 5% leachates of all litters on reproduction and mortality compared to the control, 10% herbaceous leachates increased survival and reproduction. This results is surprising, but perhaps can be explained by a greater quantity of nutrients in these leachates, whereas labile compounds in the 5 % leachates were probably not sufficient to observe a positive effect.

Leaching of leaves and litter is an important process in ecosystem functioning since a great quantity of compounds is rapidly released, contrarily to their liberation by decomposition of organic matter. Litter leachates are rarely taken into account in microcosm studies, whereas this study showed that they contain available compounds which are significant drivers of Collembola fitness.

3.5 Conclusion

Litter types significantly affected *F. candida* mortality and reproduction. Herbaceous litter increased survival and reproduction of springtails, while poplar litter had the strongest negative impact on survival and reproduction. This study also showed that leachates had greater impacts on the springtails fitness compared to litter itself, with a positive effect of herbaceous leachates, and negative effects of all other leachate types. The high mortality in microcosms that received poplar or mixed poplar/spruce leachates indicates a strong influence of the compounds contained in poplar leaves on springtails. Phenolic compounds in poplar leaves were more leachable than in spruce leaves, which could explain this stronger negative effect of poplar leachates. This study shows that litter chemistry is an important factor for *F. candida* fitness, and could be determinant for mesofauna communities in natural ecosystems.

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CHAPITRE IV

EFFETS DES HERBACÉES SUR LE PROCESSUS DE DÉCOMPOSITION

Figure 4.1 Photo d'une plantation mixte de peuplier hybride et d'épinette blanche avec un espacement de 3 x 3 m colonisée par les herbacées.

Ce chapitre correspond à un article qui sera soumis à Plant and Soil

"Effect of the mixing of herbaceous litter with tree litters on decomposition and N release in intensive sylvicultural system"

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Résumé

Depuis le 19^{e} siècle l'abandon de terres agricoles s'est répandu en Amérique du Nord. Ces terres abandonnées sont de plus en plus utilisées pour établir des plantations à croissance rapide, dans lesquelles s'installe une importante densité d'herbacées en comparaison des forêts naturelles. Ces herbacées généralement considérées comme des "mauvaises herbes" pouvant limiter la croissance des arbres en entrant en compétition pour les ressources, sont généralement éliminées dans les systèmes sylvicoles intensifs. Cependant, la présence de litière d'herbacées dans ces plantations pourrait aussi avoir des effets positifs sur la productivité des arbres en améliorant les conditions micro-environnementales, la décomposition des litières et ainsi la libération d'éléments nutritifs. Dans la présente étude nous avons voulu déterminer l'impact des herbacées sur le processus de décomposition et la libération des nutriments, des litières d'épinette blanche (*Picea glauca*) et de peuplier hybride (*Populus maximowiczii* x *P. balsamifera*) dans des plantations monospécifiques ou mixtes. Nos résultats ont montré que la présence de litière d'herbacées dans les litter bags accélérait la libération d'azote de la litière de peuplier, d'épinette et du mélange peuplier / épinette. Cette différence pourrait être directement liée à l'augmentation de l'abondance de la mésofaune et de la biomasse fongique provoquée par la présence de litière d'herbacées. La décomposition de chaque type de litière d'arbre en mélange avec les herbacées a montré que seulement la décomposition du peuplier et du mélange de peuplier/épinette a été améliorée. La litière d'épinette, quant à elle, s'est décomposée à la même vitesse quand elle était seule ou en mélange avec les herbacées. Ce résultat confirme que la performance individuelle de chaque type de litière dans le mélange dépend plus fortement de son identité que de l'identité des autres types de litières contenues dans le mélange. La litière d'herbacées semble avoir un effet positif sur le processus de décomposition et la libération de l'azote, ce qui pourrait contrebalancer l'effet négatif potentiel de la compétition pour les ressources avec les arbres.

Abstract

Widespread abandonment of agricultural land has occurred in northeastern North America over the past two centuries. These abandoned lands are increasingly used to establish fast-growing plantations, promoting a high density of herbaceous undergrowth compared to natural forests. Since weeds can inhibit growth of planted trees by competing for resources, they are generally removed in intensive silvicultural systems. However, the presence of herbaceous litter in those plantations could also have some positive effects on tree productivity by improving micro-environmental conditions, litter decomposition and associated nutrient release. In the present study we wanted to determine the impact of herbaceous species on litter decomposition processes and nutrient release of white spruce (*Picea glauca*) and hybrid poplar (*Populus maximowiczii* x *P. balsamifera*) litters in monospecific or mixed species plantations. Our results showed a large increase of N release of poplar, spruce and mixed poplar / spruce litters with the presence of herbaceous litter. This finding could be directly linked to greater abundance of decomposers and fungal biomass brought about by the herbaceous litter. Decomposition of each litter type mixed in with herbaceous litter showed that only decomposition rates of poplar and the mixture poplar/spruce litters were enhanced compared to trees' litters alone, while spruce litter decomposed at the same rate when it was alone or mixed in with herbaceous litter. This result confirmed that the individual performance of each litter types in mixture depended more strongly on its identity than on the identity of neighbor species contained in the mixture. Herbaceous litter seemed to have a great positive effect on decomposition processes and N release, which could counteract the potential negative effects of their presence on tree growth.

4.1 Introduction

There is increasing interest to establish fast-growing plantations in boreal regions to reduce harvesting pressure on natural forests. Abandoned agricultural lands are interesting to establish fast-growing plantations for two reasons: i) they are often close to the mills and decrease the need and costs of wood transportation; ii) they revitalize available lands with an economically promising alternative regarding the anticipated shortfall in fiber sources (Vouligny and Gariépy, 2008). Boreal tree plantations established on abandoned farmlands are often rapidly invaded by a high density of herbaceous undergrowth comparing to natural forests (Gachet et al., 2007). Traditionally, understorey vegetation has been considered an inhibiting factor in silviculture, because it intensifies the competition for resources (light, water and nutrients) with the planted trees (Chang et al., 1996). Thus, many authors suggested that weed suppression is essential to the establishment of trees in short-rotation intensive plantations until canopy closure outcompetes them (Dickmann et al., 2001; Labrecque et al., 1994) . However, the presence of herbaceous litter in those plantations could also have some positive effects on tree productivity by increasing litter decomposition and associated nutrient release. Indeed, litter mixtures have been found to enhance decomposition rates, mainly when litters are chemically dissimilar (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Lecerf et al., 2011) or when plant species with particular functional traits (named functional types, *i.e.*, nitrogen-fixing legumes, C4 grasses) are present in the mix (De Deyn et al., 2008; Fornara and Tilman, 2008). Furthermore, herbaceous litter can play an important role in maintaining high humidity levels (Xiong et al., 2008) and in bringing organic matter rich in labile compounds (Hoorens et al., 2002; Wise and Schaefer, 1994). Humidity and litter quality are known to be determinant factors for soil organism's abundance and for decomposition processes. More labile substrates improve decomposition processes and the activity of decomposers. For example, Milcu et al., (2006) found that collembola density was increased by 66% in the presence of grasses in mesocosms. Although this knowledge is important to optimize intensive silviculture scenarios, the understorey vegetation of plantations on abandoned agricultural land in the boreal region is a quite scantily researched topic (Soo et al., 2009; Weih et al., 2003).

In recent years, extensive areas of agricultural land have been abandoned in eastern North America, Europe, East Asia and South America (McLauchlan, 2006), mainly due to rural depopulation, industrialization or land mismanagement (Rey Benayas et al., 2007). In the province of Quebec, 100,000 ha of abandoned agricultural lands were surveyed between 1997 and 2007 (Vouligny and Gariépy, 2008) and are available to establish fast-growing hybrid poplar plantations. The rapid growth rate and high yield potential of such plantations both explain the growing interest for this type of production system (Weih, 2004). Forest regeneration standards in Canada are creating pure coniferous stands after harvest (Lieffers et al., 2008). White spruce is one of the most important conifer species for the sawmilling and pulpwood in Canada. Recent research showed that mixing both species in intensive silvicultural systems could improve productivity and carbon storage (Chomel et al., 2014a). In such plurispecific plantations with increased tree and litter diversity, does herbaceous litter contribution to nutrient cycling differ compared to monospecific plantations?

In the present study we wanted to determine the impact of herbaceous species on litter decomposition processes and nutrient release of white spruce (*Picea glauca*) and hybrid poplar (*Populus maximowiczii* x *P. balsamifera*) litters. This experiment was done in monospecific poplar or spruce plantations and in mixed plantations of poplar and spruce. A thick herbaceous understory had developed in all plantation types. We monitored soil microbial activity, fungal biomass and mesofauna abundance for a two-year period in litterbags with poplar, spruce, mixed poplar/spruce and herbaceous litters alone or in mixture in the three plantation types. We hypothesized that i) herbaceous litter increases humidity of spruce, poplar and mixed litters, ii) herbaceous litter increases mesofauna abundance and microbial activity, and so N and

C release of spruce, poplar and mixed litters iii) mixing effect with herbaceous litter would be more pronounced in spruce litter than poplar litter since the chemical composition between the two litters is more dissimilar, iii) herbaceous litter has a stronger effect in mixed plantations due to a more diverse litter.

4.2 Materials and methods

4.2.1 Site description

The study was located in the boreal region of Abitibi-Temiscamingue, Quebec, Canada. Three sites were selected for study : Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was abandoned farmland with a heavy clay soil that was dominated by grasses and sparse patches of alder (*Alnus incana* [L.] Moench ssp. *rugosa* [Du Roi] R.T. Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was an abandoned farmland site with heavy clay soil, which was also dominated by shrubs, including patches of alder, willow, and trembling aspen. Nédelec had been previously dominated by trembling aspen forest, which was commercially harvested in 2000. This last site was characterized by soils with a sandy loam texture. Based on the 30-year running climate average (1970-2000), Amos and Rivière Héva receive an annual mean 918 mm of precipitation (Amos station) and have a mean temperature of 1.2 °C, while Nédelec has mean precipitation of 916 mm year^{-1} and a mean temperature of 1.9 °C (Remigny station, Environment Canada 2014). Site preparation was conducted in 2002, where tree stumps were removed and soils were ploughed to a depth of about 30 cm. The plantations were established in 2003, using one hybrid poplar clone (*Populus maximowiczii* A.Henry x *P. balsamifera* L., clone MB915319), and an improved white spruce family (*Picea glauca* [Moench] Voss). These two species were planted in both mono-specific and mixed species plots under 1 × 1 m spacing. For the mixed plantation, each row consisted of spruce alternating with poplar. Each experimental unit contained 36 trees (6 × 6 trees).

4.2.2 Litter decomposition experiment

In late September 2010, spruce needles and hybrid poplar leaves were collected from plantations that were close to the Amos study site. Abscission of needles or leaves in which senescence was complete was aided by shaking the trees, and the fallen needles/leaves were collected on a plastic sheet that was placed on the ground beneath the trees to prevent soil contamination. Herbaceous species (majority of grasses, *i.e Poa* sp.) naturally present at the Amos site were cut at ground level during the same time and from the same plantation site. Collected leaf material was homogenized and stored at room temperature prior to the experiment. A subsample of each species was oven-dried at 60 °C to establish the relationships between air-dried and oven-dried mass. Seven grams (air-dried) of either poplar (P), spruce (S) and herbaceous litter (H) and their mixing (M for the mixture poplar/spruce, PH, SH, and MH) were placed in 1-mm mesh litter bags (10 × 15 cm for spruce mono-specific litter and 15 x 15 cm for all other litter type and their mixing) to allow colonization by soil mesofauna and microbes, while excluding macrofauna (Swift et al., 1979). We used pairs of litterbags with one bag being used for chemical and microbial measurements and the other for mesofauna extraction. To prevent losses of spruce needles through the net mesh during handling, a sheet of paper was inserted into each litterbag with spruce needles. These sheets of paper were removed and the litterbags were finally closed just before they were placed on the soil. The dimensions of the litterbags containing spruce needles was smaller than those for poplar leaves, to create the same litter incubation conditions among litter types and to prevent needle losses.

In November 2010, 12 pairs of litterbags with spruce litter, 12 pairs of litterbags with herbaceous litter, and 12 pairs of litterbags with their mixing were randomly deposited around 12 trees in the spruce plantations. The design was similar for poplar plantations, with poplar litter in place of spruce litter. In mixed plantations, 24 pairs of mixed poplar/spruce litterbags, 24 pairs of herbaceous and 12 pairs of their mixing were placed, half under poplar and half under spruce trees. This was repeated at the 3 sites (replicates), resulting in a total of 576 litterbags (2 litter species x 4 plantations types x 3 sites x 24 litterbags = 576). Freshly fallen litter was removed from the surface of the forest floor prior to placing the litterbags on the ground surface, and then replaced over the litterbags. Litterbags were fixed with one galvanized nail to prevent movement by animals or by the wind. After 5, 11, 18 and 24 months, 3 pairs (pseudo-replicates) of litterbags were retrieved from around three randomly chosen trees at each site. Sampling dates corresponded to snowmelt and anticipated snowpack development, generally mid-May and early or mid-October, respectively.

