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RÉSUMÉ

Le bois mort, constitué par les chicots et les arbres morts au sol, est un élément structural clé des écosystèmes forestiers. En forêt boréale, il représente un large réservoir de carbone (C) et une quantité substantielle de matière organique dans la couverture morte. Le passage d'un aménagement forestier équienne à un aménagement inéquienne aura un impact important sur la dynamique du bois mort et pourrait avoir un effet positif sur la capacité de séquestration de C des peuplements. Ce projet a pour objectif général de préciser les paramètres qui affectent la contribution du bois mort à la séquestration du C dans un contexte d'aménagement écosystémique. La démarche consistait à comparer la dynamique du bois mort avec celle des litières de feuillage, de façon à relativiser l'importance du bois mort pour la rétention du C. Nous amenons l'hypothèse que la coupe totale et les coupes partielles auraient une influence sur la dynamique du C à travers leurs effets sur la production et la décomposition du bois mort et des litières de feuillage. Parce que la décomposition du bois mort atteindrait une limite maximale de décomposition plus élevée et conduirait à des composés carbonés moins stables que la décomposition des litières de feuillage, les changements dans les réservoirs et la dynamique du bois mort induits par les coupes auront des incidences sur la séquestration du C.

L'étude est menée en sapinière à bouleau blanc, dans la forêt d'enseignement et de recherche du lac Duparquet, dans des peuplements dominés par le tremble et des peuplements dominés par les conifères. Afin d'étudier le rôle du bois mort et des litières de feuillage dans la rétention du C via leur limite maximale de décomposition et la formation de molécules stables, nous avons caractérisé les patrons de perte de masse et les transformations chimiques du bois mort (chicots, billes) et des litières de feuillage au cours de la décomposition de conifères et de feuillus. La composition chimique de la couverture morte a aussi été étudiée. Les analyses chimiques incluaient les méthodes de spectroscopies à résonance magnétique nucléaire et infrarouge, ainsi que la quantification des monomères de lignines par oxydation à l'oxyde de cuivre. Les effets des coupes partielles et totales sur la dynamique du bois mort et la rétention du C ont été déterminés à partir de 9 années d'inventaires (dendrométrique, bois mort, chutes de litières) et d'échantillonnage (sol, bois mort, litières de feuillage) dans des peuplements naturels dominés par le tremble et des peuplements soumis à différents degrés de prélèvement.

Ainsi, les litières de feuillage retiendraient le C en atteignant rapidement une faible limite maximale de décomposition et en formant une matière récalcitrante riche en composés alkyl et en hydrates de carbone. Au contraire, le bois mort retiendrait le C par sa décomposition lente, et permettrait la préservation de lignines et d'hydrates de carbone dans les billes bien décomposées. L'hypothèse, qui supposait que la décomposition du bois mort atteindrait une limite maximale supérieure aux litières de feuillage, se vérifiait dans le cas du tremble, mais pas pour les conifères. Dans les peuplements naturels de tremble étudiés, la production de bois mort était légèrement supérieure à celle des litières de feuilles, et le bois mort formait un plus large réservoir de C, incluant 59 % de la nécromasse. Pourtant, le bois enfoui constituait seulement 19% de la couverture morte.

Les coupes totales favorisaient les litières de feuillage, à décomposition rapide, à faible limite maximale de décomposition, et générant une matière organique récalcitrante riche en composés alkyl. Au contraire, les coupes partielles conservaient plusieurs caractéristiques des peuplements naturels, en particulier les chutes de litières et la production de bois mort, la distribution des billes dans les classes de diamètres et de décomposition, ainsi que le contenu de la couverture morte et du sol minéral. Après coupes partielles, la mortalité progressive des arbres favorisait la présence de bois mort, qui retenait le C grâce à sa décomposition lente, notamment dans les chicots. L'aménagement écosystémique pourrait donc contribuer à la séquestration du C, en choisissant des traitements de coupes adaptés, comme des coupes partielles. Les tiges résiduelles fixent le C et génèrent des litières de bois mort à décomposition lente. Le devenir et la rétention des lignines associées au bois enfoui dans la couverture morte, ainsi que le lessivage des composés organiques dissous lors de la décomposition du bois mort devront faire l'objet d'études plus approfondies afin de compléter l'importance du bois mort pour la séquestration du C.

Mots-clés : bois mort, carbone, chicots, billes au sol, décomposition, composition chimique, lignines, résonance magnétique nucléaire, coupes partielles, couverture morte, litières de feuillage.

INTRODUCTION GÉNÉRALE

0.1. Problématique

Les forêts boréales jouent un rôle majeur dans le cycle du carbone (C) terrestre (Apps et al., 1993; Bhatti et al., 2003; Pan et al., 2011). Occupant de vastes étendues dans l'hémisphère nord (Pan et al., 2011), elles constituent une réserve considérable de C, principalement dans les sols (Apps et al., 1993; Malhi et al., 1999), où la matière organique s'accumule et se décompose lentement (Van Cleve & Powers, 1995; Zhang et al., 2008). De nombreux facteurs vont influencer cette réserve et modifier la dynamique du C dans l'écosystème (Bhatti et al., 2003), déterminant ainsi la fonction de puits ou de source de C de la forêt (Liu et al., 2002). Parmi ces facteurs figurent l'âge du peuplement (Pregitzer & Euskirchen, 2004) et sa composition (Gower et al., 2001), le climat (Dixon et al., 1994), les caractéristiques du sol (Van Cleve & Powers, 1995), les perturbations naturelles (Harden et al., 2000) et les récoltes forestières (Scott et al., 2004; Martin et al., 2005).

Le bois mort, constitué principalement par les chicots et les arbres morts au sol, est un élément structural clé des écosystèmes forestiers (Harmon et al., 1986). Le bois mort joue de nombreux rôles écologiques, notamment dans la biodiversité, dans la productivité des écosystèmes et dans la géomorphologie des milieux (Harmon et al., 1986; Freedman et al., 1996; Siitonen, 2001). La quantité de bois mort dans un écosystème résulte de la balance entre la mortalité des arbres et la décomposition, la consumation ou l'exportation du bois (Harmon et al., 1986; Tinker & Knight, 2000;

Siitonen, 2001). Outre la sénescence naturelle des arbres, leur formation est favorisée par les perturbations, telles que les feux, le vent, les épidémies d'insectes, les chablis, ou les coupes forestières (Franklin et al., 1987; Krankina et al., 2002). Le bois mort représente une quantité substantielle de matière organique de la couverture morte des sols et un pool de C important dans l'écosystème forestier (Krankina & Harmon, 1995; Manies et al., 2005). Et pourtant, leur contribution dans les cycles du C et des nutriments n'est pas bien définie (Laiho & Prescott, 2004; Manies et al., 2005).

Les coupes forestières, et plus particulièrement les coupes totales, ont un impact important sur la dynamique du C dans l'écosystème. Elles changent les conditions abiotiques (Moroni & Zhu, 2012), ce qui peut avoir une incidence sur le taux de décomposition de la matière organique. Elles modifient également l'allocation du C dans les différents réservoirs, en diminuant le pool de C du couvert forestier et en générant des débris au sol (Krankina & Harmon, 1995).

Depuis quelques années, la mise en place d'un aménagement écosystémique, inspiré de la dynamique naturelle des peuplements, est proposée afin de préserver la biodiversité et de maintenir les fonctions de l'écosystème (Harvey et al., 2002). L'impact de l'aménagement écosystémique sur la dynamique du bois mort et sur le cycle du C n'est pas connu. Les coupes partielles sont un élément prépondérant de l'aménagement écosystémique et pourraient avoir une influence sur la mortalité des tiges résiduelles (Bose et al., 2014), et sur le taux de décomposition des litières (Prescott, 1997). Ainsi, elles pourraient modifier le statut de la forêt de puits ou de source de C.

L'étude est menée en sapinière à bouleau blanc, dans des peuplements dominés par le tremble et des peuplements dominés par les conifères de la forêt d'enseignement et de recherche du lac Duparquet. Les principaux objectifs de ce projet sont d'étudier le rôle du bois mort dans la rétention du C via la formation de molécules stables et d'évaluer les effets des différents types de coupes partielles et totales sur la dynamique du bois mort et la rétention du C dans les différents réservoirs de l'écosystème.

0.2. État des connaissances

0.2.1. Importance des forêts boréales dans le cycle du carbone

Les forêts boréales occupent la région circumpolaire (50°-70°N) située entre la toundra au nord et la forêt tempérée au sud (Larsen, 1980; Bellefleur & Parent, 2009). Elles s'étendent sur environ 1300 Mha (Bonan & Shugart, 1989; Apps et al., 1993), soit environ 32% de la superficie des forêts (Dixon et al., 1994; Pan et al., 2011) ou 11% des terres du globe (Bonan & Shugart, 1989; FAO & JRC, 2012), et se répartissent sur la Russie, le Canada, la Scandinavie et l'Alaska (Tableau 0.1).

La diversité en espèces est faible en forêt boréale, due à la présence relativement récente des glaciers et au faible taux de migration et d'évolution des espèces (McGlone, 1996). Les genres principaux incluent les épinettes (*Picea*), les pins (*Pinus*), les mélèzes (*Larix*), les sapins (*Abies*), les bouleaux (*Betula*), les peupliers (*Populus*), les aulnes (*Alnus*) et les saules (*Salix*), qui peuvent former des peuplements purs ou mélangés plus ou moins ouverts (Larsen, 1980).

Le climat des forêts boréales est typiquement continental, avec un été court et humide, un hiver long et froid, une moyenne annuelle de température de 0°C, de fortes variations saisonnières, et des précipitions de 400 à 800 mm distribuées régulièrement toute l'année (Larsen, 1980; Bonan & Shugart, 1989; Burton et al., 2003b; Bellefleur & Parent, 2009). Au niveau des conditions édaphiques, les sites pauvrement drainés sont organiques, tandis que les sites de haut de pente ont plutôt une texture grossière et sableuse (régosols). On trouve aussi des podzols, qui ont un horizon de surface épais, acide et organique, et un horizon minéral pauvre en nutriments (Larsen, 1980; Soil Classification Working Group, 1998). Les luvisols, présents dans cette étude, sont caractéristiques de l'argile de remblaiement lacustre bien drainée (Bergeron et al., 1983).

La séquestration du C dans les forêts boréales est un important processus de régulation du CO_2 atmosphérique (Dixon et al., 1994; Gower, 2003). La quantité de C dans les forêts boréales est estimée à 271.5 PgC, alors que les forêts du globe contiennent de 861.1 PgC (Tableau 0.1), mais les estimations varient considérablement entre les études (Dixon et al., 1994; Pan et al., 2011). De nombreux facteurs vont avoir un impact sur le taux de croissance et de mortalité des arbres, et sur le taux de décomposition de la matière organique morte, et ainsi vont influencer le stockage et les émissions de C (Liu et al., 2002). Ces facteurs incluent les caractéristiques du peuplement (Pregitzer & Euskirchen, 2004), les conditions climatiques et édaphiques (Dixon et al., 1994; Van Cleve & Powers, 1995), et les perturbations naturelles (Harden et al., 2000) et anthropiques (Martin et al., 2005).

Tableau 0.1. Superficie, réservoirs de C et flux net de C dans les forêts boréales, tempérées et tropicales (Pan et al., 2011).

	Forêts boréales	**Forêts tempérées**	**Forêts tropicales**
Superficie (Mha)	1135	767	1949
Réservoirs de C (Pg)			
Total	271.5	118.6	471
Biomasse vivante	53.9	46.6	262.1
Bois mort	16.1	3.3	53.6
Litière	27.0	12.1	4.0
Sols	174.5	56.7	151.3
Flux de C entre 2000 et 2007 (PgC/an)			
Puits de C (+) ou Sources de C (-)	+0.5	+0.78	-0.08

Mais globalement, les forêts boréales sont de faibles puits de C, en raison des feux et des épidémies d'insectes qui affectent d'importantes surfaces forestières (Goodale et al., 2002). Ces perturbations jouent un rôle majeur dans le cycle du C dans les forêts boréales, car elles génèrent la mortalité des arbres du couvert, la production de chicots et de billes au sol et le recrutement d'espèces intolérantes à l'ombre, et ainsi elles peuvent ré-initier un nouveau peuplement (Gromtsev, 2002; Youngblood & Wickman, 2002). Les épidémies d'insectes au Québec incluent les épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.; Morin et al., 1993) et les épidémies de livrée des forêts (*Malacosoma disstria* Hübner; Moulinier et al., 2011). Les feux peuvent être plus ou moins sévères et vont aussi consumer une partie des arbres, du bois mort et de la couverture morte, et former du CO_2 du CH_4, du C pyrogénique (« pyrogenic carbon » ou « black carbon » en anglais) et des cendres (Kasischke et al., 1995; González-Pérez et al., 2004). Les composés pyrogéniques incluent des charbons (résidus solides) et de la suie (composés volatiles) (Preston & Schmidt, 2006). Il est estimé qu'environ 1/3 de la productivité primaire nette dans les forêts boréales est consumé par le feu (Harden et al., 2000; Preston & Schmidt, 2006).

Les forêts boréales se caractérisent par une séquestration importante de leur C dans les sols (Dixon et al., 1994; Malhi et al., 1999) (Tableau 0.1), où la décomposition est lente et incomplète (Prescott, 2005; Zhang et al., 2008), en raison du climat froid, de la courte saison de croissance (Van Cleve et al., 1981; Van Cleve et al., 1983) et des conditions édaphiques (Van Cleve & Powers, 1995). La décomposition apparaît donc comme un processus majeur contrôlant les échanges de C entre la forêt boréale et l'atmosphère (Sellers et al., 1997). La quantité de C dans la couverture morte augmente généralement avec le temps depuis le dernier feu (Kasischke et al., 1995).

Les forêts boréales mixtes, dans lesquelles cette étude est réalisée, représentent la moitié des forêts boréales canadiennes productives (Towill, 1996). Elles bénéficient d'un climat plus doux que la moyenne des forêts boréales et se trouvent généralement sur les sols les plus fertiles (Man & Lieffers, 1999; Johansson, 2003; MacDonald & Thompson, 2003). Au Québec, elles sont présentes notamment dans le domaine de la sapinière à bouleau blanc, où les espèces dominantes changent avec le temps depuis le dernier feu.

Sur les sites mésiques, la succession des espèces après feux commence généralement avec l'établissement de peuplements purs ou mixtes de bouleau blanc (*Betula papyrifera* Marsh.), de tremble (*Populus tremuloides* Michx.) et de pin gris (*Pinus banksiana* Lamb.) qui maintiennent leur dominance pendant plus de 100 ans. Dans l'absence de perturbation majeure, le remplacement graduel de ces espèces par une mixture d'espèces tolérantes à l'ombre, comme l'épinette blanche (*Picea glauca* (Moench) Voss), l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et le sapin baumier (*Abies balsamea* (L.) Mill.) (Bergeron & Dubuc, 1989) génère la formation de peuplements mixtes. À cause de leur grande productivité, les forêts boréales mixtes peuvent jouer un rôle important dans la séquestration du C et pourraient augmenter les capacités de puits de C des forêts boréales.

0.2.2. Importance du bois mort dans la séquestration du carbone

Le bois mort est une composante structurale importante des forêts boréales naturelles et est associé à un grand nombre de processus et de fonctions (Harmon et al., 1986; Jonsson & Kruys, 2001; Harmon et al., 2004). Sous forme de chicots (arbres morts debout), de souche d'arbres, de billes au sol, de branches, de charbons ou de bois enfoui dans le sol (i.e., couverture morte lignique), le bois mort est aussi divers par la taille de ses débris, et lorsque le diamètre est supérieur à 2.5 cm, on parle de débris ligneux grossiers (Harmon et al., 1986; Tinker & Knight, 2000). Le bois mort forme une diversité d'habitats et de microhabitats pour une multitude de microorganismes et d'espèces animales et végétales (Thomas, 1979; Harmon et al., 1986). Notamment, les champignons saproxyliques, les invertébrés et les petits mammifères utilisent le bois mort comme abri et source de nourriture et favorisent ainsi la décomposition du bois mort. Le bois mort stocke d'importantes quantité d'eau, il joue également un rôle dans les cycles des nutriments (Lambert et al., 1980; Laiho & Prescott, 2004; Brais et al., 2006), notamment en fixant l'azote par des bactéries non symbiotiques (Brunner & Kimmins, 2003). À long terme, le bois mort constitue une source de matière organique du sol et participe aux propriétés physiques et chimiques, et à la fertilité du sol (Feller, 2003).

Le bois mort joue aussi un rôle important dans le cycle du C. Sur les 0.6-0.7 Pg C/an accumulés dans les forêts boréales et tempérées (Battle et al., 2000; Prentice et al., 2001; Goodale et al., 2002), 0.15 PgC/an l'était dans le bois mort, contre 0.21 PgC/an dans la biomasse vivante, et 0.13 PgC/an dans les sols (Goodale et al., 2002). Ce rôle a souvent été négligé dans les études où seulement les arbres vivants ou le sol sont considérés (Schlesinger, 1977; Woodwell et al., 1978).

Peu à peu, les connaissances sur la dynamique du bois mort se sont développées (Krankina & Harmon, 1995; Tarasov & Birdsey, 2001; Yatskov et al., 2003), notamment dans la forêt boréale mixte de l'est du Canada (Hély et al., 2000), mais rares sont les études qui considèrent l'ensemble de la dynamique, incluant la mortalité, la décomposition, la qualité et la quantité du bois mort.

0.2.2.1. Dynamique du bois mort

En forêt naturelle, la quantité de bois mort résulte de la balance entre les flux entrants, à travers la mortalité des arbres et l'élagage des branches, et les flux sortants lors de la décomposition et de la consumation par les feux (Tinker & Knight, 2000).

La mortalité des arbres est favorisée par les perturbations, comme les épidémies d'insectes, les feux le vent et les chablis (Gromtsev, 2002; Youngblood & Wickman, 2002). Mais la mort résulte généralement d'une interaction complexe entre l'arbre, son environnement, la présence d'agents de mortalité, et la succession d'événements qu'il va subir et qui fragilisent l'arbre. Parmi ces événements figurent les maladies, les blessures lors des chablis, les phénomènes de compétition ou de sénescence, et les stress environnementaux (Franklin et al., 1987; Krankina et al., 2002). La décomposition du bois mort est influencée par le climat (température, humidité, conditions lumineuses) (Aerts, 1997; Zhang et al., 2008), les conditions édaphiques (drainage, nutriments), la qualité des litières (type de litière, espèce, taille, degré de carbonisation), et la nature des microorganismes (bactéries, champignons) et de la faune (Swift et al., 1979; Coûteaux et al., 1995).

Avant même la mort de l'arbre, la colonisation plus ou moins avancée par des bactéries et des champignons va jouer un rôle dans l'initiation de la décomposition (Boddy 2001). La mort de l'arbre génère des chicots ou des billes au sol, qui transitent rapidement à travers les premiers stades de décomposition (Vanderwel et al., 2006). Le taux de chute des chicots augmente avec la décomposition (Angers et al., 2010), et lorsque les chicots tombent, ils intègrent généralement les stades de décomposition avancés. Le bois mort progresse dans les différents stades de décomposition, jusqu'à être enfouis et intégrés à la matière organique du sol.

0.2.2.2. Quantité de bois mort

Dans un peuplement naturel, la masse de bois mort peut varier de 3 $Mg{\cdot}ha^{-1}$ à 400 Mg/ha (Harmon et al., 1986; Harmon et al., 1987; Krankina & Harmon, 1995). Après un feu, l'étude de Tinker & Knight (2000) a estimé que 8% du bois mort total serait carbonisé, pour un total de 0.2 à 7.4 Mg/ha (Preston & Schmidt, 2006), soit une faible proportion du C en forêt. Les débris de bois mort sont généralement hétérogènes, différant par la taille, le stade de décomposition, l'espèce, la position, et la forme (Harmon et al., 1986), et le degré de carbonisation (Preston & Schmidt, 2006). La quantité, la qualité et la distribution spatiale du bois mort dépendent du patron de mortalité des arbres, de l'intensité des feux et la proximité dans le temps des épisodes de mortalité (Harmon et al., 1986; Jomura et al., 2007; Aakala, 2010; Kasin & Ohlson, 2013). La quantité de bois mort dépend aussi du taux de décomposition, de la productivité du site, de la composition et de la structure de la canopée et de l'histoire des perturbations (Fridman & Walheim, 2000; Hély et al., 2000; Siitonen, 2001; Krankina et al., 2002; Feller, 2003; Ranius et al., 2003).

Après une perturbation naturelle, l'abondance du bois mort en fonction du temps suit une courbe en forme de U, avec une quantité plus élevée dans les jeunes et les vieilles forêts et plus faible dans les forêts d'âge moyen (Harmon et al., 1986; Sturtevant et al., 1997; Feller, 2003; Brais et al., 2005). Ces patrons résultent de la décomposition graduelle de la grande quantité du bois mort généré par la perturbation initiale et la reformation de ce stock lorsque le peuplement de replacement devient mature et génère des débris de bois mort par la mortalité des arbres (Janisch & Harmon, 2002).

0.2.3. Importance de la décomposition dans la séquestration du carbone

La décomposition est processus complexe de dégradation des litières et aboutit à la formation de composés organiques stables (Berg & McClaugherty, 2008), de composés organiques dissous (Kalbitz et al., 2000) et de composés minéraux (Swift et al., 1979). La libération du CO_2 dans l'atmosphère ou la rétention du C dans l'humus ou le sol minéral lors de la décomposition en font un processus majeur du cycle du C.

La qualité des litières correspond aux caractéristiques physiques et chimiques qui ont un impact sur la décomposition. La qualité des litières va influencer le taux de décomposition (Melillo et al., 1982; Taylor et al., 1989), la limite maximale de décomposition (Berg et al., 1996; Berg, 2000), et dans certains cas, la composition de la matière organique issue de la décomposition (Quideau et al., 2001). Bien que la production de bois mort équivaille celle des litières de feuillage, le bois mort se décompose généralement plus lentement (Harmon et al., 1986; Laiho & Prescott, 2004), en raison de sa structure physique (Cornwell et al., 2009) et de sa composition chimique (Laiho & Prescott, 2004; Berg & McClaugherty, 2008). Le bois mort pourrait ainsi favoriser la rétention du C dans les sols (Manies et al., 2005). Et pourtant, peu d'études se sont penchées sur l'importance de la qualité du bois mort pour son intégration dans le sol et sa séquestration du C.

0.2.3.1. Qualité initiale des litières

Les feuilles et les aiguilles sont formées de cellules vivantes entourées d'une couche de cuticule qui recouvre l'épiderme, tandis que la tige de l'arbre est formée principalement de bois, où la majorité des cellules sont mortes. Les litières de feuillage et le bois mort non décomposés sont constitués de composés structuraux (cellulose, hémicelluloses, lignines, composés pectiques), de composés métaboliques primaires (sucres, lipides, protéines), et de composés phénoliques (tannins) (Panshin & de Zeeuw, 1980; Trofymow et al., 1995), en proportions différentes (Tableau 0.2).

Le bois mort contient généralement plus de cellulose et d'hémicelluloses que les litières de feuillage, mais moins de sucres simples et autres composés solubles, ainsi que moins de nutriments (Tableau 0.2) (Berg & McClaugherty, 2008). Les parois des cellules du bois sont constituées de plusieurs couches, où les lignines sont fortement imbriquées à la cellulose et aux hémicelluloses. Le duramen est pauvre en nutriments et riche en extractibles (composés phénoliques, des résines, des tropolones, des acides gras, des cires, etc.), qui se sont accumulés pendant la duraminisation (Panshin & de Zeeuw, 1980), tandis que l'écorce est plus riche en tannins et en nutriments (Hernes

& Hedges, 2004). La cuticule des feuilles contient des cires et de la cutine, qui sont résistantes à la décomposition (Lorenz et al., 2007).

Les racines, qui ne sont pas étudiées ici, peuvent être à l'origine de 50 à 70 % du carbone séquestré dans les sols des forêts boréales (Clemmensen et al., 2013). Les racines se distinguent des litières de feuillage par une concentration en azote, cellulose, hémicellulose et lignines plus élevées, mais une concentration en composés solubles et composés non polaires plus faibles (Stump & Binkley, 1993; Lemma et al., 2007; Berg & McClaugherty, 2008), mais ce n'est pas toujours le cas (Stump & Binkley, 1993; Lemma et al., 2007; Berg & McClaugherty, 2008).

Le bois et les feuilles des espèces feuillues contiennent généralement plus de cellulose, d'hémicelluloses et de nutriments, et moins de lignines que le bois et les aiguilles de conifères (Cornwell et al., 2009; Weedon et al., 2009), mais ce n'est pas toujours le cas (Tableau 0.2). Les lignines du bois d'espèces feuillues sont constituées d'unités phénoliques syringyl et vanillyl, tandis que celles de conifères sont formées principalement des unités vanillyl (Thevenot et al., 2010). Les feuilles et les aiguilles contiennent également des unités cinnamyl (Thevenot et al., 2010). Au niveau de la structure physique, les bois des espèces feuillues ont des vaisseaux pour conduire la sève, tandis que les conifères n'ont que des trachéides (Cornwell et al., 2009).

Les caractéristiques initiales du bois mort, incluant sa taille, son espèce, et sa position (debout ou au sol) influencent la décomposition. Son état de décomposition sera donc très hétérogène entre les débris de bois mort, mais également au sein d'un même débris.

Tableau 0.2. Concentrations des principaux composés organiques extraits par analyses proximales, et concentrations de carbone et d'azote (mg.g^{-1}) dans les litières de feuillage et le bois mort d'espèces feuillues et de conifères

Type de litière	**ENP**	**EPE**	**ACID**	**AUR**	**Carbone**	**Azote**
Feuilles d'espèces feuillues (Trofymow et al., 1995)						
Bouleau à papier	65	359	303	240	480	7.2
Tremble	88	354	337	144	468	6.7
Aiguilles de conifères (Trofymow et al., 1995)						
Sapin baumier	132	265	302	272	555	5.3
Épinette blanche	81	297	347	201	464	7.7
Pin gris	70	152	424	328	497	12.8
Bois d'espèces feuillues (Alban & Pastor, 1993; Beaudoin et al., 2009)						
Bouleau blanc			420[a]	190		
Tremble		57	720	200	489	1.5
Bois de conifères (Lambert et al., 1980; Alban & Pastor, 1993)						
Sapin baumier			358[a]	351	499	1.5
Épinette blanche		56	670	262	496	1.0
Pin gris		46	640	283	505	0.9

Note : ENP : extrait non polaire soluble dans le dichlorométhane (lipides, huiles, cires). EPE : extrait polaire soluble dans l'eau (sucres simples, amidon, composés phénoliques). ACID : extrait soluble dans l'acide sulfurique (cellulose et hémicelluloses). AUR : résidu non hydrolysable par l'acide (lignines, tannins, cutine, cires).

[a] correspond à la cellulose uniquement (autre méthode utilisée)

Le taux de décomposition (Tableau 0.3) est généralement plus élevé pour les billes au sol (Brais et al., 2006) que pour les chicots (Angers et al., 2012b), plus élevé pour les bois d'espèces feuillus que pour les bois de conifères (Alban & Pastor, 1993; Brais et al., 2006), et plus élevé pour des petits débris que des gros débris (Edmonds, 1987). De plus, le taux de décomposition est plus faible pour le bois mort (Moore et al., 2006) que pour les litières de feuillage (Alban & Pastor, 1993), résultant de leur différences chimiques et du rapport Surface : Volume plus élevé dans le feuillage, favorisant le contact avec le sol et les microorganismes. Les racines se décomposent également plus lentement que les litières de feuillage (Lemma et al., 2007).

Tableau 0.3. Taux de décomposition (k, année^{-1}) de litières de feuillage, de bois mort, et de racines d'espèces feuillues et de conifères

Type de litières	**k**	**Méthode utilisée**	**Période maximale de décomposition (années)**
Feuillages (Moore et al., 2006)			
Bouleau à papier	0.184	Sacs de litières	6
Tremble	0.140	Sacs de litières	6
Épinette noire	0.183	Sacs de litières	6
Pin gris	0.148	Sacs de litières	6
Billes au sol (Brais et al., 2006)			
Bouleau à papier	0.053	Chronoséquence	22
Tremble	0.060	Chronoséquence	23
Épinette blanche	0.038	Chronoséquence	64
Pin gris	0.020	Chronoséquence	75
Chicots (Angers et al., 2012b)			
Tremble	0.0274	Chronoséquence	25
Sapin baumier	0.0123	Chronoséquence	31
Épinette noire	0.0058	Chronoséquence	65
Pin gris	0.0152	Chronoséquence	39
Racines (Berg & McClaugherty, 2008)			
Pin blanc	0.109	Sacs de litières	10
Érable à sucre	0.083	Sacs de litières	10

0.2.3.2. Pertes de masse au cours de la décomposition et modèles

Au cours de la décomposition, les débris de bois mort, qu'ils soient couchés au sol ou en position debout, perdent leurs feuilles ou leurs aiguilles, leur écorce, leurs branches, ils se décomposent progressivement, et ils se fragmentent (Harmon et al., 1986; Ganjegunte et al., 2004). Les chicots chutent et deviennent des billes au sol (Angers et al., 2010). Les débris de bois mort passent ainsi par une succession de stades de décomposition (Vanderwel et al., 2006), au cours desquels la libération de dioxyde de carbone diminue, et la capacité à stocker l'eau augmente (Brais et al., 2005).

La décomposition est caractérisée par une diminution de masse et de densité des litières, souvent modélisée par une fonction exponentielle négative simple (Olson, 1963), $M_t=M_0e^{-kt}$, où t représente le temps, M_0 la masse du matériel au temps initial, M_t la masse au temps t, et k la constante de décomposition. La plupart des études portent sur les litières de feuillage mises à décomposer pendant une courte durée (0.3-2 ans) (Taylor et al., 1989; Hart et al., 1992), et dans ce cas, l'utilisation de ce modèle est satisfaisante. À plus long terme, ce modèle faillit (Trofymow et al., 2002; Brais et al., 2006), car il implique qu'une proportion constante de litière est décomposée chaque année, que tous les composés se décomposent de façon identique, et que la décomposition est complète sans synthèse de nouveaux composés (Carpenter, 1981). Or, ce n'est pas toujours le cas en forêt boréale (Prescott et al., 2000b; Prescott, 2005), où le taux de décomposition diminue au cours de la décomposition (Harmon et al., 2009).

D'autres modèles ont été appliqués, comme une fonction en plusieurs phases (Melillo et al., 1989; Coûteaux et al., 1995) ou la fonction exponentielle double (Harmon et al., 2009), qui différentient le contenu des litières en un pool labile et un pool récalcitrant. Pour le bois mort, où la colonisation initiale par les microorganismes est lente, il peut aussi y avoir un temps initial de latence (Harmon et al., 1986), où le taux de décomposition est plus faible (Herrmann & Prescott, 2008).

La décomposition peut aussi être décrite par une fonction exponentielle négative avec asymptote (Howard & Howard, 1974; Harmon et al., 2009), $M_t=L_0e^{-kt} + S_0$, où L_0 représente la limite maximale de décomposition, c'est-à-dire la fraction de la litière qui est décomposée et S_0 l'asymptote, c'est-à-dire la fraction de la litière stable. La limite maximale de décomposition (Prescott, 2005; Berg & McClaugherty, 2008) serait un indice plus intéressant que le taux de décomposition pour estimer la rétention du C au cours de la décomposition (Prescott, 2005). Cette fonction exponentielle négative avec asymptote décrit avec peu de paramètres la décomposition incomplète des litières, mais implique qu'une fraction du matériel initial ou que les produits de la décomposition sont complètement stables et ne se décomposent pas (Harmon et al., 2009). Peu d'études ont décrit la limite maximale de décomposition (Berg et al., 1996; Berg & McClaugherty, 2008).

Le taux de décomposition serait négativement corrélé au ratio lignine:azote (Melillo et al., 1982) et au rapport C:N, et positivement corrélé à la concentration en azote (Taylor et al., 1989). La limite maximale de décomposition serait reliée négativement à la concentration initiale en azote et en lignines, et positivement à la concentration en manganèse (Berg & McClaugherty, 2008).

0.2.3.3. Changements de la composition chimique au cours de la décomposition

La décomposition est influencée par la nature du substrat, notamment par la taille des molécules, le type de liaisons chimiques, la régularité des structures, et la toxicité (Chapin et al., 2002). Souvent, les études distinguent les composés labiles, rapidement décomposés (sucres, acides aminés, cellulose, hémicelluloses) et les composés récalcitrants, résistants à la décomposition (lignines, composés phénoliques, cutine) (Chapin et al., 2002).

Ainsi, les composés simples (sucres, acides aminés) sont assimilés directement, tandis que la cellulose et les hémicelluloses sont dépolymérisées par des exoenzymes en composés simples (Swift et al., 1979), avant leur assimilation par les microorganismes (Baldock & Preston, 1995). Les lignines sont plus difficilement dépolymérisées en raison de la grande diversité des liaisons covalentes entre les monomères (Kögel-Knabner, 2002). Les composés à longue chaîne carbonée, comme la cutine, les cires et les acides gras, pourraient persister plus longtemps (Lorenz et al., 2007).

Les composés récalcitrants permettraient donc de séquestrer du C à plus long terme. Les transformations successives résulteraient ainsi en la convergence de la composition chimique (Wickings et al., 2012), et en la formation de l'humus, incluant des composés très stables tels que les acides humiques, l'humine, et les acides fulviques (Swift et al., 1979).

Cependant, ces considérations ont évolué dans les dernières études (Lorenz et al., 2007; Thevenot et al., 2010; Cotrufo et al., 2013). D'une part, les lignines, longtemps considérées comme récalcitrantes en raison de leur corrélation négative avec le taux de décomposition (Taylor et al., 1989), auraient en fait un taux de recyclage assez élevé et ne persisteraient pas longtemps dans les sols (Thevenot et al., 2010). De plus, le résidu non hydrolysable par l'acide (AUR) des analyses proximales, souvent désigné comme « lignines » (Taylor et al., 1989), contient aussi des tannins, de la cutine et des cires (Preston et al., 1997).

D'autre part, l'humus serait issu de la condensation de petites molécules issues de la décomposition, et non pas des lignines résiduelles (Prescott, 2010). Pour Cotrufo (2013), ce sont principalement les composés microbiens, c'est-à-dire issu de la dégradation des composés labiles, qui formeraient la matière organique à long terme. D'une manière générale, la récalcitrance des composés ne serait pas un mécanisme de stabilisation du C à très long terme, comparé aux mécanismes d'occlusion dans des aggrégats ou d'interaction avec le sol minéral (von Lützow et al., 2006).

L'azote joue aussi un rôle majeur dans la décomposition. Il augmente tout au long de la décomposition (Alban & Pastor, 1993; Holub et al., 2001; Brais et al., 2006), résultant de la translocation par les champignons (Schimel & Hättenschwiler, 2007) et la fixation par les bactéries (Brunner & Kimmins, 2003). Il augmente initialement le taux de décomposition (Taylor et al., 1989), mais réagit avec les lignines pour former des composés récalcitrants aux stades avancés de la décomposition (Berg, 2000). Les protéines peuvent aussi être complexées par les tannins, formant alors des composés résistants à la décomposition (Kraus et al., 2003).

Les connaissances sur les changements chimiques au cours de la décomposition sont principalement issues d'études portant sur les litières de feuillage. Les études sur la décomposition du bois mort sont plus rares et montrent que le bois mort bien décomposé est majoritairement composé de lignines (Preston et al., 1998). En se décomposant, le bois mort s'intègre dans la couverture morte, où il peut constituer une fraction non négligeable et persister pendant de nombreuses décennies (Moroni et al., 2010). Cependant, peu d'études ont considéré l'influence de la nature du bois mort sur la stabilité des composés issus de la décomposition et sur la formation du bois enfoui, qui constituent pourtant d'importants facteurs de la séquestration du C dans les sols (Moroni et al., 2010; Brais & Drouin, 2012).

0.2.3.4. Effets des feux et des épidémies d'insectes sur la décomposition

Bien que leurs effets n'aient pas été étudiés ici, les perturbations naturelles influencent aussi la qualité des litières et donc la décomposition. Les insectes responsables des épidémies et les animaux herbivores en général vont, en se nourrissant des plantes, induire une réaction de défense par les plantes, généralement la formation de composés secondaires à partir des hydrates de C, des acides aminés, et des lipides (Kozlowski, 1992). Ces composés secondaires, incluant des alcaloïdes, des terpènes, des composés phénoliques, des tannins, des stéroïdes, etc., peuvent avoir un effet toxique direct, réduire la digestibilité des plantes, inhiber la croissance des insectes ou réduire la fécondité des insectes (Kozlowski, 1992). Par exemple, l'herbivorie du tremble par la Livrée des forêts induit l'expression d'un gène codant pour une enzyme, permettant la synthèse de tannins condensés (Peters & Constabel, 2002). Les tannins sont des composés phénoliques pouvant précipiter les protéines, et ont ainsi des effets biologiques importants, tels que la réduction de l'absorption des nutriments par les insectes et l'inhibition de l'activité enzymatique microbienne lors de la décomposition (Kraus et al., 2003).