4.2.3 Litter bag processing

The first litterbag of each pair was used for mesofauna extraction, after which it was oven-dried at 60°C for 3 days. An aliquot of the second litterbag was used for microbial analysis and the remainder of the sample were freeze-dried (Lyovac GT2®) for chemical analysis. To prevent soil contamination of litter, we wiped each needle/leaf thoroughly before analysis. At t_0, 26 samples of each litter type (7 g air-dried) were used to determine initial litter quality.

4.2.4 Mass loss and litter water content

Litter decomposition rates were determined from the full set of litterbags. Mass loss was expressed as the percentage of total initial dry mass. Litter water content was calculated with the ratio (remaining fresh mass – remaining dry mass) / remaining fresh mass.

4.2.5 Mesofaunal extraction

Mesofauna were extracted from fresh litter using the dry funnel method (Berlese, 1905). Organisms were stored in 70 % alcohol, counted using a binocular scope, and identified to family for Collembola (Gisin, 1960) and to order for Acari (Gamasida, Acaridida, Actinedida, Oribatida; (Coineau, 1974). Other invertebrates were separated according to taxa (e.g., Arachnida, Diplopoda, Chilopoda, Araneae, Hymenoptera, etc.).

4.2.6 Fungal biomass

Fungal biomass was determined by quantifying ergosterol, a fungal membrane constituent and good indicator of living fungal biomass (Gessner and Chauvet, 1993; Ruzicka et al., 2000). Samples were frozen and lyophilized to enable more efficient extraction of ergosterol (Gessner and Schmitt, 1996). Ergosterol was extracted from 50 mg of needles/leaves with 5 mL of an alcohol base (KOH/methanol 8 g L^{-1}) for 30 min, and purified by solid-phase extraction on a Waters® (Milford, MA, USA) Oasis HLB cartridge (Gessner and Schmitt, 1996). The extract that was produced was purified and quantified by high-performance liquid chromatography (HPLC) on a Hewlett Packard series 1050 system running with HPLC-grade methanol at a flow rate of 1.5 mL min^{-1}. Detection was performed at 282 nm, and the ergosterol peak was identified based on the retention time of an ergosterol standard.

4.2.7 Catabolic profiles of microorganisms

Microbial (fungal and bacterial) catabolic profiles were assessed using Biolog® EcoPlates (Biolog Inc., Hayward, CA, USA) for all sampling dates using a procedure adapted from (Garland and Mills, 1991). We purposely did not adjust inoculum concentration because we considered total microbial number to be an inherent characteristic of microbial communities in each sample. To have enough fresh material, the three pseudo-replicates in each plantation were pooled, with the three sites remaining as replicates. Briefly, 2 g (dry mass equiv.) of ground litter were stirred in 100 mL of a sterile 0.1% tetra-sodium pyrophosphate solution for 1 h to suspend microbial communities. Each 96-well plate contained 3 replicate blocks of a water blank and 31 of the most useful carbon sources for soil community analysis, nine of which are considered as constituents of plant root exudates (Preston-Mafham et al., 2002). A 125 µL aliquot of extract solution, diluted 1:110, was added to all 96 wells in each EcoPlate. The plates were incubated at 30 °C for 7 days, and absorbance was measured at 595 nm on a microplate spectrophotometer (Multiskan GO, Thermo Fisher Scientific). Different microbial communities can exhibit different patterns of substrate use, as revealed by the ensuing colorimetric reactions. The average metabolic response (AWCD, average well colour development) for EcoPlates is analogous to community functional abundance, and was calculated for each sample after 5 days of incubation by dividing the sum of the optical density data by 31 (total number of substrates) (Garland, 1996). The community metabolic diversity for EcoPlates is analogous to community functional richness (richness), and is calculated for each sample after 5 days of incubation by summing the number of positive responses (well color formation) observed (Stefanowicz, 2006). A threshold optical density above which the well color formation indicates carbon source utilization was set at optical density ≥ 0.2.

4.2.8 Data analyses

Through this paper, data in mixed plantations resulted to the means of data collected under poplar trees and under spruce trees in mixed plantations. All statistical analyses were performed using R version 3.1.0 (R Development Core Team 2008). Mean values (humidity, litter mass remaining, ergosterol, mesofauna abundance) were compared among decomposition times and litter types for each plantation type using linear mixed-effects models using the *lme* function in the *nlme* package (Pinheiro et al., 2014). Site replicates were treated as random effects. If the effect of treatment was significant, the different treatments were compared with pre-planned linear contrasts (differences are noted in the manuscript as a < b < c). As for biolog data, the three pseudo-replicates in each plantation were pooled, ANOVA were used to compare AWCD and catabolic richness among litter type in the different plantations, followed by Tukey tests.

4.3 Results

4.3.1 Initial litter quality

Herbaceous litter had significantly greater N content than the three other litter types (spruce, poplar, mixed; Table 4.1) and similar C content than poplar and mixed litters (Table 1). Spruce litter had greater C content than herbaceous and poplar litter, while mixed litter had intermediate values. Consequently, herbaceous litter had lower C/N ratio, and spruce litter had greater C/N ratio than poplar and mixed litters (Table 4.1). Phenolic content was significantly lower in herbaceous litter compared to the three other litter types (Table 4.1).

Table 4.1 Initial C, N, and phenolics concentrations and C/N ratio of the four different litter types (mean ± SE). Results of Anova are reported on the right side, with significant differences indicated with *0.05, **0.01, ***0.001. Different letters within a row denote significant differences according to Tukey tests (0.05 significance threshold).

Initial litter quality	Litter species				N	F value
	Poplar	Spruce	Mixed	Herbaceous		
C (% DM)	38.01 ± 1.15 (a)	42.35 ± 1.51 (b)	38.61 ± 1.45 (ab)	36.86 ± 1.09 (a)	101	4.18**
N (% DM)	0.53 ± 0.03 (a)	0.50 ± 0.02 (a)	0.50 ± 0.01 (a)	0.65 ± 0.03 (b)	101	13.47***
C/N	76.65 ± 3.98 (b)	86.73 ± 3.47 (c)	77.33 ± 2.33 (b)	58.89 ± 2.22 (a)	101	17.97***
Phenolics (mg g^{-1} DM)	52.20 ± 3.45 (b)	44.20 ± 2.61 (b)	46.26 ± 1.96 (b)	10.16 ± 1.37 (a)	28	81.99***

4.3.2 Litter water content

Globally there was no difference of litter water content between litter types. The main effect of the addition of herbaceous litter in the litterbags containing tree litter occurred at 18 months of decomposition where it greatly increased (+ 32%) the water content in the mixture spruce / herbs compared to spruce litter alone (lme, interaction litter*herbs : $F_{1,45} = 24.5$, $P < 0.01$, Table 4.2).

Table 4.2 Mean water content (%) (± SE) of each litter types with or without herbaceous during decomposition time. Different letters within each decomposition time and plantation type represent a significant difference between means according to linear contrast.

Plantation type	litter	Decomposition time (months)			
		7	11	18	24
Spruce	S	17.4 ± 3.7	17.6 ± 2.3 (ab)	3.6 ± 1.5 (a)	57.0 ± 3.4
	SH	18.3 ± 3.5	21.7 ± 3.2 (b)	35.7 ± 7.5 (c)	56.3 ± 2.2
	H	19.4 ± 5.6	13.7 ± 2.0 (a)	15.7 ± 5.1 (b)	60.5 ± 3.5
Poplar	P	16.9 ± 2.5	11.8 ± 2.2	3.2 ± 1.3	64.6 ± 1.1
	PH	15.7 ± 3.3	15.4 ± 1.3	4.2 ± 1.5	65.4 ± 1.2
	H	19.7 ± 6.0	10.5 ± 1.3	2.5 ± 0.7	61.8 ± 3.3
Mixed	M	16.2 ± 2.2	10.9 ± 1.9	3.2 ± 0.7	55.6 ±2.5 (ab)
	MH	15.3 ± 3.4	14.9 ±2.4	6.1 ± 2.2	50.3 ± 3.5 (a)
	H	17.4 ± 4.8	9.9 ± 1.5	4.6 ± 1.2	61.3 ± 2.1 (b)

4.3.3 Litter mass remaining

At 7 months of decomposition, herbaceous litter addition had no effect on mass remaining of tree litters in their corresponding plantations (Fig. 4.2). At all other sampling dates, herbaceous litter had no effect on spruce litter decomposition in spruce plantation but had positive effects on poplar litter in poplar plantations (all dates, lme, $P < 0.05$, Fig. 4.2). In mixed plantations, herbaceous increased mixed litter decomposition at 18 and 24 months. However, we observed only sporadic and slight effect of mixing herbaceous and tree litters on herbaceous litter decomposition. After two years, poplar and mixed litters were 30% and 20% more decomposed, respectively, when mixed with herbaceous litter compared to tree litter alone.

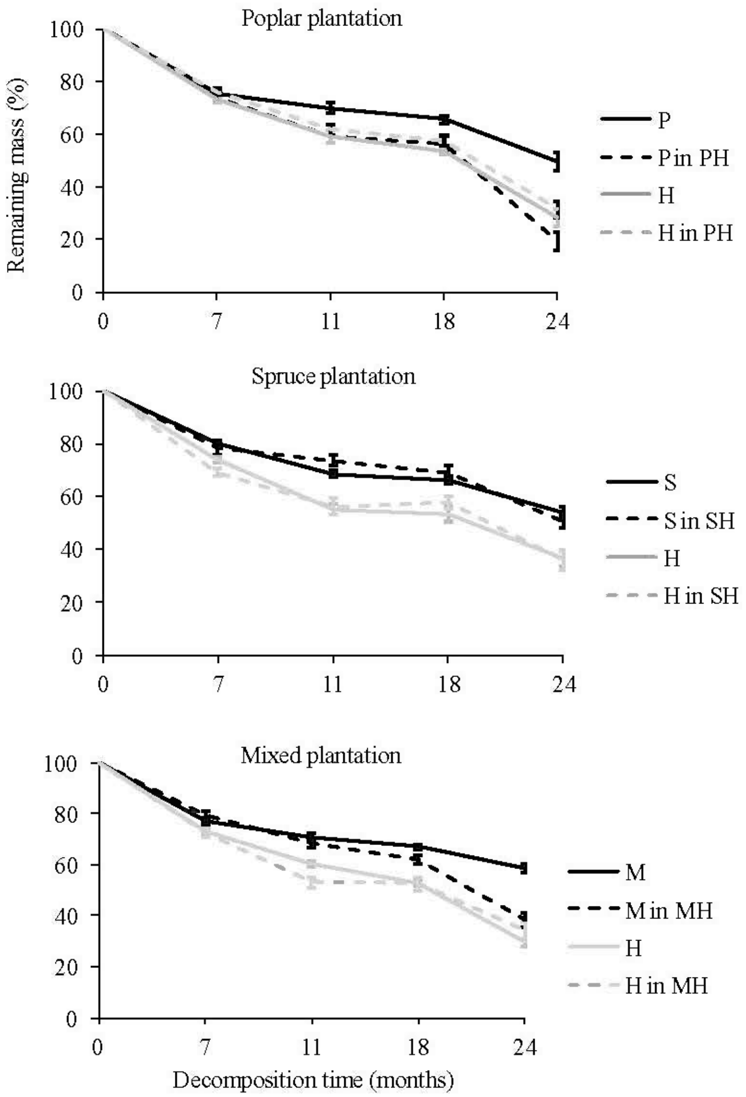


Figure 4.2 Mean (± SE) remaining mass of herbs (H), poplar (P), spruce (S) or mixed (M) tree litters in their respective plantations alone or in mixture with herbaceous litter (H), but segregated for remaining mass measurement.

4.3.4 Mesofauna

Globally, the abundance of mites was greater in herbaceous litter alone or mixed with tree litters compared to tree litters alone in the three plantation types, all along the experiment (lme, litter type, $P < 0.05$, Figure 4.3). Springtails' abundance was generally greater in herbaceous litter alone and/or added to tree litters in all plantation types, but results differed among dates and litter types; There were significantly less springtails in poplar litter compared to herbaceous or in PH mixture at 11 months of decomposition in poplar plantations (litter type, $F_{2,22} = 3.9$, $P = 0.04$). At 18 and 24 months of decomposition, springtails were more abundant in the mixture PH than in poplar and herbaceous litters alone (litter type, $F_{2,22} = 4.3$ and $F_{2,22} = 2.9$, $P < 0.05$ for 18 and 24 months respectively). Springtails' abundance in spruce plantations was significantly lower in S litter than in SH mixture, while the herbaceous litter had intermediate values (litter type, $F_{2,95} = 10.5$, $P < 0.01$, Figure 4.3). There were significantly less springtails in mixed litter compared to herbaceous and MH litters at 11 months of decomposition, in mixed plantations (litter type, $F_{2,22} = 4.2$, $P = 0.03$, Figure 4.3). At 24 months of decomposition, abundance of springtails was greater in the mixture MH compared to the two other litter types (litter type, $F_{2,22} = 5.9$, $P < 0.01$, Figure 4.3). The abundance of predators was lower in poplar litter compared to herbaceous and PH litters at 7 months of decomposition (litter type, $F_{2,22} = 3.9$, $P < 0.01$, Figure 4.3). In spruce plantations, predators had the lowest abundance in spruce litter, then in the mixture SH, and finally greater predator abundance in herbaceous litter (litter type, $F_{2,22} = 19.6$, $P < 0.01$, Figure 4.3). In mixed plantations, predator abundance was significantly greater in herbaceous litter compared to mixed and MH litters at 7 and 11 months of decomposition (litter type, $F_{2,22} = 37.5$, and $F_{2,22} = 13$, respectively, $P < 0.01$, Figure 4.3). There was no difference in predator abundance between litter types at all the other sampling dates.