Les feux vont modifier la qualité chimique des composés organiques et former des composés pyrogéniques et des cendres (González-Pérez et al., 2004). Ils changent également les conditions microclimatiques, le cycle des nutriments et l'activité microbienne, et ainsi, ils influencent la décomposition (González-Pérez et al., 2004; Certini, 2005). Les effets des feux sur la qualité de la matière organique dépendent des caractéristiques des feux (type, durée, intensité, température, oxygène) et des facteurs environnementaux (humidité de l'air et du sol, vent, température, etc.), qui influencent la combustion (Neary et al., 1999; Certini, 2005). Les composés pyrogéniques formés incluent un continuum de structures allant des matériaux de plantes partiellement carbonisés au charbon, suie et ultimement graphite, où la concentration en C augmente, les concentrations en hydrogène et en oxygène diminuent, et le nombre de groupes fonctionnels important pour la dégradabilité biologique diminue (Preston & Schmidt, 2006). Lors de la carbonisation, les hydrates de carbone diminuent, tandis que des noyaux aromatiques se forment (Czimczik et al., 2002), mais les caractéristiques des composés dépendent aussi de l'espèce initiale (Kasin & Ohlson, 2013). Toute cette variation de structures est associée à un gradient de propriétés physiques et chimiques qui peuvent affecter leur stabilité à long terme. Les charbons sont généralement considérés très stables par rapport aux autres résidus de plantes, avec des taux de décomposition négligeables et pourraient donc séquestrer du C à très long terme (Preston & Schmidt, 2006). Les charbons sont susceptibles aux pertes lors de l'oxydation par les feux suivants. Les charbons faciliteraient aussi la nitrification, permettraient la fixation et la stabilisation de composés phénoliques et favoriseraient l'activité microbienne (Zackrisson et al., 1996; DeLuca et al., 2006).

0.2.4. Effets des récoltes forestières sur le cycle du carbone

Les coupes forestières, et plus particulièrement les coupes totales, ont un impact majeur sur la structure et la composition des écosystèmes forestiers et diminuent leur complexité, ce qui affecte leurs fonctions, notamment celle d'habitats pour les espèces végétales, animales et microbiennes (Popescu & Hunter, 2011). Au Canada, sur les 348 Mha occupés par les forêts, 229 Mha sont constitués de forêts aménagées, et 0.688 Mha ont été récoltés en 2010 (Ressources naturelles Canada, 2012).

Le type d'aménagement forestier réalisé au Canada évolue constamment, en fonction des considérations économiques, sociales et écologiques. Ces dernières décennies, le concept d'aménagement écosystémique est apparu dans le but de maintenir la diversité des espèces, des structures et des fonctions des écosystèmes forestiers (Kimmins, 1992; Freedman et al., 1994). Il s'agit notamment de maintenir la variabilité naturelle des peuplements à l'échelle du paysage, en s'inspirant du régime naturel de perturbations, afin que l'aménagement crée des conditions auxquelles les écosystèmes forestiers sont adaptés.

La mise en place d'un aménagement écosystémique est complexe, étant donné la variabilité des écosystèmes forestiers, dont la structure est fortement influencée par sa composition spécifique et ses caractéristiques biophysiques, incluant sa situation géographique, le sol, le climat, et le régime de perturbations naturelles (Burton et al., 2003a). Un système de sylviculture basée sur la dynamique naturelle des écosystèmes forestiers a été proposé afin de maintenir la variabilité naturelle (Galindo-Leal & Bunnell, 1995; Bergeron & Harvey, 1997). Il repose principalement sur la diversification des interventions sylvicoles. Les coupes totales mimeraient les feux sévères, d'autant plus si elles sont associés à un brûlage dirigé, et ainsi elles ré-initieraient des peuplements équiens (Harvey et al., 2002). Les coupes partielles et sélectives seraient utilisées pour émuler la succession de la canopée et les petites perturbations générant la mort de quelques arbres. Les coupes partielles pourraient être de plus en plus utilisées en forêt boréale, particulièrement dans des peuplements où les feuillus intolérants à l'ombre atteignent leur maturité avant les conifères tolérants à l'ombre (Lieffers et al., 1996).

Les recherches sur l'aménagement écosystémique et son utilisation au niveau des industries et des ministères se développent progressivement (Thorpe & Thomas, 2007; Gauthier et al., 2008). Dans le contexte actuel, où l'on tente de limiter les émissions de CO_2 et où le secteur forestier est en crise, il s'agit de définir un aménagement pouvant favoriser la séquestration du C tout en fournissant des produits à l'industrie et maintenant l'intégrité écologique de la forêt. Les coupes totales ont un impact important sur la dynamique du C, notamment sur la dynamique du bois mort (Johnson et al., 1995; Johnson & Curtis, 2001; Howard et al., 2004; Martin et al., 2005). Cependant, l'impact des coupes partielles, et plus généralement de l'aménagement écosystémique, sur la séquestration du C reste peu étudié (Lee et al., 2002).

Les coupes totales, suite à l'exportation du bois, diminuent considérablement la quantité du C dans l'écosystème (Scott et al., 2004) et modifient la distribution du C dans les différents réservoirs. Après une coupe, la quasi-totalité du C est stockée dans les sols, répartie entre le bois mort, la couverture morte et le sol minéral (Howard et al., 2004). Avec l'augmentation de l'âge du peuplement, la quantité de C total de l'écosystème augmente. La production primaire nette augmente (Howard et al., 2004), ainsi que le pool de C de la canopée (Martin et al., 2005). Les plantes de sous-bois constituent un pool de C mineur (Martin et al., 2005), qui atteint un pic dans les années qui suivent la récolte (Howard et al., 2004).

Suite à une coupe totale, la quantité totale de bois mort est fortement diminuée par rapport aux perturbations naturelles, notamment dans les jeunes peuplements (Krankina & Harmon, 1995; Fridman & Walheim, 2000; Siitonen, 2001; Krankina et al., 2002; Gibb et al., 2005; Ekbom et al., 2006). Les effets des coupes touchent la taille des débris, leur distribution spatiale et temporelle, leur quantité, leur position (Harmon et al., 1986), et leur état de décomposition (Stokland, 2001; Gibb et al., 2005). Les peuplements après coupes sont constitués principalement de billes au sol, au détriment des chicots (Duvall & Grigal, 1999), et particulièrement des débris de petite taille, au détriment des débris de gros diamètres (Fridman & Walheim, 2000; Fraver et al., 2002; Pedlar et al., 2002; Gibb et al., 2005). Elles interrompent la continuité des débris de bois mort dans les différentes classes de décomposition (Siitonen, 2001; Gibb et al., 2005).

Les coupes totales changent le microclimat et augmentent l'exposition aux radiations solaires (Barg & Edmonds, 1999; Prévost & Pothier, 2003), et la température de l'air et du sol (Seastedt & Crossley, 1981; Moroni & Zhu, 2012). De plus, les coupes diminuent l'évapotranspiration et augmentent l'humidité du sol (Chen et al., 1999). L'impact du changement de microclimat sur la décomposition des litières et de la matière organique varie. Certaines études mettent en évidence une accélération de la décomposition, qui serait due à l'augmentation de la température (Prescott et al., 2000a; Prescott et al., 2004), d'autres une diminution du taux de décomposition (Abbott & Crossley, 1982; O'Connell, 1987; Yin et al., 1989; Prescott, 1997), du fait des effets négatifs des coupes sur la faune et les microorganismes (Seastedt & Crossley, 1981). Certaines études ne montrent pas d'effets (Lee et al., 2002).

Au niveau de la couverture morte, certaines études ont montré des réductions du réservoir de C, suite à l'accélération de la décomposition et à la diminution des chutes de litière, tandis que d'autres trouvent une augmentation ou peu d'effet (Yanai et al., 2003). Une augmentation du réservoir de C du sol minéral pourrait résulter des perturbations du sol générées par les opérations de récolte, qui mixent la couche organique et la couche minérale (Howard et al., 2004). D'une manière générale, le contenu total en C du sol semble être peu affecté par les récoltes (Johnson & Curtis, 2001; Martin et al., 2005).

Les coupes partielles ont des effets semblables à la coupe totale dépendamment de la surface terrière prélevée (Barg & Edmonds, 1999; Prévost & Pothier, 2003; Lapointe et al., 2006). Elles conservent aussi de nombreuses similarités avec les peuplements naturels (Fridman & Walheim, 2000; Pedlar et al., 2002; Rouvinen et al., 2002), malgré quelques différences, telles que l'augmentation de la végétation du sous-bois et de la régénération selon l'ouverture du couvert (Brais et al., 2004), et une diminution des billes de gros diamètres (Hansen et al., 1991; Freedman et al., 1996; Fridman & Walheim, 2000). L'étude de Scott et al. (2004) a montré une réduction du réservoir de C de la couverture morte, mais généralement peu d'études concernent les effets des coupes partielles sur la dynamique du C.

0.3. Structure de la thèse

Cette thèse propose d'enrichir les connaissances relatives à la contribution du bois mort à la séquestration du C en forêt boréale mixte dans un contexte d'aménagement écosystémique. Nous amenons l'hypothèse que *« La coupe totale et les coupes partielles auraient une influence sur la dynamique du C à travers leurs effets sur la production et la décomposition du bois mort et des litières de feuillage. Parce que la décomposition du bois mort aurait un taux de décomposition plus faible, atteindrait une limite maximale de décomposition plus élevée et conduirait à des composés carbonés moins stables que la décomposition des litières de feuillage, les changements dans les réservoirs et la dynamique du bois mort induits par les coupes* *auront des incidences sur la séquestration du C. De plus, la décomposition des litières de feuillage et du bois mort des essences résineuses conduirait à la formation de composés carbonés plus stables que ceux issus des litières de feuillus. »*

Trois chapitres ont été réalisés dans cette thèse. Afin d'établir les relations entre la dynamique du bois mort telle que modifiée par la récolte forestière et la séquestration de C, nous avons d'abord caractérisé les liens entre la qualité chimique du bois mort et des litières de feuillage au fur et à mesure de leurs décompositions et la stabilité du C. Pour cela, nous nous sommes intéressés aux effets des essences forestières sur la nature et les changements de la composition chimique du bois mort et des litières de feuillage en décomposition (chapitres I et II). Nous avons également comparé les changements chimiques dans les billes au sol et les chicots au cours de la décomposition (chapitre II). Le chapitre III porte sur la dynamique des réservoirs et des flux de C suite à la récolte totale et partielle d'un peuplement de tremble, et intègre les connaissances issues des deux premiers chapitres, afin d'apporter une vision globale des effets des coupes sur la séquestration du C dans la matière organique morte.

Cette thèse a été menée dans les sites du projet SAFE (Sylviculture et Aménagement forestier écosystémiques), mis en place en 1998 dans la forêt d'enseignement et de recherche du lac Duparquet (Brais et al., 2004). Le projet SAFE inclut une série d'études expérimentales dans la forêt boréale mixte qui testent un système d'aménagement basé sur la dynamique naturelle des peuplements. Plusieurs études ont déjà rapporté des résultats du projet SAFE, notamment sur l'effet des coupes partielles sur la température et l'humidité du sol (Brais et al., 2004), sur la végétation du sous-bois et la régénération (Brais et al., 2004), sur la mortalité et la dynamique du bois mort (Harvey & Brais, 2007; Brais et al., 2013), sur les semis et les champignons saproxyliques qui vivent sur le bois mort (Kebli et al., 2011; Kebli et al., 2012; Robert et al., 2012), et sur la faune du sol (Brais et al., 2013).

Les trois chapitres répondent à différents objectifs et reposent sur des approches de terrain différentes. Dans le chapitre I, l'objectif était de caractériser et comparer les patrons de perte de masse et les changements dans la composition chimique du bois mort et des litières de feuillage des espèces dominantes de la forêt boréale. Des sacs de litières ont été mis à décomposer in situ dans trois types de peuplements du projet SAFE. Les espèces incluaient une espèce de feuillus (tremble) et deux espèces de conifères (sapin baumier, épinette blanche) afin d'avoir des qualités chimiques contrastées. Pour la décomposition du bois mort, nous avons utilisé des blocs assez petits (5x5x10 cm) pour les intégrer dans des sacs, c'est-à-dire qu'ils n'incluaient pas tout le diamètre, mais plus probablement le bois de cœur plus large que l'aubier. Nous avons posé l'hypothèse que la décomposition du bois mort aurait un taux de décomposition plus faible et une limite maximale de décomposition plus élevée que la décomposition des litières du feuillage, en raison de la teneur en azote plus faible dans le bois (Berg et al 2000). Les composés labiles se décomposant plus facilement que les composés plus récalcitrants, nous avons supposé que la composition chimique des litières s'enrichirait avec la décomposition en composés récalcitrants, c'est-à-dire en composés alkyl très stables (Lorenz et al. 2007) pour les litières de feuillage et en lignines pour le bois mort qui est pauvre en composés alkyl.

Le chapitre II décrit les changements de la composition chimique du bois mort en fonction du degré de décomposition. Il repose sur des chronoséquences de chicots et de billes au sol représentant une gamme d'espèces et de stades de décomposition. On y compare aussi les caractéristiques des billes avec la composition chimique de la couverture morte. Nous avons émis l'hypothèse que la composition chimique du bois mort des feuillus et des conifères s'enrichirait en lignines avec la décomposition et donc convergerait entre les espèces, et ainsi la couverture morte lignique serait principalement composée de lignines. De plus, les changements chimiques dans les chicots seraient moins prononcés que dans les billes au sol. Ce chapitre souligne la différence entre les feuillus et les résineux quant à leur intégration dans la couverture morte et leur contribution à la rétention du C dans les sols.

Les chapitres I et II font appel à des techniques de pointe, caractérisant la composition chimique de la matière organique de façon plus précise que les analyses proximales habituelles. En effet, les analyses proximales réalisées dans la plupart des études (Ryan et al., 1990; Trofymow et al., 1995) utilisent différents solvants chimiques qui extraient rarement des composés purs, notamment dans le cas des litières de feuillage. Notamment, le résidu non hydrolysable par l'acide sulfurique (AUR) était communément assimilé à la lignine, cette fraction peut contenir également des tannins, de la cutine, des cires (Preston et al., 1997), des composés aromatiques produits lors de la décomposition (McTiernan et al., 2003), et des ligno-protéines (Brinkmann et al., 2002). Au contraire, la spectroscopie à résonance magnétique nucléaire (RMN) (chapitres I et II) est un outil très précis pour l'étude de la composition chimique de la matière organique du sol (Preston, 2001; Simpson & Preston, 2008). Chaque litière a une signature RMN unique, dépendamment de la chimie de ses macromolécules. Cette signature spectrale peut être utilisée pour évaluer semi-quantitativement la nature du C dans les litières (Turcotte et al., 2009). Le spectre obtenu par RMN fournit des intensités relatives aux molécules, dont le C résonne aux différentes fréquences, dépendamment de leur environnement chimique (Appendice A). D'autre part, les analyses des monomères de lignines par oxydation à l'oxyde cuprique (chapitre I) fournissent des informations additionnelles sur la nature des lignines (Appendice B), leur dégradabilité et leur état d'oxydation. (Dignac et al., 2005). Ces analyses étant coûteuses et longues à réaliser, les échantillons analysés ont été sélectionnés, de façon à représenter tous les types de litières et tout le gradient de décomposition.

Le chapitre III porte sur les effets des coupes partielles et totales sur les réservoirs et les flux de C associés au bois mort et à la matière organique morte en général. Cette étude a été réalisée dans un des dispositifs expérimentaux du projet SAFE. Les réservoirs et les flux de C y ont été mesurés sur une période de 9 ans après coupes dans des peuplements de tremble soumis à des intensités variables de prélèvement. Outre les inventaires dendrométriques, l'étude repose sur des études de décomposition des litières de feuilles et de bois, sur le suivi des chutes de feuilles, et sur des inventaires de volumes de bois mort et de sol. Nous avons émis l'hypothèse qu'avec l'augmentation de l'intensité de récolte, il y aurait une augmentation du taux de décomposition, de la limite maximale de décomposition, et de l'importance relative des chutes de litières de feuilles par rapport à la production de bois mort. De plus, les caractéristiques des billes au sol et des chicots après coupes partielles seraient plus proches du témoin que des coupes totales. De plus, ce chapitre applique les connaissances issues des deux premiers chapitres à l'interprétation des liens entre la qualité des litières et leur rétention du C, et fournit des données empiriques sur les effets des coupes partielles peu fréquentes dans la littérature scientifique.

CHAPITRE I

CHEMICAL TRANSFORMATIONS OF DEADWOOD AND FOLIAR LITTER OF MIXED BOREAL SPECIES DURING DECOMPOSITION

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1.1. Abstract

Deadwood constitutes an important input of carbon to soil, but its role in carbon sequestration over the long term is not well documented in the eastern boreal forests of Canada, especially when compared with foliar litter. The objectives of this study were to characterize and compare patterns of mass loss and changes in chemical composition of deadwood and foliar litter of trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) during a 5- to 6-year period of field decomposition, using litterbags, solid-state ^{13}C nuclear magnetic resonance analysis, and lignin monomer quantification by cupric oxide oxidation. The maximum decomposition limit was similar between foliar litter and wood material, but foliar litter decomposed faster, reached the estimated maximum decomposition limit, and converged to a composition rich in alkyl, phenolic, and carbonyl carbon. However, wood did not reach the estimated maximum decomposition limit and underwent relatively little chemical changes, remaining with high carbohydrate content. At the end of the experiment, aspen wood still had a lower lignin concentration than that of conifers, but contained higher proportions of alkyl and carbonyl carbon. Although wood contributes to a greater diversity in the chemical composition of the forest floor, foliar litter, which keeps a high alkyl C content throughout its decay, could generate more recalcitrant residual organic matter.

*Une quantité importante de carbone dans les sols vient du bois mort mais son rôle dans la séquestration du carbone à long terme, comparativement à celui des litières de feuillage, n’est pas bien documenté dans les forêts boréales de l’Est du Canada. Les objectifs de cette étude étaient de caractériser et de comparer les patrons de perte de masse et les changements dans la composition chimique du bois mort et des litières de feuillage du peuplier faux-tremble (*Populus tremuloides *Michx.), de l’épinette blanche (*Picea glauca *(Moench) Voss) et du sapin baumier (*Abies balsamea *(L.) Mill.) pendant une période d’incubation in situ de 5 à 6 ans, au moyen de sacs de litières, d’analyses par résonance magnétique nucléaire du ^{13}C en phase solide et de la quantification des monomères de lignine par oxydation à l’oxyde de cuivre. La limite maximale de décomposition des litières de feuillage et du bois mort était similaire, mais les litières de feuillage se décomposaient plus rapidement, atteignaient la limite maximale de décomposition estimée et convergeaient vers une composition riche en carbone alkyle, phénolique et carbonyle. Au contraire, le bois n’atteignait pas la limite maximale de décomposition estimée, subissait peu de changements chimiques et conservait une teneur élevée en cellulose. A la fin de l’expérimentation, le bois de peuplier faux-tremble avait toujours une concentration en lignine plus faible que celle des conifères, mais des concentrations plus élevées en carbone alkyle et carbonyle. Alors que le bois contribue à augmenter la diversité chimique de la couverture morte, les litières de feuillage, qui conservent un contenu plus élevé en composés alkyles tout au long de la décomposition, pourraient générer une matière organique résiduelle plus récalcitrante.*

1.2. Introduction

In Canada, boreal forests cover 304 Mha, representing a carbon (C) pool of 186 Pg (Bhatti et al., 2003), 84% of which is contained in soils (IPCC, 2001). Historically, wildfire and insect outbreaks were the dominant disturbances affecting boreal forests, but harvesting contributes to an increasing fraction of the overall disturbance effects (Seedre et al., 2011). Forest harvesting modifies soil C dynamics through input of logging slash, alteration of litter input from remaining vegetation, increased microbial respiration, and increased leaching (Jandl et al., 2007). In particular, partial and selective cutting promoted by ecosystem management to diversify silvicultural practices has an impact on the chemical quality of litter input, as it changes the balance between foliar litter fall, and recruitment of deadwood and dead roots (Lee et al., 2002; Harvey & Brais, 2007).

Litter quality is a significant factor controlling decomposition and carbon sequestration in soils and may influence its early decay rate (Prescott, 2010), its maximum decomposition limit (Berg et al., 1996; Berg, 2000), and in some cases, composition of the residual soil organic matter (Quideau et al., 2001). Nitrogen (N) is one of the key components of litter quality, initially enhancing decomposition but reacting with lignins to form recalcitrant complexes in later stages of decay (Berg, 2000). Although lignins were traditionally considered a major source of stable carbon, recent evidence suggests that some lignin components have a relatively rapid turnover (Thevenot et al., 2010). Tannins can sequester proteins, forming complexes resistant to decomposition (Kraus et al., 2003), whereas aliphatic compounds, including cutin, suberin, and lipids, are considered among the most recalcitrant compounds (Lorenz et al., 2007).

Litter quality, mainly described for foliar litter, is often characterized using parameters incorporating nitrogen and lignin content, and the relationship of these parameters to ease of decomposition is assessed by means of correlations with litter decay rates (Taylor et al., 1989). However, in many studies, lignin is loosely defined as the acid-unhydrolyzable residue (AUR) of the proximate analysis, although this may include other recalcitrant compounds such as tannins and cutin (Preston et al., 2009b). Moreover, the negative exponential model used to estimate decay rates (Trofymow et al., 1995) may not describe C dynamics adequately as it assumes a constant decay rate and a complete decomposition (Berg et al., 1995). In northern forests, decay rates are not constant over time and eventually drop to very low levels (Prescott, 2005, 2010), corresponding to the maximum decomposition limit of the litter (Berg et al., 1996). Quantifying changes in chemical properties with decay and the maximum decomposition limit of litters should further our understanding of how litter contributes to long-term forest soil C sequestration (Berg, 2000; Prescott, 2005, 2010).

Among boreal tree species, aspen has a relatively easily decomposable litter compared with conifers (Flanagan & Van Cleve, 1983). Aspen leaves contain more labile material and less AUR than conifers needles (Trofymow et al., 2002). Because they are demethylated faster, the syringyl units from deciduous lignins are thought to be preferentially degraded over the vanillyl units found in all plants (Otto & Simpson, 2006). Also, phenols and tannins present mainly in conifers can hinder decomposition (Kraus et al., 2003; Hernes & Hedges, 2004). Wood contains more lignin than foliage but very low amounts of nitrogen and aliphatic compounds (Alban & Pastor, 1993; Trofymow et al., 1995; Preston et al., 2009a); it also has lower decay rates (Alban & Pastor, 1993; Moore et al., 2006). An important intersite study realized in western Canada (Trofymow et al., 1995; Trofymow et al., 2002; Preston et al., 2009a; Preston et al., 2009b) showed that foliar litters became more similar in chemical composition among tree species after 6 years of decomposition when compared with their initial composition; specifically, they became more concentrated in AUR arising from a collective increase in lignins, tannins, and cutin. However, few studies have compared the decomposition of foliar litter and coarse woody debris from the same species (Krzyszowska-Waitkus et al., 2006) and their respective contribution to C retention in soils.

The objective of this study was to characterize and compare patterns of mass loss and changes in chemical composition of wood and foliar material for three boreal species of contrasting quality using a litter bag experiment, solid-state nuclear magnetic resonance (NMR) spectroscopy, and cupric oxide (CuO) oxidation analyses. (i) We expected wood to have a higher maximum decomposition limit than foliar litter, despite its slower decomposition rate, because of its low N content (Berg et al., 1996). (ii) Foliar litters, containing aliphatic compounds, were hypothesized to converge to a composition rich in alkyl C, whereas wood containing little aliphatic compounds were expected to converge to a composition rich in aromatic C from lignins. (iii) Because of the presence of syringyl units in lignins of aspen, we also expected lignins from aspen to be less recalcitrant than those of conifers and to change their composition and content during decomposition.

1.3. Materials and methods

1.3.1. Study area and experimental design

The study area is located in the Lake Duparquet Research and Teaching Forest in the Abitibi region of northern Quebec, 45 km northwest of Rouyn–Noranda, Quebec (48°86’N-48°32’N, 79°19’W-79°30’W). Mean annual temperature is 0.7 °C, and mean temperatures of the warmest and coldest months (July and January) are 16.9 and –18.2 °C, respectively. Annual precipitation is 890 mm, of which 614 mm falls as rain from April to November (Environment Canada, 2010). Soils have evolved from fine clay to fine loamy textured glaciolacustrine deposits formed by sedimentation at the bottom of glacial Lake Barlow-Ojibway (Veillette et al., 2000) under fresh to moist moisture regimes (Brais & Camiré, 1992) and are classified as Gray Luvisols

(Soil Classification Working Group, 1998). The region is situated in the mixedwood zone of the boreal shield within the western balsam fir – white birch bioclimatic domain. Forest succession on rich mesic sites generally begins with the establishment of pure or mixed stands of white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and jack pine (*Pinus banksiana* Lamb.) that maintain dominance for over 100 years. In the absence of a major disturbance, these species are gradually replaced by a mixture of shade-tolerant species such as white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), and balsam fir (*Abies balsamea* (L.) Mill.) (Bergeron & Dubuc, 1989).

The study was conducted within the SAFE (Sylviculture et Aménagement Forestier Écosystémiques) project, a series of silvicultural experiments testing an ecosystem management model based on natural dynamics (Brais et al., 2004). The project is set in three natural stand types (Table 1.1, Appendix D) originating from forest fires dating from 1923 (ASPEN stand), 1910 (MIXED stand), and 1760 (OLD stand). Trembling aspen represented 92% of the basal area of the ASPEN stand and 81% of the MIXED stand, whereas white spruce and balsam fir accounted for 18% of the total basal area of the latter stand. The oldest stand type (OLD) was affected by the 1970–1987 outbreak of spruce budworm (*Choristoneura fumiferana* Clem.) (Morin et al., 1993) and was characterized by a mixed composition of white birch, white spruce, and balsam fir.

This study was limited to control (unharvested) stands and included three replications in each stand type for a total of nine experimental units (1–2 ha). In all experimental units, five permanent sampling plots (400 m^2) were established at the onset of the study.

Table 1.1. Forest stand descriptions, number of samples and chronology of litterbag collections

Stand type	Litter type	**Year of collection (time of decay (*t*) and number of samples including wood blocs and foliar litter (*n*))**				
		Initial	1st	2nd	3rd	4th
ASPEN	Trembling aspen leaves and wood	1999* (t= 0) (n= 11)	2000* (1 year) (n= 30)	2002* (3 years) (n= 30)	2004 (5 years) (n= 30)	2005* (6 years) (n= 30)
MIXED	White spruce needles and wood	2001* (t= 0) (n= 20)	2002* (1 year) (n= 30)	2005 (4 years) (n= 30)	2007* (6 years) (n= 30)	-
OLD	Balsam fir needles and wood	2000* (t= 0) (n=11)	2001* (1 year) (n= 30)	2004 (4 years) (n= 30)	2005* (5 years) (n= 30)	-

*Samples from these collections were analyzed by NMR and CuO oxidation.

1.3.2. Litterbag decomposition experiment

Freshly fallen leaves of aspen were collected in the fall, whereas fresh needles of fir and spruce were sampled directly on trees. Wood blocks were cut (10 × 5 × 5 cm) from dimensional lumbers of each species. Foliar material (±10 g) and wood blocks (100–150 g) were enclosed in litterbags (±10 × 8 cm) made of fiberglass (1 mm mesh size), with their initial moist mass printed on DYMO tape. Five to 10 subsamples of each litter type (n = 42) were dried (48 h, 65 °C) to determine the moist-to-dry mass conversion factor and to characterize initial litter chemical composition. Five litterbags containing wood blocks and five containing foliage from one of the stands dominant species were positioned in each permanent sampling plot and left in situ to decompose. A total of 300 litterbags were collected 1 to 6 years after the start of the experiment (Table 1.1).

After collection, the exterior of each litterbag was carefully cleaned with a brush. Foliar material or wood blocks were removed from the bags and manually sorted to eliminate any mineral soil or plant remains. Material was dried (48 h, 65 °C) and weighed. Initial moist mass was converted to dry mass, and mass loss was estimated.

Materials for each collection date and litter type were pooled over experimental units, leading to 60 samples. A total of 102 samples (42 nondecomposed samples and 60 field-incubated samples) were ground to 0.5 mm for chemical analyses. A subset of 60 samples (three undecayed samples per litter type and samples at different times of decay; see Table 1.1) was analyzed by NMR and CuO oxidation.

1.3.3. Laboratory analyses

Solid-state ^{13}C cross-polarization with magic angle spinning (CPMAS) NMR analyses were carried out using a Bruker Avance 400 spectrometer (B_0 = 9.4T, $v_L(^{13}C)$ = 100.6 MHz) with ramped cross-polarization (RAMP-CP) according to the procedure followed by Thiffault et al. (2008) and Turcotte et al. (2009). Spectra were acquired with a ^1H 90° pulse length of 4 µs, a pulse delay of 5.0 s, a cross-polarization contact time of 1.0 ms, an acquisition time of 17.1 ms, and a spinning frequency of 13 kHz. A ramped ^1H pulse was used to circumvent spin modulation of Hartmann–Hahn conditions. Four or eight thousand scans were processed, depending on the samples, using line broadening set at 200 Hz. Chemical shifts were reported relative to tetramethylsilane (TMS) at 0 ppm, with the reference frequency set using adamantane.

The Bruker's WIN-NMR package was used to estimate the relative integrated areas of the different spectral regions between 0 and 222 ppm, after corrections for spinning sidebands. Spectra were divided into a total of seven chemical shift regions according to the studies of Baldock et al. (1992) and Knicker & Lüdemann (1995): (1) alkyl C (0–46 ppm) region from lipids, cutin, and amino acids; (2) methoxyl C (46–58 ppm), (3) *O*-alkyl C (58–93 ppm), and (4) di-*O*-alkyl C (93–111 ppm) regions from carbohydrates, amino acids, and methoxyl C of lignins (= *O*/*N*-alkyl C, which includes regions 2, 3, and 4); (5) aromatic C (111–142 ppm) and (6) phenolic C (142–166 ppm) regions from lignins, tannins and olefins; and (7) carbonyl C (166–222 ppm) region from carboxylic acid, amide, ester, aldehyde, and ketone in lignins, proteins, lipids, carbohydrates, and tannins. Although there are limitations in the quantitative reliability of CPMAS spectra (Preston et al., 1990), it is appropriate to use NMR to compare intensity distribution and study structural features when samples do not differ widely in composition and are run under similar experimental conditions (Preston, 1996), as was the case for our study.

To obtain further information on C structures, dipolar dephased (DD) spectra were generated for six samples (one of each initial litter type) by inserting a delay period of 40 μs without ^{1}H decoupling between the cross-polarization and acquisition portions of the CPMAS pulse sequence (Thiffault et al., 2008). All DD spectra were obtained using the TOSS sequence for total suppression of spinning sidebands (Lorenz et al., 2000).

The analysis of lignin monomers by CuO oxidation provides additional information on the nature of lignins, their degradability, and their oxidation state (Dignac et al., 2005). Cupric oxide oxidation was carried out according to the method developed by Hedges & Ertel (1982) and modified by Kögel & Bochter (1985) and Turcotte (2009). Each sample (50 mg) was added to a PARR stainless steel Teflon bomb (no. 4749) containing CuO (1 g), iron (II) ammonium sulphate hexahydrate (0.1 g), and 15 mL of 2 mol·L^{-1} NaOH. The bomb was placed in an oven (model no. 1330GMS, VWR International, Cornelius, Oregon) and heated at 150 °C for 3 h. After cooling under running water, the sample was centrifuged at 4000 rpm for 20 min. The supernatant was transferred into a beaker, and the litter residue was washed with 10 mL deionized water, vortexed, centrifuged, and added to the beaker containing the supernatant. The solution was acidified with 6 mol·L^{-1} HCl to a pH of 1.8–2.2. Ethylvanillin (100 μL at 200 ppm) was added to the sample as a recovery standard. After being kept in the dark overnight, the sample was filtered through a SPE C18 column (50 μm particle size, 60 Å pore size, 8 cm^3 column size) (Alltech Associates, Inc., Deerfield, Illinois). The final phenolic products were eluted with 0.8

mL ethyl acetate, dried, and derivatized to their silylated forms by adding BSTFA (*N*,*O*-Bis(trimethylsilyl)trifluoroacetamide) as the derivatizing agent and pyridine as the final solvent. Phenylacetic acid (100 µL at 200 ppm) was added as an internal standard. Samples were analysed immediately by a gas chromatograph – flame ionization detector (GC-FID) on a HP GC 5890 equipped with a HP Ultra 2 (cross-linked Ph Me Silicone) (25 m × 0.32 mm × 0.52 µm). The initial temperature was 120 °C for 2 min, increased to 160 °C at a rate of 8 $°C \cdot min^{-1}$, increased to 170 °C at a rate of 4 $°C \cdot min^{-1}$, and increased to 300 °C at a rate of 20 $°C \cdot min^{-1}$. The injector was kept at 280 °C, and the detector was kept at 350 °C. Samples were injected in split mode (1:5). Results from GC-FID analyses with a recovery below 30% were discarded.

From the GC-FID chromatographs, 11 lignin phenols were quantified. The sum of vanillin (Val), vanillic acid (Vac), and acetovanillone (Vc) constitutes the vanillyl phenols (V); the sum of syringaldehyde (Sal), syringic acid (Sac), and acetosyringone (Sc) comprises the syringyl phenols (S); the *p*-hydroxy phenols (P) include *p*-hydroxybenzaldehyde (Pal), *p*-hydroxybenzoic acid (Pac), and *p*-hydroxyacetophenone (Pc); and the sum of *p*-coumaryl acid (Cco) and ferulic acid (Cfe) corresponds to the cinnamyl phenols (Cn). The sum of vanillyl, syringyl, cinnamyl, and *p*-hydroxy phenols represents the total phenolic constituents (TPC). The resolution of GC peaks of the syringyl phenols in foliage was not well resolved, so we removed these data from the results.

Total C and N contents were determined by dry combustion using a CNS 2000 analyzer (LECO Corporation, St. Joseph, Michigan).

1.3.4. Data analyses

The proportion of initial mass remaining (residual mass), as well as the percentage of initial mass of N and C remaining at each collection date, were calculated for all individual litterbags. The maximum decomposition limit was estimated for each litter type using a single negative exponential model with an asymptote (Harmon et al., 2009):

$$M_t = L_0 \times e^{-kt} + S_0$$

where M_t is the residual mass (%) at time t (years), L_0 is the initial mass of material subject to loss (%), S_0 is the asymptote (%), and k is the decomposition rate. The sum of L_0 and S_0 is 100%, and an estimate of one can be used to derive the other (Harmon et al., 2009). Parameters of the model were estimated using a nonlinear regression with the nls function of the R software (R Development Core Team, 2012). The amount of N remaining (as a percentage of initial mass) was plotted over the amount of C remaining (as a percentage of initial mass). The polynomial regression was used to predict the C content remaining at the maximum N content (Moore et al., 2006) and then establish the critical C:N quotient, indicating the point after which there was a net loss of N.

The effects of material (wood vs. foliage), tree species, and time of decomposition on litter characteristics were assessed by means of linear mixed models and Wald's *t* test (Pinheiro & Bates, 2000) using the lme function included in the nlme library of R software (R Development Core Team, 2012). Experimental units within stand types were treated as a random factor. Material, species (two contrasts: C1, aspen vs. conifers; C2, fir vs. spruce) and time of decomposition, as well as their two and three-way interactions, were treated as fixed factors. Interactions were removed from the models when found to be nonsignificant. Response variables were C and N concentrations, C:N ratio, alkyl:*O*/*N*-alkyl ratio, which corresponds to the division of alkyl (0–46 ppm) by the sum of methoxyl, *O*-alkyl, and di-*O*-alkyl (46– 111 ppm) (Baldock & Preston, 1995), phenolic:*O*-alkyl ratio (Dignac et al., 2002), as well as ratios of lignin phenols, the acid:aldehyde ratios (Vac:Val, Sac:Sal, Pac:Pal), which can be used to estimate the oxidation state of lignins, the S:V ratio, as an indicator of angiosperm contribution, the Cn:V ratio, an indicator of nonwoody tissues contribution, and the P:V ratio (Hedges et al., 1988). The corCAR argument was used to account for the correlation between measures with time. Normality and homogeneity of variances were verified by visual assessment of residuals. When these assumptions were not met, square-root or logarithmic transformations were applied.

To synthetize information generated by NMR spectroscopy, spectral NMR areas from all litter types and collection dates were analyzed using the nonmetric multidimensional scaling (NMDS) method (Kruskal, 1964) with the PC-ORD software (McCune et al., 2002). This ordination method is well suited to nonnormal or semiquantitative data such as the integrated spectral NMR areas. The Sorensen (Bray–Curtis) distance measure was used. The variables included in the first matrix were the seven integrated spectral NMR areas (alkyl, methoxyl, *O*-alkyl, di-*O*-alkyl, aromatic, phenolic, and carbonyl), relativized by row and standardized using the arcsine square-root transformation. The second matrix contained the NMR areas to map these vectors over the first matrix, as well as three variables: material (wood vs. foliage), tree species, and time of decomposition. In addition, the multiresponse permutation procedure (MRPP) analysis with the Sorensen distance was used to compare distances in the ordination space between different litter types and decomposition times to determine whether these groups of litters were statistically different. In addition to the p value, MRPP results include the T value, which indicates separation among groups (with larger values for stronger separation), and the A value, which indicates within-group homogeneity compared with random expectation.

1.4. Results

1.4.1. Maximum decomposition limit, decay rates, and residual biomass

Predicted residual organic matter (S_0, asymptote) ranged from 22.4% to 53.8% (Table 1.2a; Figs. 1.1A, 1.1B, and 1.1C). Maximum decomposition limits were similar between foliar litters and wood blocks and among species (overlap of confidence intervals; Table 1.2a). Balsam fir needles decayed significantly faster than other foliar litters, and aspen wood decayed faster than spruce wood. Decay rates did not differ significantly between aspen and spruce foliar litters and aspen wood blocks (Figs. 1.1A and 1.1B). The model for balsam fir wood was not significant because of the high variation in residual mass following 5 years of decay (Fig. 1.1C), but maximum decomposition limit was marginally significant (p = 0.084; Table 1.2a). After 5 to 6 years of decay, the observed amount of foliage residual mass ranged from 23.5% to 32.4% (Table 1.2a), indicating that foliar litters had almost reached their maximum decomposition limits. This was not the case for the wood blocks, especially for conifers as their residual masses were still between 39.7% and 66.7%.

1.4.2. Carbon and nitrogen dynamics

Initial C concentrations differed slightly between litter types (results not shown), and initial N concentrations were significantly ($p < 0.001$) higher in foliage than in wood (Tables 1.3 and 1.4). Increases in N concentrations with time were faster for wood than for foliage ($p = 0.003$). Wood N concentrations increased significantly ($p = 0.048$) faster for aspen than for fir and spruce, and by the end of the incubation period, concentrations were 9.1, 4.6, and 3 times higher than initial concentrations for aspen, spruce, and fir wood, respectively (Table 1.3). In terms of the foliage, the three species reached similar N concentrations (19.6–21.3 $\text{mg}\cdot\text{g}^{-1}$) by the end of the experiment. Initial C:N ratios were lower in foliar material than in wood (Tables 1.3 and 1.4). The decrease in C:N ratio with time was significantly ($p = 0.020$) faster for aspen than for coniferous species and significantly (*p* = 0.006) faster for wood than for foliar material (Table 1.4).

The N content in foliar litters increased during the first part of the experiment, until the N content reached between 123% and 132% of the initial amount (Figs. 1.1D, 1.1E, 1.1F); the critical C:N ratios after which there was a net loss of N were between 25.7 and 35.8 (Table 1.2b), which is higher than final C:N ratios in foliar litters (22.3–25.1; Table 1.3). For wood material, the data were highly variable, resulting in poor polynomial regressions (Figs. 1.1D, 1.1E, 1.1F). There was a net gain of N in wood followed by a net loss when C:N ratios reached values between 196 to 259 (Table 1.2b). These critical C:N ratios were reached by the end of the experiment by aspen and spruce wood litters, but not by fir wood (Table 1.3), in which the polynomial regression does not describe adequately changes of N content (Fig. 1.1F).

1.4.3. CPMAS NMR spectra

All ^{13}C CPMAS NMR spectra (Fig. 1.2; Appendix C) were dominated by the *O*/*N*-alkyl region (46–111 ppm), which represented a higher proportion in wood (78%–83%) than in foliar litter (51%–66%). The most prominent signal at 73 ppm was characteristic of the C-2, C-3, and C-5 of pyranoside rings in cellulose and hemicelluloses (Preston et al., 2000). The di-*O*-alkyl peak at 105 ppm was assigned to anomeric C (C-1), whereas the peak at 65 ppm corresponded to the C-6 of these carbohydrates. The shoulders at 83 and 89 ppm may be due to C-4 of cellulose. The shoulder at 56 ppm was a signal for the methoxyl C characteristic of lignins. The *O*/*N*-alkyl region could also include some signals of condensed and hydrolysable tannins and contributions in the methoxyl region from *N*-alkyl C of proteins. The carbonyl region (166–222 ppm) was the least important on all spectra, although it was larger in foliar litter (4%–7%) than in wood (2%–3%) spectra. The peak at 173 ppm was attributed to carboxylic acids, amides, and esters (Fig. 1.2).

Table 1.2. (a) Residual biomass of foliar litters (FL) and wood blocks (WB) from three boreal species after one year and at the end of a field decomposition experiment and model of residual mass (Figs. 1A, 1B, 1C). (b) Carbon and nitrogen remaining and model of nitrogen remaining (Figs. 1D, 1E, 1F).

a) Residual mass vs time model

	Residual mass (% of initial mass)		**Model of residual mass with time $M_t = L_0 \times e^{-kt} + S_0$**				
Litter types	After 1 year	After 5-6 years	Asymptote S_0 (%)	L_0 (= 1-S_0) (%)	p	k (years^{-1})	p
Aspen FL	72.7 ± 3.2	32.4 ± 7.3	30.4 ± 6.5	69.6 ± 6.5	<0.001	0.550 ± 0.168	<0.001
Spruce FL	71.4 ± 2.1	31.2 ± 4.3	29.2 ± 5.5	70.8 ± 5.5	<0.001	0.472 ± 0.109	<0.001
Fir FL	57.6 ± 3.9	23.5 ± 4.0	22.4 ± 3.0	77.6 ± 3.0	<0.001	0.788 ± 0.115	<0.001
Aspen WB	73.9 ± 4.2	33.0 ± 7.1	27.1 ± 7.9	72.9 ± 7.9	<0.001	0.451 ± 0.138	<0.001
Spruce WB	78.7 ± 4.8	39.7 ± 8.9	22.9 ± 36.7	77.1 ± 36.7	<0.001	0.229 ± 0.199	0.028
Fir WB	91.5 ± 3.7	66.7 ± 13.2	53.8 ± 51.5	46.2 ± 51.5	0.084	0.274 ± 0.578	0.358

b) N remaining vs C remaining model

	C remaining (% of initial content)		**N remaining (% of initial content)**		**Model of N remaining with C remaining $N = a*C^2 + b*C + (1-a-b)$**				
							Maximum of curve		
Litter types	After 1 year	After 5-6 years	After 1 year	After 5-6 years	Equation	p (a, b)	C_m (%)	N_m (%)	$C:N_m$
Aspen FL	71.9 ± 3.0	29.9 ± 7.2	117.8 ± 7.6	83.3 ± 21.4	$N=-3.20*C^2+4.37*C-0.17$	<0.001	68	132	35.8
Spruce FL	71.8 ± 2.5	31.9 ± 4.4	112.0 ± 2.8	97.0 ± 13.4	$N=-2.33*C^2+3.14*C+0.18$	<0.001	68	124	32.7
Fir FL	55.3 ± 3.8	24.3 ± 4.2	119.8 ± 8.3	41.9 ± 7.1	$N=-3.10*C^2+4.51*C-0.41$	<0.001	73	123	25.7
Aspen WB	73.6 ± 4.1	33.9 ± 7.2	182.2 ± 33.7	270.8 ±61.0	$N=-5.19*C^2+4.64*C+1.55$	<0.001	45	259	149.1
Spruce WB	75.9 ± 5.8	40.9 ± 9.1	139.9 ± 14.1	176.2 ± 37.5	$N=-6.21*C^2+7.55*C-0.34$	<0.001	61	196	244.7
Fir WB	93.6 ± 3.9	69.2 ± 13.4	159.5 ± 20.6	196.9 ± 35.4	$N=-11.0*C^2+14.96*C-2.97$	<0.001	68	212	244.5

Note: Mean values (n = 15) ± confidence intervals. L_0, percentage of initial mass of material subject to loss; S_0, asymptote; k, decomposition rate; p, p value for individual parameters; a and b, parameters of polynomial regression model; $p(a,b)$, p value for a and b parameters; C_m, value of C remaining when N remaining is maximum in model; N_m, maximum of N remaining in model; $C:N_m$, C:N ratio when N remaining is maximum in model.

Table 1.3. Carbon, nitrogen concentrations and C:N ratios of foliar litters (FL) and wood blocks (WB) from three boreal species at the start, after one year, and at the end of a field incubation experiment.

Litter types	C (mg.g^{-1})			N (mg.g^{-1})			C:N ratio		
	Initial	1st year	Final	Initial	1st year	Final	Initial	1st year	Final
Aspen FL	479 (1)	474 (6)	433 (33)	8.0 (0.2)	13.0 (2.1)	19.6 (3.2)	60.2 (1.3)	37.2 (6.2)	22.3 (2.2)
Spruce FL	473 (5)	476 (14)	485 (3)	6.8 (0.4)	10.7 (0.6)	21.3 (0.4)	69.4 (3.9)	44.4 (2.4)	22.8 (0.3)
Fir FL	515 (3)	494 (7)	533 (2)	11.9 (0.1)	24.7 (0.6)	21.3 (0.7)	43.3 (0.3)	20.0 (0.3)	25.1 (0.9)
Aspen WB	480 (5)	478 (4)	493 (5)	0.6 (0.1)	1.5 (0.5)	5.5 (2.7)	806.0 (131.4)	347.6 (109.7)	105.3 (51.4)
Spruce WB	473 (11)	455 (35)	487 (4)	0.5 (0.3)	1.0 (0.2)	2.5 (0.7)	987.4 (298.2)	485.2 (98.3)	202.8 (63.2)
Fir WB	487 (11)	498 (1)	508 (20)	0.6 (0.05)	1.1 (0.4)	1.9 (0.4)	766.5 (61.6)	478.5 (132.5)	266.0 (40.9)

Note: Mean values are reported (*n* = 3, each from five pooled samples) and standard deviations are indicated in parentheses.

Table 1.4. Effects of material (foliage vs wood), tree species (aspen, spruce and fir) and time of incubation on the chemical composition of litters assessed by means of mixed linear models.

Fixed factors	**N (log)**		**C:N (log)**		**Alkyl:O/N-alkyl (sqrt)**		**Phenolic:O-alkyl**	
	E	*p*	*E*	*p*	*E*	*p*	*E*	*p*
(Intercept)	-2.61	<0.001	6.48	<0.001	0.255	<0.001	0.0577	<0.001
Material (foliage)	2.65	<0.001	-2.63	<0.001	0.426	<0.001	0.0484	<0.001
C1 (aspen vs conifers)	0.12	0.071	-0.10	0.089	0.011	0.129	-0.0094	0.008
C2 (fir vs spruce)	-0.12	0.236	0.10	0.300	-0.002	0.878	-0.0032	0.493
Time	0.25	<0.001	-0.24	<0.001	0.008	0.005	0.0034	0.003
Material (foliage) * C1	-0.20	0.001	0.18	0.004	-0.001	0.873	0.0105	0.003
Material (foliage) * C2	-0.18	0.089	0.17	0.121	-0.154	<0.001	-0.0141	0.023
Time * C1	0.02	0.048	-0.02	0.020	0.002	0.180	0.0003	0.671
Time * C2	0.03	0.076	-0.03	0.072	0.001	0.722	-0.0027	0.051
Material (foliage) * Time	-0.11	0.003	0.10	0.006	-0.005	0.193	0.0019	0.198
Material (foliage) * Time * C1	(−)	(−)	(−)	(−)	-0.005	0.035	-0.0002	0.808
Material (foliage) * Time * C2	(−)	(−)	(−)	(−)	0.010	0.027	0.0060	0.003

Table 1.4 (suite)

Fixed factors	**V (log)**		**S:V (sqrt), in wood**		**C:V (sqrt)**		**Vac:Val**	
	E	*p*	*E*	*p*	*E*	*p*	*E*	*p*
(Intercept)	2.493	<0.001	0.650	<0.001	0.147	<0.001	0.251	<0.001
Material (foliage)	-1.278	<0.001	(−)	(−)	0.586	<0.001	-0.081	<0.001
C1 (aspen vs conifers)	-0.216	<0.001	0.487	<0.001	-0.008	0.518	0.191	<0.001
C2 (fir vs spruce)	0.032	0.618	0.017	0.493	-0.032	0.199	0.009	0.672
Time	-0.045	0.008	-0.011	0.102	0.002	0.786	0.017	<0.001
Material (foliage) * C1	0.054	0.279	(−)	(−)	0.042	0.007	-0.220	<0.001
Material (foliage) * C2	-0.061	0.495	(−)	(−)	0.018	0.514	-0.016	0.586
Time * C1	-0.042	<0.001	-0.011	0.022	-0.007	0.029	(−)	(−)
Time * C2	-0.014	0.501	0.001	0.892	0.004	0.526	(−)	(−)
Material (foliage) * Time	0.091	<0.001	(−)	(−)	-0.036	<0.001	(−)	(−)
Material (foliage) * Time * C1	0.036	0.021	(−)	(−)	(−)	(−)	(−)	(−)
Material (foliage) * Time * C2	0.024	0.384	(−)	(−)	(−)	(−)	(−)	(−)

Note: The reference level for material is wood. The first contrast (C1) is positive when the parameter is higher for aspen than for conifers; the second contrast (C2) is positive when the parameter is higher for spruce than for fir. Transformations realized to reach normality and homogeneity assumptions are indicated in parentheses. *E*, estimated value of the model; *p*, *p* value of *t* test for individual parameters; (−), nonsignificant interaction removed from model. Transformations: log, logarithmic; sqrt, square-root. N, nitrogen concentration; C, carbon concentration. NMR: alkyl, 0-46 ppm; *O*/*N*-alkyl, 46-111 ppm; phenolic, 142-166 ppm; *O*-alkyl, 58-93 ppm. V, vanillyl phenols; S, syringyl phenols; C, cinnamyl phenols; Vac, vanillic acid; Val, vanillin.

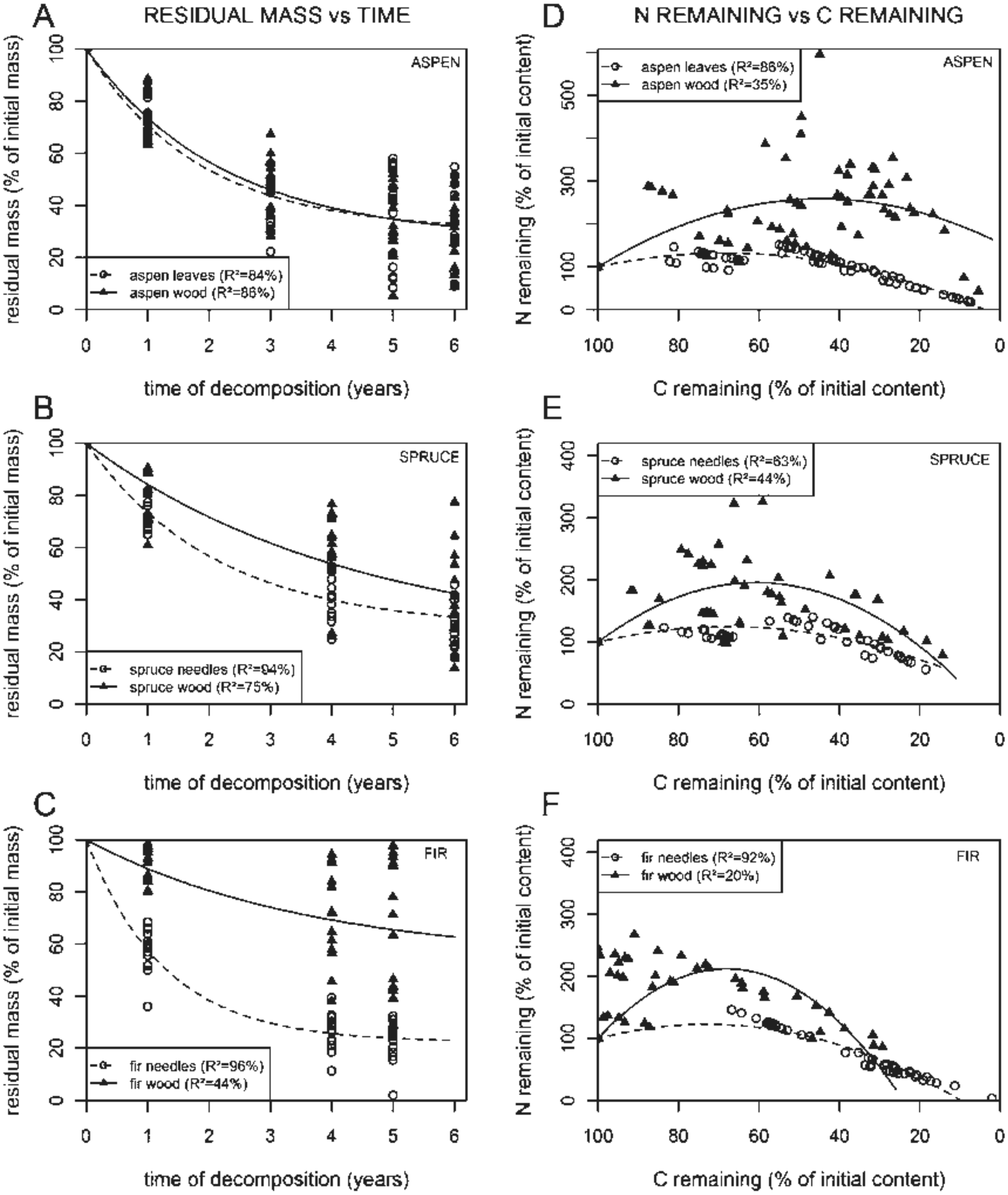

Fig. 1.1. Changes in residual mass with time of decomposition of foliar litters and wood blocks from (A) trembling aspen, (B) white spruce and (C) balsam fir. Changes of nitrogen remaining with carbon remaining of foliar litters and wood blocks from (D) trembling aspen, (E) white spruce and (F) balsam fir.

Note: Parameters of the models are described in Table 2.

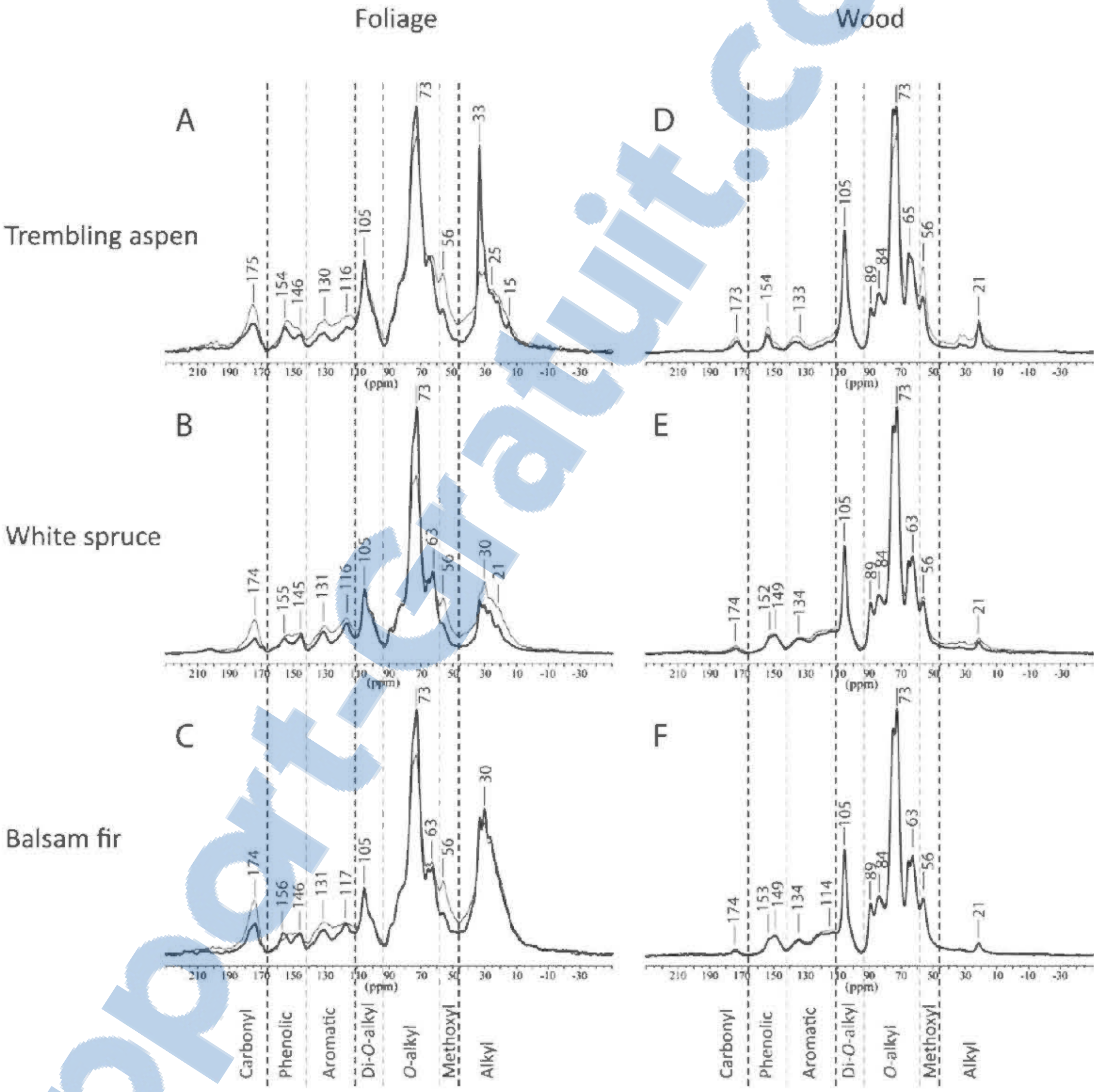

Fig. 1.2. Cross-polarization magic angle spinning (CPMAS) ^{13}C NMR spectra of fresh foliage and wood material (thick line) and spectra of material decayed for 5 to 6 years (thin line).

The alkyl region (0–46 ppm) represented a higher proportion of the spectra for foliar litter (16%–32%) than for wood material (5%–7%). Three peaks at 25–33 ppm arising from aliphatic compounds such as waxes, cutin, and lipids were present on the foliar litter spectra but not on the wood blocks spectra (Fig. 1.2). All spectra displayed a peak at 21 ppm corresponding to methyl C of the acetyl groups of hemicelluloses (Kolodziejski et al., 1982). Additionally, amino acids may contribute to the intensity of the alkyl and carbonyl regions (Almendros et al., 2000).

The aromatic and phenolic regions (111–166 ppm) were quite different among litter types (Fig. 1.2). On the spectra of the aspen wood blocks, there was a small peak at 154 ppm, produced by C-3 and C-5 of etherified structures in syringyl units of lignins, and a broad shoulder at 136 ppm from C-4 in syringyl units (Preston et al., 2000). The C-2 and C-6 of syringyl units likely contributed to the peak at 105 ppm. Coniferous wood blocks spectra displayed a large signal from 112 to 123 ppm, which may be derived from the C-2, C-5, and C-6 of guaiacyl units, whereas the shoulder around 133 ppm resulted from the C-1, the shoulder at 149 ppm from the C-3, and the shoulder at 153 ppm from the C-4 of guaiacyl units. Signals from tannins were not detected on any wood spectra, which presented no characteristic split peak at 144 and 154 ppm. The foliar litter spectra indicated a mixture of lignins and tannins structures, with four broad peaks at 116, 131, 145–146, and 155–156 ppm. The DD spectra for wood blocks showed the predominance of lignin versus tannin structures, with an important peak at 56 ppm and a small one at 105 ppm (results not shown). The DD spectra for foliar litters had peaks at 105, 145, and 155 ppm (results not shown), supporting the presence of condensed tannins (Lorenz et al., 2000). The methoxyl peak at 56 ppm also indicated the presence of lignins.

In summary, fresh wood material was characterized by higher proportions of *O*/*N*-alkyl C, mainly arising from carbohydrate C, whereas foliar material contained a higher proportion of alkyl C resulting from cutin, waxes, and other lipids and a higher proportion of carbonyl C (Fig. 1.3). Furthermore, the aromatic and phenolic regions (Fig. 1.2) resulted from the presence of lignins in wood and from a mixture of lignins and tannins in foliage. Aspen wood had a higher proportion of carbohydrates and a lower proportion of lignins than coniferous species. Differences in foliage composition were linked to a higher proportion of alkyl C in fir, a higher proportion of *O*/*N*-alkyl C in spruce, and a higher proportion of carbonyl C in aspen.

During decomposition, shoulders appeared on foliar litter spectra in the aromatic region, mainly between 145 and 155 ppm and between 115 and 130 ppm (Figs. 1.2A, 1.2B, and 1.2C). Peaks at 157 and 154 ppm in decayed aspen leaf litter may be from syringyl units, and peaks at 146, 148, and 153 ppm in decayed coniferous foliar litters are characteristic of guaiacyl units (Preston et al., 2000). Following 5 or 6 years of decay, foliar litters had a chemical composition very different from initial compositions ($p < 0.001$; Table 1.5; Fig. 1.3). Differences among the three tree species had narrowed down compared with initial compositions, as indicated by the decrease in the T value of the MRPP analysis (Table 1.5; Fig. 1.3), but the three species still had distinct chemical compositions ($p = 0.003$; Table 1.5; Fig. 1.3), mainly arising from different alkyl C proportions. The decay of spruce needles was characterized by a decrease in the proportion of the *O*-alkyl C group and an increase of the proportions of alkyl, phenolic, and carbonyl C (Fig. 1.3). For aspen and fir foliar litters, the proportion of *O*-alkyl C initially decreased, while the proportions of alkyl, phenolic, and carbonyl C increased. Thereafter, the phenolic and *O*-alkyl C increased, while the proportion of the alkyl C group decreased (Fig. 1.3).

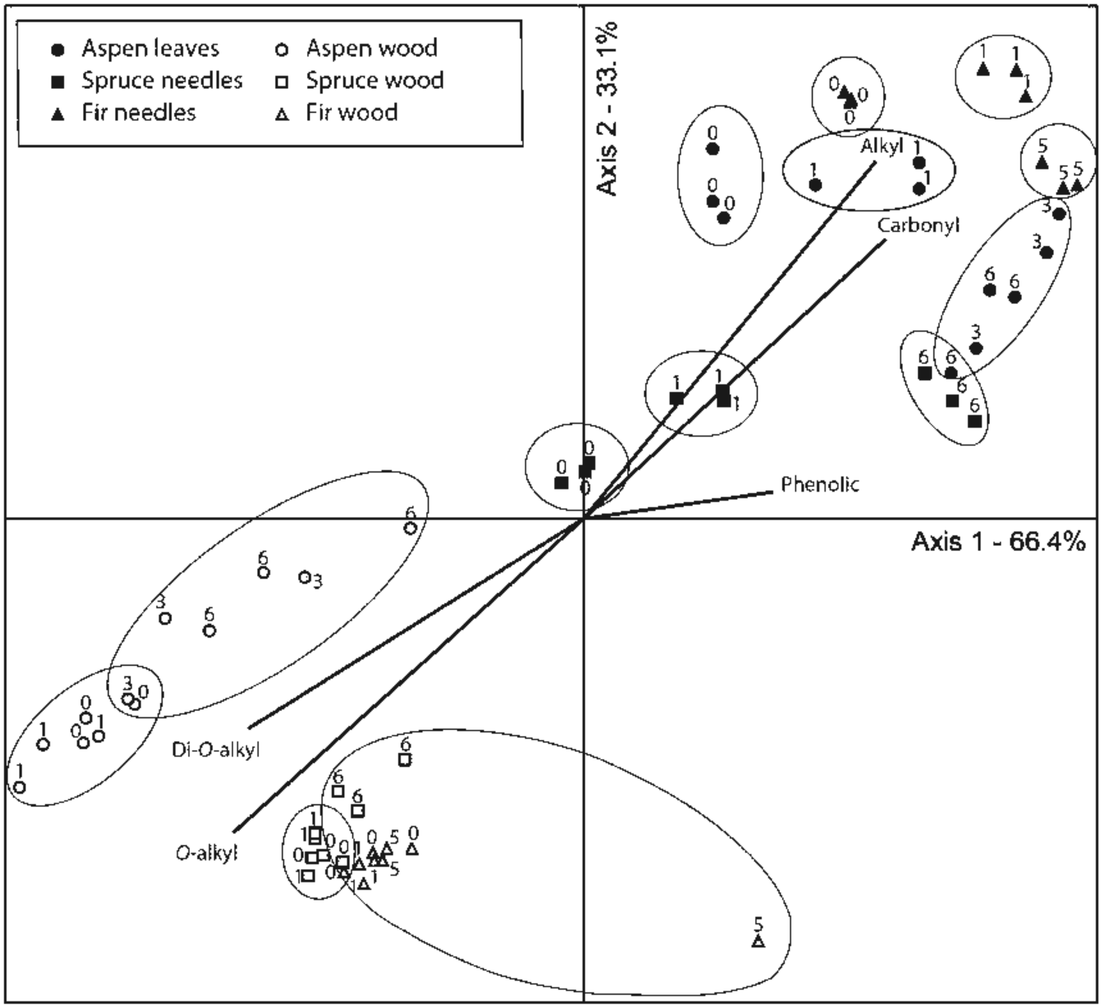

Fig. 1.3. Nonmetric multidimensional scaling (NMDS) ordination of ^{13}C NMR integral areas from aspen, fir and spruce foliar litter and wood blocks.

Note: Numbers on top of symbols (circles, squares and triangles) indicate time of decay (years). The spectral NMR areas to map the vectors are the alkyl (0-46 ppm), the methoxyl (46-58 ppm), the *O*-alkyl (58-93 ppm), the di-*O*-alkyl (93-111 ppm), the aromatic (111-142 ppm), the phenolic (142-166 ppm) and the carbonyl (166-222 ppm) regions. Groupings based upon multiresponse permutation procedure (MRPP) analysis are encircled. Cutoff for correlation vectors was set at r^2=0.5. NMDS ordination produced a solution with a stress of 2.87, which was achieved after 73 iterations.

Table 1.5. Distances in the nonmetric multidimensional scaling (NMDS) ordination space between litter types at the start and at the end of a field incubation experiment, obtained by multiresponse permutation procedure (MRPP) analysis with the Sorensen distance.

Distance type	*T*	*A*	*p*
Distances between foliar litters and wood blocks			
Initial	-10.25	0.531	<0.001
Final	-10.94	0.566	<0.001
Distances between species and time of decay (foliar litters)			
Initial distance between species	-4.68	0.850	<0.001
Final distance between species	-3.92	0.593	0.003
Distance between initial and final foliar litters	-7.74	0.292	<0.001
Distances between species and time of decay (wood blocks)			
Initial distance between species	-3.82	0.708	0.003
Final distance between species	-2.87	0.280	0.010
Distance between initial and final wood blocks	-1.49	0.050	0.083

Note: *T* value, separation among groups; *A* value, within group heterogeneity; *p* value, significance of the difference.

Decayed wood blocks kept a chemical composition clearly distinct from that of foliar litters ($p < 0.001$; Table 1.5; Fig. 1.3). Although the decrease of the *T* value indicated more similarity of chemical composition between wood blocks at the end of the experiment (Table 1.5), initial and final wood blocks were not significantly different ($p = 0.083$; Table 1.5). Few changes in composition appeared during the study period for coniferous wood, as revealed by the small differences between the initial and final spectra (Figs. 1.2E, 1.2F). Similarly, all observations representing initial and final composition stayed closely clustered on the NMDS ordination, with the exception of one fir wood block that showed an increase in the proportion of alkyl, phenolic, and carbonyl C groups and a decrease in the percentage of *O*-alkyl C (Fig. 1.3). In aspen wood, few changes appeared during the first year of decomposition, except for a small increase in the concentration of *O*-alkyl C. After the first year, the proportion of *O*-alkyl C group decreased and the proportion of alkyl, phenolic, and carbonyl C increased (Fig. 1.3). Species kept distinct wood compositions at the end of the experiment ($p = 0.010$; Table 1.5), differing by their proportions of alkyl, *O*-alkyl, phenolic, and carbonyl C.

Changes in the alkyl:*O*/*N*-alkyl ratio differed significantly ($p = 0.035$) between the aspen leaf litter and the other litter types (Table 1.4) for which the ratio increased ($p = 0.005$). The alkyl:*O*/*N*-alkyl ratio increased faster for spruce foliar litter than for the other coniferous litters ($p = 0.027$), as the fir foliar litter showed little changes (Fig. 1.4). The phenolic:*O*-alkyl ratio increased significantly ($p = 0.003$) for aspen and coniferous litters over the 5- to 6-year period (Table 1.4; Fig. 1.4B), but this increase was very little for spruce wood and larger for spruce than for fir foliar litter.

1.4.4. Lignin monomers

The V phenols were significantly ($p < 0.001$) higher in coniferous litters than in aspen litters and remained significantly higher in wood than in foliar material throughout the incubation period (Tables 1.4 and 1.6), whereas the Cn phenols did not differ between species and were higher in foliage than in wood. Initial Cn:V ratios in foliage ranged from 0.47 to 0.75 and were significantly ($p < 0.001$) higher than in wood (Fig. 1.4D). Initially, the P phenols constituted a high amount of the phenols in spruce foliar litter, contrary to other litters (Table 1.6). The main phenol in all litters was vanillin. The S:V ratio was higher in aspen than in coniferous wood ($p < 0.001$). The results yielded initial V:S:Cn ratios of 51:136:1 for aspen, 51:2:1 for spruce, and 63:2:3 for fir wood blocks. The Vac:Val ratio was higher in wood blocks than in foliar litters ($p < 0.001$) and higher in aspen than in coniferous wood ($p < 0.001$) but lower ($p < 0.001$) in aspen leaves than in coniferous needles (Fig. 1.4D; Table 1.4). The P: V, Pac:Pal, and Sac:Sal ratios did not show any trend except for a higher P:V ratio in spruce foliar litter (results not shown).

The amount of V phenols decreased significantly ($p < 0.001$) in aspen wood compared with coniferous wood (Table 1.4) and increased significantly in foliar litters ($p < 0.001$). Amounts of TPC decreased with time in aspen wood but not in coniferous wood. Decreases of Cn:V ratios with time were significant ($p < 0.001$) in foliar litters (Table 1.4; Fig. 1.4C) and higher in aspen than in coniferous litters ($p = 0.029$), and decreases of the S:V ratio were significant ($p = 0.022$) in aspen wood. The Vac:Val ratio increased significantly ($p < 0.001$) with time in all litters (Fig. 1.4D; Table 1.4). Lignins from the aspen wood had a high proportion of syringyl phenols, but the Sac:Sal ratio remained low throughout the decomposition study (results not presented).

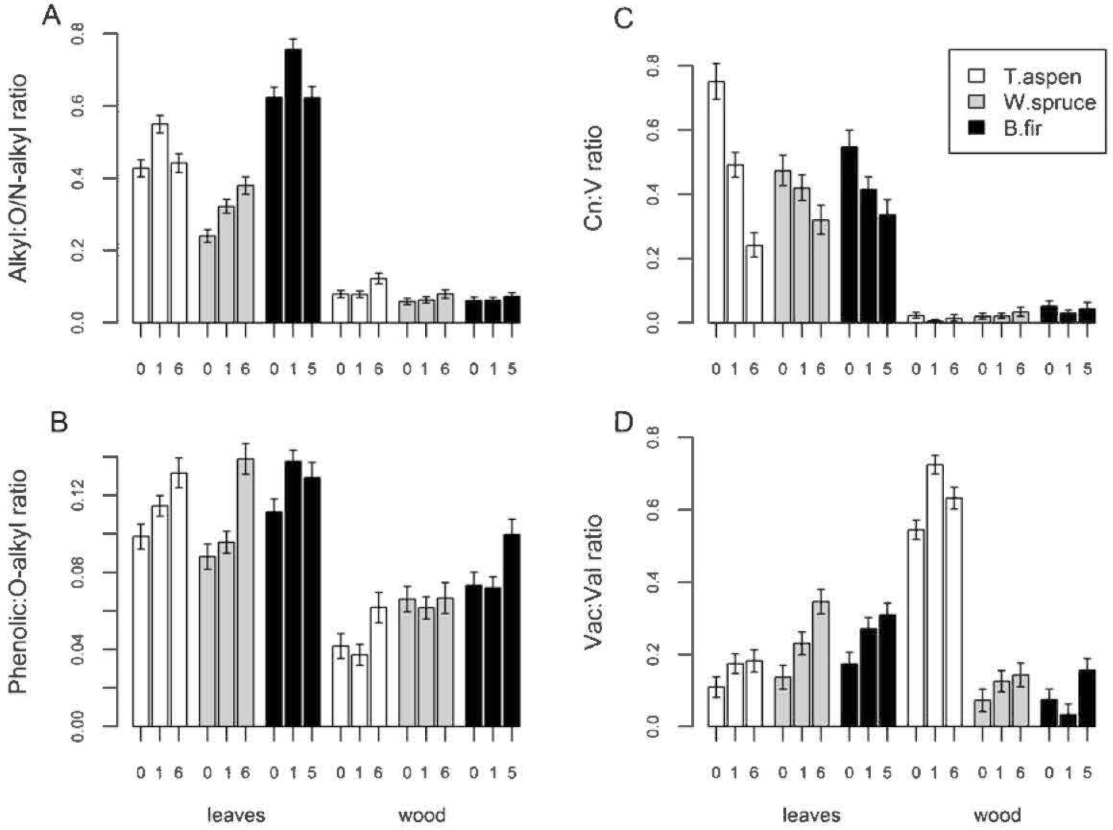

Fig. 1.4. Integrated spectral ^{13}C NMR area and lignins phenolic ratios in foliar litters and wood blocks from three boreal species of northwestern Quebec at initial time (0), after 1 year of decay, and after either 5 or 6 years of decay. (A) alkyl:*O*/*N*-alkyl ratio; (B) phenolic:*O*-alkyl ratio; (C) Cn:V ratio; (D) Vac:Val ratio.