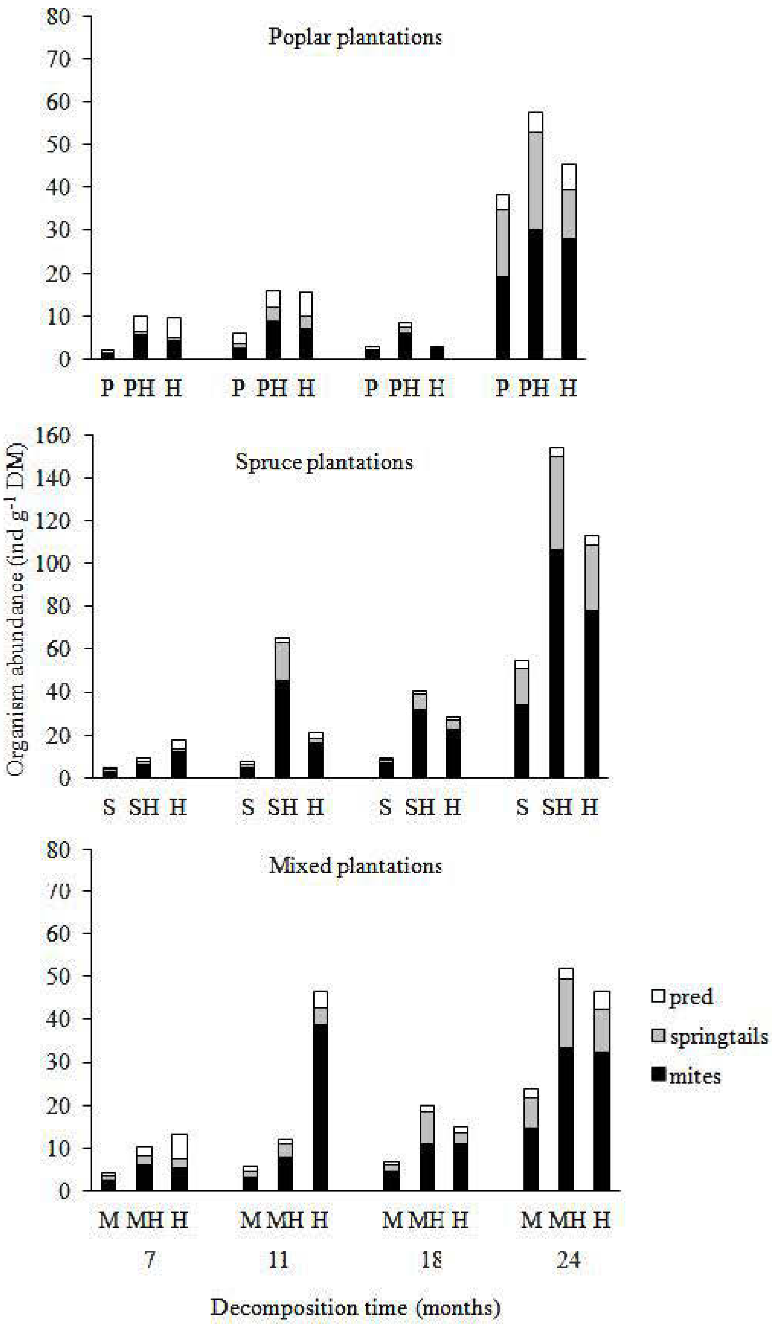


Figure 4.3 Mean abundance of the three main groups of organisms (predators, springtails and mites) in the different litter types, herbaceous (H), poplar (P), spruce (S) or mixed (M) litters in their respective plantations alone or in mixture with H litter.

4.3.5 Microorganisms

Fungal biomass was significantly greater in herbaceous litter compared to tree litters without herbs (poplar, spruce and mixed litters) all along the experiment, in all three plantation types (linear contrasts, $P < 0.01$, Figure 4.4). At 7 and 11 months of decomposition, the addition of herbaceous litter to tree litters (PH, SH, and MH) increased fungal biomass compared to tree litters alone but remained lower than values of herbaceous litter alone. However at 18 and 24 months of decomposition, fungal biomass in the PH and SH litters was similar to fungal biomass found in herbaceous litter (linear contrasts, $P < 0.01$, Figure 4.4). In mixed plantations, fungal biomass found in the MH litter reached similar values to that found in the mixed litter (linear contrasts, $P < 0.01$, Figure 4.4).

We represented overall microbial activity using the Average Well Color Development (AWCD), and found no difference between litter types in poplar plantations (Figure 4.4). However, AWCD was greater in herbaceous and SH litter compared to spruce litter at 7 months of decomposition, in spruce plantations. At 18 months of decomposition, only the SH litter had greater AWCD than S litter alone in spruce plantations (Tukey test, $P < 0.05$, Figure 4.4). Mixed plantation had greater AWCD in herbaceous litter compared to mixed litter at 7 months of decomposition, while the MH litter had intermediate values (Tukey test, $P < 0.05$, Figure 4.4).

Concerning richness of the catabolic activity (mean of the number of substrates used), at 7 months of decomposition P litter had lower catabolic richness than the PH litter, spruce litter had lower richness than herbaceous and SH litters, and mixed litter had lower catabolic richness than herbaceous litter (Tukey test, $P < 0.05$, Figure 4.4). After this sampling date there was no longer a difference between litter types, except at 18 months of decomposition where catabolic richness in spruce litter was lower than herbaceous and SH litters. In poplar and mixed plantations, catabolic richness was significantly lower at 18 months of decomposition compared to the three other sampling dates (lme, decomposition time, P< 0.05), whereas in spruce plantations this difference was observed only for spruce litter.

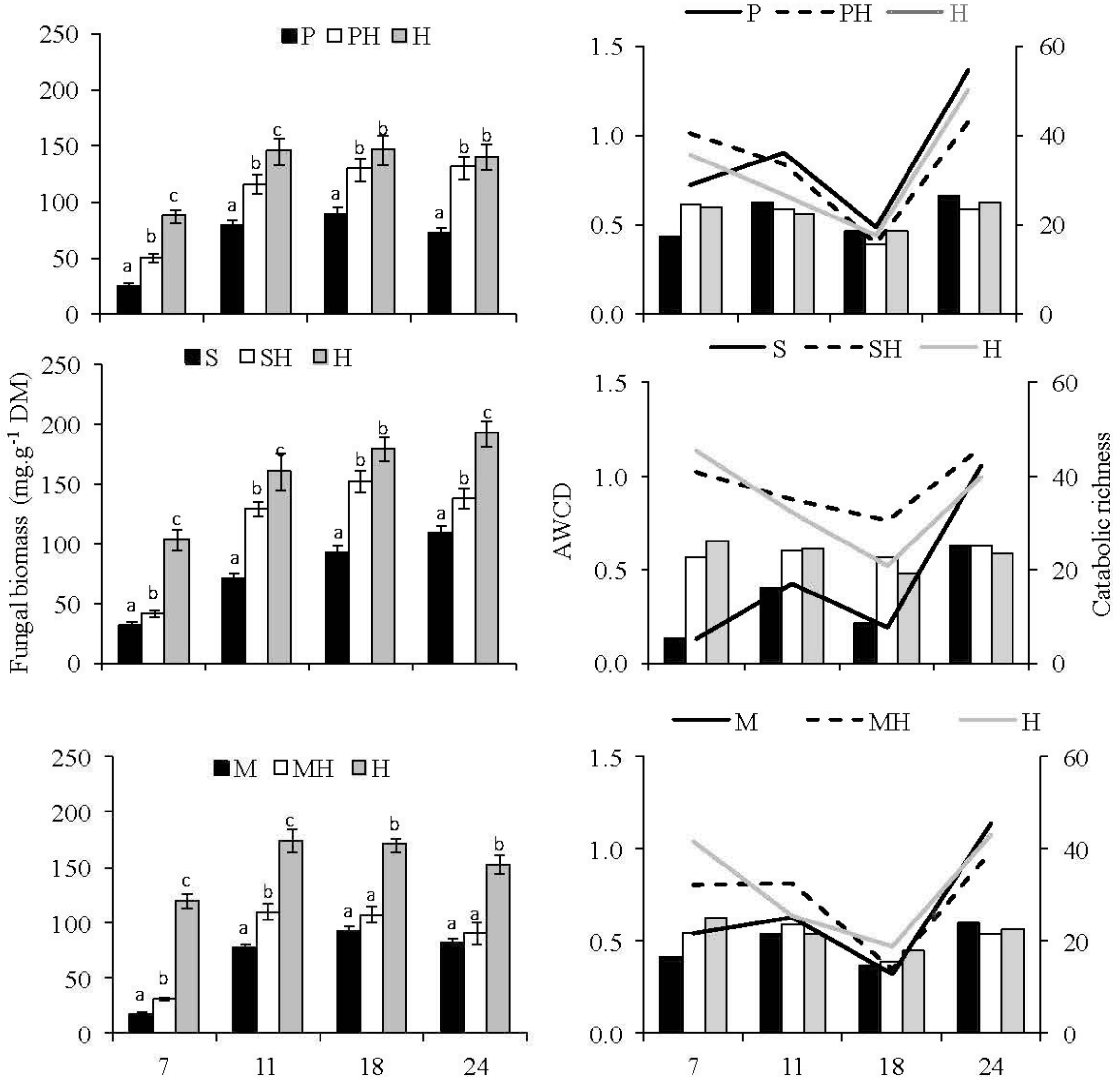
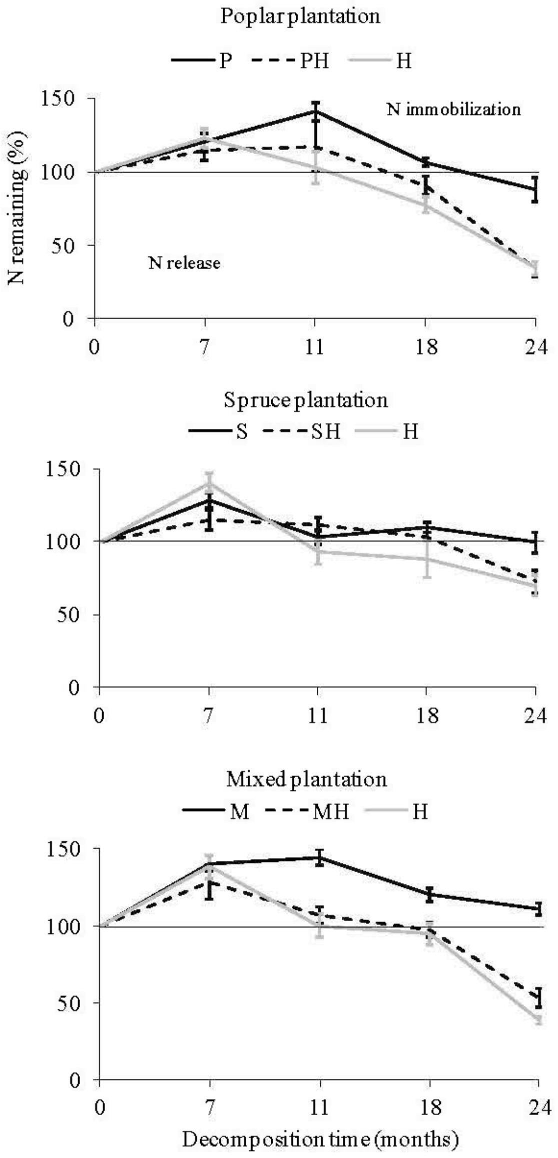


Figure 4.4 Mean (± SE) of fungal biomass (left side), Average Well Color Development (AWCD) (right side, curve) and mean number of substrate use (right side, histogram) in each litter type (poplar P, spruce S, mixed M, herbaceous H) and their different mixing. Different letters within each decomposition time represent a significant difference between means according to linear contrasts.

4.3.6 Nitrogen release

Nitrogen remaining in litter (% of initial N content) showed similar patterns between the poplar and mixed plantations; It was lower in herbaceous litter than in poplar or mixed litter at 11, 18 and 24 months of decomposition (linear contrast, $P< 0.05$, Figure 4.5). In poplar plantations, the PH litter had intermediate values, and differed from poplar or herbaceous litters at 18 months of decomposition, but at 24 months of decomposition N remaining in PH litter had values similar to herbaceous litter (linear contrast, $P< 0.05$, Figure 4.5). In mixed plantations, MH litter had similar values of N remaining to herbaceous litter at 11 and 18 months of decomposition, and had intermediate and different values from herbaceous or mixed litters at 24 months of decomposition (linear contrast, $P< 0.05$, Figure 4.5). In spruce plantations, greater N remaining was observed in herbaceous litter compared to SH litter at 7 months of decomposition, and after 24 months of decomposition S litter had significantly greater N remaining than herbaceous and SH litter (linear contrast, $P< 0.05$, Figure 4.5).