Note: V, vanillyl phenols; Cn, cinnamyl phenols; Vac, vanillic acid; Val, vanillin

Table 1.6. Initial and final concentrations of phenolic degradation products obtained from the CuO oxidation of foliar litters and wood blocks of three boreal species.

Litter type	Time of decay (years)	**CuO oxidation products (mg.g^{-1} dry weight)**				
		V	S	Cn	P	TPC
Aspen leaves	0	2.52 (0.96)	n.d.	1.70 (0.52)	0.41 (0.23)	n.d.
	6	3.29 (1.46)	n.d.	0.74 (0.12)	0.35 (0.16)	n.d.
Spruce needles	0	3.64 (1.39)	n.d.	1.72 (1.32)	4.35 (0.25)	n.d.
	6	5.69 (0.88)	n.d.	1.81 (0.27)	0.57 (0.04)	n.d.
Fir needles	0	4.21 (1.33)	n.d.	2.50 (1.99)	0.70 (0.32)	n.d.
	5	5.09 (0.84)	n.d.	1.68 (0.04)	0.29 (0.07)	n.d.
Aspen wood	0	8.15 (2.07)	21.73 (5.71)	0.16 (0.09)	0.68 (0.47)	30.73 (8.19)
	6	3.95 (0.61)	8.65 (2.79)	0.06 (0.05)	0.35 (0.20)	13.02 (3.65)
Spruce wood	0	15.71 (1.77)	0.65 (0.46)	0.31 (0.06)	0.13 (0.12)	16.80 (2.20)
	6	16.07 (3.80)	0.62 (0.06)	0.56 (0.19)	0.42 (0.42)	17.67 (4.48)
Fir wood	0	14.81 (5.28)	0.47 (0.15)	0.76 (0.31)	0.06 (0.02)	16.09 (5.63)
	5	15.40 (0.40)	0.36 (0.03)	0.66 (0.09)	0.19 (0.07)	16.62 (0.46)

Note: Mean values ($n = 3$) and standard deviations in parentheses. n.d., no data; TPC, total phenolic constituents (sum of vanillyl phenols (V), syringyl phenols (S), cinnamyl phenols (Cn), and *p*-hydroxy phenols (P)).

1.5. Discussion

Our results underline the differences in biochemical composition between foliage and wood material during the first 5 to 6 years of decomposition. Similar predicted maximum decomposition limits were found for foliage and wood. However, decomposition of aspen, fir, and spruce foliar litters generated organic matter rich in alkyl, phenolic, and carbonyl C, whereas few changes appeared in wood of all three species as their cellulose content remained high.

1.5.1. Maximum decomposition limit

The exponential model with an asymptote used to estimate maximum decomposition limits gave satisfactory results (Fig. 1.1), except for balsam fir wood, which was characterized by low mass losses. Slow decomposition of balsam fir wood has been reported for logs or branches (Edmonds, 1987). Losses of mass of other litters were within the range reported after 6 years of decay by the study of Preston et al. (2009a). The maximum decomposition limit of foliar litters was in the same range as what has been reported by Berg et al. (1996). To our knowledge, our study is the first one reporting maximum decomposition limit values for wood. Aspen wood differed from coniferous wood by decomposing faster, and similarly to the foliar litters, aspen wood was close to reaching its maximum decomposition limit at the end of the experiment.

Previous studies (Berg, 2000; Prescott, 2010) have indicated that low-molecular-mass N compounds such as ammonium and amino acids influence decomposition by repressing the formation of lignolytic enzymes in white-rot fungi and by reacting with products of degradation forming recalcitrant compounds. Despite lower initial N concentrations, the maximum decomposition limit in wood was similar to that of foliar litters, indicating that other factors were coming into play. Berg (2000) found a negative correlation between lignin concentrations and maximum decomposition limit in Norway spruce needle litter. Although lignins can have a rapid turnover (Lorenz et al., 2007), they have been shown to react during decay with N or residual carbohydrates to form a recalcitrant matrix (Berg, 2000). Hence, they could impede the completeness of decay in wood, mainly composed of cellulose, hemicelluloses, and lignins, as reflected on the ^{13}C CPMAS NMR spectra dominated by *O*/*N*-alkyl, aromatic, and phenolic C groups (Figs. 2 and 4). Moreover, low nutrient content in wood (Laiho & Prescott, 2004) and extractives (Cornwell et al., 2009) could influence decomposition (Berg, 2000; Hättenschwiler & Vitousek, 2000), although these were not studied here. Regardless of the underlying processes responsible for this phenomenon, it was interesting to note that for the boreal tree species that we studied, maximum decomposition limit values for wood were similar to those for foliage, contrary to our first hypothesis.

1.5.2. Foliar litter decomposition patterns

The gain of N in all litters during the early phase of decay is mainly due to immobilization by saprotrophic fungi that can overcome local nutrient deficiency through mycelial translocation (Schimel & Hättenschwiler, 2007; Boberg et al., 2010). Carbon and nitrogen concentrations were in the same range as other published data for aspen (Moore et al., 2006) and white spruce (Trofymow et al., 1995) foliar litters. However, N concentration in balsam fir foliar litter was higher in this study (11.9 $mg \cdot g^{-1}$) than in Trofymow et al. (1995) (5.3 $mg \cdot g^{-1}$) . Balsam fir is a tree species demanding high levels of nutrients (Paré et al., 2002) that can accumulate a high level of nitrogen, depending on soil richness. The critical C:N ratios in which N is released found in this experiment were lower than those of aspen (54) and black spruce (63) found in the study of Moore et al. (2006), which may result from differences between sites. The N concentration reached an asymptote in foliar litters (results not shown), with the C:N ratio of the decayed material stabilizing between 22.3 and 25.1. Soil fungi and bacteria typically have lower C:N ratios of 10 and 4, respectively (Vance & Chapin, 2001). The C:N ratio of the forest floor for the same stands (29; Brais et al., 2004) was higher than the C:N ratio of the decayed foliar litters, which suggests litter inputs having higher C:N ratios such as wood material.

Contrary to wood, leaves and needles contained a high proportion of alkyl C (Fig. 1.3) from cutin, waxes, and other lipids located in the cuticle surrounding their epidermis (Kögel-Knabner, 2002). These biopolymers are considered highly recalcitrant to decomposition (Lorenz et al., 2007), and the alkyl:*O*/*N*-alkyl ratio is often reported as a sensitive index of the extent of decomposition, as decomposition is often associated with an increased content of alkyl C and a decreased content of *O*/*N*-alkyl C (Baldock & Preston, 1995). The alkyl:*O*/*N*-alkyl ratio and the concentration of alkyl C increased in spruce foliar litter (Fig. 4). However, in aspen and fir foliar litters where the initial alkyl C proportion was high, the alkyl:*O*/*N*-alkyl ratio remained stable, indicating a concomitant decrease of the content in alkyl C and *O*/*N*-alkyl C compounds resulting from concomitant decomposition of celluloses and aliphatic compounds initially present and also from degradation of microbial products such as proteins and lipids that resonate in the alkyl region (Quideau et al., 2005). Because only a small proportion of the initial alkyl C was preserved after 5 or 6 years of decay for aspen and fir foliage, we conclude that the enrichment in alkyl C expected during decomposition of foliar litters is not universal but instead is species-dependant.

However, all foliar litters were enriched in phenolic C during decomposition (Fig. 1.3). The aromatic and phenolic regions in spectra of initial foliar litters were dominated by peaks characteristic of tannins, but these peaks disappeared during decomposition, whereas peaks characteristic of guaiacyl or syringyl phenols of lignins appeared. This can result from a loss of the soluble tannins from the foliar litters, likely by leaching (Lorenz et al., 2000; Preston et al., 2009b), that left a residue in which the majority of aromatic C was part of lignin moieties. The observed increase in phenolic C of foliar litters likely resulted from a relative increase in lignin concentrations compared with more labile litter biomolecules, but also from the formation of aromatic by-products of decomposition such as aromatic humus precursors (Berg et al., 1996; Prescott, 2010). Moreover, the significant increase in the amount of V phenols with decomposition as obtained by CuO oxidation clearly indicated their recalcitrance. The significant decrease of the Cn:V ratio in foliar litters (Fig. 1.4C) was more important in aspen than in coniferous foliar litters and indicated a preferential degradation of the cinnamyl phenols over the vanillyl phenols, which has been documented previously (Otto & Simpson, 2006). The Cn:V ratios of initial foliar litters were consistent with those in other studies (Hedges & Mann, 1979; Kögel & Bochter, 1985; Otto & Simpson, 2006). The high level of P phenols in spruce leaf litter was very close to the value reported for black spruce by Williams et al. (1998). The Vac:Val ratio was higher in coniferous foliar litters than in aspen throughout the incubation period, as found for Norway spruce and European beech in the study of Klotzbücher et al. (2011).

Therefore, our third hypothesis was not confirmed in this study, as the Cn phenols were more degraded in aspen foliage, whereas the P phenols were more degraded in spruce foliage. However, the P phenols can also be derived from proteins and tannins (Otto & Simpson, 2006), and the S phenols characteristic of deciduous lignins are thought to be preferentially degraded over the V phenols (Otto & Simpson, 2006). Contrary to what our second hypothesis suggested, there was no enrichment in alkyl C in all foliar litters. However, despite large initial differences in chemical composition (Fig. 1.3; Table 1.5), foliar litters of aspen, spruce, and fir converged to a chemical composition similarly rich in alkyl, phenolic, and carbonyl C. Preston et al. (2009a); Preston et al. (2009b) found a similar convergence for white birch, jack pine, aspen, black spruce, and other species of western Canada over a 6-year period. Although Berg (2000) postulated that it should be possible to distinguish differences in humus buildup among tree species, our results suggest that all foliar litters had comparable maximum decomposition limits and an increasing similarity in composition, which would lead to an equivalent contribution to long-term C sequestration and similar humus composition.

1.5.3. Wood decomposition patterns

Nitrogen concentrations in deadwood were similar to those in other studies (Lambert et al., 1980; Laiho & Prescott, 1999). Nitrogen gain during wood decomposition was important relative to its low N content, and N concentration reached more than twice the initial values. The critical C:N ratio at which N is lost was far higher than in foliar litter. Hart (1999) suggested that N release in decaying wood occurs at ratios higher than those of the microbial biomass due to a decrease in C availability.

Our findings for lignin oxidation products (V, S, and Cn) (16–30.7 $\text{mg}\cdot\text{g}^{-1}$) are within the range of other studies, extending from 5.1 $\text{mg}\cdot\text{g}^{-1}$ for brown leaves of quaking aspen (Otto & Simpson, 2006) to 102.9 $\text{mg}\cdot\text{g}^{-1}$ for wood of silver maple (Hedges & Mann, 1979). The CuO oxidation method is a semiquantitative method that can release between 25% and 75% of the outer part of lignin in the form of monomers (Hedges & Ertel, 1982; Otto & Simpson, 2006), which explains the large variation between studies. However, CuO oxidation is indicative of lignin composition and content. The V:S:Cn ratios of initial wood blocks were consistent with those in other studies, with a predominance of vanillyl phenols in gymnosperms and a predominance of syringyl in angiosperms (Hedges & Mann, 1979; Otto & Simpson, 2006). Aspen wood had lower initial concentrations of aromatic and phenolic C from lignins than coniferous species and its S:V ratio was higher, indicating that lignins from aspen wood were more susceptible to degradation than those of coniferous wood. Little changes were observed during the first year of aspen wood decomposition, but lignin concentrations increased thereafter (Fig. 1.3).

Nonetheless, aspen wood composition remained distinct from both coniferous species to the end of the study period, i.e., aspen wood contained a lower proportion of lignins but higher proportions of alkyl and carbonyl C. Other studies (Preston et al., 1990; Fukasawa et al., 2009) have documented a third phase of wood decomposition in which chemical composition remains stable in well-decomposed logs. In our study, aspen wood had almost reached its maximum decomposition limit and would probably undergo small transformations in chemical composition with further decay.

Coniferous wood underwent only minor changes in composition during our study, which is consistent with results obtained by Preston et al. (2009a) for western hemlock wood. The amount of total phenolic constituents remained stable in coniferous wood, suggesting preservation of the chemical structure of lignins (Table 1.6) mainly composed of recalcitrant vanillyl phenols. The phenolic:*O*-alkyl ratio increased slightly, arising from an increase of the concentration of lignins and lignin-like by-products (Baldock & Preston, 1995; Berg et al., 1996). The Vac:Val ratio increased with time, accompanied by an increase of the carbonyl C group, which arise from side-chain oxidation of lignins by the oxidative enzymes secreted by microorganisms (Otto & Simpson, 2006). The Vac:Val ratio of coniferous wood blocks after 6 years of decay reached low values from 0.14 to 0.16 and would probably increase with further decay. Coniferous wood would require additional time to enter a stable state. Further changes in composition would depend on the microorganisms involved (Baldock & Preston, 1995). Although white-rot fungi can degrade both lignins and carbohydrates, brown-rot and soft-rot fungi degrade mainly carbohydrates (Baldock & Preston, 1995; Fukasawa et al., 2009). Differences in decomposition patterns between aspen and the coniferous species could have resulted from differences in environmental forest stand characteristics as litterbags from each species were placed in different stand types (e.g., aspen litter was left to decompose in aspen stands, etc). However, a parallel study conducted in the same stands compared the composition of fungal communities on decaying aspen and balsam fir wood blocks and found no differences in these communities between stand types, with most differences in fungal communities being linked to wood species (H. Kebli, personal communication).

In summary, our second hypothesis was not verified in wood material. Although wood chemical composition became enriched in phenolic C, as well as slightly enriched in alkyl C, few changes appeared overall during decomposition. As we expected in our third hypothesis, lignins of coniferous wood were more recalcitrant than those of aspen, which could explain the slower decomposition of coniferous wood. Although wood has the potential to create a higher diversity in the residual organic matter composition than foliar litters, its importance in C sequestration will depend on its final composition once it reaches its maximum decomposition limit.

1.6. Conclusions

The maximum decomposition limit constitutes an important parameter of the C cycle, and our results indicate that foliar litter and decomposing wood reach similar limits. The chemical composition of organic matter resulting from foliage decomposition was rich in alkyl, phenolic, and carbonyl C, whereas the residual material from decomposing wood was still rich in celluloses. Once litters have reached their maximum decomposition limit, the residual organic matter is assumed to be composed of fairly stabilized fractions. Hence, organic matter resulting from foliage decomposition may be more stable compared with wood due to its relatively high proportion of aliphatic compounds. However, wood takes more time to reach its maximum decomposition limit and generates a more diverse composition for the resulting organic matter, contributing to the chemical and physical complexity of the forest floor. Further study is necessary to determine the specific factors and mechanisms involved in the formation of organic matter until the maximum decomposition limit in wood is reached. This study considered decomposition of small heartwood blocks during a 6-year experiment, without sapwood and bark. Understanding longer term decay patterns for whole coarse woody debris is necessary to assess precisely the contribution of deadwood to C sequestration.

1.7. Acknowledgements

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CHAPITRE II

CHEMICAL TRANSFORMATIONS IN DOWNED LOGS AND SNAGS OF MIXED BOREAL SPECIES DURING DECOMPOSITION

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2.1. Abstract

Snags and downed logs are substantial components of the detrital carbon pool in boreal forests. Effects of their decomposition on chemical and physical characteristics of the forest floor remain relatively unknown. The main objective of this study was to characterize chemical transformations of decaying logs and snags of common tree species in the boreal mixedwood forest. Logs and snags from a wide range of decay classes were sampled and analyzed by solid-state ^{13}C nuclear magnetic resonance spectroscopy and by near-infrared spectroscopy. Little or moderate chemical changes appeared in fresh and moderately decayed snags and logs, but in well-decayed logs, substantial degradation of carbohydrates and increases in lignin concentrations occurred. Deciduous species had initially more carbohydrates than coniferous species, but decomposition narrowed their differences, and in well-decayed logs, species differed mainly in terms of their lignin concentrations. Well-decayed deciduous logs reached very low wood densities, and their integration into the forest floor and long-term preservation remains questionable. In contrast, chemical composition of well-decayed coniferous logs resembles that of lignic forest floor (i.e., forest floor originating from deadwood decomposition), with preserved lignins, carbohydrates, and alkyl carbon compounds. Decomposed coniferous wood thus contributes to chemical heterogeneity of the forest floor, possibly promoting diversity of decomposers as well as carbon retention in soils.

Les chicots et les billes au sol sont des composantes substantielles du réservoir de carbone détritique en forêt boréale. Les effets de leur décomposition sur les caractéristiques physiques et chimiques de la couverture morte restent méconnus. Le principal objectif de cette étude était de caractériser les transformations chimiques des billes et des chicots en décomposition d'espèces d'arbres communes en foret boréale mixte. Des billes et des chicots de différentes classes de décomposition ont été échantillonnés et analysés par résonance magnétique nucléaire du ^{13}C *en phase solide et par spectroscopie dans le proche infra-rouge. Des changements chimiques faibles ou modérés apparaissaient dans les billes et les chicots frais ou modérément décomposés, mais dans les billes bien décomposées, une dégradation substantielle des hydrates de carbone et une augmentation de la concentration en lignines avaient lieu. Les espèces décidues avaient initialement plus d'hydrates de carbone que les conifères, mais la décomposition réduisaient leurs différences, et dans les billes bien décomposées, les espèces ne différaient que par leur teneur en lignines. Les billes bien décomposées des espèces décidues atteignaient des densités de bois très faibles, et leur intégration dans la couverture morte et leur préservation à long-terme restait questionnable. Au contraire, la composition chimique des billes bien décomposées de conifères ressemblait à celle de la couverture morte lignique (c'est-à-dire la couverture morte provenant de la décomposition du bois mort), avec préservation des lignines, des hydrates de carbone et des composes alkylés. Le bois décomposé de conifères contribue à l'hétérogénéité chimique de la couverture morte, favorisant la diversité des décomposeurs et la rétention du carbone dans les sols.*

2.2. Introduction

Coarse woody debris (CWD), which includes standing snags and downed logs on the forest floor, is a prominent attribute of temperate and boreal forests (Harmon et al., 1986). Because of its relatively low nutrient content (Laiho & Prescott, 2004) and large size (Cornwell et al., 2009), CWD generally decomposes more slowly than fine litters (Harmon et al., 1986; Laiho & Prescott, 2004; Strukelj et al., 2012, Chapitre I) and is recognized as an important long-term pool of forest carbon (C) (Manies et al., 2005). Forest harvesting alters CWD dynamics and reduces its abundance (Ekbom et al., 2006), and the management of CWD as a key factor in the forest C cycle needs to be addressed. However, our limited understanding of how different tree species modulate wood chemistry and organic matter stability during CWD decomposition (Weedon et al., 2009) reduces our ability to do so.

Studies conducted in temperate and boreal forests have shown that CWD decomposition results in a loss of carbohydrates and increases in lignins, waxes, and resins (Preston et al., 1990; Preston et al., 1998; Fukasawa et al., 2009). Several studies have also reported little change in wood chemical composition with decomposition (Lambert et al., 1980; Preston et al., 1990). As CWD decomposes, nitrogen (N) concentrations generally increase because of translocation and retention by fungi (Lambert et al., 1980; Schimel & Hättenschwiler, 2007) and fixation by bacteria (Brunner & Kimmins, 2003), resulting in a continuous decrease in C:N ratio, which is initially high in CWD (Herrmann & Prescott, 2008; Strukelj et al., 2012, Chapitre I). With time, CWD becomes incorporated into surface organic soil horizons (de Montigny et al., 1993; Brais & Drouin, 2012), where it contributes to the chemical heterogeneity of the forest floor by maintaining a chemical composition distinct from the material originating from foliar litter (de Montigny et al., 1993; Krzyszowska-Waitkus et al., 2006; Brais & Drouin, 2012) and from well-decayed logs lying on the forest floor (Brais & Drouin, 2012).

Compared with logs, very few studies have characterized chemical changes in snags before they reach the ground (Fukasawa et al., 2009; Mukhortova et al., 2009). Changes in wood density should take place more slowly in snags than in logs (Boulanger & Sirois, 2006), as a result of lower moisture content (Fukasawa et al., 2009) and restricted access to decomposer microorganisms on the forest floor. However, similar fungal communities have been found on logs and snags of trembling aspen (*Populus tremuloides* Michx.; Kebli et al., 2012). Furthermore, large decreases in snag wood density with decay have been observed for some species (Angers et al., 2012b). Because of their low decay rates, snags constitute an important pool of slow-release C (Boulanger & Sirois, 2006), and studying changes in their chemical properties with decay will improve our understanding of their contributions to long-term C sequestration.

Deciduous species have generally higher wood densities than coniferous species (Weedon et al., 2009), together with higher carbohydrate contents, lower lignin contents, and a fine-scale anatomy more favourable to fungal activity (Cornwell et al., 2009). In addition, angiosperm and gymnosperm woods differ in the chemistry of their lignins, in the quality of their hemicelluloses, and in the quantity and quality of their resins (Cornwell et al., 2009). These differences may have important effects on degradation by microbes and C sequestration. In boreal forests, few studies have been conducted on the decomposition of deciduous CWD (Brais et al., 2006) compared with coniferous CWD. In a previous study (Strukelj et al., 2012, Chapitre I), we found that trembling aspen wood lying on the forest floor became enriched in phenolic C and alkyl C, whereas little change was apparent during earlywood decomposition of white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.). Angiosperm and gymnosperm foliar litters have been shown to become more similar with decomposition (Preston et al., 2009a). We do not know yet if a similar trend can be found for wood.

The primary objective of this study was to characterize the chemical composition of decaying snags and logs of common deciduous and coniferous boreal species, including white birch (*Betula papyrifera* Marshall), trembling aspen, balsam fir, jack pine (*Pinus banksiana* Lamb.), white spruce, and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) over a broad range of decomposition states. A secondary objective was to compare the chemical composition of well-decayed logs with forest floor originating from logs (lignic forest floor) and forest floor originating from foliar litter (alignic forest floor; Kayahara et al., 1996; Brais & Drouin, 2012). This information will improve our understanding of the contribution of individual tree species to C stability (Lorenz et al., 2007) and soil organic matter chemical heterogeneity. Our hypotheses are as follows: (*i*) We expect snags and logs to become richer in lignins with decomposition, whereas their C:N ratios will decrease. (*ii*) We also expect wood chemical composition to converge among species as decomposition proceeds. (*iii*) These changes in chemical composition will be less pronounced in snags than in logs. (*iv*) Finally, the chemical composition of well-decayed logs will remain distinct from that of lignic forest floor, which will consist mainly of lignins and modified lignins, whereas the composition of alignic forest floor will be characterized by high alkyl content (Strukelj et al., 2012, Chapitre I).

2.3. Material and methods

2.3.1. Study area

The study was conducted in the Lake Duparquet Research and Teaching Forest (48°86’N-48°32’N, 79°19’W-79°30’W), which is located in the Abitibi region of northern Quebec, 45 km northwest of the city of Rouyn-Noranda. The climate is continental with a mean annual temperature of 0.7 °C. Annual precipitation is 890 mm, of which 614 mm falls as rain from April to November (Environment Canada, 2010). The region is situated in the mixedwood zone of the boreal shield, within the western balsam fir – white birch bioclimatic domain. Forest succession on rich mesic sites generally begins with the establishment of pure or mixed stands of white birch, trembling aspen, and jack pine. In the absence of major disturbance, these species are gradually replaced by a mixture of white spruce, black spruce, and balsam fir (Bergeron & Dansereau, 1993). The dominant soils of the region have evolved from fine clayey to fine loamy textured glaciolacustrine deposits that were formed at the bottom of proglacial Lake Barlow-Ojibway (Bergeron & Dansereau, 1993), and which are classified as Gray Luvisols (Soil Classification Working Group, 1998).

2.3.2. Sampling design

Snags and logs were sampled in stands of fire origin that dated from 1760 to 1923 and that represented a gradient of stand composition typical of natural succession on rich mesic sites (Bergeron & Dansereau, 1993). Snags were sampled by Angers et al. (2010), whereas logs were sampled over the course of two other studies (Kebli et al., 2011; Robert et al., 2012).

2.3.2.1. Sampling of snags

Snags were sampled from 16 plots that were defined by year of stand initiation by fire and dominant tree species (for complete stand descriptions see Angers et al., 2010; and Appendix E). To determine decay class, characterization of snags included species, diameter at breast height, height, stem integrity (entire or broken), and presence of foliage, twigs, branches, and bark (Table 2.1). A five-class system was used, from decay class S-I representing fresh snags to decay class S-V representing well-decayed snags (Table 2.1). A subset of 84 snag samples, covering four species (white birch, trembling aspen, balsam fir, and jack pine) was selected to represent a gradient of wood density (Appendix E). Cross sections taken at breast height from each snag were oven-dried at 60 °C to constant mass. After removal of the bark, sections were cut into subsamples (10 cm × 5 cm × 2 cm) for chemical analyses.

Table 2.1. Standing snags, downed logs, and lignic forest floor descriptions.

Decay class	**Description**
Snags (adapted from Imbeau and Desrochers, 2002)	
S-I	Recently dead snag, with hard wood, firm bark cover, 0% green foliage, large and small branches and twigs still present.
S-II	Dead snag for some time, with hard wood, but no dead foliage, no small branches and no twigs.
S-III	Pole, with hard wood, loose bark cover, broken top, reaching more than 50% of the height of living trees, a few large branches.
S-IV	Half-pole, with soft, decomposed wood, broken top, reaching less than 50% of the height of living trees, bark peeling or absent.
S-V	Stump, less than 2m in height.
Logs (adapted from Daniels et al., 1997)	
L-I	Freshly fallen logs, with sound bark and wood, and with presence of twigs.
L-II	Sound bark and wood mainly, branches are present but twigs are absent.
L-III	Logs maintain structural integrity, bark is detached or absent, wood is decayed but still structurally sound.
L-IV	Logs are oval, bark is absent, and wood is soft due to decay, branch stubs can be removed.
L-V	Logs lack structural integrity and are being incorporated into the forest floor. Log height over the forest floor > half log diameter.
Lignic forest floor (buried wood; Brais and Drouin, 2012)	
	Wood buried within the forest floor, from whole logs to aggregates of well decomposed wood fibres. Log height over the forest floor < half log diameter.

2.3.2.2. Sampling of logs

Log sampling was conducted in 2006 and 2007 in four different stand types that were defined in terms of year of stand initiation by fire (Bergeron & Dansereau, 1993) and dominant tree species (see Brais & Drouin, 2012; Robert et al., 2012; and Appendix D for stand descriptions). Logs were located within permanent sampling plots, nested within three individual stands per stand type (Appendix F). A total of 164 logs with butt-end diameters >10 cm were sampled from a range of decay classes representing a gradient of decomposition from freshly fallen to well-decayed logs (Daniels et al., 1997). White birch, trembling aspen, balsam fir, jack pine, white spruce, and black spruce were included in this collection. Decay classes were based on visual criteria such as the presence of foliage, twigs, branches, bark and moss, the shape of the bole, and the softness of the wood (Table 2.1). A five-class system was used to characterize decay, from L-I representing fresh logs to L-V representing well-decayed logs (Table 2.1). When species identification of logs could not be made in the field, a wood sample was taken from the least decomposed part of the log and the species was identified from structural and anatomical features under a microscope (Kebli et al., 2011). This technique did not allow us to distinguish between white and black spruce, which were pooled as “spruce spp.”

A cross section ~5 cm thick was removed with a chainsaw from the half section of the log closest to the butt end. All sections were kept frozen at –20 °C prior to analyses. Log sections were cut into subsamples (10 cm × 5 cm × 2 cm), after removal of the bark and wood that had been in contact with the chainsaw. Two subsamples were kept for density measurements. The others were air-dried (20–25 °C) to constant mass for chemical analyses.

2.3.2.3. Sampling of forest floor

Lignic and alignic forest floor material was collected in 2007 in a parallel study (M. Strukelj, S. Brais, and D. Paré, manuscript in preparation, Chapitre III), in the same permanent sampling plots of three stand types where logs were sampled. Sampling consisted of removing 1 m^2 of lignic forest floor (~3 kg of material) and 0.125 m^2 of alignic forest floor (~2 kg of material) from each plot. Lignic forest floor was recognizable by its red to brown colour, its shape, or its fibrous texture, which differed from alignic forest floor. For this study, three 30 g samples of lignic forest floor and of alignic forest floor (one of each per stand type) were randomly selected from 45 samples and sieved for chemical analyses.

2.3.3. Measures of wood density

Although decay classification systems based on external morphological attributes constituted a simple method to sample a gradient of decomposition of CWD in forest, they provided rough approximations of time-since-death or wood density, particularly in snags (Daniels et al., 1997; Angers et al., 2012a). Wood density that decreases with decomposition as a result of C mineralization (Harmon et al., 1986) is recognized as a good and more objective indicator of decomposition than decay classes, and was easily measured in the laboratory.

Wood density of snags was estimated by Angers et al. (2012b). After drying and removal of the bark, the dry mass of each cross section was measured. The volume was estimated from upper and lower stem diameters and the average thickness of the section using a cylinder formula. As wood moisture in snags often fluctuates with environmental conditions and influences fresh volume (Boulanger & Sirois, 2006), wood density was calculated as the ratio of the cross-section dry mass to its dry volume (instead of fresh volume for logs).

Wood density of logs was estimated from two subsamples of each log section. The first subsample was weighed (wet mass) and coated in hot paraffin before its volume was measured by water displacement. The second subsample was weighed (wet mass) and oven-dried at 65 °C for moisture determination. The density was estimated from the first section after its fresh mass was corrected for moisture content (Brais & Drouin, 2012). This method gives somewhat lower values of wood density than the method used for snags (Kennedy, 1965).

2.3.4. Chemical analyses

All wood and forest floor samples were ground in a ball mill (Retsch MM200, Haan, Germany) to pass a 0.5 mm mesh screen for chemical analyses. Total C and N concentrations were determined by dry combustion (Rutherford et al., 2008) using a CNS 2000 analyzer (LECO Corporation, St. Joseph, Michigan).

Lignin, cellulose, and hemicellulose concentrations were determined on all samples by near-infrared spectroscopy (NIRS), following calibration between the spectral absorbance of a subset of samples and reference values obtained by proximate chemical analyses. Samples were scanned from 400 to 2498 nm in 2 nm intervals using a NIR spectrophotometer (model 6500, FOSS – NIRSystems). Data were analyzed with WinISI II chemometric software (ISI (Infrasoft International LLC), 1999). Acid- and neutral-detergent fibre (ADF and NDF) contents were determined on 100 samples (Kebli et al., 2011) using the method of Goering & Van Soest (1970). ADF lignin, which corresponded to the acid-unhydrolyzable residue ("AUR" fraction), was determined using the method of Brinkmann et al. (2002). A fraction containing mostly hemicelluloses was calculated as (NDF–ADF) and was referred to as "hemicelluloses$_{GV}$" (GV for the method of Goering and Van Soest), because it also includes products from microbial decomposition. Also, a fraction referred to as "cellulose$_{GV}$" was calculated as (ADF–AUR), and contained mainly cellulose and also products from microbial decomposition (Coûteaux et al., 1998; McTiernan et al., 2003). The "nonstructural" fraction (cell content) was calculated as (100–NDF) and contained mainly soluble compounds (soluble carbohydrates, starch, pectin, nonprotein N, soluble proteins, and lipids). The regression equations between spectral absorbance and reference values were developed by Kebli et al. (2011) using modified partial least-squares regression (Gillon et al., 1999) after pretreatment of the spectral data to eliminate noise (detrending and standard normal variate corrections).

Solid-state ^{13}C cross-polarization with magic angle spinning (CPMAS) nuclear magnetic resonance (NMR) analyses were carried out according to the procedure followed by Thiffault et al. (2008). We used a Bruker Avance 400 spectrometer (B_0 = 9.4 T, $\nu_L(^{13}C)$ = 100.6 MHz) with ramped cross-polarization (RAMP-CP). This technique is time-consuming and, therefore, on the 164 log samples, we selected a subset of 41 samples, which consisted mainly of fresh and well-decayed logs. We also included the six samples of lignic and alignic forest floors. Spectra were acquired with a ^1H 90° pulse length of 4 μs, a pulse delay of 5.0 s, a cross-polarization contact time of 1.0 ms, an acquisition time of 17.1 ms, and a spinning frequency of 13 kHz. A ramped ^1H pulse was used to circumvent spin modulation of Hartmann–Hahn conditions. Depending upon the sample, four or eight thousand scans were processed, using line broadening set at 200 Hz. Chemical shifts were reported relative to tetramethylsilane (TMS) at 0 ppm, with the reference frequency set using adamantane ($C_{10}H_{16}$). The Bruker WIN-NMR package estimated the relative integrated areas of the different spectral regions between 0 and 222 ppm, after correction for spinning sidebands.

The spectra that were acquired by CPMAS NMR were divided into seven chemical shift regions, according to the study of Knicker & Lüdemann (1995): (1) alkyl C (0–50 ppm) region from lipids, cutins, and amino acids; (2) methoxyl C (50–59 ppm), (3) *O*-alkyl C (59–94 ppm), and (4) di-*O*-alkyl C (94–109 ppm) regions from carbohydrates, amino acids, and methoxyl C of lignins (as *O*/*N*-alkyl C, which includes regions 2, 3, and 4); (5) aromatic C (109–142 ppm) and (6) phenolic C (142–166 ppm) regions from lignins, tannins, and olefins; and (7) carbonyl C (166–230 ppm) region from carboxylic acids, amides, esters, aldehydes, and ketones in lignins, proteins, lipids, carbohydrates, and tannins. Although there are limitations to the quantitative reliability of CPMAS spectra (Preston et al., 1990), it is appropriate to use NMR to compare intensity distributions and study structural features when samples do not differ widely in composition (Preston et al., 1997), as was the case for our study. To obtain further information on C structures, dipolar dephased (DD) spectra were generated for seven samples (one fresh log of each species, one lignic forest floor, and one alignic forest floor) by inserting a delay period of 40 μs without ^{1}H decoupling between the cross-polarization and acquisition portions of the CPMAS pulse sequence (Thiffault et al., 2008). All DD spectra were obtained using the TOSS sequence for total suppression of spinning sidebands (Lorenz et al., 2000).

2.3.5. Data analyses

Because of the different sampling methodologies used for snags and logs, data were analyzed separately but using similar statistical models. The effects of tree species and decay state on response variables were assessed by means of a linear mixed model and Wald's *t* test ($\alpha = 0.05$; Pinheiro & Bates, 2000) using the lme function included in the nlme library of R software (R Development Core Team, 2012). The fixed factors of our mixed models were wood density, tree species, their interaction, and the square of wood density. We chose wood density as an indicator of decay state in our mixed models rather than decay class or time-since- death. However, to facilitate comparisons with other studies, decay classes were also indicated in the tables and figures. The effects of tree species were tested by directed contrasts between deciduous and coniferous species (C1), between deciduous species (C2) and among coniferous species (C3 and C4; see Table 2.3 for snags and Table 2.4 for logs). The square of wood density was also included in the models when opposite changes in concentrations (an increase followed by a decrease or vice versa) or a plateau, such as that often occurring at the beginning of decomposition (Preston et al., 1998; Strukelj et al., 2012, Chapitre I), were expected. Interactions and the square of wood density were removed from the models when their *p* value was >0.10. Random factors were sampling plots for snags, sampling plots nested within stands, and stands nested within stand types for logs. Normality and homogeneity of variance assumptions were verified by visual assessment of residuals. When these assumptions were not met, logarithmic transformations were applied to achieve normality and homogeneity of variance.

To synthesize the multivariate information generated by NMR spectroscopy for logs and forest floor samples, all spectral NMR areas were analyzed using nonmetric multidimensional scaling (NMDS; Kruskal, 1964) with PC-ORD software (McCune et al., 2002). This ordination method is well-suited to non-normal or semiquantitative data, such as the integrated spectral NMR areas. In addition to the 47 NMR samples that were analyzed in this study, we included three samples in the ordination that were obtained from a previous study (Strukelj et al., 2012, Chapitre I), and which corresponded to the means of three samples of trembling aspen, balsam fir, and white spruce foliar litters that had decayed over a 5 to 6 year period. The Bray–Curtis index (also referred to as Sorensen distance) was used as our measure of dissimilarity. The variables (columns) that were included in the first matrix of 50 samples (rows) of NMR data were the seven integrated spectral areas (alkyl, methoxyl, *O*-alkyl, di-*O*-alkyl, aromatic, phenolic, and carbonyl), which we converted to proportions (by row) and applied arcsine square-root transformation prior to ordination to normalize data. The second matrix contained the NMR areas to map these vectors over the first matrix, as well as tree species, decay class, and litter (lignic forest floor, alignic forest floor, logs, and decayed foliage).

A multiresponse permutation procedure (MRPP) analysis (Biondini et al., 1988) with Bray–Curtis dissimilarity index was realized with PC-ORD software (McCune et al., 2002). The MRPP analysis was used in the ordination space to compare the chemical signatures of different groups of samples, that were defined by their species, their decay class, or their litter type, and to determine whether these groups were statistically different. After calculating the delta (δ) for given groups (i.e., the weighted mean within-group dissimilarity), MRPP estimated the p, T, and A values. The T-test statistic is the difference between the observed and expected δ divided by the square root of the variance in δ. The T value describes the separation between groups. The p value associated with T is determined by numerical integration of the Pearson distribution (McCune et al., 2002). The A value measures the within-group homogeneity compared to the random expectation.

Forty-one wood samples were analyzed by both NMR and NIR spectroscopy. To link results from the two methods, we computed the correlations between alkyl, methoxyl, *O*-alkyl, di-*O*-alkyl, aromatic, phenolic, and carbonyl integral areas versus concentrations of hemicelluloses$_{GV}$, cellulose$_{GV}$, AUR, and nonstructural compounds.

2.4. Results

2.4.1. Changes in concentrations of C and N with wood density

Wood density of snags ranged from 175 to 628 kg·m^{-3}, and for logs, from 79 to 469 kg·m^{-3} (Fig. 2.1). Despite a general decrease in wood density with snag and log decay classes, densities of adjacent decay classes overlapped for all species (Table 2.2), and large variations in wood density were observed within each decay class.

The C:N ratio of snags decreased significantly with decreasing wood density (Table 2.3 and Fig. 2.1) because of increases in N concentrations and stable C concentrations (Tables 2.2 and 2.3). The decrease in C:N ratio was significantly greater in trembling aspen snags compared with white birch snags. Nitrogen concentrations in jack pine snags were below the detection limit (0.2 mg·g^{-1}).

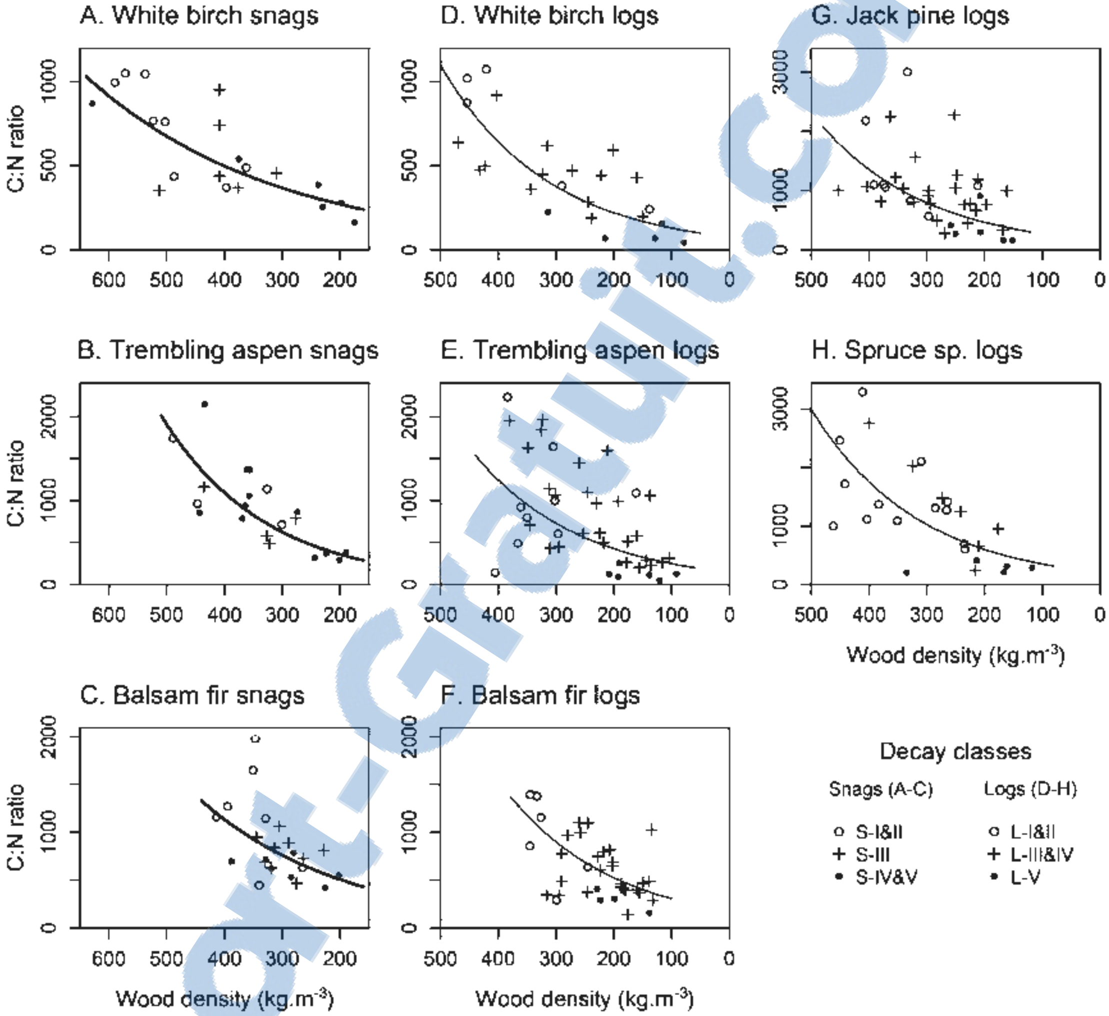

Fig. 2.1. Changes in C:N ratio with decreasing wood density in (A–C) snags and (D–H) logs of common boreal tree species.

Note: Data were transformed to their original scale. In jack pine snags, N concentrations were below the limit of detection in most samples, and C:N ratio is not presented.

Table 2.2. Changes in wood density (kg·m^{-3}), and changes in concentrations of carbon, nitrogen, acid-unhydrolyzable residue (AUR), cellulose$_{GV}$, hemicelluloses$_{GV}$ (Hcell$_{GV}$), and nonstructural compounds (NS cpds) (mg·g^{-1}) with decay classes in snags (n = 84) and logs (n = 164) of boreal tree species.

Species	Decay class	n	**Density**	**Carbon**	**Nitrogen**	**AUR**	**Cellulose$_{GV}$**	**Hcell$_{GV}$**	**NS cpds**
Snags									
White birch	S-I	3	502 ± 105	495 ± 1	0.76 ± 0.56	109 ± 13	564 ± 12	203 ± 22	124 ± 28
	S-II	5	493 ± 73	497 ± 3	0.79 ± 0.24	123 ± 21	543 ± 36	198 ± 18	136 ± 25
	S-III	6	404 ± 53	496 ± 4	1.02 ± 0.29	129 ± 20	539 ± 24	187 ± 16	146 ± 18
	S-IV&V[a]	6	307 ± 138	499 ± 3	1.60 ± 0.71	183 ± 30	475 ± 41	162 ± 17	180 ± 28
Trembling aspen	S-I	2	387 ± 118	490 ± 7	0.47 ± 0.08	130 ± 18	532 ± 23	190 ± 03	149 ± 43
	S-II	2	395 ± 184	492 ± 3	0.49 ± 0.40	125 ± 13	555 ± 20	201 ± 27	120 ± 34
	S-III	4	340 ± 66	498 ± 9	0.73 ± 0.25	130 ± 01	517 ± 24	185 ± 07	169 ± 25
	S-IV&V[a]	12	318 ± 50	495 ± 3	0.81 ± 0.30	154 ± 21	508 ± 33	185 ± 11	153 ± 23
Balsam fir	S-I	2	373 ± 44	507 ± 8	0.35 ± 0.08	321 ± 04	415 ± 35	121 ± 01	144 ± 32
	S-II	5	339 ± 47	502 ± 2	0.61 ± 0.30	313 ± 05	427 ± 08	122 ± 07	138 ± 14
	S-III	9	297 ± 24	502 ± 3	0.68 ± 0.12	303 ± 07	431 ± 09	121 ± 04	145 ± 05
	S-IV&V[a]	7	290 ± 47	500 ± 2	0.84 ± 0.14	296 ± 08	428 ± 06	120 ± 08	156 ± 14
Jack pine	S-I	8	479 ± 26	514 ± 3	<0.2[b]	320 ± 08	415 ± 19	137 ± 11	129 ± 17
	S-II	9	453 ± 30	514 ± 5	<0.2[b]	330 ± 12	395 ± 26	133 ± 08	142 ± 16
	S-III	2	385 ± 185	518 ± 2	<0.2[b]	351 ± 12	345 ± 03	123 ± 09	182 ± 18
	S-IV&V[a]	2	347 ± 74	514 ± 23	0.24 ± 0.33	335 ± 61	369 ± 124	121 ±28	176 ±92

Table 2.2. (suite)

Species	Decay class	n	**Density**	**Carbon**	**Nitrogen**	**AUR**	**Cellulose$_{GV}$**	**Hcell$_{GV}$**	**NS cpds**
Logs									
White birch	L-I&II[a]	5	351 ± 120	498 ± 2	0.98 ± 0.58	142 ± 39	537 ± 52	185 ± 22	137 ± 34
	L-III	10	303 ± 64	505 ± 10	1.12 ± 0.35	179 ± 34	478 ± 56	177 ± 13	166 ± 29
	L-IV	4	293 ± 120	508 ± 11	1.73 ± 0.64	204 ± 41	454 ± 55	157 ±16	186 ± 21
	L-V	5	171 ± 83	501 ± 11	6.32 ± 3.18	302 ± 70	310 ± 106	101 ± 39	286 ± 75
Trembling aspen	L-I&II[a]	9	326 ± 47	489 ± 5	0.87 ± 0.64	129 ± 17	550 ± 20	188 ± 13	132 ± 23
	L-III	18	244 ± 39	499 ± 4	0.71 ± 0.23	156 ± 19	517 ± 26	181 ± 10	146 ± 14
	L-IV	8	211 ± 48	493 ± 5	1.36 ± 0.56	172 ± 20	495 ± 30	170 ± 16	164 ± 22
	L-V	6	157 ± 38	498 ± 12	4.95 ± 2.12	239 ± 26	366 ± 51	130 ± 28	265 ± 44
Balsam fir	L-I&II[a]	6	316 ± 31	501 ± 8	0.73 ± 0.44	298 ± 28	442 ± 28	115 ± 06	146 ± 19
	L-III	11	223 ± 28	511 ± 9	0.93 ± 0.24	333 ± 26	383 ± 52	115 ± 13	170 ± 35
	L-IV	15	207 ± 30	512 ± 9	1.18 ± 0.36	338 ± 21	383 ± 37	111 ± 09	168 ± 20
	L-V	4	197 ± 41	502 ± 8	1.93 ± 0.86	302 ± 27	410 ± 36	96 ± 11	192 ± 39
Jack pine	L-I&II[a]	8	339 ± 44	515 ± 7	0.49 ± 0.15	325 ± 08	420 ± 15	127 ± 07	128 ± 11
	L-III	12	289 ± 45	532 ± 11	0.65 ± 0.26	366 ± 30	331 ± 59	116 ± 15	187 ± 33
	L-IV	12	275 ± 40	530 ± 11	0.68 ± 0.19	354 ± 38	344 ± 43	113 ± 15	189 ± 22
	L-V	6	207 ± 34	533 ± 18	2.07 ± 0.86	393 ± 47	257 ± 91	99 ± 19	251 ± 52
Spruce sp.	L-I&II[a]	13	346 ± 46	503 ± 2	0.42 ± 0.10	297 ± 09	449 ± 16	132 ± 08	123 ± 18
	L-III	5	283 ± 74	501 ± 5	0.32 ± 0.11	283 ± 09	474 ± 18	130 ± 13	113 ± 27
	L-IV	2	213 ± 6	527 ± 2	1.50 ± 1.37	334 ± 33	364 ± 103	92 ± 25	211 ± 95
	L-V	5	199 ± 73	519 ± 21	1.98 ± 0.49	360 ± 53	327 ± 85	104 ± 18	209 ± 26

Note: Mean values ± confidence intervals. GV, determined using method of Goering and Van Soest.

[a] Snags samples from decay class S-IV and S-V were grouped in a single class because samples from decay class S-V were rare for all tree species. Similarly, logs of decay class L-I and L-II were grouped because of the scarcity of decay class L-I for all species.

[b] Below the detection limit (0.2 $mg \cdot g^{-1}$).

Table 2.3. Effects of tree species (white birch, trembling aspen, jack pine and balsam fir) on the chemical composition of decaying snags assessed by means of mixed linear models.

Fixed factors	**Carbon**		**Nitrogen**[a]		**C:N**[a, b]		**Cellulose**$_{\text{GV}}$	
	E	*p*	*E*	*p*	*E*	*p*	*E*	*p*
(Intercept)	502.2	<0.001	2.12	<0.001	5.07	<0.001	310.9	<0.001
Density	-0.8	0.919	-3.64	<0.001	4.20	<0.001	637.5	0.013
(Density)^2							-574.0	0.092
C1 (dec. vs con.)	-0.5	0.879	0.16	<0.001	-0.18	0.232	3.6	0.834
C2 (birch vs aspen)	0.02	0.995	0.31	<0.001	0.11	0.573	-2.9	0.877
C3 (pine vs fir)	8.0	0.130					-68.2	0.032
Density * C1	-16.0	0.058			0.10	0.835	152.3	0.001
Density * C2	4.2	0.630			-1.26	0.023	-11.3	0.828
Density * C3	-6.8	0.627					127.0	0.132

Fixed factors	**Hemicelluloses**$_{\text{GV}}$		**AUR**		**NS compounds**	
	E	*p*	*E*	*p*	*E*	*p*
(Intercept)	109.4	<0.001	345.0	<0.001	234.1	<0.001
Density	123.9	<0.001	-540.3	<0.001	-227.6	<0.001
(Density)^2			606.5	0.005		
C1 (dec. vs con.)	29.8	<0.001	-33.1	0.003	2.8	0.292
C2 (birch vs aspen)	-5.8	0.009	13.2	0.247	7.1	0.088
C3 (pine vs fir)	-2.8	0.228	59.1	0.004	14.5	0.002
Density * C1			-160.0	<0.001		
Density * C2			-22.8	0.470		
Density * C3			-139.7	0.010		

Note: Wood density is used as an index of decay state. The first contrast (C1) is positive when the parameter is higher for deciduous (dec.) than for coniferous (con.) species; the second contrast (C2) is positive when the parameter is higher for birch than for aspen; and the third contrast (C3) is positive when the parameter is higher for pine than for fir. AUR, acid-unhydrolyzable residue; GV, determined using method of Goering and Van Soest; NS, nonstructural.

[a] The contrast C3 was not calculated, because N concentrations in most jack pine snags were below detection limits.

[b] Logarithmic transformation was applied.

In logs, C concentrations increased significantly with decreasing density, from 492 to 502 mg·g^{-1} in deciduous species, from 523 to 531 mg·g^{-1} in jack pine, and from 503 to 511 mg·g^{-1} in spruce spp. and balsam fir (Tables 2.2 and 2.4). Nitrogen concentrations in logs also significantly increased with decreasing wood density (Tables 2.2 and 2.4), but remained higher in deciduous logs than in coniferous logs throughout decomposition, and higher in white birch than in trembling aspen.

In logs, C:N ratios decreased significantly with decreasing wood density (Table 2.4 and Fig. 2.1). The C:N ratios of deciduous logs remained lower than those of coniferous logs as density decreased, and were lower for white birch than for trembling aspen. The variability in log C:N ratios that was observed both within species and among species decreased with wood density (Fig. 2.1). In logs from decay class L-V, C:N ratios attained values of around 100 in deciduous species and 300 in coniferous species. Lignic forest floor C:N ratios ranged from 30 to 47 (mean = 38), whereas alignic forest floor C:N ratios ranged from 16 to 24 (mean = 21).

2.4.2. Changes in concentrations of carbohydrates, AUR, and nonstructural compounds

In snags, cellulose$_{\mathrm{GV}}$ concentrations decreased significantly with decreasing wood density (Tables 2.2 and 2.3 and Figs. 2.2A–2.2D), but this decrease was limited mainly to deciduous snags (Figs. 2.2A–2.2D); at low wood density, the cellulose$_{\mathrm{GV}}$ concentrations of deciduous snags reached values similar to those of coniferous species (Table 2.3). The decrease in concentrations of hemicelluloses$_{\mathrm{GV}}$ with wood density was similar among tree species (Table 2.3 and Figs. 2.2A–2.2D).

Table 2.4. Effects of tree species (white birch, trembling aspen, jack pine, balsam fir and spruce spp.) on the chemical composition of decaying logs assessed by means of mixed linear models.

Fixed factors	**Carbon**		**Nitrogen**[a]		**C:N**[a]		**Cellulose$_{GV}$**	
	E	*p*	*E*	*p*	*E*	*p*	*E*	*p*
(Intercept)	514	<0.001	1.27	<0.001	4.98	<0.001	219	<0.001
Density	-28	0.030	-5.46	<0.001	5.38	<0.001	1252	0.003
(Density)^2							-1511	0.045
C1 (dec. vs con.)	-3	<0.001	0.10	<0.001	-0.11	<0.001	4	0.584
C2 (birch vs aspen)	4	0.070	0.34	<0.001	-0.32	<0.001	-48	0.071
C3 (pine vs spruce/fir)	7	<0.001	0.08	0.138	-0.07	0.178	-35	0.071
C4 (spruce vs fir)	1	0.623	-0.06	0.477	0.06	0.495	-34	0.325
Density * C1							58	0.034
Density * C2							72	0.450
Density * C3							-4	0.954
Density * C4							145	0.270

Fixed factors	**Hemicelluloses$_{GV}$**		**AUR**		**NS compounds**	
	E	*p*	*E*	*p*	*E*	*p*
(Intercept)	77	<0.001	398	<0.001	305	<0.001
Density	363	0.005	-787	0.002	-822	0.002
(Density)^2	-470	0.041	995	0.029	980	0.043
C1 (dec. vs con.)	1	0.776	-15	0.002	10	0.039
C2 (birch vs aspen)	-19	0.017	38	0.017	29	0.090
C3 (pine vs spruce/fir)	6	0.281	15	0.209	15	0.241
C4 (spruce vs fir)	-18	0.089	12	0.554	40	0.073
Density * C1	36	<0.001	-58	<0.001	-36	0.037
Density * C2	44	0.135	-61	0.288	-54	0.372
Density * C3	-32	0.125	21	0.618	14	0.745
Density * C4	78	0.052	-61	0.440	-163	0.055

Note: Wood density is used as an index of decay state. The first contrast (C1) is positive when the parameter is higher for deciduous (dec.) than for coniferous (con.) species; the second contrast (C2) is positive when the parameter is higher for birch than for aspen; the third contrast (C3) is positive when the parameter is higher for pine than for spruce/fir; and the fourth contrast (C4) is positive when the parameter is higher for spruce than for fir. AUR, acid-unhydrolyzable residue; GV, determined using method of Goering and Van Soest; NS, nonstructural.

[a] Logarithmic transformation was applied.

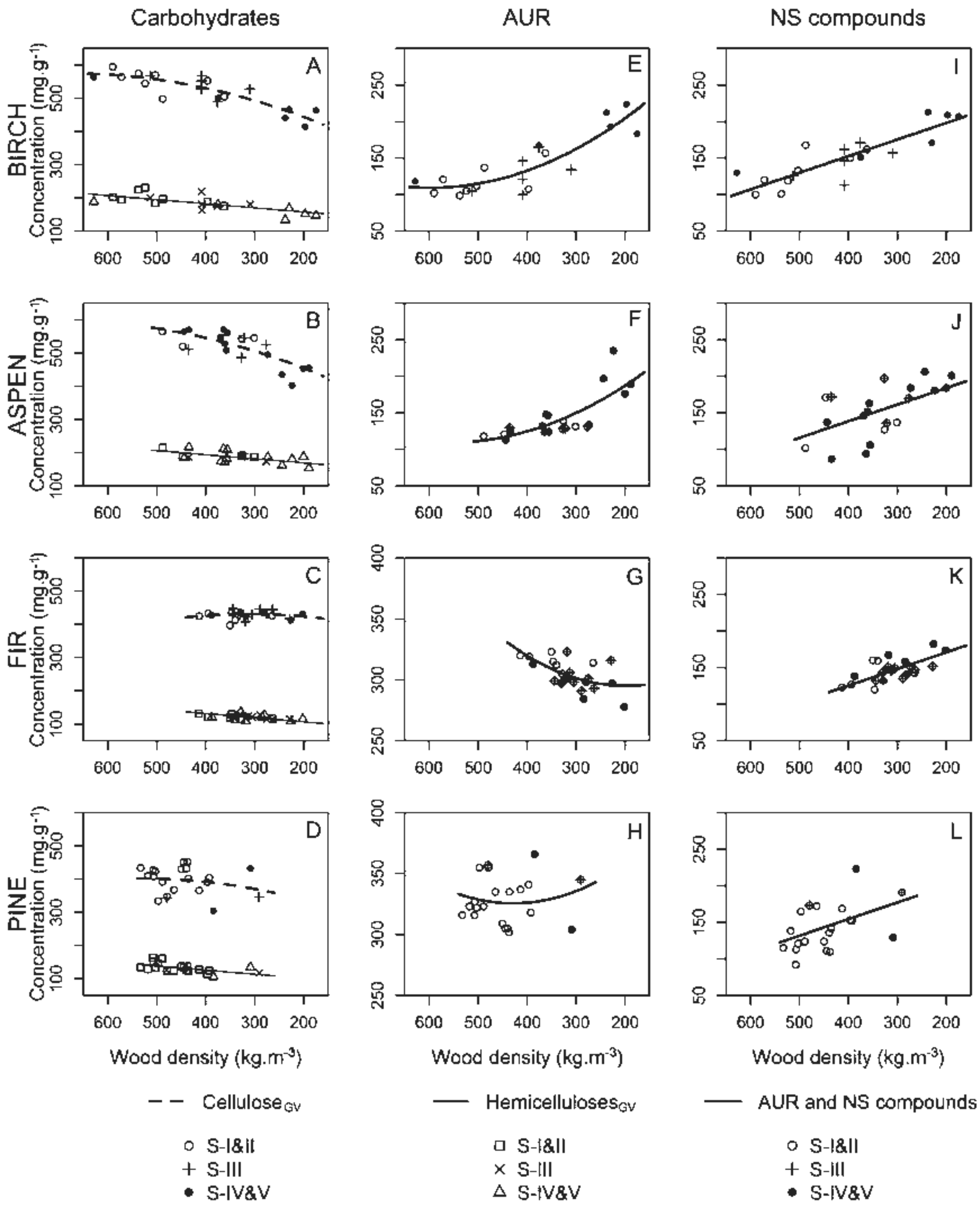

Fig. 2.2. Changes in concentrations (mg·g^{-1}) of cellulose$_{GV}$, hemicelluloses$_{GV}$, acid-unhydrolyzable residue (AUR) and nonstructural (NS) organic compound fractions with wood density in snags of four common boreal tree species.

In deciduous snags, changes in AUR concentrations with decreasing wood density were characterized by an initial stable phase until wood density reached ~350 kg·m^{-3} and then an increase to 200 mg·g^{-1} (Table 2.3 and Figs. 2.2E–2.2H). Concentrations of AUR in deciduous snags remained significantly lower than in coniferous species, where concentrations remained almost stable throughout decomposition. Concentrations of nonstructural compounds in snags increased with decreasing density in a similar manner for all species (Table 2.3 and Figs. 2.2I–2.2L).

For logs, the relationships between concentrations of carbohydrates (hemicelluloses$_{GV}$ or cellulose$_{GV}$) and squared wood density were significant (Table 2.4), indicating a first phase characterized by little change, followed by a second phase characterized by a decrease in concentrations with decreasing wood density (Figs. 2.3A–2.3E). In jack pine and spruce spp. logs, a slight increase in cellulose$_{GV}$ concentrations was observed at the beginning of the first phase of decay (Figs. 2.3A–2.3E). The transition between the first and second phases occurred when wood density reached 300–350 kg·m^{-3} in deciduous logs and 200–250 kg·m^{-3} in coniferous logs (Figs. 2.3A–2.3E). Decreases in cellulose$_{GV}$ and hemicelluloses$_{GV}$ concentrations were significantly more pronounced in deciduous than in coniferous logs, where hemicelluloses$_{GV}$ concentrations remained stable (Table 2.4 and Figs. 2.3A–2.3E). At low wood density, deciduous and coniferous logs reached similar concentrations of cellulose$_{GV}$ and hemicelluloses$_{GV}$, but hemicelluloses$_{GV}$ concentrations were lower for white birch than for trembling aspen.

In logs, concentrations of AUR remained stable during a first phase of decomposition and increased thereafter with decreasing wood density (Table 2.4 and Figs. 2.3F–2.3J). The turning point was observed at wood densities that were similar to those observed for cellulose$_{GV}$ concentrations, i.e., 300–350 kg·m^{-3} in deciduous logs and 200–250 kg·m^{-3} in coniferous logs. The increase in AUR concentrations with decreasing wood density was more pronounced for deciduous than coniferous logs (Table 2.4 and Figs. 2.3F–2.3J). In jack pine and spruce spp. logs, a slight decrease in AUR was observed at the beginning of the decomposition. The AUR fraction reached significantly higher concentrations in coniferous logs than in deciduous logs, and higher concentrations in white birch than in trembling aspen (Table 2.4). Concentrations of nonstructural compounds in logs increased with decreasing wood density in all species (Figs. 2.3K–2.3O). This increase was more pronounced for deciduous logs than for coniferous logs, and more pronounced for spruce spp. than for jack pine and balsam fir (Table 2.4). At low wood density, concentrations were higher for deciduous logs than for coniferous logs.

2.4.3. Nuclear magnetic resonance spectra

All signals in the CPMAS ^{13}C NMR spectra were assigned to the dominant forms of C according to previous NMR studies conducted on wood and lignin (Preston et al., 1990; de Montigny et al., 1993; Preston et al., 1998). All spectra for fresh logs (see Fig. 2.4A for selected spectra and Table 2.5) were dominated by the *O*/*N*-alkyl region (50–109 ppm), resulting mainly from the presence of cellulose and hemicelluloses. This region was higher for deciduous than for coniferous fresh logs (Figs. 2.4A and 2.5). Signals of carbohydrates included a main peak of high intensity with a shoulder at 73 and 75 ppm (C-2, C-3, and C-5 of cellulose), another peak with a shoulder at 63 and 65 ppm (C-6 of cellulose), other peaks at 83 and 89 ppm (C-4 of cellulose), and 105 ppm (C-1 of cellulose). Lignins also contributed to resonance in the *O*/*N*-alkyl region: the C-2 and C-6 of syringyl units of deciduous species likely contributed to the peak at 105 ppm, lignin side chains resonated at 73 ppm, and the methoxyl group of lignins resonated at 56 ppm. Also, the nonprotonated C-4a and C-8 of tannins resonated at 105–108 ppm (de Montigny et al., 1993; Lorenz et al., 2000).

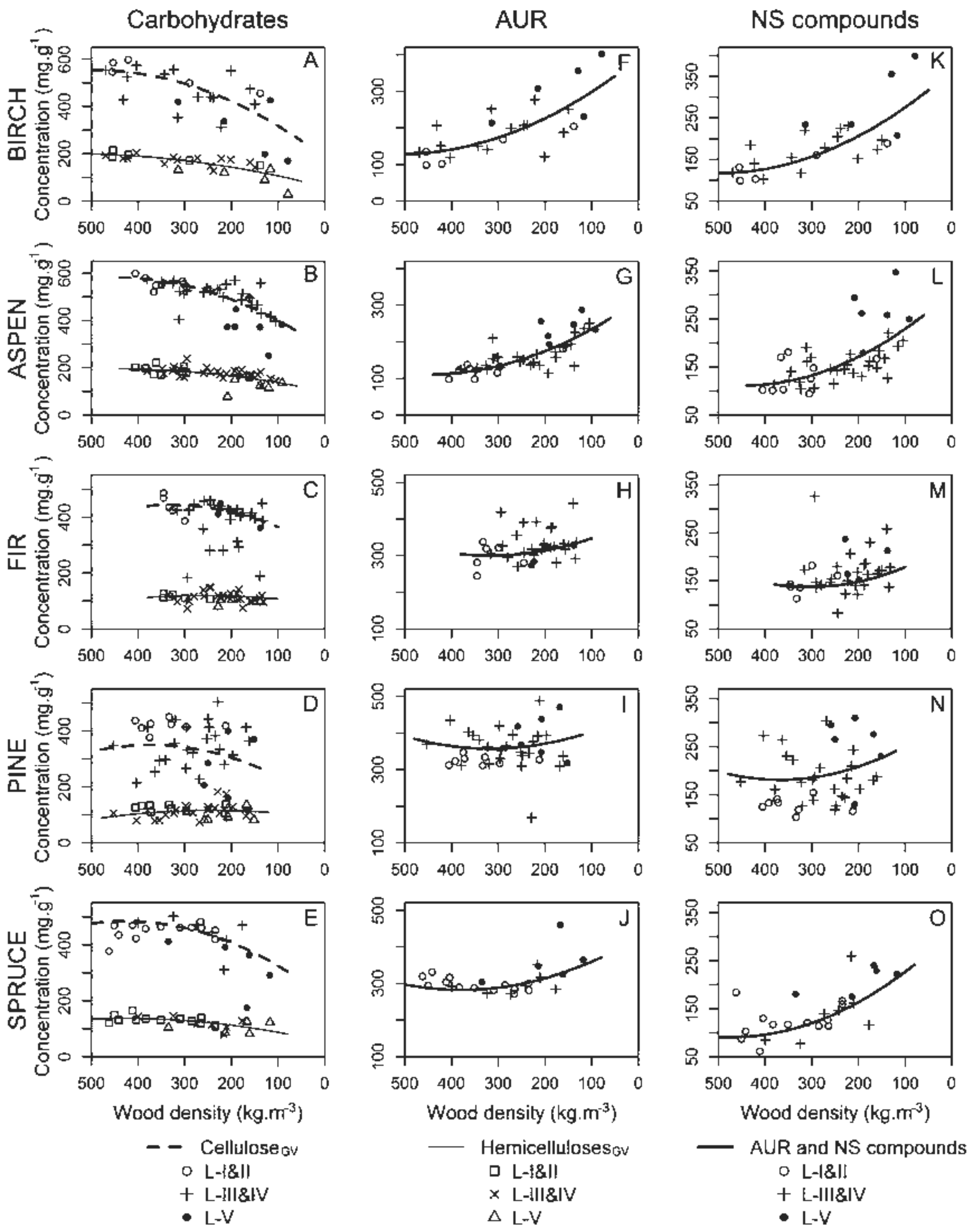

Fig. 2.3. Changes in concentrations (mg·g^{-1}) of cellulose$_{GV}$, hemicelluloses$_{GV}$, acid-unhydrolyzable residue (AUR) and nonstructural (NS) organic compound fractions with wood density in logs of five common boreal species.

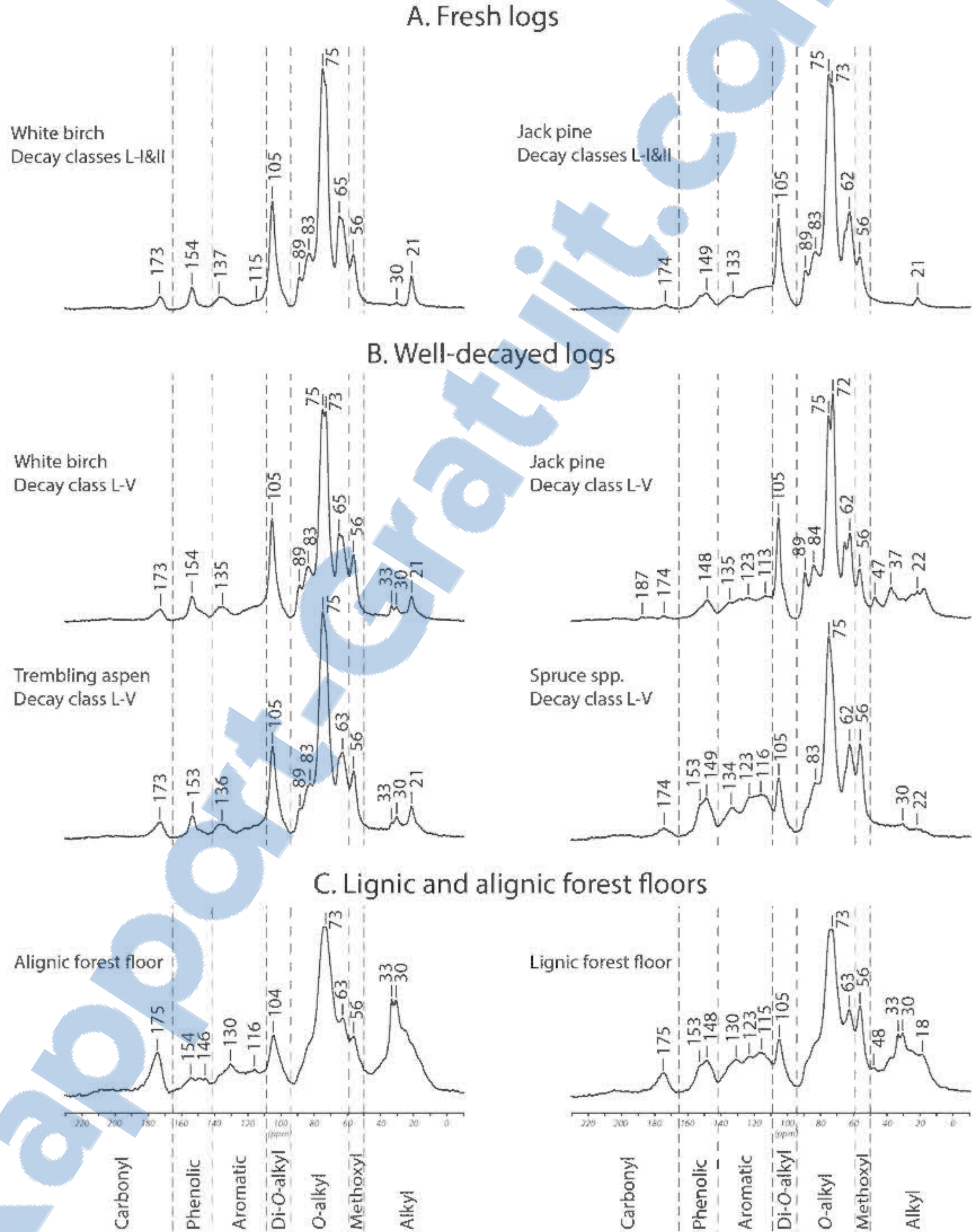

Fig. 2.4. Cross-polarization magic angle spinning (CPMAS) ^{13}C NMR spectra of (A) white birch and jack pine fresh logs, (B) well-decayed logs of white birch, trembling aspen, jack pine and spruce spp., and (C) lignic and alignic forest floors from boreal mixedwood stands.

Table 2.5. Integration values of the major C-types (% of total area) in the ^{13}C NMR spectra of decaying logs and forest floor.