Poplar plantation

Spruce plantation

Mixed plantation

Figure 4.5 Mean (± SE) N remaining (% of initial litter content) in the different litter types (poplar: P, spruce: S, mixed: M and herbaceous: H) and their respective mixing in the different plantation types along decomposition time. Values above the 100% line represent N immobilization, whereas values below the 100% line represent N release.

4.4 Discussion

Nitrogen release in decaying litter is an essential process to maintain soil fertility, especially in boreal regions, where nutrient cycling is slow due to cold temperatures and a short growing season (McMillan et al., 2007). As expected in our second hypothesis, nitrogen release of the studied tree litters (poplar, spruce, and mixed poplar / spruce) was improved in the presence of herbaceous litter by an increase of 54, 27 and 58 %, respectively, comparing to these three litter types alone, after 24 months of decomposition. Furthermore, the release of N began earlier (after one year) in the decomposition process with herbaceous litter compared to tree litters alone (after 18 or 24 months). Herbaceous litter had a mean C/N ratio of 59, whereas the C/N ratio of the three other litter types were more than 76. C/N has been recognized for a long time as a great indicator of litter quality (Aerts, 1997): lower C/N ratios generally indicate greater amounts of nitrogen and of labile compounds in litter. Furthermore our results showed lower phenolic content in herbaceous litter, emphazing the “good” quality of this litter. The acceleration of N release in mixtures of herbaceous with tree litters may be partially driven by the increased supply of labile nutrients (especially N) from the herbaceous litter because microbes decomposing fresh litter are frequently N-limited (Berg and McClaugherty, 2008). The increase of N release by adding herbaceous litter to tree litter can thus be directly linked to the greater colonization of the mixture by decomposers and the greater catabolic activity at 6 months of decomposition compared to tree litter alone.

Herbaceous litter had the highest colonization by fungi in all plantation types, and the addition of herbaceous litter to poplar, spruce or mixed poplar / spruce litter bags increased fungal biomass compared to tree litters alone. Fungal biomass dynamics across the different litter types can be directly linked to detritivorous mites abundance during the decomposition experiment as their dynamics were similar by bottom-up effect. Interestingly, springtails abundance were less linked to fungal abundance, and the mixture of tree litters with the herbaceous litter increased the abundance of

Collembola compared to tree litters and herbaceous litter alone at 24 months of decomposition, where fungal biomass was not the greater. The mixture of tree litter and herbaceous litter implied mixed diets for detritivorous springtails, which has been shown to increase their fitness (Scheu and Simmerling, 2004). We can conclude that for fungi and mites the quality of litter is more determinant, which is in line with the theory that chemical composition is more important than chemical diversity during microbial decomposition (Meier and Bowman, 2008), whereas for springtails the diversity of resources seemed to be more important than the litter quality *per se*.

These differences in abundance of decomposers and fungal biomass was not really due to an increase of humidity resulting from herbaceous litter addition, since herbaceous litter didn't increase litter humidity when it was mixed with tree litters, contrary to our first hypothesis. Only at 18 months of decomposition greater litter water content was observed in the herbaceous litter and the mixture spruce / herbaceous compared to spruce litter alone. This greater humidity could explain the greater microbial activity in these litters compared to spruce litter alone at 18 months of decomposition.

Our study differs from most previous litter mixture experiments in that we separated litters from all individual species within mixtures at the end of the experiment. This allowed us to identify strong species-specific responses in mixtures. The presence of herbaceous litter in the litter bags increased the decomposition of poplar and the mixed (spruce / poplar) litter, with an increase of 30 and 20% of mass loss, respectively. However, contrary to our third hypothesis, spruce litter decomposition was not improved by the presence of herbaceous litter while their chemical dissimilarity was greater than poplar and herbaceous litter. Nevertheless we found greater fungal biomass and detritivorous abundance associated with spruce litter when it was mixed with herbaceous litter; In spruce plantation, we previously observed that the abundance of decomposers and fungi was relatively high compared to poplar and mixed plantations (Chomel et al., 2014c). We hypothesized that the high abundance of decomposers in the experimental site could depress the expected positive effect of the increased abundance with herbaceous on litter mixture decomposition. Functional redundancy within the decomposers communities could explain this lack of effect on decomposition. Moreover, in a previous study we found that spruce litter was less decomposed in the presence of poplar litter. This could be linked to the attraction of opportunist organisms (r-strategy) by a more labile litter type, which outcompete specialized organisms (k-strategy) more able to degrade spruce litter which contains great quantities of structural compounds such as lignin (Chap. 2a).

We also hypothesized that the effect of the addition of herbaceous litter in mixed tree litter (poplar/spruce) would be more pronounced compared to each litter taken separately due to a more diverse micro-habitats and resources for decomposers. However we did not find support for this hypothesis, as the effect was globally similar to the results observed when adding herbaceous to poplar litter, and confirmed that the number of species included in the litter mixture is less important for the prediction of decomposition processes compared to their composition (Barantal et al., 2011; Hättenschwiler and Jorgensen, 2010; Jonsson and Wardle, 2008). Results on decomposition of herbaceous litter gave support to this assertion, as decomposition rate of the herbaceous litter added to the tree litters was similar to the herbaceous litter by itself. Relative individual performance of various litter types depended more strongly on the identity of target species than on the identity of neighbor species contained in the mixture (Barantal et al., 2011).

4.5 Conclusion

Herbaceous litter was characterized by a great colonization of decomposers (detritivores and fungi) and a great catabolic richness of microorganisms. Therefore the addition of herbaceous litter to tree litters (poplar, spruce or mixed poplar/spruce) increased the abundance of decomposers and fungal biomass compared to tree litter alone, without affecting humidity. These differences conduced to earlier and greater nitrogen release of tree litters in mixture with herbaceous litter. The presence of herbaceous litter in the litter bags increased the decomposition of poplar and the mixed (spruce / poplar) litter, but had no effect on herbaceous and spruce litter decomposition. The individual performance of each litter type in the mixture depended more strongly on the identity of target species than on the identity of neighbor species contained in the mixture. Herbaceous litter seemed to have a great positive effect on decomposition processes and N release, which could counteract the potential negative effect of their presence on growth of planted trees.

CHAPITRE V

EFFETS DE LA MIXITÉ SUR LE STOCK AÉRIEN ET SOUTERRAIN DE CARBONE

Figure 5.1 Photo des quadrats utilisés pour évaluer le stockage de carbone dans les différents horizons du sol.

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"Non-additive effects of mixing hybrid poplar and white spruce on aboveground and soil carbon storage in boreal plantations"

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Keywords: Boreal forest, Carbon storage, Mixed-species plantations, Productivity, Soil horizon, Synergistic effect.

Résumé

La sylviculture intensive est particulièrement intéressante pour la production rapide de fibre de bois dans les régions boréales. Dans des plantations mixtes, l'utilisation de diverses essences forestières qui ont des niches écologiques complémentaires, comme le peuplier hybride et l'épinette blanche, peut potentiellement maximiser l'utilisation des ressources et, par conséquent, augmenter la productivité. Dans le contexte du changement climatique, un intérêt particulier est porté sur la séquestration de carbone par la végétation et le sol, car elle pourrait être un moyen de compensation des émissions de CO_2. Une augmentation de la productivité induit une augmentation de la séquestration de CO_2. Ainsi l'utilisation des plantations mixtes pourrait améliorer le service écosystémique du stockage de carbone en comparaison avec des plantations mono-spécifiques. Nous avons comparé le stockage de carbone dans la végétation et dans le sol dans des plantations mono-spécifiques de peuplier hybride et d'épinette blanche âgées de neuf ans avec des plantations de ces deux espèces en mélange. Le stockage de carbone a été mesuré en échantillonnant les quatre premiers horizons du sol, et le stockage dans la végétation a été mesuré à partir de la biomasse estimée par des équations allométriques. Le mélange de l'épinette blanche et du peuplier exerce un effet synergique sur le stockage de carbone dans le sol et dans la végétation. Cet effet positif est principalement dû à une productivité plus importante du peuplier (augmentation de 47% de la biomasse) et une plus grande accumulation de la litière dans les horizons superficiels (augmentation de 52% de carbone dans l'horizon OL) dans les plantations mixtes en comparaison avec les plantations pures. Ces résultats suggèrent qu'en plus d'une augmentation de la production des peupliers, les plantations mixtes du peuplier et de l'épinette favoriseraient le stockage de carbone en comparaison avec les plantations monospécifiques.

Abstract

The use of trees under intensive management is particularly important for rapid fibre production in boreal regions. Mixed-species plantations using species that have complementary ecological niches, such as hybrid poplar and white spruce, potentially can maximize the use of resources and, consequently, increase productivity. In the context of climate change, vegetation and soil carbon sequestration is of a particular interest as part of a possible means of compensating for CO_2 emissions. Since higher productivity leads to higher CO_2 sequestration, the use of mixed-species plantations could improve the ecological service of carbon storage compared to mono-specific plantations. We compared above-ground and soil C storage of nine-year-old mono-specific plantations of white spruce and hybrid poplar with mixed plantations of these two species. Soil carbon was evaluated by separately sampling four soil horizons, while aboveground carbon was assessed from tree biomass estimates using allometric relationships. Mixing white spruce and hybrid poplar exerted a substantial synergistic effect on above-ground and soil carbon storage. This positive effect was due to greater productivity of poplar (47% of biomass increase) and great accumulation of litter in soil surface horizons (52% L-horizon carbon increase) of mixed-species compared to mono-specific plantations. These results imply that in addition to wood production gains by poplar trees, mixed-species plantations of hybrid poplar and white spruce promotes greater carbon sequestration than mono-specific plantations of either hybrid poplar or white spruce, an important aspect of forest ecosystem services.

5.1 Introduction

In 2010, the total area of planted forests was estimated to cover 264 million hectares worldwide (FAO, 2010). Although they constituted only 7% of global forest cover (FAO, 2010), these plantations were estimated to supplied about 35% of global roundwood needs (Shvidenko et al., 2005). The use of trees under intensive management is particularly important for rapid fibre production in boreal regions of Canada, where growth rates of natural forests are relatively low (Pothier and Savard, 1998). Within this biome, short-rotation forestry has great potential for supporting ecosystem services in (1) valuing abandoned agricultural lands and degraded forests, (2) reducing harvesting pressure on natural forests (FAO, 2010), (3) becoming sustainable sources of wood supplies, and (4) promoting carbon storage (Kelty, 2006). Many researchers have focused upon vegetation and soil carbon sequestration in natural or planted ecosystems, as a possible means of compensating for CO_2 emissions, which is particularly important in the context of climate change (IPCC, 2007). Soil carbon storage could represent from 50% of total carbon storage in tropical forests to 98% in cropland systems; boreal forests have an intermediate level, with soil organic carbon concentrations corresponding to 84% of total carbon storage at the ecosystem level (Bolin et al., 2000). In this context, maximizing the potential for carbon storage by tree plantations becomes an interesting proposition for increasing compensation for or offsetting increasing CO_2 emissions. For example, afforestation of crop fields and pastures of central Saskatchewan with trembling aspen (*Populus tremuloides* Michaux) was shown to have the potential to sequester 30-75 Mg ha^{-1} of carbon over the next 50-100 years (Fitzsimmons et al., 2004). Forest management has traditionally relied upon mono-specific plantations, which are easier to establish, tend and harvest compared to mixed-species plantations. The former have been criticized for having poor ecological characteristics (Erskine et al., 2006; Lamb et al., 2005) and greater risks for the spread of diseases that are incurred by fungal pathogens (Burdon, 2001). In contrast, mixedwoods may have many advantages over pure stands such as higher productivity (Johansson, 2003; Man and Lieffers, 1999) and greater resistance to abiotic and biotic stresses, including damage caused by pests or fungal pathogens (Burdon, 2001; McCracken and Dawson, 1997). However, the productivity benefits that are derived from mixed stands depend upon species composition, because such benefits are not consistently observed in studies of mixture effects (Piotto, 2008; Rothe and Binkley, 2001). Mixed-species stands can be more productive than mono-specific stands through two mechanisms: facilitation between species, *i.e.,* one species improves environmental conditions and, thereafter, the growth of another; or niche segregation, where there is divergence in the use of resources between species with different functional traits, which leads to decreased competition and a better efficiency in using local resources (Vandermeer, 1989).

Mixedwood forests of trembling aspen and white spruce (*Picea glauca* [Moench] Voss) are common across boreal Canada. These two species have complementary ecological niches (*i.e.*, they exhibit niche segregation) resulting in maximal use of resources (Kelty, 1992, 2006; Man and Lieffers, 1999): white spruce is a slow-growing, superficially rooted and moderate shade-tolerant species, while aspen (like hybrid poplar) is a fast-growing, more deeply rooted and shade-intolerant species. Due to this complementarity, boreal mixedwoods could be more productive than single-species forest ecosystems (Chen and Popadiouk, 2002). Yet this hypothesis has not always been confirmed. In natural forests, some studies have found greater productivity of mixed compared to pure stands (Martin et al., 2005), with a positive effect of aspen (if less than 41% of total stand basal area) on spruce growth in mixtures (Légaré et al., 2004). Others have found negative effects of spruce on aspen productivity (MacPherson et al., 2001), negative effects of aspen on spruce productivity (Kabzems et al., 2007), or no effect of mixed compared to mono-specific stands (Cavard et al., 2010). In plantations, at least one previous study found positive effects of mixing hybrid poplar (*P. maximowiczii* × *balsamifera clone*) and white spruce in intimate mixtures on the growth of the two species (Benomar et al., 2013).