Litter type	Decay class	**Alkyl (0-50 ppm)**	**Methoxyl (50-59 ppm)**	**O-alkyl (59-94 ppm)**	**Di-O-alkyl (94-109 ppm)**	**Aromatic (109-142 ppm)**	**Phenolic (142-166 ppm)**	**Carbonyl (166-230 ppm)**
Logs								
White birch	L-I&II	6.76 (0.49)	6.60 (0.09)	61.49 (1.78)	13.43 (0.36)	5.89 (1.02)	2.97 (0.49)	2.83 (0.22)
	L-V	8.92 (0.80)	6.88 (0.84)	55.39 (2.72)	11.89 (0.59)	8.94 (0.88)	4.21 (0.49)	3.78 (0.65)
Trembling aspen	L-I&II	7.10 (0.95)	6.62 (0.33)	62.40 (0.71)	13.21 (0.13)	5.74 (0.79)	2.48 (0.42)	2.45 (0.64)
	L-III&IV	7.34 (0.29)	6.37 (1.01)	61.85 (3.44)	13.08 (0.39)	5.74 (1.16)	2.70 (0.93)	2.92 (0.60)
	L-V	10.93 (0.59)	7.13 (0.59)	54.67 (1.48)	11.50 (0.12)	7.84 (0.65)	3.60 (0.51)	4.33 (0.14)
Balsam fir	L-I&II	5.54 (0.74)	6.70 (0.42)	60.29 (1.90)	10.51 (0.50)	10.82 (1.05)	4.23 (0.57)	1.92 (0.07)
	L-III&IV	6.04 (1.07)	6.87 (0.64)	58.37 (1.71)	10.12 (0.51)	11.65 (0.79)	4.62 (0.23)	2.34 (0.28)
	L-V	6.46 (1.43)	6.82 (0.47)	57.77 (3.34)	10.11 (0.81)	11.73 (1.27)	4.59 (0.70)	2.52 (0.68)
Jack pine	L-I&II	7.01 (1.10)	6.35 (0.19)	59.59 (1.13)	10.46 (0.08)	10.96 (0.22)	3.91 (0.15)	1.72 (0.22)
	L-V	14.54 (5.55)	7.00 (2.14)	45.71 (8.56)	7.72 (1.98)	15.60 (5.32)	6.16 (2.46)	3.28 (0.83)
Spruce spp.	L-I&II	5.99 (0.67)	6.55 (0.17)	59.44 (2.43)	10.35 (0.54)	11.21 (1.38)	4.36 (0.71)	2.09 (0.22)
	L-III&IV	6.84 (2.28)	6.97 (1.22)	56.29 (5.82)	9.64 (1.42)	12.96 (2.72)	4.96 (0.82)	2.33 (0.35)
	L-V	8.26 (2.16)	8.55 (1.35)	47.22 (7.94)	7.48 (1.72)	18.01 (3.76)	7.25 (1.69)	3.24 (0.86)
Forest floor								
Lignic forest floor		19.50 (2.86)	7.79 (0.47)	37.41 (0.87)	7.01 (0.85)	15.99 (1.42)	6.56 (0.40)	5.76 (0.34)
Alignic forest floor		26.90 (4.16)	5.61 (0.53)	36.73 (1.81)	7.44 (0.50)	10.86 (1.20)	4.49 (0.46)	7.98 (0.59)

Note: Mean values and standard deviations (in parentheses).

Aromatic and phenolic regions (109–166 ppm) formed the second largest region of the spectra (Fig. 2.4A), and indicated the presence of lignins, tannins, and other phenolic compounds. These regions were more prominent for coniferous than for deciduous fresh logs. Peaks characteristic of lignin guaiacyl units (113, 122, 134, 149, and 152 ppm) were present in coniferous spectra, whereas peaks characteristic of lignin syringyl units (136 and 154 ppm) were present in deciduous spectra (Preston et al., 2000). The characteristic split peaks of tannins at 144 and 154 ppm (Lorenz et al., 2000) were absent from spectra of all logs that were analyzed. In DD spectra (not shown), a prominent peak at 56 ppm and a small one at 105 ppm confirmed the predominance of lignins over condensed tannins (Lorenz et al., 2000).

The alkyl (0–50 ppm) and carbonyl (166–230 ppm) regions were low for all species of fresh logs, and were greater for deciduous than for coniferous logs. The alkyl region was dominated by a single peak at 21 ppm, characteristic of hemicellulose acetates (Fig. 2.4A).

In spectra of well-decayed deciduous logs, peaks at 30 and 33 ppm increased compared with fresh logs, peaks at 154 ppm and 136 ppm became larger and less defined, but few changes appeared in the *O*-alkyl region (Fig. 2.4B). Decay of spruce logs was accompanied by an increase in the signals of aromatic C, phenolic C, and methoxyl C, whereas spectra of well-decayed pine were characterized by a strong increase in the signals of alkyl C. Well-decayed logs of fir remained similar to fresh ones (Fig. 2.4B).

Compared with well-decayed logs, lignic forest floor spectra (Fig. 2.4C) exhibited stronger signals at 56, 115, 123, 130, 148, and 153 ppm, which corresponded to guaiacyl units of lignin, and also stronger signals at 30, 33, and 175 ppm, resulting from alkyl and carbonyl C compounds. Smaller peaks at 73 ppm, and shoulders at 83 and 89 ppm, likely resulted from lignins and the remaining carbohydrates. In DD spectra (not shown), a weak signal at 105 ppm suggested little condensed tannins. Alignic forest floor spectra (Fig. 2.4C) also had remaining peaks characteristic of cellulose and hemicelluloses, a high signal intensity in the alkyl and carbonyl region, and an aromatic region with large signals suggesting mixing between lignins and tannins, confirmed by the presence of the 105 ppm peak on the DD spectra (not shown).

Ordination summarized chemical signatures for a range of log species and decay states, as well as decayed foliage and forest floors of lignic and alignic origins according to the seven integrated spectral NMR areas (Fig. 2.5). A first MRPP analysis compared chemical signatures of fresh conifers and determined that fresh balsam fir, spruce spp., and jack pine logs were similar in composition (MRPP test, $p = 0.525$). Also, fresh trembling aspen and white birch logs formed a single group (MRPP test, $p = 0.379$) that was distinct from that formed by coniferous logs (Table 2.6a) and which had lower proportions of aromatic and phenolic C and higher proportions of *O*-alkyl and di-*O*alkyl C. Only small changes appeared between fresh and moderately decayed logs (Fig. 2.5). In well-decayed logs of all species, proportions of alkyl C, carbonyl C, and aromatic and phenolic C were higher than in the fresher classes, whereas proportions of *O*-alkyl C and di-*O*-alkyl C were lower (Fig. 2.5).

The *T* value of the MRPP analysis is an indication of the separation between groups with larger negative values for larger distances. Comparing fresh and well-decayed logs, the *T* value was larger for deciduous species than for coniferous species (Table 2.6b), indicating greater chemical changes during the decay of deciduous species. The distance between deciduous and coniferous species narrowed in well-decayed logs (Fig. 2.5), as indicated by the decrease in the *T* value from –9.43 to –5.03 (Table 2.6a), but deciduous and coniferous logs maintained distinct chemical compositions (Table 2.6a), which mainly arose from differences in aromatic and phenolic C.

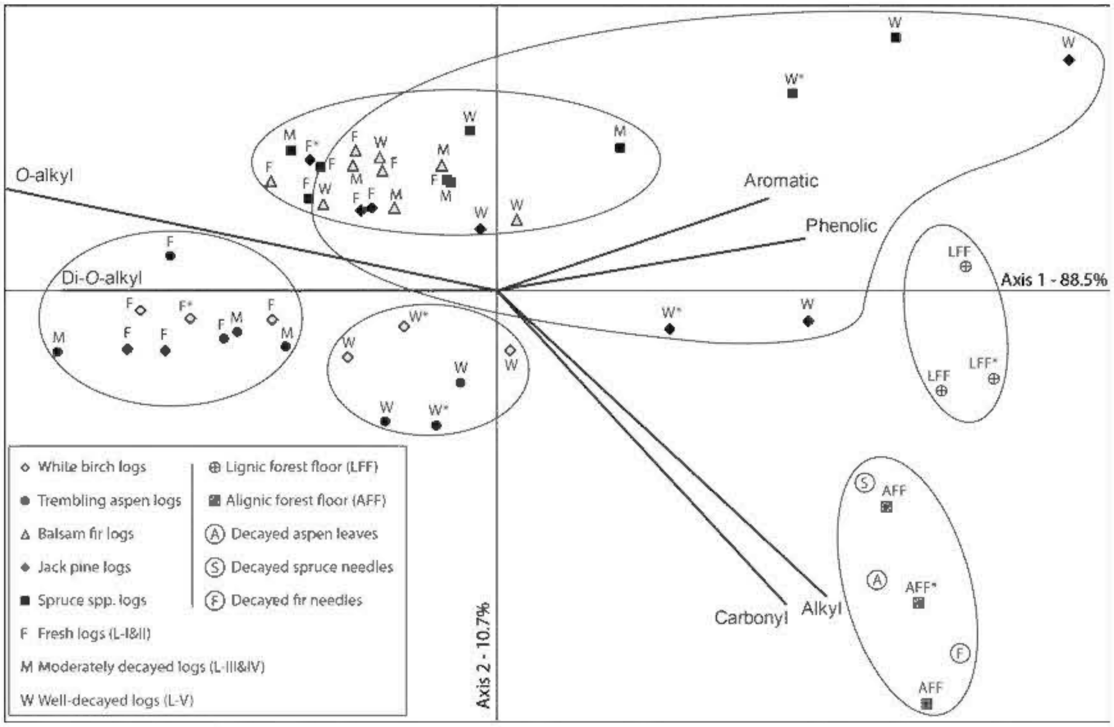

Fig. 2.5. Nonmetric multidimensional scaling (NMDS) ordination of ^{13}C NMR integral areas for logs of white birch, trembling aspen, balsam fir, jack pine and spruce spp.

Note: Letters (F, M, W) above the symbols (◇, ●, △, ◆, ■) indicate decay state of each species. The spectral NMR areas are the following: alkyl (0-50 ppm), methoxyl (50-59 ppm), *O*-alkyl (59-94 ppm), di-*O*-alkyl (94-109 ppm), aromatic (109-142 ppm), phenolic (142-166 ppm) and carbonyl (166-230 ppm) regions. Grouping based upon multiresponse permutation procedure (MRPP) analysis is highlighted with circles. Cutoff for correlation vectors was set at $r^2 = 0.5$. NMDS produced a two-dimensional solution with a stress of 4.32, which was achieved after 78 iterations.

Table 2.6. Distances in the nonmetric multidimensional scaling (NMDS) ordination space among logs of five boreal species of different decay states, obtained by multiresponse permutation procedure (MRPP) analysis with the Bray-Curtis dissimilarity.

Distance type	*T*	*A*	*p*
(a) Distances between coniferous and deciduous species			
In fresh logs (L-I&II)	-9.43	0.450	<0.001
In well-decayed logs (L-V)	-5.03	0.189	0.001
(b) Distances between fresh and well-decayed logs			
For deciduous species	-7.06	0.425	<0.001
For coniferous species	-5.45	0.210	0.001
(c) Distances between lignic forest floor and:			
Fresh deciduous logs	-5.87	0.742	<0.001
Fresh coniferous logs	-7.18	0.683	<0.001
Well-decayed deciduous logs	-5.11	0.625	0.001
Well-decayed coniferous logs	-3.09	0.191	0.012
(d) Distances between alignic forest floor and:			
Well-decayed deciduous logs	-5.12	0.628	0.001
Well-decayed coniferous logs	-4.94	0.285	0.001
Decayed foliage	0.01	-0.001	0.415
Lignic forest floor	-2.75	0.389	0.023

Note: *T*, separation among groups: the more negative is the *T* value, the stronger is the separation. *A*, within group heterogeneity: when all items are identical within groups, then $A = 1$; if heterogeneity within groups equals expectation by chance, then $A = 0$; if there is more heterogeneity within groups than expected by chance, then $A < 0$. *p*, significance of the separation.

With ongoing decomposition, the chemical composition of logs became more similar to that of lignic forest floor (Table 2.6*c*), as shown by the decrease of the *T* value from fresh to well-decayed logs. Particularly well-decayed coniferous logs closely resembled lignic forest floor, but remained distinct in their composition (Table 2.6c). Decomposition of coniferous logs resulted in a large variation of their chemical compositions, whereas the three samples of lignic forest floor spectra were closely clustered (Fig. 2.5).

Lignic and alignic forest floors had distinct chemical compositions (Table 2.6d), with lower alkyl C and higher aromatic and phenolic C compounds in the lignic forest floor (Fig. 2.5). Chemical composition of trembling aspen, balsam fir, and white spruce foliage, after 5–6 years of decomposition, did not significantly differ from samples of alignic forest floor (Table 2.6d). Well-decayed coniferous logs remained separate from alignic forest floor compared with lignic forest floor (Table 2.6d), but this was less the case for deciduous logs.

2.4.4. Correspondence between NIR and NMR analyses

The AUR fraction obtained by NIR was positively correlated with the aromatic and phenolic regions of NMR (Table 2.7), and negatively correlated with the di-*O*-alkyl and *O*-alkyl regions. The opposite trend was observed for the cellulose$_{GV}$ fraction. The hemicelluloses$_{GV}$ fraction did not have any strong correlation with NMR areas, but was lightly positively correlated with the di-*O*-alkyl region (Table 2.7). The nonstructural fraction was positively correlated with the alkyl and carbonyl regions of the spectra.

Table 2.7. Pearson correlations (r ± confidence intervals) between variables from near-infrared (NIR) spectroscopy (columns) and variables from NMR spectroscopy (rows) based on 41 samples.

	Cellulose$_{GV}$	**Hemicelluloses$_{GV}$**	**AUR**	**NS compounds**
Alkyl	**-0.715 ± 0.158**	-0.246 ± 0.224	0.390 ± 0.265	**0.810 ± 0.113**
Methoxyl	-0.470 ± 0.245	-0.040 ± 0.307	0.368 ± 0.269	0.291 ± 0.284
O-alkyl	**0.938 ± 0.040**	0.400 ± 0.262	**-0.743 ± 0.145**	**-0.754 ± 0.140**
Di-*O*-alkyl	**0.883 ± 0.073**	0.659 ± 0.182	**-0.949 ± 0.033**	-0.491 ± 0.239
Aromatic	**-0.833 ± 0.101**	-0.573 ± 0.213	**0.909 ± 0.058**	0.413 ± 0.259
Phenolic	**-0.828 ± 0.103**	-0.464 ± 0.246	**0.835 ± 0.100**	0.456 ± 0.249
Carbonyl	-0.431 ± 0.255	0.014 ± 0.308	0.033 ± 0.307	**0.703 ± 0.163**

Note: We considered $r > 0.7$ as indicative of strong correlation. AUR, acid-unhydrolyzable residue; GV, determined using method of Goering and Van Soest; NS, nonstructural.

2.5. Discussion

2.5.1. Differences in patterns of decomposition among tree species

The main objective of the study was to assess the effects of common mixed boreal species on the decomposition patterns of snags and logs. For all studied species, changes in chemical composition with decreasing wood density were characterized by two distinct phases. During the first phase, concentrations of all organic fractions remained more or less stable, as would be the case if all organic compounds were being degraded simultaneously; during the second phase, preferential degradation of cellulose and hemicelluloses resulted in increases in lignins and alkyl C and carbonyl C compounds, affirming our first hypothesis. This pattern has been observed for coniferous species (Preston et al., 1998) and also for Japanese beech (*Fagus crenata* Blume; Fukasawa et al., 2009), and is generally explained by the action of white rot fungi during the first phase followed by brown and soft rot fungi during the second phase (Kirk & Farrell, 1987; Preston et al., 1998). However, the succession could be more complex, as white, brown, and soft rot fungi have all been detected in fresh and well-decayed CWD collected from our stands (Kebli et al., 2011; Kebli et al., 2012). A third phase with few changes in composition in well-decayed wood has also been described (Preston et al., 1990), but such a phase was not reached in our study as the chemical composition of well-decayed logs remained highly variable, i.e., unstable.

For deciduous species, the second phase of decomposition was attained at higher wood densities compared with coniferous species. With C mineralization rates much higher for white birch and trembling aspen than for spruce and jack pine (Brais et al., 2006), the densities corresponding to the onset of the second phase of decomposition would be reached much sooner for deciduous species. The degradation of carbohydrates during the second phase was more pronounced for deciduous than for coniferous species, resulting in a larger increase of AUR and nonstructural compound concentrations in deciduous species. In particular, balsam fir wood underwent little change in chemical composition, but changes could appear with further decomposition, i.e., in logs buried within the forest floor (lignic forest floor; Lambert et al., 1980). In well-decayed snags and logs, cellulose concentrations converged between deciduous and coniferous species, but, contrary to our second hypothesis, AUR concentrations remained lower in deciduous species, particularly in trembling aspen.

The AUR fraction likely contains lignins, lignin-like aromatic by-products of decomposition (McTiernan et al., 2003; Prescott, 2010) and lignoproteins (Brinkmann et al., 2002), but little tannin and cutin, considering our NMR spectra and results reported by Hernes & Hedges (2004) and Kögel-Knabner (2002). As revealed by NMR spectra, lignins of deciduous wood were dominated by syringyl units in fresh logs and by a mixture of syringyl and guaiacyl units in well-decayed logs. These changes likely result from preferential degradation of syringyl units compared with guaiacyl units, which are also present in the lignins of deciduous wood (Hedges & Mann, 1979; Strukelj et al., 2012, Chapitre I) and are more resistant to microbial attack (Cornwell et al., 2009). Despite some lignin degradation, we observed aromatic and phenolic C enrichment of deciduous wood during decomposition, which could have resulted from slower degradation of lignins compared with carbohydrates or from the formation of lignin-like aromatic by-products during decomposition.

In contrast, lignins of coniferous wood had a stable composition dominated by guaiacyl units throughout decomposition. Despite the relative recalcitrance of guaiacyl lignins (Cornwell et al., 2009), we observed similar degradation rates for lignins and carbohydrates of coniferous logs that resulted in few overall changes in their chemical composition during decomposition. In addition to the chemical nature of the units, covalent linkages among the phenols of lignins and covalent linkages between lignins and carbohydrates would be important determinants of recalcitrance (Talbot et al., 2012), which would explain why only a fraction of guaiacyl lignins is recalcitrant for conifers.

Moreover, decreases in wood density from those of fresh to well-decayed snags and logs were accompanied by a continuous decrease in their C:N ratios, as suggested by our first hypothesis. This decrease likely resulted from mycelial N translocation by saprotrophic fungi (Schimel & Hättenschwiler, 2007) and by asymbiotic N fixation (Brunner & Kimmins, 2003). Low-molecular N compounds, such as ammonia or amino acids, can react with lignins and products of lignin degradation (Coûteaux et al., 1998; Berg, 2000) to create complexes that are recalcitrant to further decomposition. In addition, low-molecular N compounds may repress the synthesis of lignin-degrading enzymes in white rot fungi (Kirk & Farrell, 1987; Berg, 2000). These processes could explain the decreased range of C:N ratios that we observed within and among species with decomposition (Herrmann & Prescott, 2008). Well-decayed deciduous logs attained a lower C:N ratio than did coniferous species, but well-decayed logs still underwent chemical changes, as previously indicated.

Nonstructural compounds increased in concentration with wood decay more than lignins did. This nonstructural fraction likely included microbial products, such as proteins (as suggested by the high correlation of this fraction with the alkyl C region), together with soluble by-products of decomposition, such as organic acids (as suggested by the high correlation with the carbonyl region). In jack pine wood, characterized by high alkyl C compounds and low N content, a nonstructural fraction could also result from high concentrations of resin acids, which are typically present in pine species (Lindberg et al., 2004) and could be very resistant to decomposition (Lorenz et al., 2007). Further studies are necessary to more precisely define the composition of the nonstructural fraction.

2.5.2. Differences in patterns of decomposition between snags and logs

The range of snag wood densities was higher in deciduous than in coniferous species, and very close to that observed in logs. However, snags would take longer to reach the lower end of the density range, because of the lower decay rates reported for snags (Angers et al., 2012b) than those of logs (Brais et al., 2006). Decreases in wood density and C:N ratios of snags indicate fungal activity and N-immobilization despite the limited access of microorganisms to snags (Boulanger & Sirois, 2006) and a limiting moisture content (Rayner & Boddy, 1988; Fukasawa et al., 2009). Wood decay is readily present in living trees (Boddy, 2001) and in snags (Kebli et al., 2012), resulting from heart rot, pathogens, unspecialized opportunists, or fungi that are present in the functional sapwood.

As expected, fewer changes occurred in snags than in logs during decomposition, affirming our third hypothesis. The selective degradation of cellulose and hemicelluloses and concomitant increases in lignins and nonstructural fractions was only apparent in deciduous snags. Studies on snag organic chemical composition are very rare. Fukasawa et al. (2009) found a similar decrease in density and carbohydrates, and an increase in the AUR fraction in Japanese beech snags, whereas Mukhortova et al. (2009) observed little change in the composition of Siberian larch (*Larix sibirica* Ledeb.) and Siberian spruce (*Picea obovata* Ledeb.) snags with decomposition. As snag susceptibility to breakage increases with decreasing wood density (Angers et al., 2012b), well-decayed snags likely fall before they achieve the degradation state of well-decayed logs.

2.5.3. Differences of chemical composition among well-decayed logs and lignic and alignic forest floors

Lignic forest floor had a chemical composition rich in aromatic, phenolic, and alkyl C compounds. Whereas well-decayed spruce spp. and jack pine logs developed compositions closer to that of lignic forest floor, well-decayed deciduous logs retained lower lignin contents. As logs decompose and become covered by the surrounding forest floor and mosses (Robert et al., 2012), their water-holding capacity (Brais et al., 2005) and their water content (Fukasawa et al., 2009) increase. Under high water content, anoxic conditions can inhibit the degradation of lignins by white rot fungi (Hedges et al., 1988) and promote bacteria and soft rot fungi (Rayner & Boddy, 1988). The high N concentrations of the lignic forest floor, twofold higher than those of well-decayed logs, could also cause the inhibition of lignolytic enzyme production by white rot fungi (Berg, 2000) as well as promote the formation of recalcitrant condensation products between lignins and low-molecular- weight N compounds. Contrary to previous findings (de Montigny et al., 1993), lignins were not the main compounds of lignic forest floor. Their unexpectedly high carbohydrate contents probably resulted from microbial products and preservation of carbohydrates linked to lignins (Talbot et al., 2012).

Alignic forest floor had a chemical composition differing from that of lignic forest floor, with higher proportions of alkyl C and carbonyl C compounds, and lower proportions of aromatic and phenolic C compounds. Alignic forest floor chemical composition was similar to that of 5- to 6-year-old decayed foliar material, irrespective of tree species and stand type. Higher alkyl concentrations of the alignic forest floor are associated with foliar protein content (Almendros et al., 2000), that is higher than in wood. Also, alkyl C compounds come from cutin in the cuticle of foliage and from resins in wood. These alkyl compounds are more resistant to decomposition than lignins (Kögel-Knabner, 2002; Lorenz et al., 2007), explaining their increasing concentrations with increasing decay.

2.6. Conclusions and implications for carbon retention

As wood decomposed, changes in chemical composition followed a two-phase pattern. This pattern was observed in all studied species, in snags as well as in logs. The first phase involved nonselective degradation of all chemical compounds. Degradation was more selective in the second phase, with the loss of carbohydrates, preservation of lignins, and formation of nonstructural compounds and by-products of lignin degradation enriched in N. Jack pine wood with its high lignin and alkyl C compounds mineralized slowly and, hence, has high C sequestration potential. In contrast, trembling aspen would have the lowest potential, because of its high degree of decomposability and fast decay rate.

Changes in wood quality concurrent with wood decomposition and burial within the forest floor could affect fungal communities and lead to the production of highly stabilized wood residues. This has strong implications in managed forests, where a reduction in deadwood availability could decrease the chemical heterogeneity of soils. Although recent studies have shown that lignins have a higher turnover rate than previously thought, these studies have considered neither wood lignins nor lignins in boreal forests (Berg et al., 1982; Kiem & Kögel-Knabner, 2003; Thevenot et al., 2010). The implications of initial wood lignin composition as strong determinants of soil C sequestration should undergo further assessment.

Chronosequence studies might create a bias toward well-decayed logs that are inhabited by brown rot fungi. On one hand, these logs are more likely over-represented on the forest floor. On the other hand, logs in which white rot is more active, could be mineralized almost completely, thereby becoming indistinguishable from the surrounding humus. Wood decomposition rates in the latter stages of decay are controlled not only by its initial composition and its associated suite of microbial decomposers, but also by ongoing environmental conditions and substrate nutrient concentrations. Controlled experiments are thus required to gain a better understanding of wood decay in boreal forests.

2.7. Acknowledgements

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CHAPITRE III

CHANGES IN DEAD ORGANIC MATTER POOLS AND ABOVEGROUND LITTER DYNAMICS FOLLOWING DIFFERENT INTENSITY OF CANOPY REMOVAL IN MIXED BOREAL FOREST STANDS

Manuella Strukelj, Suzanne Brais, David Paré

3.1. Abstract

Changes in carbon pools of dead organic matter following forest harvesting have major implications for forest land carbon budgets. We used a replicated experiment to assess changes in mineral soil, forest floor, deadwood (standing snags, downed logs) and live tree carbon pools over a 9-year period. The experiment included an unharvested control, two variants of partial harvesting, and a clear-cut. We also assessed rates of litter input and decay for deadwood and foliage. Carbon flux through leaf litterfall recovered rapidly following harvesting, but the leaf litterfall:deadwood production ratio diverged strongly among clear-cut and partially harvested treatments. The forest floor carbon pool in clear-cuts remained higher than in other treatments over the 9-year period. Generally, harvesting had little effect on forest floor and mineral soil carbon pools or their carbon:nitrogen ratios. Contrary to what was observed in clear-cuts, carbon flux from live trees to the deadwood pools was a dominant process in partially harvested stands, where snags and downed log carbon pools remained close to those of natural stands. The absence of large woody debris recruitment in clear-cuts could have consequences for the forest floor carbon pool, as 20% of forest floor mass consisted of lignic material originating from deadwood decay.

Après récoltes forestières, les changements dans les réservoirs de carbone de la matière organique morte ont des implications majeures sur le budget du carbone en forêt. Nous avons réalisé un suivi des réservoirs de carbone du sol minéral, de la couverture morte, du bois mort (chicots, billes au sol) et des arbres sur une période de neuf ans après coupes dans des peuplements de tremble. L'expérimentation incluait un témoin non coupé, deux variantes de coupes partielles, et une coupe totale, avec trois réplications de chaque traitement. Nous avons aussi évalué les taux de production et de décomposition des litières de feuilles et de bois de tremble. Le flux de carbone associé aux chutes de litières de feuilles a récupéré rapidement après coupes, mais le ratio des chutes de litières de feuilles sur la production de bois mort divergeait fortement entre les types de coupes. Le réservoir de carbone de la couverture morte restait plus élevé dans les coupes totales que dans les autres traitements tout au long des 9 ans. Mais généralement, la récolte avait peu d'effet sur les réservoirs de carbone de la couverture morte et du sol minéral et sur leurs ratios Carbone:Azote. Contrairement à ce qui a été observé dans les coupes totales, le flux de carbone associé à la mortalité des arbres vivants était un processus dominant dans les peuplements récoltés partiellement, où les réservoirs de carbone des chicots et des billes au sol restaient proches de ceux des peuplements naturels. L'absence de recrutement de large débris ligneux dans les coupes totales pourrait avoir des conséquences sur le réservoir de carbone de la couverture morte, car 20% de la masse de couverture morte consistait de matériaux ligniques provenant de la décomposition du bois.

3.2. Introduction

Forest harvesting has major implications for forest stock budgets at the site and landscape scales (Stinson et al., 2011). In the boreal forest, soils represent the largest carbon (C) pool (Pan et al., 2011) and could undergo large impacts from forest harvesting. However, to this day, the effects of forest harvesting on soil C dynamics and pools differ substantially across studies and ecosystems (Nave et al., 2010). The study of Covington (1981) predicts a decline of soil C pool following harvesting and then a recovery of soil C pool, whereas other studies found an increase in soil C pool due to the presence of harvest residues or few changes following harvesting (Yanai et al., 2003; Nave et al., 2009). Little empirical information exists regarding the effects of canopy removal on the dynamics of dead organic matter (DOM) pools beyond the very first few years following harvesting. A better understanding of the processes affected by harvesting and their magnitudes is necessary to assess the C sequestration in forest at the site and landscape scales.

The effects of harvesting on soil C pools can result from several processes, including changes in litter production, litter quality, and litter decomposition (Yanai et al., 2003). Specifically, harvesting activity produces copious, small fresh woody debris and stumps, and crushes well-decomposed logs (Wei et al., 1997; Brais et al., 2004; Jandl et al., 2007). Following harvesting, the removal of large trees that would otherwise die results in a substantial decrease in the deadwood component that includes snags, downed logs and buried wood. Consequently, the size- and decay-class distributions of logs (Wei et al., 1997; Siitonen et al., 2000) are altered and the number of snags is strongly reduced, when compared to natural disturbances (Lee et al., 2002; Pedlar et al., 2002; Rouvinen et al., 2002). Moreover, despite numerous studies estimating organic matter decomposition rates following forest harvesting, no consensus on how changes in stand conditions affect decomposition rates has emerged (Yin et al., 1989; Prescott, 1997; Wei et al., 1997; Lee et al., 2002).

Integrating concomitant changes in stand growth, deadwood and foliar litter dynamics, dead organic matter decomposition, and soil pools would improve our understanding of C dynamics following harvesting (Seedre et al., 2011).

Mixedwood forests occupy a large extent of boreal regions and have the potential to sequester large amounts of C (Cavard et al., 2010; Laganière et al., 2012), as they are frequently found on the most fertile and productive sites (Lee et al., 2002). In recent years, forest ecosystem management (FEM) or natural disturbance-based approaches have been proposed for the Canadian boreal mixedwoods (Bergeron & Harvey, 1997; Perera et al., 2004; Work et al., 2004). These approaches have aimed at maintaining forest diversity, ecological functions, and sustainability. While forest management has strong effects on C dynamics and sequestration (Wei et al., 1997; Johnson & Curtis, 2001; Jandl et al., 2007), the implications of FEM for the C cycle have yet to be investigated (Lee et al., 2002). Compared to even-aged management, FEM implies diversification of silvicultural practices, including various forms of retention harvest and partial cutting. Partially harvested stands have retained some characteristics of natural stands, such as live residual stems and downed log recruitment. These originate from fallen snags and large cull trees left after harvesting (Lee et al., 2002; Harvey & Brais, 2007; Brais et al., 2013).

One of the first ecosystem-based silvicultural experiments that was established in the Canadian boreal mixedwood is the SAFE (Sylviculture et aménagement forestier écosystémique) Project (Brais et al., 2004; Brais et al., 2013). SAFE is a series of experiments that are aimed at testing the conceptual model of mixedwood dynamics and silviculture, first proposed by Bergeron & Harvey (1997). The first phase of the SAFE project was set up in 1998 in stands of even-aged trembling aspen (Populus tremuloides Michx.) that originated from fire. These stands have been monitored since 1998 for C pools and fluxes. Treatments have included four levels of harvesting. We aimed to answer the following questions: (1) What are the effects of partial harvesting on quality, production, and decomposition of aboveground litters? (2) What are the effects of partial harvesting on stand C fluxes and pools and on C sequestration in the stand?

With an increasing level of harvesting, we expected an increase in the decay rates and maximum decomposition limits of woody and foliar litters (Taylor et al., 1991; Prescott, 2010), together with an increase in downed log volume immediately after harvesting. Due to the capacity of aspen stands to re-establish their leaf biomass through suckering following disturbance, we expected leaf litterfall to rapidly reach similar levels in all treatments (Covington & Aber, 1980). Thus, the importance of leaf litterfall relative to deadwood recruitment would increase with increasing level of harvesting. This would decrease, in turn, the C:N ratios of the forest floor and mineral soil organic matter (Strukelj et al., 2012, Chapitre I). We also expected snag and downed log characteristics and recruitment in partially harvested stands to be closer to those of undisturbed control than to those of clear-cut stands (Siitonen et al., 2000).

3.3. Material and methods

3.3.1. Study area

The study area is located in the Lake Duparquet Research and Teaching Forest (LDRTF; 48°86'N-48°32'N, 79°19'W-79°30'W). LDRTF lies within the Abitibi region of northwestern Quebec. The climate of the region is continental with a mean annual temperature of 0.7 °C. Mean temperatures of the warmest and coldest months are 16.9 °C (July) and -18.2 °C (January), respectively. Annual precipitation is 890 mm, of which 614 mm falls as rain from April to November (Environment Canada, 2010). The region is situated in the mixedwood zone of the Boreal Shield, within the western balsam fir-white birch bioclimatic domain. The dominant soils of the region have evolved from fine clayey to fine loamy textured glaciolacustrine deposits that were formed by sedimentation at the bottom of glacial Lake Barlow-Ojibway (Veillette et al., 2000) under fresh to moist moisture regimes (Brais & Camiré, 1992), and which are classified as Grey Luvisols (Soil Classification Working Group, 1998).

3.3.2. Experimental design and treatments

This study was conducted in aspen-dominated stands of fire origin that dated from 1923 (Table 3.1; for a complete description of harvested stands, see Brais et al., 2004). Four levels of forest harvesting were applied in the winter of 1998-1999, according to a complete block design with 3 replications per treatment and experimental units ranging in area from 1 to 2.5 ha. Treatments included a control ("Control"), a clear-cut ("CC") and two partial cut treatments. In the first partial cut ("1/3 PC") and the second partial cut ("2/3 PC"), pre-harvest basal areas were lower than in the two other treatments (Table 3.1). Harvesting of stems (> 9 cm dbh) removed respectively 31 % (1/3 PC) and 62 % (2/3 PC) of basal area, compared to controls. In the 1/3 PC treatment, non-vigorous aspen stems were preferentially removed, whereas in the 2/3 PC treatment, stands were crown-thinned with the larger, vigorous aspen stems preferentially selected (Table 3.1). In all harvesting treatments, stems were delimbed on site.

3.3.3. Field methods

3.3.3.1. Live stem and snag inventories

In the autumn of 1998 (before harvesting), five permanent circular sampling plots (PSP, 400 m^2, radius = 11.28 m) were established in each experimental unit, for a total of 60 PSP. Within each PSP, all live trees ≥ 5.0 cm dbh (diameter at breast height, 1.3 m) were identified to species, measured (dbh) and tagged for further measurements. In the north-east quarter of each plot (100 m^2), all stems with dbh ranging from 2.0 to 4.99 cm were also identified to species, measured (dbh), and tagged. In the spring of 1999 (after harvesting), a tally of the remaining stems was conducted in all PSP on the partial cuts to estimate residual basal area and changes in stem density. Forest inventories were conducted again in autumn of 2001, 2004 and 2007.

From 2001 to 2007, a similar inventory was conducted for snags within PSP. Snags (dead stems > 1.3 m in height) were identified to species, measured (dbh), and tagged. In 2007, snags were also measured for height and assigned to one of five decomposition classes (see Table 2.1). All stems that bore no tags in 2001 were assumed to have been dead and standing at the time of the tally (1999). Pre-harvest (1998) values for snags in partial and clear-cutting experimental units could not be reconstructed and, consequently, the average value that had been determined for the control experimental units in 1999 was attributed to all treatments for 1998.

Table 3.1. Characteristics of boreal aspen stands immediately following partial cut (PC) and clear-cut (CC) harvesting.

		Control	**1/3 PC**	**2/3 PC**	**CC**
Residual tree basal area (m^2/ha)	2 ≤ dbh ≤ 20 cm	8.87	6.55	8.11	0.03
		(2.08)	(2.63)	(2.39)	(0.03)
	dbh > 20 cm	36.08	24.64	8.94	0
		(2.13)	(4.48)	(3.89)	
	Total (dbh ≥ 2 cm)	44.95	31.19	17.05	0.03
		(1.79)	(1.92)	(1.59)	(0.03)
Harvested basal area (m^2/ha)	Total (dbh ≥ 9 cm)	0	10.12	21.47	43.40
			(1.35)	(0.67)	(6.05)
Snag basal area (m^2/ha)	Total (dbh ≥ 2 cm)	2.80	2.46	3.30	0.10
		(0.96)	(0.83)	(1.90)	(0.09)
Log volume (m^3/ha)	0.5 ≤ diameter < 2.5 cm	7.79	9.28	13.90	31.06
		(0.77)	(1.32)	(4.58)	(9.55)
	diameter ≥ 2.5 cm	96.04	122.92	93.02	155.65
		(63.56)	(30.55)	(8.25)	(44.62)

Note: Mean values and standard deviations (in parentheses).

3.3.3.2. Downed log inventory

Inventories of downed logs were conducted in 1998 (before harvesting), in 1999 (after harvesting), and again in 2001, 2004 and 2007. The volume of downed logs was estimated by the triangular transect method (Van Wagner, 1982). One 30 m-sided triangle was sampled in each experimental unit (each for a total length of 90 m), except in 2007 when two triangles were sampled in each experimental unit (180 m length). Along each transect line, the frequency of downed logs was recorded by species, diameter class (2.5-7.5 cm;7.6-12.5 cm; 12.6-17.5 cm; >17.6 cm), and five decay classes (see Table 2.1). The mid-points of these diameter classes were 5 cm, 10 cm, 15 cm and 20 cm, respectively. In 1999, an additional diameter class (1.5 cm, 0.5-2.4 cm) was recorded.

3.3.3.3. Soil sampling

In 1998 (before harvesting), 1999 (first year after harvesting), and 2007, soils were sampled for the determination of dry mass, and N and C content. The forest floor and the uppermost 10 cm of mineral soil were sampled at two locations that were close to each PSP, i.e., 12 m from the PSP centre in opposite directions. In 1998 and 1999, sampled forest floor material included all organic material lying on top of mineral soil. In 2007, alignic forest floor (i.e., originating from fine litter) and lignic forest floor (i.e., originating from woody debris) were sampled separately. Forest floor (FH layers) was cut out, extracted using a square frame (25x25 cm), and weighed in the field. Prior to sampling, all live plant material inside the frame and the L layer (fresh leaves and woody debris) were removed. In 2007, we proceeded in a similar manner for the alignic forest floor, but the lignic forest floor was sampled separately with a larger square frame (71 x 71 cm), to take into account its greater heterogeneity. Lignic forest floor was recognisable by its red to brown colour, its shape or its fibrous texture, which differed from alignic forest floor. At each sampling location, a bulk sample of the forest floor (alignic and lignic) was taken for dry mass estimation and laboratory analyses, and a bulk sample of mineral soil (0-10 cm) was collected. In 1998, the bulk density of mineral soil (0-10 cm) was also measured using a double-cylinder. Samples were kept cool (<4°C) until they were processed.

3.3.3.4. Leaf litterfall

In the summer of 1999, one litter trap (0.5 m²) was positioned in the centre of each PSP. Litter was collected twice a year from spring 1999 to spring 2002 and from spring 2005 to spring 2008.

3.3.3.5. Leaf and wood decomposition rate

Freshly fallen leaves of aspen were collected in the fall of 1999, whereas wood blocks were cut (10 × 5 × 5 cm) from dimensional lumbers of aspen. Foliar material (± 10 g) and wood blocks (100-150 g) were enclosed in litterbags (±10 × 8 cm) made of fibreglass (1 mm mesh size), with their initial moist mass printed on DYMO tape. Five subsamples of each litter type were dried (48 h, 65 °C) to determine the moist-to-dry mass conversion factors and to characterise initial litter chemical composition. In autumn of 1999, five litterbags containing wood blocks and five containing leaves were placed on the litter layer in each PSP and left to decompose in situ. A total of 240 litterbags were collected 1, 3, 5, and 6 years after the start of the experiment.

3.3.4. Laboratory methods

Leaf litter collected from litter traps was dried (48 h, 65°C) and weighed. After collection of litterbags, the exterior was carefully cleaned with a brush. Leaf litter or wood blocks were removed from the bags, manually sorted to eliminate any mineral soil or plant remains, dried (48 h, 65 °C), and weighed. Initial moist weights were corrected for their respective moisture content. For each collection date, materials from litter traps and from wood and leaf litterbags were pooled over experimental units. Samples were ground to 0.5 mm for C content analyses.

A total of 120 samples of forest floor and 120 samples of mineral soil have been collected and analysed in 1998, 1999 and 2007. In 2007, an additional 120 samples of lignic forest floor were analysed. Subsamples of the forest floor were weighed before and after drying (48 h, 65 °C) to determine the gravimetric moisture content. Forest floor masses that had been measured in the field were corrected to a dry-mass basis from their respective moisture contents.

Forest floor and mineral soil samples were air-dried (20-25°C) and sieved to 2 mm before grinding to 250 µm. In 1998 and 1999, soil C and N concentrations were determined by wet-digestion (Parkinson & Allen, 1975). In 2007, C and N analyses were conducted by high temperature dry-combustion using an elemental analyser (LECO, St. Joseph, Michigan) on samples collected in 2007 and a portion of the 1999 samples (re-analysis). Carbon and N concentrations that had been assessed by wet digestion were converted to combustion values based on a linear regression conducted on the 1999 samples that had been analysed using both methods.

3.3.5. Calculations

3.3.5.1. Carbon pools

The aboveground biomass of live trees and snags was estimated using specific allometric equations that were based on dbh (Lambert et al., 2005). The mass of each tree was assessed by adding the mass of stems (wood and bark), branches and foliage. The mass of snags was assessed with the same equations, but excluding some of tree components as implied by our snag classification criteria (see Table 2.1). Masses of snags of decay classes S-I and S-II included stems and branches, but 50% of branch mass was removed for snags of decay class S-II. Masses of snags in decay classes S-III, S-IV and S-V were estimated with the stem equations, but 33%, 66%, and 100% of bark mass was removed, respectively. Percentage loss of wood density corresponding to a snag decomposition class (Angers et al., 2012a) was applied to the estimated snag masses. The mass of snags in decay classes S-III, S-IV, and S-V with broken tops was further reduced by a factor corresponding to the ratio of their remaining volume to that of an intact pole of the same dbh. The volume of snags was estimated as the frustrum of a paraboloid (Husch et al., 2003), using the estimated initial height (Poulin et al., 2008; Beaudet et al., 2011) and the measured height of the snag.

The C pool of live trees was estimated from their aboveground biomass and specific C concentrations that were obtained from Lamlom & Savidge (2003). For species that were not reported, we used C concentrations of species within the same genera. The same C concentrations were used for snags, as a previous study found no changes in C concentrations with snag decay (Strukelj et al., 2013, Chapitre II). To estimate the aboveground C pool of snags in 1999, 2001 and 2004, where the height and decay class of snags was not determined, we estimated the C content of snags in each PSP from their basal areas, using a regression between basal area and C content that had been obtained from data collected in 2007 (R^2 = 88%).

Density of downed logs was based on values that were determined from parallel studies (Brais et al., 2004; Harvey & Brais, 2007) for each combination of species-decomposition classes. Changes in C concentrations of logs with decomposition were assessed in a previous study (Strukelj et al., 2013, Chapitre II).

The C pool of the forest floor was calculated by multiplying the C concentration by the dry mass of material. The C pool of the mineral soil (0-10 cm) was estimated by multiplying its C concentration, by its bulk density and by the volume of the 0-10 cm mineral soil.

3.3.5.2. Carbon fluxes

Carbon fluxes incurred by harvesting were estimated using specific allometric equations that were based on harvested tree dbh (Lambert et al., 2005). Carbon flux from live trees to logging slash included C mass of branches of harvested trees, whereas C flux from live trees to forest products included C masses of stem wood and stem bark. Carbon fluxes from live trees to deadwood through tree mortality were based on the same equations (branches, stem wood, and stem bark; Lambert et al., 2005) and changes in tree status between forest inventories over the 9-year period.

Carbon content in leaf litterfall of each year was obtained by multiplying measured C concentrations by the dry mass of leaf litterfall. To obtain the cumulative C fluxes that were associated with leaf litterfall over the nine years following treatments, leaf litterfall from 2002 to 2005 was estimated by considering (for each PSP) a linear increase or decrease in leaf litterfall between data that had been obtained for 2002 and for 2005.

The C content of each decomposition litterbag was estimated from its mass and C concentration at the time of sampling. Residual C (%) in litterbags is the ratio of C content at time of sampling divided by the initial C content. To estimate decomposition rates and decomposition limits from leaves and wood, a negative exponential model that included an asymptote (Berg et al., 1996; Harmon et al., 2009) was applied to data from the litterbags that had been collected from each experimental unit, according to the following equation:

$$C_t = C_0\, \mathrm{e}^{-kt} + S_0$$

where C_t is the residual C content (%) at time t (years), C_0 is the initial C content of material subject to loss (%), S_0 is the asymptote (%), and k is the decay rate (year^{-1}). The sum of C_0 and S_0 is constrained to equal 100% and, consequently, an estimate of one parameter can be used to derive the other (Harmon et al., 2009). Consistent with previous authors (Howard & Howard, 1974), we refer to this equation simply as the asymptotic model.

3.3.6. Data analyses

The effects of harvesting on the response variables (except for S_0 and k, see below) were assessed by means of linear mixed-effects models and Wald's t tests ($\alpha = 0.05$; Pinheiro & Bates, 2000) using the lme function that is included in the nlme library of R (R Development Core Team, 2012). Fixed factors in the models included treatment (control, 1/3 partial cut, 2/3 partial cut, clear-cut), time-since-treatment, and their interaction. Leaf litterfall was analysed as a function of residual tree basal area, basal area-squared, time-since-harvesting, and the interactions between basal area and time. Interactions were removed from all models when their p values were > 0.10. For C pools, the pre-harvest values (1998) of the response variables were used as covariates to account for pre-harvest differences among experimental units, but were removed when they were not significant. When treatment was used as a categorical fixed factor, the reference level of treatment was control, against which the three other treatments were compared. The significance of treatment effects on S_0 and k was assessed with non-linear mixed-effects models using the nlme function, for which the fixed factors were treatment, material (wood vs leaves), and their interaction.

Random factors were sampling plots, which were nested within experimental unit, and experimental units, which were nested within block, except for logs that were sampled at the experimental unit scale. Normality and homogeneity of variance assumptions were verified by visual assessment of residuals. When these assumptions were not met, logarithmic or square-root transformations were applied.

In clear-cut experimental units, differences among trees of medium and large sizes, and snag pools and C flux through tree mortality were negligible; the clear-cut treatment was removed from the analysis to respect the homoskedasticity assumption. Observed values are nonetheless presented in figures 3.1 and 3.2.

3.4. Results

3.4.1. Direct and immediate effects of harvesting on carbon pools

Tree harvesting exported 19.5 $MgC{\cdot}ha^{-1}$, 44.6 $MgC{\cdot}ha^{-1}$, and 86.1 $MgC{\cdot}ha^{-1}$ in forest products from the 1/3 partial cut, 2/3 partial cut and clear-cut treatments, respectively. On-site delimbing of stems left fresh branches and tops on the ground, corresponding to C inputs of 2.5 $MgC{\cdot}ha^{-1}$, 5.6 $MgC{\cdot}ha^{-1}$, and 11.3 $MgC{\cdot}ha^{-1}$ in the 1/3 partial cut, 2/3 partial cut and clear-cut treatments, respectively (Fig. 3.1).

Carbon pools that were associated with small-sized trees ($2\text{ cm} < \text{dbh} \leq 12.5\text{ cm}$) were not affected by partial harvesting, but were significantly reduced by clear-cutting (Table 3.2, Fig. 3.2). The C pool that was associated with medium-sized trees ($12.5\text{ cm} < \text{dbh} \leq 20\text{ cm}$) was reduced by the 1/3 partial cut (Fig. 3.2), while the C pool of large-sized trees ($\text{dbh} > 20\text{ cm}$) was reduced by all harvesting treatments (Table 3.2, Fig. 3.2).

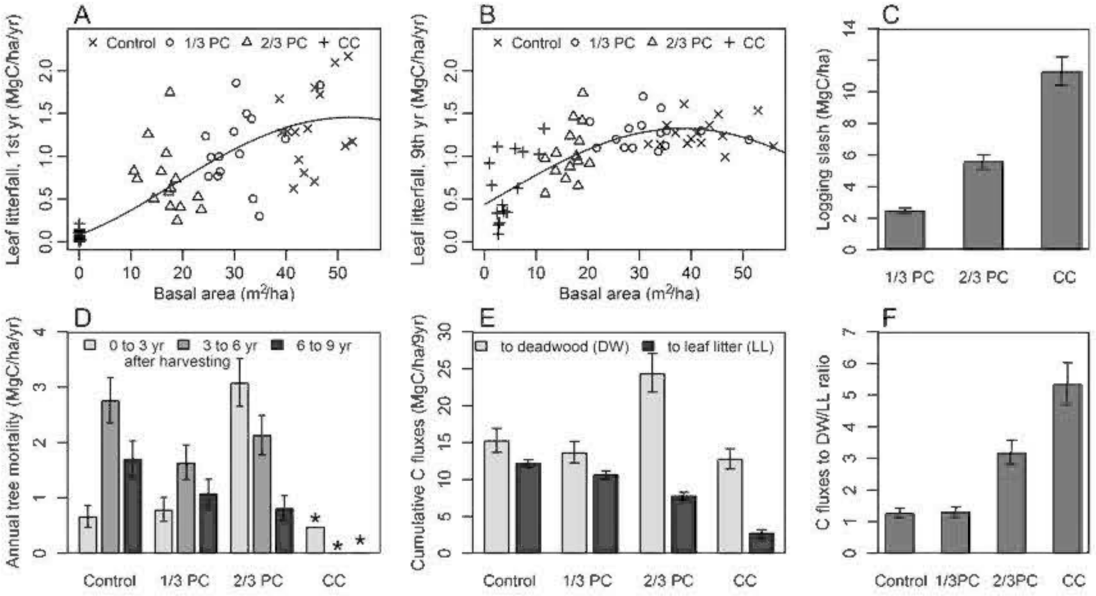

Fig. 3.1. Effects of partial cut (PC) and clear-cut (CC) harvesting on ecosystem aboveground C fluxes over a nine-year period following harvesting in boreal aspen stands. Carbon fluxes associated with annual leaf litterfall during (A) the first and (B) the ninth years following harvesting. (C) Carbon fluxes to deadwood through logging slash at time of harvesting. (D) Annual carbon fluxes from tree biomass to deadwood (tree mortality) according to time since harvesting. (E) Nine year cumulative C fluxes from tree biomass to deadwood (DW) and C fluxes to leaf litter (LL) associated with leaf litterfall. (F) Ratio of C flux to deadwood over C flux to leaf litter.

* Clear-cut values are observed values, as they were removed from the statistical analyses (close to 0).

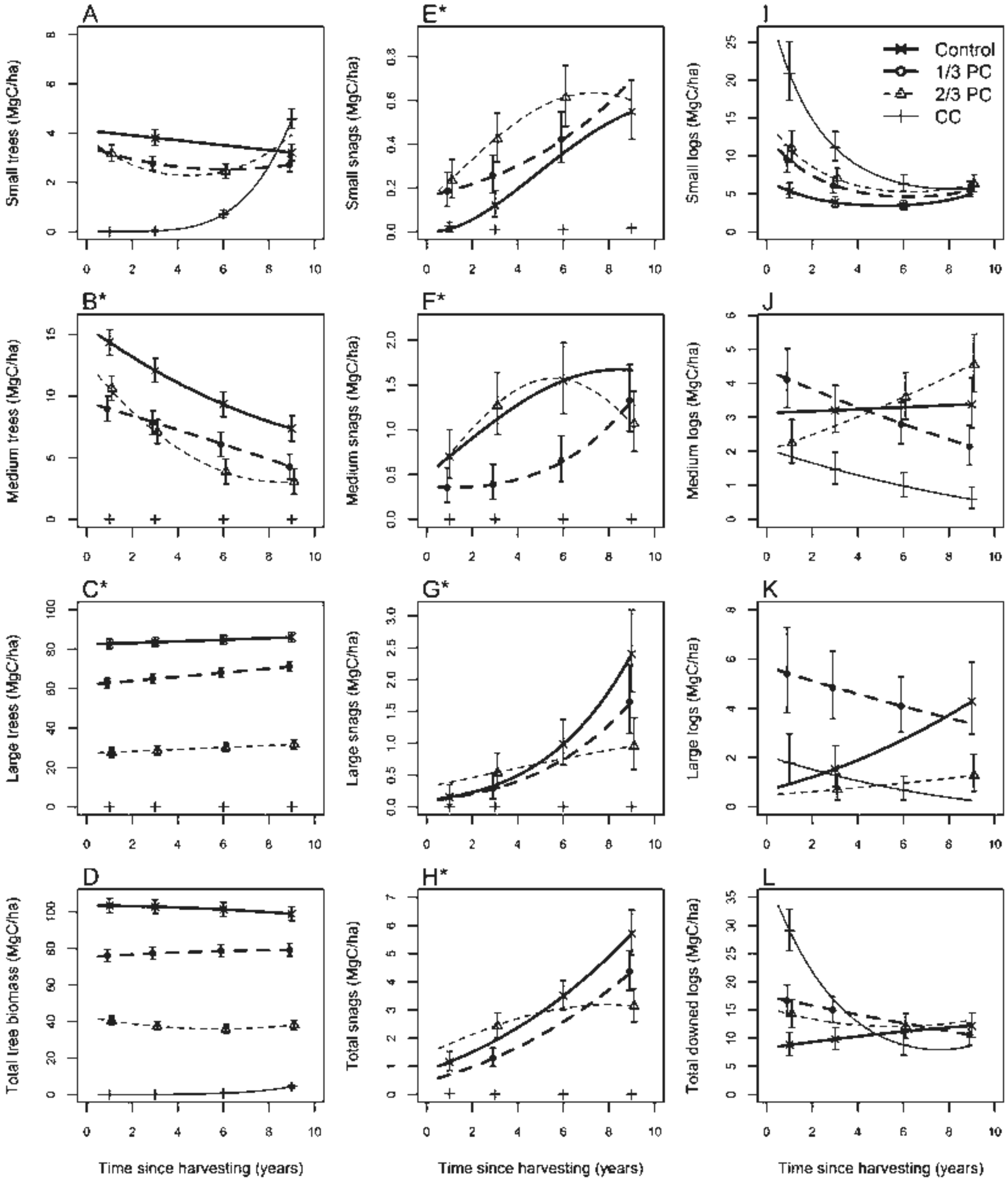

Fig. 3.2. Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C pools associated with (A) small trees, (B) medium trees*, (C) large trees*, (D) total tree biomass, (E) small snags*, (F) medium snags*, (G) large snags*, (H) total snags*, (I) small downed logs, (J) medium downed logs, (K) large downed logs, (L) total downed logs.

* Clear-cut values are observed values, as they were removed from the statistical analyses (close to 0).

Table 3.2. Effect of partial cut (PC) and clear-cut (CC) harvesting and time since harvesting on C fluxes associated with annual tree mortality and on standing C pools in boreal aspen stands.

Variable	**Pre-harvest**	**1/3PC**	**2/3PC**	**CC**	**Time**	**Time^2**	**Interaction: Time x**			**Interaction: Time^2 x**		
							1/3PC	**2/3PC**	**CC**	**1/3PC**	**2/3PC**	**CC**
Tree mortality[a]		NS	*		***	***	+	**		NS	+	
Tree biomass												
Small trees[b]	***	NS	NS	***	NS	NS	NS	*	NS	NS	***	***
Medium trees[b]	***	*	NS		***	NS	NS	+		NS	+	
Large trees[b]	***	**	***		NS		+	NS				
Total[b]	***	**	***	***	NS	NS	NS	*	NS	NS	**	***
Snags												
Small snags[b]		*	*		***	+	*	NS		+	NS	
Medium snags[b]		NS	NS		*	NS	*	NS		*	NS	
Large snags[b]		NS	NS		NS	NS				NS	*	
Total[b]		NS	NS		**	NS				NS	**	

Note: ***: $p < 0.001$; **: $0.001 < p < 0.010$; *: $0.010 < p < 0.050$; +: $0.050 < p < 0.100$; NS: $p > 0.100$. The significance of the effects was assessed by means of linear mixed models. The reference level of treatment was control.

[a] Logarithmic transformation.

[b] Square-root transformation.

Fresh logs were absent prior to harvesting, but harvesting caused an influx of fresh logs in all treatments. An input of 5.8 $MgC \cdot ha^{-1}$ was estimated for control stands in the year following harvesting (Fig. 3.3). Inputs of fresh logs were higher in the 1/3 partial cut, 2/3 partial cut, and clear-cut treatments, compared to the control (Table 3.3, Fig. 3.3). Increases in moderately decayed logs were much higher following clear-cutting and marginally higher after the 2/3 partial cut, compared to the control (Table 3.3, Fig. 3.3). The C pool of well-decayed logs was smaller following clear-cutting than in the control or other treatments (Table 3.3, Fig. 3.3). The C pool of very small (0.5 cm < Diameter < 2.5 cm) and small (2.5 cm < Diameter ≤ 12.5 cm) downed logs was larger in stands following harvesting than in control stands (Tables 3.1 and 3.3, Fig. 3.2). The C pool of large downed logs was initially larger after the 1/3 partial cut treatment than that of the control (p=0.042) or other treatments (Table 3.3, Fig. 3.2).

After clear-cutting, C pools, C concentrations, and the depth of the forest floor increased. Differences among the two partial cut treatments and the control were minor (Table 3.3, Fig. 3.3). No difference was observed among treatments in terms of the C pool of the mineral soil (Table 3.3, Fig. 3.3).

3.4.2. Carbon fluxes through tree mortality and leaf litterfall after harvesting

During the first year following harvesting (1999), annual C flux through leaf litterfall decreased with decreasing residual basal area ($p<0.001$, Table 3.4). These fluxes averaged 1.34, 1.10, 0.72, and 0.07 $MgC \cdot ha^{-1} \cdot yr^{-1}$ in the control, the 1/3 partial cut, the 2/3 partial cut, and the clear-cut treatments, respectively (Fig. 3.1). Over the 9-year period, leaf litterfall increased ($p<0.001$) more strongly in stands with lower basal area ($p<0.001$).

Nine years after harvest, annual C flux through the leaf litterfall averaged 1.27, 1.27, 1.04, and 0.65 MgC·ha^{-1}·yr^{-1} in the control, the 1/3 partial cut, the 2/3 partial cut, and the clear-cut treatments, respectively. Few differences were observed between partial cutting and the control in terms of leaf litterfall, although basal area remained very different among treatments (Fig. 3.1). Over the nine years following the harvest, cumulative C inputs from leaf litter increased almost five-fold with increasing basal area, from 2.7 MgC·ha^{-1} in the clear-cut to 12.2 MgC/ha in the control (Table 3.4, Fig. 3.1).

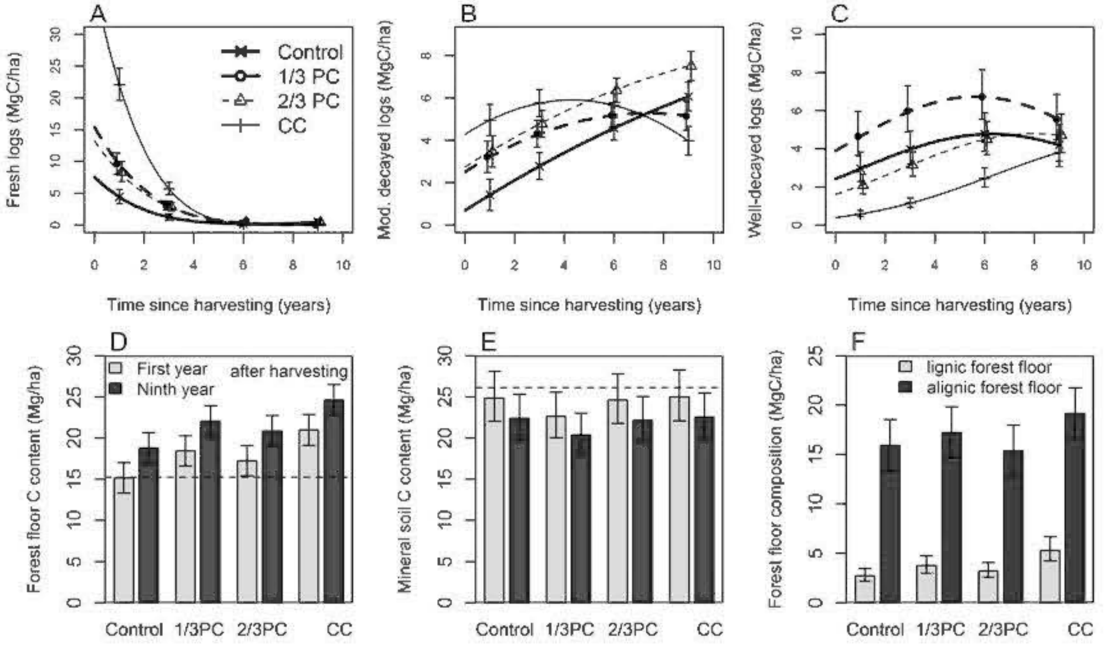

Fig. 3.3. Effects of partial cut (PC) and clear-cut (CC) harvesting and of time since harvesting in boreal aspen stands on C pools associated with (A) fresh downed logs of decay classes L-I&II, (B) moderately decayed logs of decay class L-III, and (C) well-decayed logs of decay classes L-IV&V, (D) forest floor, (E) and mineral soil (0-10 cm). (F) Effects of PC and CC harvesting on the composition of the forest floor nine years following harvesting.

Note: Broken line: average of variable before harvesting (1998), all sites and treatment confounded, used in models as covariable.

Table 3.3. Effect of partial cut (PC) and clear-cut (CC) harvesting and time since harvesting on dead organic matter (DOM) C pools, including downed logs, forest floor and mineral soil (0-10 cm) in boreal aspen stands.

Variable	**Pre-harvest**	**1/3PC**	**2/3PC**	**CC**	**Time**	**Time^2**	**Interaction: Time x**			**Interaction: Time^2 x**		
							1/3PC	**2/3PC**	**CC**	**1/3PC**	**2/3PC**	**CC**
Downed logs												
Small logs^a		+	*	**	***	***	*	*	***			
Medium logs^b		NS	NS	NS	NS		*	*	*			
Large logs^b	*	*	NS	NS	*		*	NS	**			
Fresh logs^b		*	*	***	***	***	**	+	***			
Mod.d. logs^b		NS	+	**	*	NS				*	NS	***
Well-d. logs^a	**	NS	NS	**	*	+	NS	NS	***			
Total	*	+	NS	**	NS	NS	NS	NS	***	NS	NS	**
Soil												
Forest floor	***	NS	NS	+	**							
Mineral soil^a	***	NS	NS	NS								

Note: ***: $p < 0.001$; **: $0.001 < p < 0.010$; *: $0.010 < p < 0.050$; +: $0.050 < p < 0.100$; NS: $p > 0.100$. The significance of the effects was assessed by means of linear mixed models. The reference level of treatment was control. Fresh, including L-I and L-II decay classes; Mod.d., moderately decayed, including L-III decay class; Well-d., well-decayed, including L-IV and L-V decay classes.

[a] Logarithmic transformation.

[b] Square-root transformation.

Table 3.4. (a) Effect of harvesting (*i.e.*, residual tree basal area variable) and time since harvesting on C fluxes associated with annual leaf litterfall. (b) Effects of partial cut (PC) and clear-cut (CC) harvesting on cumulative C fluxes associated with leaf litterfall, tree mortality and snag fall over a 9-year period following harvesting of boreal aspen stands.

a) C fluxes associated with annual leaf litterfall

Variable	**Basal area**	**Basal area^2**	**Time**	**Basal area x Time**
Annual leaf litterfall[a]	***	***	***	***

b) Cumulative C fluxes associated with leaf litterfall, tree mortality, and snag fall

Variable	**1/3 PC**	**2/3 PC**	**CC**
C flux through leaf litterfall	*	***	***
C flux from live trees to snags[a, c]	NS	NS	
C flux from live trees to downed logs[a]	NS	+	NS
C flux from snags to downed logs[a, c]	NS	NS	
Total C flux from live trees to deadwood[b, d]	NS	*	NS
DW/LL ratio of C flux[b, e]	NS	**	***

Note: ***: $p < 0.001$; **: $0.001 < p < 0.010$; *: $0.010 < p < 0.050$; +: $0.050 < p < 0.100$; NS: $p > 0.100$. The significance of the effects was assessed by means of linear mixed models. The reference level of treatment was control.

[a] Square-root transformation.

[b] Logarithmic transformation.

[c] Clear-cutting treatment excluded of the model, because values=0.

[d] Including C flux to snags and to downed logs, associated with tree mortality and logging slash.

[e] Ratio of C flux to deadwood (DW) on C flux to leaf litter (LL).

In the control, C fluxes from live tree biomass to deadwood (tree mortality inputs) was lowest in the first three years following harvesting and highest between 3 and 6 years following the harvest (Table 3.2, Fig. 3.1). At this point, mean flux was significantly higher in the control than in partial cut treatments. The 1/3 partial cut reduced tree mortality relative to the control, but the pattern of mortality through time in this treatment was similar to that of the control (Table 3.2, Fig. 3.1). In the 2/3 partial cut, C fluxes through tree mortality were higher than in other treatments during the first 3 years following harvesting, but decreased thereafter (Table 3.2, Fig. 3.1). From years 6 to 9, tree mortality reflected remaining basal area ($p<0.001$) in the control and partial cut treatments (Table 3.3, Fig. 3.1). Following clear-cutting, C fluxes were associated with the mortality of shrubs and small trees during harvesting operations, but they were close to 0 thereafter (Fig. 3.1). Over the 9-year period, total C fluxes from tree biomass to the deadwood pool through tree mortality and logging slash were higher in the 2/3 partial cut than in the control ($p = 0.022$), whereas other treatments were similar to the control (Table 3.4, Fig. 3.1). The ratio of wood to leaf litter inputs was higher in stands with lower basal area (Fig. 3.1).

3.4.3. Carbon fluxes through decomposition after harvesting

The asymptotic model predicted similar residual C contents (S_0, asymptote, Table 3.5) for leaf litters deployed in the four treatments and for wood in the clear-cuts, ranging from 28.7 to 35.4% (Fig. 3.4). Wood in the control and partial cut treatments had lower S_0-value ($p<0.001$, Table 3.5), ranging from 8.7 to 14.9% (Fig. 3.4). Predicted decay rates of leaf litter were higher in the partial cuts and the control than in the clear-cut (Table 3.5). Conversely, decay rates of wood were lower in the partial cut and the control than in the clear-cut (Fig. 3.4). Consequently, in the clear-cuts, decay rates were lower for leaf litter than for wood, whereas in the control and partial cut treatments, decay rates were higher for leaf litter than for wood.

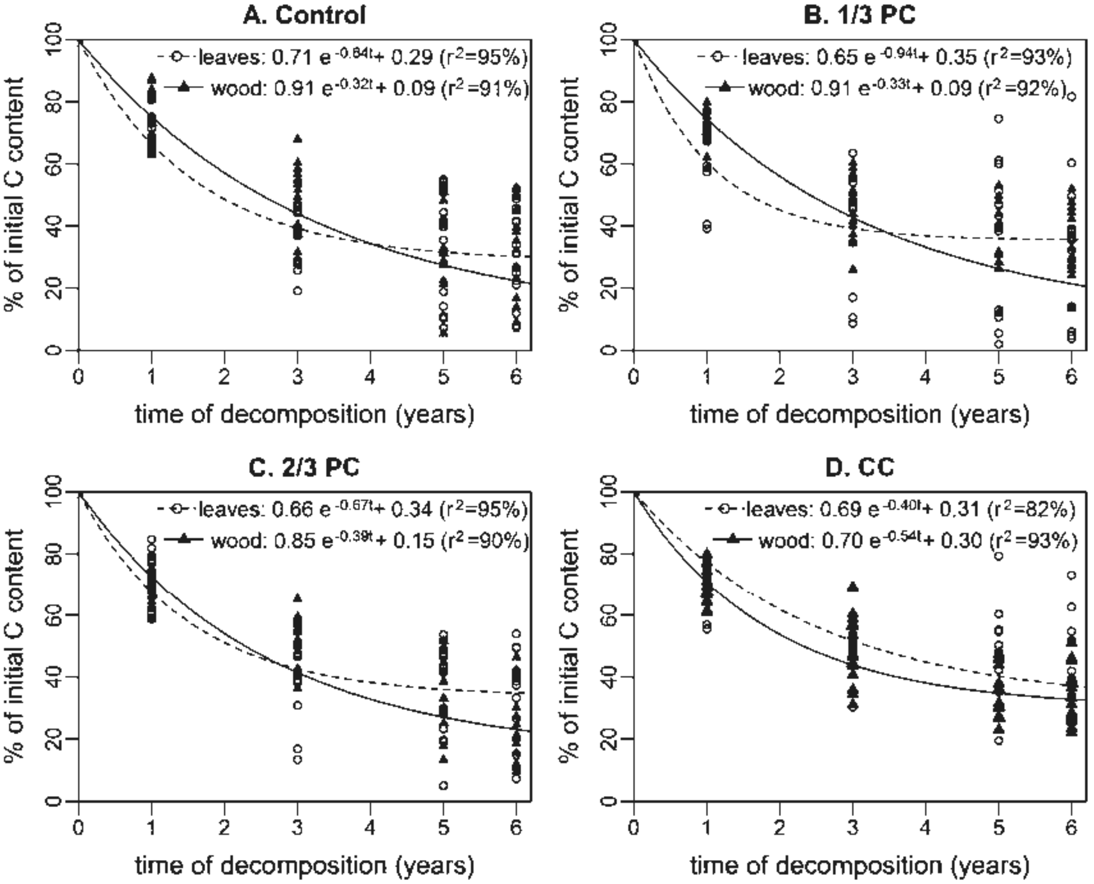

Fig. 3.4. Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C fluxes from decaying leaf litters and wood of trembling aspen.

Note: Values are expressed as the proportion (%) of initial decomposition bag C content.

Table 3.5. Effect of partial cut (PC) and clear-cut (CC) harvesting on aspen leaf litter (LL) and deadwood (DW) decomposition in boreal aspen stands.

Variable	**1/3PC**	**2/3PC**	**CC**	**Litter (DW)**	**Interaction: Litter x**		
					1/3PC	**2/3PC**	**CC**
Asymptote (S_0)	+	NS	NS	***	+	NS	***
Decay rate (k)	**	NS	***	***	**	NS	***
Residual C content after 6 years of decomposition	NS	NS	*	NS	NS	+	+

Note: ***: $p < 0.001$; **: $0.001 < p < 0.010$; *: $0.010 < p < 0.050$; +: $0.050 < p < 0.100$; NS: $p > 0.100$. The significance of the effects was assessed by means of non linear mixed models, and linear mixed models. The reference level of treatment was control for treatment and leaf litter for litter type.

After 6 years of decomposition, residual C content in decayed leaf litter was similar between the partial cut treatments and the control, but higher in the clear-cut treatment than in the control (Table 3.5, Fig. 3.4). Residual C content in wood was similar among treatments (Fig. 3.4). After 6 years of decomposition, the observed C content in leaf litter ranged from 29.9 in the control to 43.7% in the clear-cut. These values are close to the asymptotes estimated for the partial cuts and the control, indicating that leaf litters had almost reached their maximum decomposition limits, except for the clear-cut. This was not the case for the wood blocks, where observed C contents were still between 25.4 % and 33.9 %, versus predicted asymptote estimates ranging from 9 % to 30 %.

3.4.4. Changes in carbon pools of tree biomass after harvesting

With time-since-harvesting, the C pool of small trees increased significantly following clear-cutting from 0 to 4.4 MgC·ha^{-1} (Table 3.2, Fig. 3.2). In the 2/3 partial cut, small tree C pools initially decreased before increasing from year 6 onward. Small tree C pools remained stable in the 1/3 partial cut and control (Table 3.2). The C pool associated with medium sized trees decreased in partially harvested treatments and the control (Table 3.2, Fig. 3.2). Nine years after harvesting, both partially harvesting treatments had similar medium sized tree C pools, averaging 3.7 MgC·ha^{-1}, compared to 7.4 MgC·ha^{-1} in control stands.

The C pool of large trees remained more or less constant in partially harvested and control stands (p=0.107, Table 3.2, Fig. 3.2), while C pools of medium- and large-sized trees remained close to 0 in the clear-cuts. Over the 9-year period, C pools of tree biomass (stem > 2 cm dbh) did not change significantly in the control and 1/3 partial cut treatments. In the 2/3 partial cut treatment, the live tree C pool first decreased before increasing from year 6 after harvesting and onward (Table 3.2, Fig. 3.2). The C pool in tree biomass after clear-cutting followed the pattern of the small-sized tree C pools. Trees > 20 cm (dbh) accounted for most of the tree biomass C over the nine-year period in the control and partial cut treatments. Nine years following harvesting, total tree biomass C pools were 97.8, 79.1, 39.5, and 4.6 MgC·ha^{-1} in control stands and in stands following 1/3 partial cut, 2/3 partial cut, and clear-cut, respectively.

3.4.5. Changes in carbon pools of snags and downed logs after harvesting

Carbon pools of small, medium, and large snags increased in both partial harvesting treatments and in the control over the nine year post-harvest period, but the increase were not significant for large snags (Table 3.2, Figs. 3.2). The C pool that was contributed by snags remained negligible over the nine years following clear-cutting. The C pool of small snags in the control was lower than in either partial cutting treatments (Table 3.2, Fig. 3.2), whereas the C pools of medium and large snags were similar across treatments (Fig. 3.2).

Changes in snag C pools within the different size classes followed different dynamics. Nine years after harvest, few differences in small snags remained among treatments. In contrast, the C pool of medium snags was larger in the control than the

1/3 partial cut, whereas the C pool of large snags was smaller in the 2/3 partial cut than in the control and 1/3 partial cut treatment.

Carbon fluxes from snags to downed logs averaged 0.96, 0.58 and 1.33 $\mathrm{MgC \cdot ha^{-1}}$ over the 9-year period in the control, 1/3 partial cut and 2/3 partial cut treatments, respectively. However, the differences among treatments were not significant (Table 3.4).