Since greater tree productivity leads to greater CO_2 sequestration, the use of mixed species plantations could improve the ecological service of aboveground carbon storage compared to mono-specific plantations. Furthermore, increases in forest productivity can also increase litter production and litterfall (Liu et al., 2005; Rothe and Binkley, 2001), leading to greater accumulation of organic matter on the forest floor (Leff et al., 2012; Sayer et al., 2011), which may result in an increase in soil carbon storage. Soil carbon storage depends upon the balance between C input rates, *i.e.*, senescent organic matter (branches, leaves, and roots), and output rates, *i.e.*, the decomposition of this organic matter. Some studies found a positive effect of mixing litters on decomposition rates; however, like the effects of mixtures on tree productivity, mixture effects on litter decomposition are also largely dependent upon the particular species that are present in the mixture (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Needle litter of conifers is often acidic, complex in terms of its chemistry, and generally less palatable for soil decomposers compared with the leaf litter shed by broadleaf deciduous species. In boreal mixedwoods, aspen improved litter decomposition relative to spruce through an increase of soil organism abundance, together with an improvement in litter quality and soil physical and chemical properties (Laganière et al., 2009; Légaré et al., 2005). Consequently, aspen forests store less soil carbon than black spruce forests (*Picea mariana* [BSP] Miller), given the faster rates of decomposition processes in the former compared to the latter (Gower et al., 2000; Laganière et al., 2011; Vance and Chapin, 2001).

In tree plantations, studies have generally focused on tree growth and productivity to determine the best management practices that promote higher timber yield, whereas soil carbon storage is largely less thoroughly investigated. This paucity of information contrasts with studies that have been conducted in natural forest environments (Johnson, 1992). In this paper, we compared above-ground and soil carbon storage in nine-year-old mono-specific plantations of white spruce and hybrid poplar *versus* mixed plantations of these two species. For this purpose, we examined hybrid poplar and white spruce growth, together with humus morphology, in the different planted plots. Quantities of soil carbon were estimated by separately sampling four soil horizons, whereas the quantity of aboveground carbon was assessed from tree biomass, which was calculated using allometric relationships.

We hypothesized the following: (i) Based on the low resource quality of spruce needles and slow decomposition rates in natural spruce forests, we expected that carbon storage would be greater in surface soil horizons of mono-specific spruce plantations compared to mono-specific hybrid poplar and mixed plantations. (ii) Due to an increase in productivity, we expected carbon storage in aerial biomass to be higher in mixed plantations compared to mono-specific plantations. iii) Given a potentially positive effect of mixing species on organic matter decomposition rates compared to mono-specific plots, we expected lower carbon storage within the soil surface horizons (non-additive effect).

5.2 Materials and methods

5.2.1 Study area

The study was located in the boreal region of Abitibi-Témiscamingue, Quebec, Canada. Three sites were selected for study : Amos (48°36′N, 78°04′W), Rivière Héva (48°11′N, 78°16′W), and Nédelec (47°45′N, 79°22′W). The Amos site was abandoned farmland with a heavy clay soil that was dominated by grasses and sparse patches of speckled alder (*Alnus incana* [L.] Moench ssp. *rugosa* [Du Roi] R.T. Clausen), willow (*Salix* spp.), and trembling aspen. Rivière Héva was an abandoned farmland site with heavy clay soil, which was also dominated by shrubs, including patches of alder, willow, and aspen. Nédelec had been previously dominated by trembling aspen forest, which was commercially harvested in 2000. In addition to aspen, the main species that were present included white or paper birch (*Betula papyrifera* Marshall) and pin cherry (*Prunus pensylvanica* L.f.), which were growing on soil with a sandy loam texture. Soil type of the three sites ranged from a Brunisol with a Bm-layer to a grey Luvisol with a Bt-layer or Gleysol (Soil Classification Working Group, 1998). Based on a 30-year running climate average (1970–2000), Amos and Rivière Héva annually receive an average of 918 mm year^{-1} (Amos station) and have a mean temperature of 1.2 °C, while Nédelec has mean precipitation of 916 mm year^{-1} and a mean temperature of 1.9 °C (Remigny station, Environment Canada 2014). Site preparation before planting was conducted in 2002. A bulldozer was used to remove tree stumps at Nédelec, while shrubby vegetation at Rivière Héva was removed using a brush shredder mounted on a farm tractor. At Amos, scattered tree stumps and shrub clumps were removed using chains and a farm tractor. Sites were then ploughed to a depth of about 30 cm, followed by disking in spring 2003 to level the soil surface and remove most woody debris (Benomar et al., 2011). The plantations were established in 2003, using one hybrid poplar clone (*Populus maximowiczii* A. Henry × *P. balsamifera* L., clone MB915319), and an improved white spruce family from a provincial seed orchard. These two species were planted in mono-specific plots of 36 trees (6 × 6 trees) with 1 × 1 m spacing, and in mixed species plots, where rows of spruce alternated with rows of poplar, which was also planted under a spacing of 1 × 1 m. Spacing corresponded to a tree density of 10,000 stems ha^{-1} (Figure 5.2). Each experimental unit thus contained 36 trees, of which only the 16 interior trees were considered for the study. This left a 1 row-wide buffer along each plot edge. The experiment was designed as a split-split-plot layout, with replicate sites as the whole-plot factor, and plantation type as the subplot factor. Soil horizon or tree parts were a sub-sub-plot factor nested in plantation type. Weed management was done during the first five years after planting, using a manual rototiller between rows and trees.

Figure 5.2 Photographs of the three plantation types at the Nédelec site. Spruce, mixed-species and poplar plantations are depicted from left to right.

5.2.2 Aboveground tree biomass and carbon storage

Height, stem basal diameter (at 10 cm above the soil surface) and diameter at breast height (DBH, 1.3 m) were measured on the 16 interior trees at the end of the ninth growing season (mid-October 2011). Above-ground biomass of stems, branches and needles of the spruces were estimated from allometric equations that related biomass to basal diameter (D10), according to (Pitt and Bell, 2004). Above-ground biomass of stems, branches and leaves of the poplars were estimated from allometric equations that related biomass to DBH, based on (Benomar et al., 2012). According to these allometric equations, the relationship between DBH and the biomass of stems, branches or leaves/needles was a power function model, and data were fitted to the following equation:

$$W = a \, \mathrm{DBH}^{b}$$

where W is the biomass of stems, or branches, or leaves (kg dry mass), DBH is the diameter at breast height (cm), and a and b are parameters that are estimated from the model. At the plot level, aboveground biomass (Mg ha $^{-1}$ of dry mass) was estimated by multiplying aboveground tree biomass by tree density at planting.

For aboveground carbon storage (Mg ha^{-1}), we assumed that the organic matter contains 50% carbon (Lieth, 1975). The quantity of carbon per tree that had been obtained from biomass measurements was multiplied by tree density (stems per hectare). For mixed plantations, we performed the same calculation, but spruce and poplar densities were each 5000 stems ha^{-1}.

5.2.3 Litterfall

Annual litterfall was assessed using litter traps. Spruce branches were about 20 cm above the ground, while poplar branches were more than 1 m off the ground surface; the littertraps were adapted to the structure and height of each tree species. Each trap consisted of a wooden frame measuring 40 × 60 cm (corresponding to 0.24 m^2) for the poplar leaf harvest, or 30 x 50 cm (corresponding to 0.15 m^2) for the spruce needle harvest. The traps were each supported by four legs that were 40 and 20 cm high, respectively. Steel 2-cm mesh screening was placed on the sides and bottom of the frames for poplars. Nylon screening (2-mm mesh), which was covered with a permeable fabric to prevent needle loss, was attached to the sides and bottom of the wooden frames for spruce. Four traps were placed within each mono-specific plot, and eight traps were placed within the mixed-species plots (4 traps under poplar, and 4 under spruce trees), for a total of 48 traps. The traps were installed in October 2011. Litterfall was collected weekly during poplar leaf fall, and once a month otherwise, from October 2011 to October 2012. After collection of litterfall, the litter was oven-dried at 65 °C to constant mass and weighed.

5.2.4 Field procedures and carbon concentrations

The soil samples were divided into four layers according to the Canadian system of soil classification (Agriculture Canada Expert Committee on Soil Survey, 1987): two organic layers, *i.e.*, L (fresh litter) and F (fermentation layer); one organo-mineral layer that had been disturbed by plowing (Ap); and one mineral layer (Bm or Bt). Sampling took place within the centre space located among 4 trees, and with 5 replicates being taken in each plot (spruce, poplar, and mixed). Soil sampling from L, F and Ap horizons was performed using a wooden frame (20 cm × 20 cm). For the B horizon, sampling was done with a steel cylinder (6 cm deep, 170 cm^3). Only the first

6 cm were sampled because we considered that possible changes in carbon concentration in this horizon mainly involved the uppermost few centimeters of soil, due to the young age of the plantations. For this reason, we further assumed that for this study, the B horizon was only 6 cm thick. Ap-layer materials were sieved to pass a 2-mm mesh, and sieve residues (i.e. leaves, needles, twigs, bark, seeds, and cones) were added to the F-layer, while live roots were removed and discarded. In total, 180 samples were oven-dried at 60 °C to constant mass, and weighed to determine their dry mass.

Soil samples were finely ground with a ball mill (MM301, Retsch Inc., Newtown, PA), and carbon concentration were determined with a C/N elemental analyser (Flash EA 1112 series, ThermoScientific, Rodano, Italy). To determine the bulk density of the B-horizon in each plantation, B-layer mass was divided by the volume of the steel cylinder (170 cm^3). To determine soil carbon storage (Mg ha^{-1}), the mass of each soil horizon was multiplied by its carbon concentration, and the values were scaled to one hectare from the surface area of the wooden sampling frame.

5.2.5 Data analyses

Mean values (soil carbon concentrations, litterfall, tree aboveground biomass and C storage) were compared among plantation types and soil layers, or tree aerial parts for aboveground biomass, with hierarchical linear mixed-effects models using the *lme* function in the *nlme* package (Pinheiro et al., 2014) of R (Version 2.15.1, R Development Core Team 2008). Site replicates were treated as random effects, and plantation type was nested in site replicates to reflect the structure of our data set (split-split-plot design).

To better meet the assumptions of normality and homoskedasticity, the data for carbon storage were ln-transformed. Means were separated using Tukey's multiple comparison tests (differences are noted thereafter as, for example, a < b < c < d). The significance threshold was set at $\alpha = 0.05$. For further evaluation of mixed plantation effects on carbon storage, we calculated the relative effects of mixing species by comparing the observed values with the predicted values of carbon storage, based on the respective mono-specific plantation treatments. Predicted values for the mixed plantation were estimated by averaging carbon storage of the component species that had been planted in mono-specific plots in the site-specific replicates. According to Wardle *et al.* (1997), the relative mixture effect can be calculated as the ratio : [(observed − predicted)/predicted] * 100. If this ratio differs from zero, it would indicate non-additive effects of mixing species on carbon storage. Negative and positive deviations from zero are referred to as antagonistic and synergistic effects, respectively. To test if the observed vs predicted ratios of carbon storage in mixed plantations differed significantly from zero, we used one-sample Student's *t*-tests with 95% confidence intervals.

5.3 Results

5.3.1 Tree growth and litter productivity

Basal stem diameter, DBH and total height of poplar trees were greater in mixed compared to mono-specific plantations ($P < 0.01$), but litterfall was similar among plantation types ($P = 0.17$) (Table 5.1). In contrast, basal diameter and DBH of spruce trees were smaller in mixed compared to mono-specific plantations ($P < 0.001$ and $P = 0.024$, respectively). However, total height ($P = 0.30$) and litterfall ($P = 0.70$) of spruce trees was not affected by plantation type (Table 5.1). Aboveground biomass of spruce was 38% lower in mixed plots than pure plots. In contrast, poplar biomass was 47% greater in mixed plots than in pure plots ($P < 0.001$; Table 5.1).

Table 5.1 Mean (± SE) of height, basal stem diameter, diameter at breast height (DBH) and litterfall of hybrid poplar and white spruce growing in monospecific and mixed plantations. Different letters for each species within a row represent a significant difference between means according to Tukey test.

Species	N	Spruce		Poplar	
		Pure	Mixed	Pure	Mixed
Tree height (m)	118	2.66 ± 0.09 (a)	2.49 ± 0.14 (a)	7.73 ± 0.29 (a)	9.33 ± 0.26 (b)
Basal stem diameter (cm)	118	5.12 ± 0.17 (b)	4.19 ± 0.20 (a)	7.38 ± 0.27 (a)	10.18 ± 0.36 (b)
DBH (cm)	118	2.45 ± 0.14 (b)	1.92 ± 0.17 (a)	5.33 ± 0.26 (a)	7.75 ± 0.35 (b)
Biomass (kg tree^{-1})	118	3.22 ± 0.26 (b)	2.00 ± 0.22 (a)	7.02 ± 0.56 (a)	13.19 ± 0.97 (b)
Litterfall (Mg ha^{-1}yr^{-1})	48	0.50 ± 0.10 (a)	0.37 ± 0.09 (a)	3.79 ± 0.30 (a)	4.02 ± 0.23 (a)

5.3.2 Carbon concentration of soil horizons and bulk density

Carbon concentration of each horizon is reported in Table 5.2 (3 plantation types combined, as there were no differences among plantation type), and differed significantly among soil layers from the superficial horizons to the mineral soil (results of the linear mixed model are reported in Table 5.3). Bulk density (mean ± standard error) of the B-horizon was 0.86 g cm^3 ± 0.04 g cm^3, 0.91 g cm^3 ± 0.04 g cm^3, and 0.87 g cm^3 ± 0.02 g cm^3 for spruce, poplar and mixed plantations respectively, but did not significantly differ among plantation types (linear mixed model, numDF = 2, denDF = 4, F = 0.43, P = 0.68).

Table 5.2 Mean (±SE) values of C (%) in the soil horizons (N = 144). Different letters within %C across horizon represent a significant difference between means according to Tukey test.

Horizons	C (%)		
	Spruce	Poplar	mixed
L	43.2 ± 0.8 (d)	43.2 ± 1.3 (d)	43.6 ± 1.3 (d)
F	27.5 ± 2.6 (c)	25.6 ± 3.3 (c)	29.5 ± 2.6 (c)
Ap	9.8 ± 0.8 (b)	7.9 ± 0.7 (ab)	9.7 ± 0.7 (b)
B	4.0 ± 0.3 (a)	4.0 ± 0.3 (a)	4.5 ± 0.2 (a)

5.3.3 Carbon storage

Soil carbon storage

Soil C storage across the whole soil profile was similar among plantation types. However, when we decomposed carbon storage into each of the four soil layers, differences between plantations emerged for the three uppermost horizons (Table 5.3). In the L horizon, carbon storage was greater in mixed (2.67 Mg ha^{-1} of carbon) compared to mono-specific (1.40 Mg ha^{-1} of C for spruce and 1.30 Mg ha^{-1} of C for poplar) plots. In the F horizon, carbon storage was greater in spruce (2.46 Mg ha^{-1} of carbon) than in poplar and mixed (1.17 and 1.45 Mg ha^{-1} of carbon, respectively) plots. Finally, for the Ap horizon, we observed greater carbon storage in mono-specific poplar and mixed-species (3.44 and 3.01 Mg ha^{-1} of carbon, respectively) than in mono-specific spruce (1.98 Mg ha^{-1} of carbon) plots (Table 5.3, Figure 5.3).

Aboveground carbon storage

The effect of plantation type on aboveground carbon storage depended upon the tree part that was being considered. When we examined stems or branches, carbon storage was greater in mono-specific poplar (15.25 and 14.66 Mg ha^{-1} of carbon, respectively) and mixed-species (17.40 and 15 Mg ha^{-1} of carbon, respectively) plots, compared with mono-specific spruce plots (4.40 and 4.19 Mg ha^{-1} of carbon, respectively). However, carbon storage did not significantly differ among plantation types for leaves and needles (Figure 5.3, Table 5.3). With respect to carbon storage distribution, carbon storage was greater in leaves in spruce plantations, whereas it was greater in stems and branches in poplar and mixed plantations (Figure 5.3).

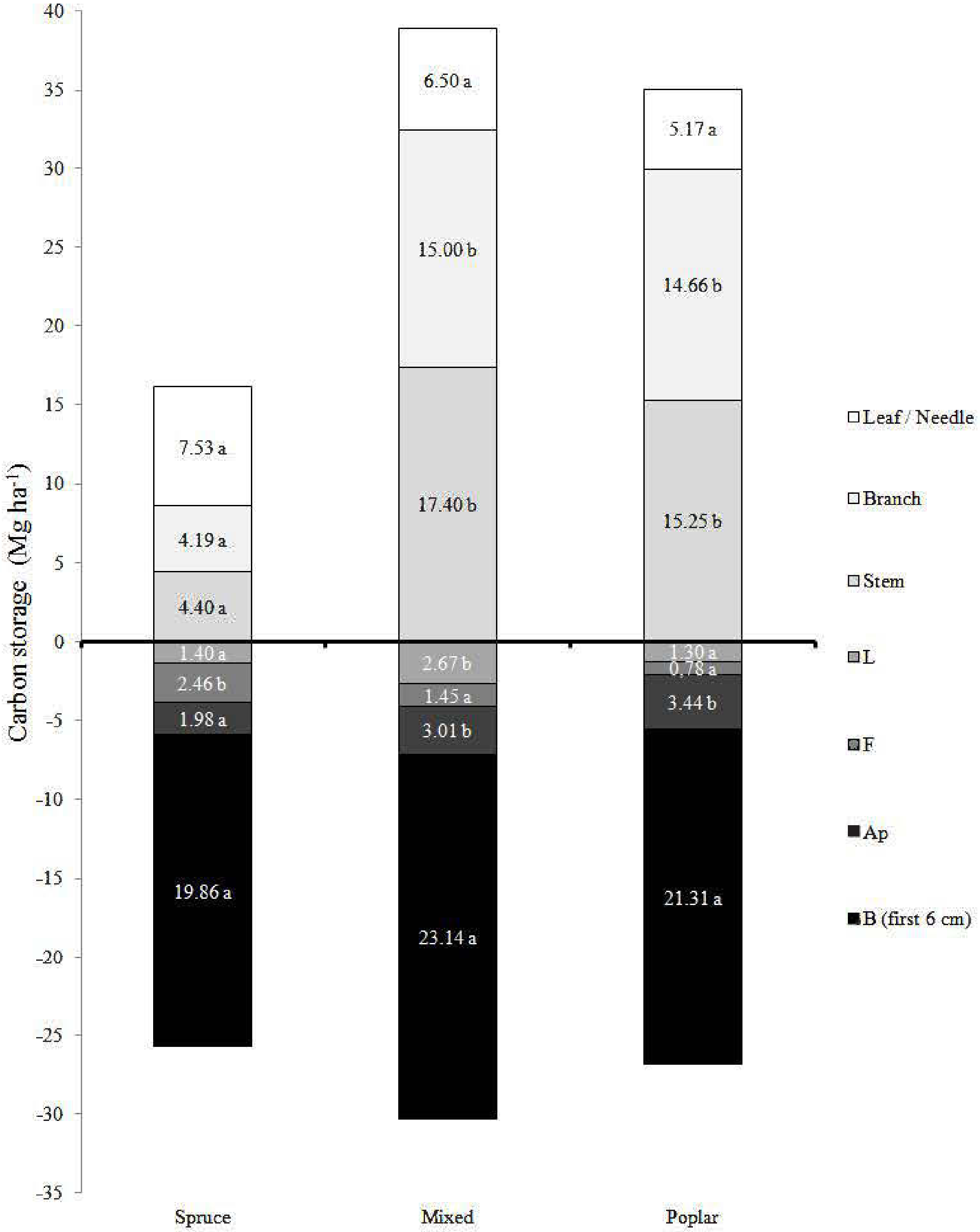

Figure 5.3 Aboveground (above the X-axis) and soil (below the X-axis) carbon storage in the different plantation types. Across plantation types, different letters within each compartment represent a significant difference between means according to Tukey test.

Sum of above and soil carbon storage

Total carbon storage (above-ground + soil carbon storage) was lower in spruce plantations (42 Mg ha^{-1} of carbon) compared to poplar and mixed-species plantations (63 and 69 Mg ha^{-1} of carbon respectively; linear mixed model: poplar plantation, P = 0.02; mixed plantation, P = 0.01). With respect to the comparison between above-ground versus soil carbon storage, spruce stands stored less carbon in the aboveground compartment (on average only 37%), compared to poplar and mixed-species stands (57 and 56% respectively; linear mixed-model, poplar plantation : P = 0.04; mixed plantation, P = 0.05).

Table 5.3 Results of mixed-effects model analysis of plantation types and soil horizons on mean soil C and soil C storage, and effects of plantation type and tree aerial parts on mean aboveground C storage. N = 180 for soil characteristics, N = 282 for aboveground characteristics.

Fixed effects	df	C concentration (%)		C storage			
				Belowground		Aboveground	
		F-statistic	*P*-value	F-statistic	*P*-value	F-statistic	*P*-value
Plantation type	2	1.98	0.14	1.0139	0.37	111.9902	<0.001
Horizon / Trees part	3	727.97	<0.001	353.1347	<0.001	9.8374	<0.001
Interaction	6	0.43	0.86	4.5584	<0.001	40.348	<0.001

Note : df = Degrees of freedom.

5.3.4 Net effect of mixed species plantation on carbon storage

Non-additive effects (NAE) of species mixing on total aboveground and soil carbon storage were recorded, but only synergistic effects were significant. NAE on aboveground carbon storage was + 68% and differed significantly from zero (One-sample t-test : t = 5.84, DF = 22, P < 0.001). The mean net effect of species mixing on soil carbon storage represented an increase of 15% and differed significantly from zero (One-sample t-test : t = 3.36, DF = 14, P = 0.005) (Figure 5.4). When decomposed into various above-ground and soil compartments (Figure 5.4), significant positive NAE of species mixing were observed for stems (One-sample *t*-test: $t = 5.86$, $DF = 22$, $P < 0.001$), branches (One-sample *t*-test: $t = 5.78$, $DF = 22$, $P < 0.001$), and for the L (One-sample *t*-test: $t = 3.45$, $DF = 14$, $P = 0.004$) and B (One-sample *t*-test : $t = 3.33$, $DF = 14$, $P = 0.005$) horizons.

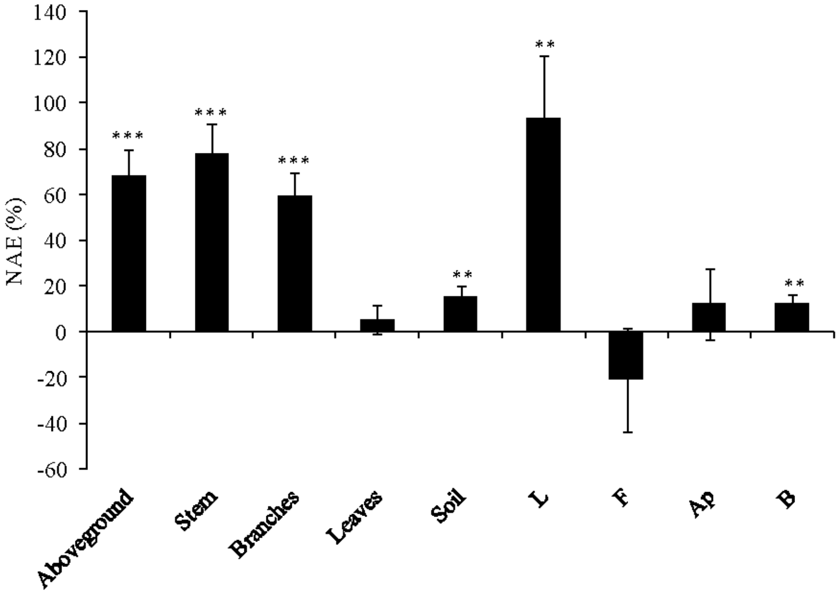

Figure 5.4 Net effect of mixed plantation on carbon storage (Mean ± SE) in various soil and vegetation compartments. Non-additive effects (NAE) were calculated as 100× (observed - predicted) / predicted. NAE that significantly different from zero, according to one-sample Student's *t*-tests, are indicated by * ($P < 0.05$), ** ($P < 0.01$), or *** for ($P < 0.001$).

5.4 Discussion

5.4.1 Effect of plantation types on soil horizons and carbon storage

Stands containing hybrid poplars (monocultures and mixed plots) stored lower quantities of carbon in the F-layer compared to mono-specific spruce plots, and conversely, they stored greater amounts of carbon in the Ap-layer. Among the factors that are known to influence organic layer characteristics, the activity of soil biota and the composition of the biota that are present profoundly affect litter degradation and incorporation of organic materials into mineral soil horizons (e.g. (Chauvat et al., 2007; Wolters, 2000). The F-horizon is the site of major soil faunal activity, where the organic matter is partially fragmented and degraded until it is eventually incorporated into the Ap-layer. In spruce plots, the activity of decomposers seemed to be less efficient than in the other plantation types, in that organic matter accumulated in the F-horizon. In mixed plots, poplar litter can promote the abundance and activity of organisms (Laganière et al., 2009; Saetre et al., 1999) and seems to counteract the negative effects that were imposed by spruce litter on decomposers in the F-horizon. Carbon content of the deeper mineral soil layer (B-layer) did not significantly differ among plantation types, demonstrating that trees influenced only the uppermost layers during 9 years that had elapsed since planting.

5.4.2 Effect of mixing species on tree growth and productivity

The productivity of mixed-species plots was the greatest (4322 kg ha^{-1} year^{-1}of carbon) when compared to mono-specific plots (spruce and poplar, 1791 and 3897 kg ha^{-1} year^{-1} of carbon, respectively), but the difference was significant only compared to spruce plantations. Our estimates for the mono-specific plots are similar to those reported in the literature for older natural forests of spruce or trembling aspen (Alexander et al., 2012; Gower et al., 1997). Hybrid poplars attained greater heights and diameters in mixed plots, while spruce had reduced diameter growth in mixed-species compared to mono-specific plots. Hybrid poplars averaged 21% greater heights and 45% greater DBH in mixed than in mono-specific plots, while spruce had 25% lower DBH in mixed compared to mono-specific plots. These results confirm preliminary findings that were obtained by Benomar *et al* (2013) for these same plantations after six growing seasons, except for the spruce, which had greater height growth in mixed compared to mono-specific plots. The canopy was more open after six growing seasons, and competition for light induced greater allocation of carbon to height rather than to diameter growth (Grams and Andersen, 2007). After nine growing seasons, hybrid poplars were closing the canopy in mixed-species plots, while the canopy was still open in the spruce monocultures, which could retard spruce height growth in the mixed plots. In natural forests, Légaré *et al.* (2004) found a positive effect of aspen on black spruce (*Picea mariana* [Miller] BSP) growth, but only when aspen represented < 40% of stand basal area. In our study, hybrid poplars represented a stand basal area above this threshold, which could explain the negative effects of mixing spruce with poplar on spruce growth. These results suggest that mixed plantings would benefit poplar harvesting, at least after 10 years of growth; they would be negative for spruce unless thinning of the poplars was preformed soon after canopy closure. However, the spacing that was used in this study (1 × 1 m) is not representative of what is normally practiced in forestry for wood production (i.e. 3 to 6 m spacing between hybrid poplars). Greater spacing between trees would probably delay canopy closure and allow hybrid poplars to reach maturity (*ca.* 20 years, (Dickmann et al., 2001) before growth of spruce was excessively and negatively affected. As suggested by Kelty (2006), managers could also reduce the proportion of the taller species in the mixed plantations to increase productivity of the lower canopy species.

5.4.3 Non-additive effects of mixing species on carbon storage

The comparison between predicted carbon storage from mono-specific plantations and observed carbon storage in mixed-species plantations showed that mixing hybrid poplar and white spruce trees affected both above-ground and soil carbon storage through synergistic effects. Examination of the different ecosystem compartments revealed that this positive effect of species mixing was mainly due to carbon storage gains aboveground for stems and branches, and in L- horizon for the soil. Calculation of non-additive effects is commonly employed in litter decomposition studies (Barantal et al., 2011; Bonanomi et al., 2010; Coq et al., 2011; Wardle et al., 1997), but this technique is rarely used in forest productivity and carbon storage analyses.

Compared to manipulative experiments with different litter mixtures in litter bags for decomposition studies, observational experiments on natural or planted forests is more constraining. One explanation is the difficulty involved in finding strictly mono-specific forests and mixtures of two species under natural conditions, that would allow non-additive effects of species mixing to be evaluated. Simple comparisons between productivity of mixed stands of aspen and spruce compared to pure aspen stands showed positive effects of mixing species on productivity (MacPherson et al., 2001; Martin et al., 2005). In the present study, spruce growth was not enhanced by planting this species in mixtures with poplar, but poplar productivity was sufficiently increased so that greater productivity in mixed-species plantations was attained than would be expected (*i.e.*, mean of the mono-specific poplar and spruce plot productivities). Thus, spruce did not affect poplar carbon storage and, indeed, adding spruce to poplar benefitted poplar wood production, at least over the short-term. We can attribute this positive finding for poplar trees to the favorable microclimatic conditions that were provided by mixing, with greater canopy space available and less competition for light and nutrients in these tightly spaced plots (Benomar et al., 2013), and more efficient biogeochemical cycling (Chen and Popadiouk, 2002). This finding is consistent with the theory that mixed stands are more productive than monocultures (Vandermeer, 1989), and with other reports showing that stands with shade-intolerant hardwoods growing over shade-tolerant conifers were more productive than shade-intolerant hardwoods growing alone (Kelty, 1989; Man and Lieffers, 1999).

In the present study, we observed that mixed plots had greater carbon accumulation in the L-horizon. Considering that litter production of spruce and poplar in mixed plots was similar to mono-specific plots, these higher accumulations of litter in mixed plots could have resulted from lower decomposition rates. Moreover, capture of light resources can increase in mixtures through canopy stratification, where less shade-tolerant species over-top more shade-tolerant species and light interception is increased (Richards et al., 2010). Increased light interception may have induced colder microclimatic conditions at the soil surface, which could have retarded decomposition processes (Chapin et al., 2002). Further, spruce induced the formation of a denser understory habitat within mixed plots because of their size and shape, possibly limiting the dispersal of poplar leaves by the wind, which could have contributed to a greater accumulation of poplar litter in the mixed plots compared to poplar monocultures.

5.5 Conclusion

This study showed that aboveground poplar growth was enhanced in mixed-species compared to mono-specific poplar plantations. Conversely mixed-species planting was detrimental to spruce growth. These results suggest that mixed plantations would be positive only for the growth of poplar (at least under this tight spacing), which should reach merchantable sizes before the poplars in that were established mono-specific plantations. Mixed plantations negatively affected spruce growth after 9 years; however, since the conifers reach maturity much later than poplars, their growth could be enhanced by selective harvesting of the poplars before being severely hindered by interspecific competition. A greater accumulation of carbon was observed in the L-horizon in mixed-species plantations, probably due to colder microclimatic conditions that were brought on by greater light interception of the mixed canopy and a denser understory layer that limited the export of litter.

These differences in the aboveground and soil compartments led to greater carbon storage in mixed-species plots than was expected, demonstrating a synergistic effect of mixing (*i.e.*, mean of the mono-specific poplar and spruce plot carbon storage values).

In addition to an increase in poplar timber yield (a desirable aspect for the forest industry), this study showed that mixed-species plantations of white spruce and hybrid poplar also promoted carbon sequestration, which is an important strategy for compensating CO_2 emissions, and for plantations management within boreal regions. Finally, these synergistic effects were found only 9 years following afforestation and should be subjected to further study to confirm sustained positive trends in the longer-term.

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CHAPITRE VI

DISCUSSION GÉNÉRALE

Plantations mono-spécifiques
ou pluri-spécifiques ?

Figure 6.1 Plantations monospécifique (en haut) ou mixte (en bas) de nos sites d'étude

Cette thèse visait à mieux comprendre l'influence de la mixité de deux essences forestières plantées en comparaison à des plantations pures, à savoir l'épinette blanche et le peuplier hybride, sur le fonctionnement de l'écosystème à travers l'étude du processus de décomposition des litières. Les espèces végétales sont susceptibles d'influencer le processus de décomposition selon deux mécanismes qui opèrent à différentes échelles :

i) d'une part par la production de litière possédant des caractéristiques physiques et chimiques propres qui constituent la ressource nutritive pour les décomposeurs, *i.e.* l'effet ressource;

ii) d'autre part avec un effet à plus long terme de l'arbre sur son environnement en influençant les microconditions climatiques et édaphiques, et les communautés d'organismes présents dans le sol, *i.e.* l'effet habitat.

L'hypothèse principale était que la mixité des espèces et donc des litières favoriserait le processus de décomposition et la remise à disposition des nutriments dans le sol. En effet cette mixité engendrerait une plus grande diversité d'habitats et de ressources favorisant une plus grande diversité et abondance des organismes décomposeurs. Cette étude a été menée sur des plantations intensivement aménagées installées sur trois sites correspondant à deux anciennes friches agricoles et un ancien site forestier, qui étaient largement colonisés par des herbacées. Ainsi une autre partie de cette thèse consistait à déterminer si la présence d'herbacées était bénéfique au processus de décomposition des litières et au relargage des éléments nutritifs dans les différentes plantations mono — ou pluri-spécifiques. Finalement, pour relier ces données avec le fonctionnement global de l'écosystème, le stockage de carbone aérien et dans le sol a été étudié. La partie qui suit constitue un bilan des conclusions intégrant les différentes études effectuées lors de cette thèse, en présentant tout d'abord le premier niveau de complexité, à savoir le fonctionnement des plantations monospécifiques et la décomposition des litières monospécifiques, puis l'effet du mélange des espèces et des litières.

6.1 Influence des espèces végétales et de la qualité de leur litière sur la décomposition et le stockage de carbone

La comparaison de la composition chimique de feuilles sénescentes des différentes espèces étudiées a tout d'abord permis de définir la "qualité" de leur litière respective : les aiguilles d'épinette présentent un ratio C/N élevé ainsi qu'une grande proportion de composés phénoliques. De plus, il est connu que cette litière possède une forte teneur en lignine (32%, Johansson 1984) impliquant une importante stabilité structurale. Les feuilles de peuplier possèdent un ratio C/N inférieur, mais possèdent tout de même une forte teneur en composés phénoliques, similaires à celle des aiguilles d'épinette. Et enfin les herbacées présentent un ratio C/N encore plus faible ainsi qu'une faible teneur en composés phénoliques, confirmant leur forte propriété labile. Les résultats obtenus après 2 ans de décomposition dans nos diverses expérimentations ont confirmé le fait que la qualité de la litière était un des facteurs déterminants de la décomposition, avec une décomposition plus rapide de la litière d'herbacées, suivie du peuplier et de l'épinette (moyenne de 69%, 45% et 39% de perte de masse respectivement après 2 ans de décomposition, voir Figure 6.2). La qualité initiale de la litière est un facteur important pour la décomposition, mais il faut également prendre en compte la biodisponibilité des composés chimiques qu'elle contient et leur capacité à être lessivés. L'étude en laboratoire (Chapitre 3b) nous permet de dire que les composés présents dans la litière de peuplier et d'herbacées, tout au moins les composés phénoliques, sont plus lessivables que les composés contenus dans la litière d'épinette. La litière de peuplier pourrait ainsi se "détoxifier" par lessivage, ce qui pourrait expliquer la plus grande colonisation de cette litière par les champignons et les acariens détritivores (Chomel et al., 2014b). De plus la litière de peuplier était colonisée par des microorganismes possédant une plus grande activité et diversité catabolique en comparaison avec la litière d'épinette, ce qui a induit une décomposition plus rapide, et donc un relargage de C et de N plus important après 2 ans de décomposition (Chapitre 3a). L'étude en microcosmes

(Chapitre 3b) a montré que les lixiviats de litière de peuplier, plus chargés en composés phénoliques que ceux de la litière d'épinette, ont eu un effet très néfaste sur une espèce cible de collemboles (*Folsomia candida*) provoquant rapidement 100% de mortalité au cours de l'expérimentation.

Parmi les différents types de litière mises à décomposer (peuplier, épinette et herbacées) une faible abondance de la mésofaune et une biomasse fongique moindre ont été observées dans les plantations monospécifiques de peuplier par rapport aux autres plantations (Chapitre 3a et 4). Cependant, lorsqu'on a examiné la décomposition de la litière de peuplier dans les autres types de plantations, on a parfois observé une colonisation plus importante des organismes décomposeurs et une décomposition relativement rapide par rapport aux autres litières (Chapitre 3a). Ce résultat indique qu'à l'inverse d'un effet ressource "peuplier" qui semble être favorable pour les décomposeurs, l'influence de l'arbre à plus long terme, *i.e.* l'effet habitat "peuplier", n'était pas propice à la colonisation des décomposeurs et à la décomposition. On peut émettre l'hypothèse que les pluviolessivats de peuplier, plus abondants dans cette plantation, créent un environnement moins propice à la colonisation des organismes. De plus la décomposition du peuplier était relativement rapide (53% de perte de masse en moyenne après 2 ans), ce qui peut induire un relargage puis un lessivage trop rapide des éléments nutritifs, engendrant un sol relativement pauvre en nutriments disponibles. Ces résultats sont corroborés par l'étude du stockage de carbone (Chapitre 5), qui nous indique une faible accumulation de carbone dans les horizons superficiels (OL et OF) traduisant une transformation rapide de la litière de peuplier.

En accord avec notre hypothèse de départ, la litière d'épinette était plus récalcitrante à la décomposition, traduisant un effet "ressource" important. En revanche les plantations monospécifiques d'épinettes ont montré un important « home field advantage », c'est-à-dire que la litière se décomposait mieux dans sa propre plantation (en moyenne 46% de perte de masse) que dans les autres types de plantations (en moyenne 37% de perte de masse). L'abondance des acariens détritivores et la biomasse des champignons y étaient également plus importantes. Ces derniers étant généralement reconnus pour être plus efficaces dans la dégradation des composés plus récalcitrants, leur plus grande abondance pourrait expliquer la décomposition plus rapide de l'épinette. Dans nos sites expérimentaux la température et l'humidité du sol n'étaient pas plus élevées dans les plantations monospécifiques d'épinettes en comparaison avec les autres plantations, ce qui signifie que cette plus grande abondance de décomposeurs était réellement due à l'environnement chimique et structurel créé par la litière. En revanche, la cellulose et l'herbe se décomposaient moins vite dans les plantations monospécifiques d'épinettes comparées aux autres types de plantations; Ces résultats confirment que les organismes présents sous les épinettes sont capables de dégrader plus efficacement la litière d'épinette, ce qui n'était pas simplement dû à une plus grande capacité de dégradation de tous types de litières. Dans les plantations monospécifiques d'épinettes, l'horizon de fragmentation (OF) était beaucoup plus important et l'horizon organo-minéral (A) moins important que dans les deux autres types de plantations (Chapitre 5). Cette accumulation de matière organique dans l'horizon OF semble constituer un important "réservoir" de décomposeurs, comme le montre la plus grande abondance des acariens et des champignons. Sur le terrain nous avons en effet observé un horizon OF constitué de feuilles fragmentées et largement colonisées par le mycélium.

L'étude de l'influence des arbres sur leur environnement a été complétée par l'étude de la décomposition de la cellulose à différentes distances de l'arbre. Ainsi, dans les plantations monospécifiques d'épinettes, la cellulose se décomposait mieux entre les arbres plutôt que directement sous les arbres. Ce résultat confirme que l'épinette crée un microhabitat très spécifique, mais très localisé sous sa canopée. À l'inverse, dans les plantations monospécifiques de peuplier, la cellulose se décomposait de manière similaire sous les arbres ou entre les arbres.

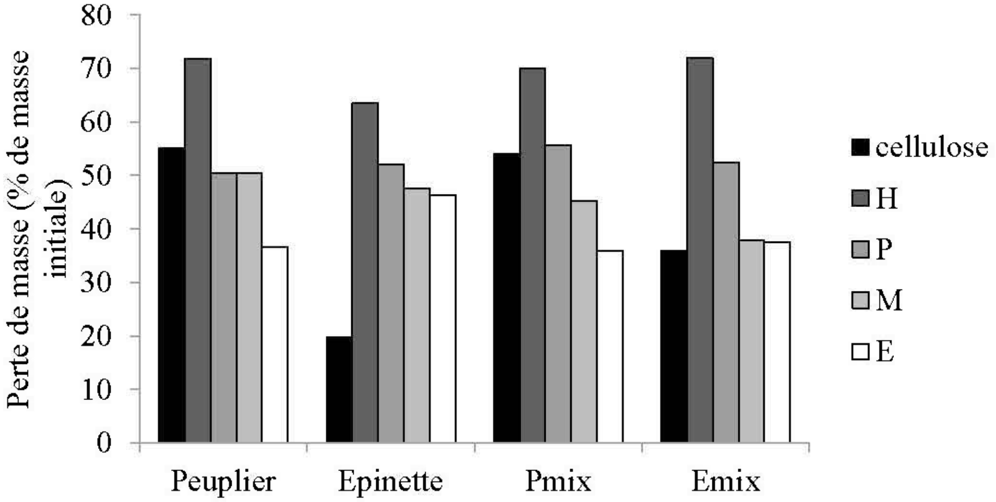

Figure 6.2 Perte de masse des différentes litières (cellulose, herbacées H, peuplier P, mixte M et épinette E) dans les différentes plantations (monospécifiques de peuplier et d'épinette, et mixtes sous les peupliers Pmix ou sous les épinettes Emix) après 2 ans de décomposition.

6.2 Des espèces seules aux mélanges d'espèces : effet de la mixité forestière

Contrairement à nos hypothèses de départ, la diversité des communautés de décomposeurs et la vitesse de décomposition n'ont généralement pas été stimulées par le mélange des arbres ou des litières de peuplier et d'épinette. En revanche le mélange avec les herbacées a généralement apporté une amélioration du processus de décomposition. Il y avait toutefois des différences selon les litières prises en compte; Lorsque les litières ont été séparées individuellement dans les mélanges, nous avons observé que la décomposition de la litière d'épinette n'a pas été améliorée par l'apport d'herbacées, et sa décomposition a même été ralentie par l'apport de peuplier. La théorie du "priming effect", i.e. l'augmentation de la vitesse de décomposition d'un mélange de litières avec un apport de litière labile, n'est donc pas vérifiée pour la litière d'épinette, litière la plus récalcitrante. Il a été proposé que le "priming effect" résultait de l'intensité de compétition entre des microorganismes à stratégie-r (à fort taux de croissance, utilisant des formes de C riches en énergie), et des microorganismes à stratégie-k utilisant les formes récalcitrantes du C (Fontaine et al., 2003). Ainsi nous pouvons penser que dans les mélanges avec la litière d'épinette, des microorganismes à stratégie-r sont attirés par la litière plus labile (les herbacées ou le peuplier) et supplantent les microorganismes à stratégie-k, adaptés à décomposer la litière d'épinette. Ainsi ces organismes colonisant le mélange seraient moins efficaces dans la dégradation de l'épinette, et donc au lieu d'une amélioration de sa décomposition nous n'observons pas d'effet ou un effet négatif du mélange avec une litière labile. Nos expérimentations *in situ* ont en effet montré que les microorganismes colonisant la litière d'épinette avaient une plus faible diversité catabolique, mais que leur activité était plus basée sur la dégradation des polymères en début du processus de décomposition, contrairement aux microorganismes qui colonisent les herbacées ou le peuplier. En revanche, la décomposition de la litière de peuplier et du mélange peuplier / épinette a fortement été accélérée par l'ajout d'herbacées. Les herbes n'augmentaient pas forcément l'humidité dans nos expérimentations, mais elles attiraient une grande abondance d'organismes, ce qui signifie que cette différence d'abondance était réellement due à la qualité chimique de la litière. De plus, les microorganismes qui colonisaient la litière d'herbacées ou les mélanges de litières avec les herbacées avaient une activité et une diversité cataboliques plus élevées que les litières d'arbres seuls à 7 mois de décomposition, ce qui reflète le caractère opportuniste de ces organismes, qui sont capables de dégrader rapidement une grande diversité de composés. Les collemboles étaient même plus abondants dans les mélanges avec les herbacées que dans les herbacées seules. Il a été démontré qu'un régime alimentaire mixte pouvait augmenter la fitness des collemboles (Scheu and Simmerling, 2004), et notre étude en microcosmes (Chapitre 3b) a permis de démontrer que les herbacées augmentaient la reproduction de *F. candida*. Ainsi les mélanges de litière avec des herbacées semblent favoriser l'abondance des collemboles. Toutes ces différences mettent en évidence l'amélioration du processus de décomposition avec l'apport d'herbacées. Grâce à cette addition de matière organique labile, la libération de l'azote a été accélérée dans tous les types de litières dans les plantations correspondantes (Chapitre 4). Cet aspect est intéressant pour la fertilité des plantations sous systèmes d'aménagement intensif, sachant que l'azote est généralement considéré comme un des principaux facteurs limitant la croissance des végétaux.

Au niveau de « l'effet habitat », tout comme « l'effet ressource », nous n'avons pas observé une plus grande diversité ou abondance de décomposeurs, ni d'amélioration du processus de décomposition par le mélange des deux espèces forestières. Nous avons calculé les effets non additifs, généralement utilisés pour évaluer l'effet du mélange de litière sur le taux de décomposition. Lorsque nous l'appliquons à l'effet habitat nous supposons que la vitesse de décomposition dans les plantations mixtes correspond à la moyenne des vitesses de décomposition dans chacune des plantations pures. Ainsi, grâce à ces calculs, nous avons pu mettre en évidence que les litières de peuplier, d'épinette et de cellulose se décomposaient comme prédit dans les plantations mixtes sous épinette. En revanche sous les peupliers dans les plantations mixtes, nous avons observé un effet non additif positif de la décomposition du peuplier et de la cellulose et un effet non-additif négatif de la décomposition de l'épinette. Ces résultats signifient que l'épinette crée des conditions spécifiques qui se retrouvent dans les plantations mixtes. Même si les différences ne sont pas flagrantes, ces résultats pourraient indiquer une séparation spatiale des organismes ce qui expliquerait en partie l'absence d'une augmentation de la diversité d'organismes en mélangeant les litières.

Les résultats de notre étude (Chapitre 5) montrent que les plantations mixtes augmentent le stockage de carbone par rapport aux plantations monospécifiques. Du fait d'une croissance plus importante des peupliers dans les plantations mixtes (augmentation de 47% de la biomasse) en comparaison aux plantations monospécifiques, le stockage de carbone dans la biomasse végétale était plus important. En ce qui concerne le stockage de carbone dans les sols (excluant les racines), nous avons observé une augmentation de 52% de carbone dans l'horizon superficiel (OL) par rapport à la moyenne des deux plantations pures. Cet aspect présente un double avantage, d'une part cette réserve de matière organique dans l'horizon OL permettrait d'avoir un apport plus progressif d'éléments minéraux suite à la décomposition graduelle de la litière et d'autre part une optimisation du stockage de carbone serait favorable dans le contexte actuel de changement climatique.

6.3 Synthèse générale et enjeux pour l'aménagement forestier

La complexité du processus de décomposition provient du fait qu'il est la résultante de nombreux processus biotiques et abiotiques interdépendants qui agissent de manière simultanée, et qui sont eux-mêmes régis par de nombreux facteurs de contrôle. Bien qu'il ait été difficile de dissocier chacun de ces paramètres, cette thèse a permis de mieux comprendre les mécanismes induits par chaque espèce végétale de manière individuelle, mais également lorsqu'elles sont en association.

Relativement peu d'études ont couplé à la fois l'effet ressource et l'effet habitat pour comprendre l'effet de la mixité forestière sur le fonctionnement de l'écosystème. Nous pouvons affirmer que l'épinette et le peuplier modifient rapidement leur environnement, car après 10 ans on observait déjà une différentiation au niveau du fonctionnement des différentes plantations. L'ensemble des résultats obtenus a permis de mettre en évidence que les arbres et leur litière induisent une sélection des communautés de décomposeurs en modifiant l'environnement physico-chimique. Nos résultats ont montré un effet ressource important, car nous avons observé des différences en terme de communautés de décomposeurs et de vitesse de décomposition entre les différents types de litière. Cependant l'effet habitat influençait de manière plus marquée les communautés de décomposeurs et le processus de décomposition, traduisant un effet plus important que l'effet ressource.

Le mélange des espèces d'arbres n'a pas induit une plus grande diversité d'organismes ni une amélioration du processus de décomposition, que ce soit au niveau du mélange de ressources ou au niveau d'une diversification d'habitats. Cependant nous avons observé une augmentation de la productivité du peuplier et une augmentation de la quantité de matière organique dans l'horizon superficiel du sol (OL). Ces différences ont conduit à une amélioration du stockage de carbone dans ces plantations mixtes par rapport aux plantations monospécifiques. Une augmentation de la vitesse du processus de décomposition est généralement considérée comme bénéfique pour la libération d'éléments nutritifs dans le sol. Mais comme nous l'avons supposé dans les plantations pures de peuplier, une décomposition trop rapide et donc une faible épaisseur des horizons superficiels du sol semblaient, parmi d'autres facteurs, diminuer la colonisation par les organismes. Ainsi, on peut se demander si un processus de décomposition relativement plus lent et donc une minéralisation des nutriments plus progressive dans les plantations mixtes ne serait pas plus avantageux ?

Les résultats de cette étude montrent divers avantages (stockage de carbone, production de bois, fonctionnement) aux plantations mixtes par rapport aux plantations monospécifiques. Il faut toutefois étudier ces processus sur le plus long terme pour pouvoir identifier avec certitude les meilleures solutions possibles pour l'aménagement forestier. De plus, les herbacées semblent être bénéfiques pour la diversité d'organismes et favorisent la libération d'azote des litières. Cet aspect pourrait contrebalancer l'effet négatif de la présence d'herbacées qui entrent en compétition avec les arbres pour les ressources.

6.4 Perspectives

Les résultats de cette thèse sont des prémices dans la compréhension du fonctionnement des relations sol / plantes dans les systèmes de sylviculture intensifs et de nombreuses pistes pour de futures recherches émergent.

Une des premières perspectives serait de poursuivre ces recherches dans des plantations arrivées à la maturité de récolte pour confirmer ces résultats sur le plus long terme et pouvoir déterminer le meilleur aménagement possible afin d'optimiser à la fois la quantité de bois récolté, le relargage naturel d'éléments nutritifs dans le sol pour limiter les apports exogènes, ainsi que le stockage de carbone dans les systèmes sylvicoles en région boréale. De plus, il serait nécessaire de réaliser des études avec divers espacements plus fréquemment utilisés en sylviculture (de 3 à 6 m pour les peupliers hybrides) pour vérifier si ces résultats se confirment dans d'autres conditions.

Dans cette thèse, le processus de décomposition a été appréhendé seulement par l'activité des microorganismes et de la mésofaune. Cependant, la macrofaune a un rôle très important dans le processus de décomposition, car elle régule les communautés d'organismes par des effets négatifs de prédation ou des effets positifs en réalisant une première fragmentation de la litière. La contribution respective des différents groupes est mal connue et des études concernant les taux de consommation et d'assimilation de chaque groupe dans les réseaux trophiques permettraient de clarifier leurs effets.

Le rôle des métabolites secondaires semble être primordial dans la compréhension des relations plantes / décomposeurs. Nous nous sommes intéressés ici seulement au dosage des phénols totaux, qui n'est qu'un indicateur du contenu total en phénols. Les terpènes et les tanins (composé phénolique) peuvent jouer un rôle important dans le processus de décomposition, et leur prise en compte dans ce type d'études pourrait améliorer la compréhension du lien entre la litière et les organismes. Il serait en particulier intéressant d'étudier en laboratoire l'effet de chaque groupe de composés secondaires sur les différents groupes de décomposeurs avec des métabolites secondaires extraits et isolés à partir des litières.

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