The C pool of small downed logs significantly decreased with time following the application of all treatments, more strongly so with increasing level of harvesting. After 9 years, the C pool of small logs attained similar values in all treatments (Table 3.3, Fig. 3.2). The C pool of medium logs did not change with time in the control, decreased rapidly in the clear-cut (p = 0.024) and 1/3 partial cut (p = 0.031), but increased in the 2/3 partial cut compared to the control (p = 0.050, Table 3.3, Fig. 3.2). With time-since-harvesting, the C pool of large downed logs increased significantly in the control (p = 0.014), while decreasing in the partial cuts and clear-cut (Table 3.3, Fig. 3.2).

The C pool of fresh downed logs decreased with time-since-treatment ($p <$ 0.001), more strongly in the treatments that had higher inputs during harvesting (Table 3.3, Fig. 3.3). After 9 years, few differences remained among treatments. The C pool of moderately decayed logs increased in all treatments with time-since-harvesting (p = 0.030), more strongly in the 2/3 partial cut and the control treatments, while the increase slowed down and decreased in the two other treatments (Table 3.3, Fig. 3.3). The C pool of well-decayed logs increased following partial cut and control treatments and reached a plateau after 6 years (Table 3.3, Fig. 3.3).

During the nine years following harvesting, the C pool of downed logs decreased in the clear-cuts, but did not change significantly in the other treatments (Table 3.3, Fig. 3.2). Moreover, the ratio of snags to logs did not differ among treatments (not shown), nor did the C fluxes from live trees to snags (Table 3.4). Over 9 years, C fluxes from live trees to downed logs averaged 1.47, 1.58, 2.57, and 1.15 MgC·ha^{-1} in the control, the 1/3 partial cut, the 2/3 partial cut and the clear-cut treatments, respectively. Mean flux was marginally higher in the 2/3 partial cut compared to the two other treatments (Table 3.4).

3.4.6. Changes in carbon pools of forest floor and 0-10 cm mineral soil after harvesting

Over the nine-year period following harvesting, the C pool of forest floor increased in a similar fashion across all treatments (Table 3.3, Fig. 3.3). After nine years, our results indicated marginally significantly higher lignic forest floor C pool in clear-cuts versus the other treatments (p= 0.081, Fig. 3.3), but similar alignic forest floor C content. Forest floor C:N ratio did not differ among treatments, but a decrease in N concentrations from 1999 to 2007 resulted in an increase in the C:N ratio in all treatments (not shown).

In mineral soil, no difference was observed among treatments, but a decrease in the C pool and in C concentrations occurred over the nine-year period following harvesting (Table 3.2, Fig. 3.3). The C:N ratio of mineral soil did not differ among treatments, except for a difference between the two partial cut treatments in 1999 (not shown).

3.4.7. Net changes in total C pools after harvesting

The balance between losses and gains of C between pre- and post-harvest conditions showed net ecosystem losses of C with harvesting, compared to few changes in the control stands (Fig. 3.5). Losses with harvesting resulted mainly from the exportation of harvested stems to forest products, while the logging slash was incorporated into deadwood and forest floor C pools. Over the nine years following harvesting, there were net ecosystem losses of C in the 2/3 partial cut and the clear-cut treatments, and net gains in the two other treatments (Fig. 3.5). Increases in snag C pools were observed in the control and partial cut treatments, whereas decreases in log C pools were found in the three harvesting treatments. Tree biomass accumulated in the 1/3 partial cut and clear-cut treatments, but decreased in the control and 2/3 partial cut treatment. After nine years, DOM C pools were very similar between the control and harvesting treatments, whereas large differences in tree biomass were still apparent. The composition of DOM and snag C pools was very similar between the control and partial cut treatments, but following clear-cutting, there was a higher forest floor content, but no snags (Fig. 3.5).

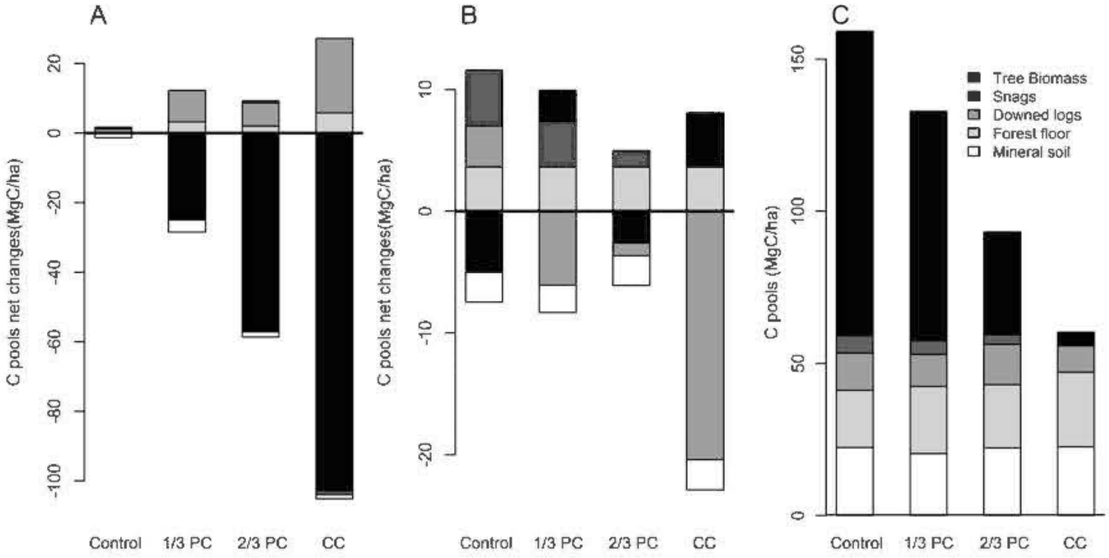

Fig. 3.5. Effect of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C pools over a nine-year period following harvesting. Net positive and negative changes of aspen stand C pools (A) between pre-harvest and post-harvest stand conditions, and (B) between post-harvest stand condition and nine years following harvesting. (C) Total soil and aboveground C pools nine years after harvesting.

3.5. Discussion

Our study provides a detailed examination of aboveground C pools, DOM pools, and fluxes over a 9-year period following partial and clear-cut harvesting of boreal aspen stands. The working hypothesis of the study was that besides an increase in decay rates and biomass accumulation following harvesting, other mechanisms such as deadwood dynamics and changes in aboveground litter quality would alter C sequestration in these stands. It was expected that snag and downed log characteristics and recruitment in partially harvested stands would remain similar to those in the undisturbed control. Given the capacity of aspen stands to re-establish their leaf biomass rapidly, we expected that the ratio of C fluxes associated with deadwood recruitment to C fluxes associated with litterfall would decrease with an increasing harvesting intensity. In turn, this would decrease the C:N ratios of the forest floor and mineral soil organic matter.

3.5.1. Carbon sequestration in tree biomass after harvesting

Boreal mature aspen stands can sequester large amounts of C in tree biomass (Paré & Bergeron, 1995). The 97.8 $\mathrm{MgC \cdot ha^{-1}}$ that was reported for the 84-year-old control stands was within the range found by Cavard et al. (2010) and Lee et al. (2002), and is large when compared to coniferous stands (Paré & Bergeron, 1995). In these stands, tree biomass represented 63 % of total C storage, while deadwood (snags and downed logs) C pools were similar to that of the forest floor, i.e., 11%.

Harvesting resulted in a reduction of tree biomass C pools that was proportional to harvesting intensity. Following both clear-cutting and 2/3 partial cut, rapid trembling aspen regeneration through suckering (Brais et al., 2004) hastened C sequestration in tree biomass. This process was likely to increase exponentially in the coming years. In contrast, larger trees were the major C pool in the 1/3 partial cut and control stands, and were still sequestering C despite their age.

3.5.2. Deadwood dynamics after harvesting

The 84-year-old control stands were characterised by the production of a large quantity of deadwood and, more particularly, a high snag input. High mortality rates in the medium and large tree size classes that were due to self-thinning accounted for most of the C flux from tree biomass to DOM. Also, an outbreak of forest tent caterpillar moth (*Malacosoma disstria* Hübner), which occurred in these stands in 2000, was responsible for the peak in aspen mortality that was observed between 2001 and 2004 (A. Bose, B. Harvey and S. Brais, manuscript in preparation). The absence of fresh logs in natural stands can be explained by the low uprooting occurrence of aspen (Angers et al., 2010) and the fast decay rates of aspen downed logs (Brais et al., 2006). Size class distributions of snags and downed logs in natural forests were fairly even among small, medium and large size classes.

Following harvesting, stands and more particularly clear-cuts were characterised by large quantities of fresh logging slash and by a large increase in moderately decayed logs, which could have resulted from the fall of snags during harvesting operations. Moreover, partial harvesting could have accelerated mortality of residual trees through increased tree fall by windthrow in post-harvest stands and through physical damage to residual stems during windthrow events (Bose et al., submitted). The high C flux associated with mortality in the 2/3 partial cut was also a result of the harvesting prescription, which left mostly non-vigorous stems (Harvey & Brais, 2007).

As expected in our hypotheses, partial cutting did not alter the distribution of deadwood that remained as standing snags or downed logs, in contrast to clear-cutting, where snags were almost absent. Lower decay rates (*k* values) have been reported for trembling aspen snags ($0.027\cdot\text{year}^{-1}$, Angers et al., 2012) than for logs of ($0.06\cdot\text{year}^{-1}$, Brais et al., 2006). These estimates corresponded to mass losses of 50% after 27 and 12 years for snags and logs, respectively. By leaving standing dead trees and allowing for snag recruitment, partial cutting would then promote medium-term C retention.

The size class distribution of downed logs after partial cutting approximated that of natural forest, despite a decrease in logs of medium and large size after 1/3 partial cutting and a greater increase in logs of medium size in the 2/3 partial cut. Contrastingly, during the nine years following clear-cutting, the distribution of downed logs was largely skewed towards small diameter classes, due to the input of logging slash and the absence of tree mortality (Fridman & Walheim, 2000; Fraver et al., 2002; Pedlar et al., 2002). Debris size constitutes another factor that affects decay rates, as small-diameter debris has been shown to decompose faster than large-diameter debris (Edmonds et al., 1986). Following clear-cutting, a rapid transition from fresh logs to moderately decayed logs to well-decayed logs was observed, highlighting the rapid decomposition of logging slash (Fraver et al., 2002).

3.5.3. Leaf litterfall after harvesting

After harvesting, C fluxes that were associated with leaf litterfall decreased in proportion to the degree of canopy removal. With time, increases in shrubs and saplings (Bourgeois et al., 2004; Brais et al., 2004) and lateral expansion of branches of the overstorey trees into openings lead to rapid recovery of litterfall in partial cuts. Vigorous suckering of aspen following stand replacing disturbance also allows for rapid foliar biomass re-establishment (Lieffers et al., 2002). Nine years following clear-cutting, the C flux through leaf litterfall was half that of control stands, but bound to increase in subsequent years and reach values comparable to those of mature stands (Klemmedson et al., 1990; Hughes & Fahey, 1994), as we expected in our hypotheses. Such a rapid resumption has also been observed in previous studies (Covington & Aber, 1980; Hendrickson, 1988; Lee et al., 2002). Rapid litterfall recovery contributes to C sequestration in the soil.

3.5.4. Litter quality and decomposition of wood and leaf litter after harvesting

Deadwood and leaf litter have very distinct chemical characteristics and decomposition patterns. Deadwood is characterised by a higher C:N ratio and higher lignin and cellulose contents, whereas leaf litter has higher tannin and alkyl C content (Strukelj et al., 2012, Chapitre I). Non-linear mixed-effects models yielded significantly higher asymptote value (*i.e.*, lower maximum decomposition limits) for leaf litter than for wood of aspen. Despite its higher lignin content, aspen deadwood exhibited very low decomposition limits. In contrast, the higher C sequestration potential of leaf litter (Strukelj et al., 2012, Chapitre I) could be linked to higher concentrations of low-molecular-mass N compounds, such as ammonium and amino acids (Berg, 2000; Cotrufo et al., 2013), as well as higher labile water-soluble constituents (e.g., sugars, amino acids, and phenols) that are degraded more rapidly. These characteristics could lead to relatively higher accumulations of microbial products and concomitant stable soil organic matter formation (Cotrufo et al., 2013).

Immediately following clear-cutting and the 2/3 partial cut, the forest floor was replenished by high input of deadwoods, whereas leaf litter inputs mainly occurred after 3 years. The 1/3 partial cut and control had a greater balance of inputs between leaf litter and deadwood. This response would subsequently have an effect upon the decomposition of forest floor, the chemical heterogeneity and C retention characteristics of the soil.

Forest harvesting generally increases air and soil temperature (Seastedt & Crossley, 1981; O'Connell, 1987; Moroni & Zhu, 2012), due to increased ground surface exposure to incident solar radiation (Barg & Edmonds, 1999; Prévost & Pothier, 2003). Also, soil moisture is increased, due to lower evapotranspiration rate. Changes in both properties would be expected to increase rates of decomposition. However, the decay rate of leaf litter in clear-cut stands was lower than that observed under partial harvesting and in the control stands, despite similar maximum decomposition limits (Fig. 3.4) and higher soil moisture contents (Brais et al., 2004). Lower decomposition rates have also previously been reported for clear-cuts when compared with control stands and partial cuts for boreal mixedwood stands (Lee et al., 2002) and for other forests (Prescott, 1997). This response could be attributed to decreases in soil fungal biomass and densities of microarthropods, which contribute to litter comminution, modification of the substrate, selective grazing, and microbial stimulation (Seastedt & Crossley, 1981). Effects of harvesting on decomposition should be exerted over the short-term, given that with increase of shading by regeneration, microclimatic and biological conditions should rapidly return to pre-cut levels (O'Connell, 1987; Blair & Crossley, 1988).

Compared to natural stands, partial cutting has been shown to decrease microbial biomass (Lindo & Visser, 2003) and decomposition rates (Prescott, 1997). Yet, previous studies that were conducted in the same or in similar stands reported minor effects of partial cutting on microclimate (Brais et al., 2004), macrofauna (Brais et al., 2013), and microorganisms (Kebli et al., 2012). This could explain the similar decomposition patterns observed here between natural and partially harvested stands. Then, contrary to what we expected, an increasing level of harvesting did not result in an increase of the decay rates and maximum decomposition limits of woody and foliar litters.

3.5.5. Soil carbon pools after harvesting

The organic matter pools of the forest floor and mineral soil are controlled by the balance between C inputs through rhizodeposition, leaf litter and deadwood, and the release of C by respiration and leaching (Jandl et al., 2007). Forest floor C pool increased in all treatments, likely resulting from two different processes: changes in litter quality with natural succession from hardwood to softwood species in control and partially harvested stands (Paré et al., 1993), and inputs of logging slash in harvested stands.

During the nine years following treatments, the forest floor and mineral soil C pools of partially harvested stands remained similar to those of the control stands. The large inputs of harvesting debris may have compensated the decrease in leaf litterfall that had been incurred through partial cutting (de Wit & Kvindesland, 1999), despite the lowered stability of C forms that originated from wood and the higher DW:LL ratio of C fluxes in the harvested stands. Our results were similar to those of Lee et al. (2002), who did not find an effect of partial cutting on the forest floor of boreal mixedwood stands 7 years after harvesting.

In clear-cut stands, the high input of logging slash and crushing of well-decomposed debris during harvesting (Brais et al., 2004) could explain the presence of higher forest floor C concentrations and C pools, and the higher lignic forest floor C pool (see Table 2.1). After harvesting, C fluxes to forest floor were mainly limited to leaf litter, a trend that is expected to continue for some decades. The observed decrease in decomposition rate may also contribute to increased C content in forest floor. Although many studies have reported a decline in forest floor mass 5 to 15 years following clear-cutting (Covington, 1981; Federer, 1984; Brais et al., 1995), due to accelerated decomposition and decreases in wood and leaf litter inputs, increases in forest floor mass the first year following treatment has also commonly reported (Johnson et al., 1985; Mattson & Swank, 1989). Over the longer term, the DW:LL ratio should decrease in clear-cuts, which in turn might promote soil C sequestration. Further studies are necessary to assess the longevity of residual organic matter and the nature of compounds that leach into mineral soil (Cotrufo et al., 2013).

Mineral soil is a major C storage pool, which is supplied by the decomposition of organic matter from forest floor. Following clear-cutting, losses of C from the forest floor that result from increased leaching of dissolved organic C has been commonly reported; this DOC consists of mainly lignin-derived compounds (Dai et al., 2001; Piirainen et al., 2002; Kalbitz et al., 2004). Leached C is transferred to the mineral soil, where it is largely retained and resistant to decomposition (Piirainen et al., 2002; Kalbitz et al., 2004). Yet, higher forest floor C content following clear-cutting had no impact on mineral soil C content. Few effects of harvesting on mineral soil C have been found for hardwood forests (Mattson & Swank, 1989; Johnson, 1992; Johnson & Curtis, 2001; Nave et al., 2009), in contrast to coniferous forests (Johnson & Curtis, 2001).

Despite differences in the quality of litter inputs among the harvesting treatments, the C:N ratio of forest floor and mineral soil was not affected by harvesting treatment (Black & Harden, 1995), contrary to what we expected. Kranabetter & Coates (2004) likewise found few effects of partial and clear-cutting on the C:N ratio of mineral soil, but they observed a weak decrease in the C:N ratio of the forest floor. During litter decomposition, the preferential loss of easily degradable compounds (e.g., protein, starch, cellulose), the persistence of recalcitrant compounds (lignin, alkyl C compounds), and the formation of microbial products (Cotrufo et al., 2013) would lead ultimately to convergence in litter chemical composition (Wickings et al., 2012). All compounds would necessarily pass through the same physiological "funnel," due to a limited set of biochemical pathways during decomposition (Fierer et al., 2009).

3.6. Conclusion

Carbon dynamics after partial cutting conserved many characteristics of natural stands. In particular, leaf litter and deadwood inputs, decomposition patterns, snag recruitment, the distribution of logs within decay and size classes, and the content of forest floor and mineral soil in partial cuts were close to those observed in control stands. However, the two methods of partial cutting that were used had strong implications for C dynamics. The 2/3 partial cut resulted in a large recruitment of deadwood immediately following harvesting, while recruitment of snags was more limited in the 1/3 partial cuts, where the imminent mortality was harvested. In the 2/3 partial cut, aggressive aspen regeneration also fostered C sequestration. In the coming years, deadwood inputs in the 2/3 partial cutting will be closer to those observed in clear-cuts. Clear-cutting strongly altered deadwood inputs, and produced large amounts of small fresh debris, which decompose quickly and become integrated into the forest floor, whereas partial cutting created more diverse types of dead organic matter, which allowed for longer C retention. In summary, harvesting prescriptions had large impacts on C pools and fluxes. Live biomass, snag and downed log C pools were the components that were most affected by the harvesting treatments, while the forest floor and mineral soil appeared to be more resilient. Interesting, net ecosystem C losses that are commonly assumed post-harvest were only found in the most intensive removal treatments, viz., the clear-cut and 2/3 partial cut. Diversifying harvesting prescriptions, as proposed by ecosystem management, could have important implications, both for C sequestration at the landscape level and at the site level for conserving high and continuous deadwood inputs, which would decompose and become slowly integrated into the forest floor layer.

3.7. Acknowledgements

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CONCLUSION GÉNÉRALE

Cette thèse, réalisée dans le cadre du projet SAFE de la forêt d'enseignement et de recherche du lac Duparquet, a permis d'approfondir plusieurs aspects de la contribution du bois mort à la rétention du carbone (C) dans un contexte d'aménagement écosystémique. Par rapport aux études précédentes, la thèse a appréhendé la séquestration du C dans le bois mort de façon plus globale, et porté un intérêt sur des aspects moins documentés de la dynamique du C dans les écosystèmes forestiers, notamment l'évolution de la nature des composés carbonés au cours de la décomposition du bois mort, ainsi que les effets des coupes partielles sur la dynamique du bois mort. La comparaison de la dynamique du bois mort avec celle des litières de feuillage constituait une approche intéressante pour mettre en évidence l'importance du réservoir de C dans le bois mort. La première partie de cette conclusion consiste donc à présenter l'intérêt de la démarche utilisée, ainsi que les principaux résultats. La deuxième partie poursuivra avec les perspectives de recherche et les applications.

4.1. Principaux résultats

4.1.1. Patron de décomposition dans le bois mort

Nous avons décrit la décomposition par un modèle exponentiel négatif avec asymptote. Le modèle exponentiel négatif avec asymptote inclut deux paramètres, le taux de décomposition et la limite maximale de décomposition. La limite maximale de décomposition serait, selon Prescott (2005), le paramètre le plus important pour évaluer la séquestration du C. Cependant, nos études ont mis en évidence que le taux de décomposition était aussi pertinent, notamment pour le bois mort qui nécessite une longue période pour atteindre sa limite de décomposition.

L'utilisation de sacs de litières a permis de mettre en relation les changements chimiques au cours de la décomposition avec la perte de masse jusqu'à la limite maximale de décomposition, et donc de mieux comprendre les implications de la nature chimique du bois mort et du feuillage pour la séquestration du C. L'échantillonnage le long d'une chronoséquence de chicots et de billes au sol a aussi permis de préciser la composition chimique du bois mort pour des stades de décomposition plus avancés que ceux obtenus avec les sacs de litières.

Ainsi, le bois mort se décomposait plus lentement que les litières de feuillage. L'hypothèse principale, qui supposait que la décomposition du bois mort atteindrait une limite maximale supérieure aux litières de feuillage, se vérifiait dans le cas du tremble, mais pas pour les conifères. Les différents types de litières ont montré différents mécanismes de rétention du C. Les litières de feuillage retiendraient le C en atteignant rapidement une faible limite maximale de décomposition et en formant une matière récalcitrante riche en composés alkyl et en hydrates de carbone. Au contraire, le bois mort retiendrait le C par sa décomposition lente, et permettrait la préservation de lignines et d'hydrates de carbone dans les billes bien décomposées.

Le bois mort de conifères se décomposait plus lentement que les espèces feuillues, et pourrait atteindre une limite maximale de décomposition plus faible. De plus, la décomposition du bois mort de conifères générait une matière organique plus riche en lignines et en composés alkyl, qui serait plus stable, confirmant l'hypothèse principale. Le bois mort de conifères aurait donc un plus grand potentiel de séquestration du C que celui des feuillus. En particulier, le bois mort de tremble avait le plus faible potentiel de séquestration du C, du fait de sa faible teneur en lignines, sa limite maximale de décomposition élevée et son taux de décomposition élevés. Au contraire, le bois mort de pin gris minéralisait lentement et générait la matière organique la plus riche en lignines et en composés alkyl, donc la plus récalcitrante.

Les composés alkyl incluraient des produits microbiens (protéines, lipides), de la cutine, des cires et des résines. Ils sont considérés comme très récalcitrants (Lorenz et al., 2007). Au contraire, les lignines auraient un taux de recyclage élevé d'après les études récentes (Thevenot et al., 2010). La teneur élevée en lignines dans les billes bien décomposées et dans la couverture morte lignique impliquerait pourtant leur préservation à plus long terme. Cette préservation pourrait être liée aux conditions anoxiques générées par une teneur en eau élevée dans les billes bien décomposées. De plus, la nature initiale des lignines, leur oxydation et leurs réactions avec les composés azotés au cours de la décomposition pourraient favoriser la récalcitrance des lignines.

Ainsi, le bois mort et les litières de feuillage situés au-dessus des couches FH de la couverture morte avaient une forte hétérogénéité chimique dépendamment de l'espèce. Les débris de bois mort présentaient aussi une forte hétérogénéité chimique en fonction de leur stade de décomposition. Les différences s'estompaient dans la couche FH, mais subsistaient des différences entre la couverture morte alignique et la couverture morte lignique. Ainsi, le bois mort et la couverture morte lignique contribuent fortement à la diversité chimique de la matière organique du sol, notamment au niveau spatial, et favoriseraient la diversité des décomposeurs.

4.1.2. Quantité totale de C dans le bois mort

Afin de mettre en évidence la contribution du bois mort à la séquestration du C, la démarche a consisté à mesurer la quantité du bois mort et des litières de feuillage sur une période de 9 ans dans des peuplements naturels. Les peuplements étudiés, issus du feu de 1923, étaient dominés par le tremble, et atteignaient ou devraient atteindre prochainement l'âge de sénescence. Dans ces peuplements, le bois mort était constitué de billes au sol bien décomposées issues du feu de 1923 et du peuplement précédent ce feu, et également des chicots et des billes issus de la mortalité par auto-éclaircie des arbres co-dominants.

La production de bois mort était légèrement supérieure à celle des litières de feuilles, mais le bois mort de tremble se décomposait plus lentement et formait ainsi un plus large réservoir de C. Sous forme de chicots, de billes au sol et de bois enfoui, la matière organique issue du bois mort représentait 21.5 MgC/ha, soit 59 % de la nécromasse. La quantité de bois mort serait donc supérieure à la quantité trouvée avant le processus d'auto-éclaircie mais inférieure à la quantité qui se produirait avec la mortalité subite des arbres dominants, qui représentaient 100 MgC/ha.

Tout cela souligne l'importance du réservoir de C dans le bois mort dans les peuplements de tremble étudiés en particulier, et aussi dans la sapinière à bouleau blanc en général.

- Quantité de C séquestré dans les chicots

Les changements chimiques dans les chicots, peu documentés jusque-là (Fukasawa et al., 2009), étaient similaires à ceux des billes au sol, mais prenaient place plus lentement. Cependant, les chicots tombaient avant d'atteindre la composition chimique des billes bien décomposées. La plus lente décomposition des chicots permettait une plus longue séquestration du C. Dans les peuplements étudiés, les chicots correspondaient à 5.7 MgC/ha, soit 27 % du bois mort. La mortalité du tremble générant principalement des chicots, la faible proportion de chicots indiquait qu'une partie significative du bois mort de notre peuplement était issue d'une mortalité ancienne.

- Quantité de C séquestré dans le bois mort enfoui (couverture morte lignique)

Le bois enfoui représente un réservoir de C non négligeable, estimé à 3.6 MgC/ha dans les peuplements étudiés, ce qui correspondait à 17% du bois mort. Bien que le bois mort, sous formes de billes au sol et de chicots, forme un plus grand réservoir de C que les litières de feuilles avant leur intégration dans la couche FH de la couverture morte, il constituait seulement 19 % de la couverture morte. Cela résultait de la décomposition plus lente et de la limite maximale de décomposition plus élevée pour le bois mort que pour les litières de feuilles. Si on considère que le bois mort s'intègre dans la couverture morte après avoir atteint la limite maximale de décomposition, cela signifierait que 9 à 27 % du bois mort frais deviendrait enfoui, dépendamment de l'espèce (chapitres I-III), alors que 22 à 30 % des litières de feuilles entreraient dans la couche FH de la couverture morte (chapitre I).

Plusieurs éléments tendraient à montrer que le bois enfoui serait principalement composé de conifères. D'une part, la composition chimique des billes bien décomposées de conifères étaient très proches de celle du bois enfoui. D'autre part, les billes bien décomposées de tremble et de bouleau blanc atteignaient des densités très faibles par rapport aux billes de conifères. La décomposition du bois mort de conifères atteindrait une limite maximale de décomposition plus faible que la décomposition des espèces feuillues. Ainsi, la matière organique issue de la décomposition des conifères serait suffisamment stable pour intégrer la couverture morte avant d'être décomposée, tandis que le bois mort de feuillus qui se décompose plus rapidement aurait le temps de se décomposer en quasi-totalité, avant d'atteindre une teneur en eau trop élevée pour générer des conditions anoxiques et avant d'être intégré dans la couverture morte.

4.1.3. Effets des coupes totales et partielles

La diversification des prescriptions de récoltes proposée par l'aménagement écosystémique pourrait avoir des implications pour la séquestration du C à l'échelle du paysage et du peuplement. Par rapport aux peuplements naturels, les coupes totales ont fortement altéré la dynamique du C. L'effet immédiat était la production d'une importante quantité de débris de coupes, qui sont passés du stade frais au stade bien décomposé dans les 9 ans que durait cette étude. Ces débris pourraient se minéraliser en grande partie (chapitre III), et aussi participer à l'augmentation du réservoir de la couverture morte. Après les coupes totales, les apports de C au sol se faisaient principalement via les chutes de litières de feuillage, qui avaient récupéré de moitié 9 ans après coupes. À court et moyen termes, les coupes totales favoriseraient donc les litières à décomposition rapide, à faible limite maximale de décomposition, et générant une matière organique récalcitrante riche en composés alkyl. À long terme, l'absence de production de larges débris après coupes diminuerait le réservoir de C de la couverture morte et modifierait sa qualité.

Les coupes partielles produisaient également des débris de coupes, mais la mortalité progressive des arbres après coupes favorisait le recrutement continu de bois mort, contrairement aux coupes totales. Les gros débris de bois mort permettaient ainsi la rétention du C par leur décomposition lente, notamment dans les chicots. Après coupes partielles, les chutes de litières de feuilles récupéraient rapidement les valeurs des peuplements naturels. La décomposition du bois mort génèrerait une matière organique et une couverture morte caractérisées par une teneur en lignines et un rapport C:N élevés, ce qui contrasterait avec la décomposition des litières de feuilles qui formait une matière riche en composés alkyl et avec un rapport C:N faible. Les coupes partielles conservaient donc de nombreuses caractéristiques des peuplements naturels, et n'altéraient pas la dynamique de décomposition des litières ni les réservoirs de C de la couverture morte et du sol minéral. De plus, les coupes partielles maintenaient le recrutement en conifères, qui génèrent des litières plus récalcitrantes que les feuillus.

Ainsi, les coupes totales homogénéisent la qualité des composés carbonés, tandis que les coupes partielles favorisent une grande hétérogénéité des composés carbonés du sol, ce qui pourrait avoir des implications pour la biodiversité, l'activité des organismes décomposeurs, la productivité et la séquestration du C dans les peuplements.

4.2. Limites de recherche

Les sacs de litières sont une méthode qui a permis d'apporter une meilleure compréhension de la décomposition et des facteurs qui la contrôlent. Un inconvénient de cette technique est l'exclusion des millipèdes, des isopodes, et des gros vers de terre (Swift et al., 1979), qui pourraient favoriser d'une part la minéralisation de la matière organique, et d'autre part la stabilisation de la matière organique dans le sol minéral (Wolters, 2000). Un autre inconvénient de cette méthode est de considérer comme non minéralisée la masse restante dans le sac, et non pas le matériel perdu par fragmentation ou lessivage (Cotrufo et al., 2013), ni le carbone transféré par les champignons ou les invertébrés en dehors du sac (Wolters, 2000; Boberg et al., 2010). Tous ces facteurs pourraient donc influencer les pertes de masses au cours de la décomposition et donc les modèles utilisés pour la décrire.

Les chronoséquences permettent l'étude de la décomposition du bois mort, qui, en conditions naturelles, se déroule sur des dizaines d'années. Le principal inconvénient de la méthode de la chronoséquence est qu'avec la substitution du temps par l'espace, les conditions environnementales qui changent dans le temps et dans l'espace peuvent influencer les résultats (Pickett, 1989). De plus, certaines billes pourraient se décomposer totalement et, par conséquent, ne pas être représentées dans la chronoséquence.

Les effets des coupes sur les peuplements de tremble ne peuvent pas être généralisés à des peuplements surannés ou des peuplements de conifères. De même, seulement deux types de coupes partielles ont été testés. La taille des parcelles pourraient influencer certains résultats, du fait des effets de lisières.

4.3. Perspectives de recherche et applications

La limite maximale de décomposition pourrait constituer un facteur important de la séquestration du C et de la préservation des lignines lors de la décomposition du bois mort et les litières de feuillage. À cette limite, la matière organique résiduelle est riche en azote et contient des composés récalcitrants non décomposés, des produits de la décomposition et des produits microbiens. Bien que les modèles de décomposition avec asymptote représentent les données plus adéquatement que les autres modèles, il serait important de vérifier l'existence de cette limite, qui est souvent considérée comme un artéfact de la méthode des sacs de décomposition. La matière organique du sol constitue la principale source d'énergie pour les organismes décomposeurs. La limite maximale de décomposition aurait donc de fortes implications pour ces organismes décomposeurs, notamment après coupes totales, où les apports de litières sont réduits. De plus, il serait intéressant de vérifier si les différentes limites trouvées dans les différents types de litières permettent d'estimer la participation de ces litières à la couverture morte.

La décomposition et l'humification de la matière résiduelle issue de la décomposition du bois mort et des litières de feuilles devraient aussi être étudiées de façon plus approfondie. On pourrait comparer les taux de décomposition des couvertures mortes alignique et lignique, et évaluer les effets des racines des plantes qui peuvent s'y développer et de la macrofaune, qui pourraient influencer cette seconde phase de la décomposition. Plus précisément, il serait important d'évaluer la préservation et le taux de recyclage des lignines et des hydrates de carbone dans la couverture morte lignique, et aussi de déterminer si ces hydrates de carbone proviennent des microorganismes ou des celluloses initiales du bois. L'utilisation de la modélisation permettrait de vérifier si les taux de décomposition de la matière résiduelle sont réalistes, afin de valider l'existence de la limite.

Dans les peuplements étudiés, les 10 premiers centimètres du sol minéral était un large réservoir de C, séquestrant l'équivalent de 37.9% du C de la matière organique morte superficielle. Cela laisse entrevoir l'importance du sol minéral dans son ensemble. Le lessivage des composés organiques dissous produits lors de la décomposition, ainsi que le transfert de C par les racines dans le sol minéral pourraient constituer des facteurs majeurs de la dynamique du C (Clemmensen et al., 2013). Le lessivage des composés organiques dissous devrait être évalué et comparé entre le bois mort et les litières de feuillage.

La présence de bois mort avec un rapport C:N élevé (contenu en C élevé) pourrait permettre la décomposition de la matière organique stable de faible rapport C:N mais riche en nutriments. Cela serait un facteur supplémentaire expliquant la faible décomposition dans les coupes totales. L'hétérogénéité chimique de la couverture morte générée par la présence de bois enfoui pourrait aussi permettre de conserver une plus grande diversité de microorganismes, et donc favoriser la décomposition, la libération des nutriments et la productivité de l'écosystème.

Les effets des coupes sur la qualité des litières et la qualité de la matière organique du sol ont été inférés à partir des connaissances établies dans des peuplements naturels. Il serait important d'étudier directement la composition chimique de la couverture morte après coupes totales et partielles, afin de vérifier les assertions.

Dans un cadre d'aménagement écosystémique, les brûlages dirigés pourraient faire partie intégrante des traitements appliqués et génèreraient la formation de composés pyrogéniques, notamment de charbons. Ces charbons, considérés comme très récalcitrants, pourraient influencer la décomposition des débris non carbonisés, et donc avoir une influence majeure sur la séquestration du C. D'une manière générale, les connaissances relatives à la quantité de charbons et à leur effet sur le C devraient être approfondies.

Le type de coupes a de fortes implications pour la dynamique du bois mort et la séquestration du C dans le peuplement résiduel. Favoriser le bois mort dans un peuplement pourrait donc se faire par la mise en place de coupes partielles, laissant des tiges non vigoureuses qui vont avoir une mortalité à court terme et des tiges vigoureuses qui vont former le bois mort à moyen terme, ce qui permettrait un recrutement continu en bois mort. Cela pourra aussi favoriser la rétention du C, notamment en conservant des larges tiges qui vont séquestrer le C par photosynthèse. D'une manière générale, une meilleure connaissance des effets des coupes permettrait de choisir un aménagement adéquat selon les objectifs.

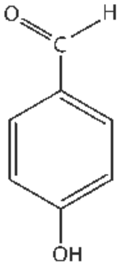
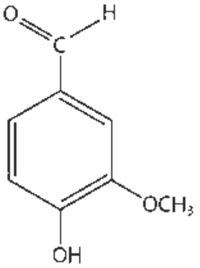
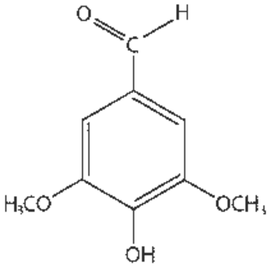
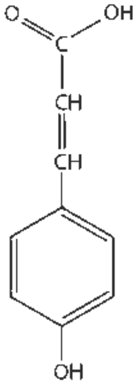
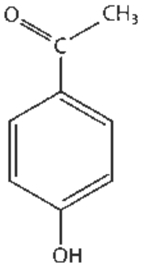
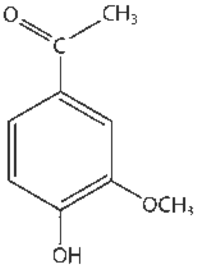
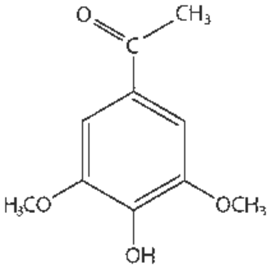
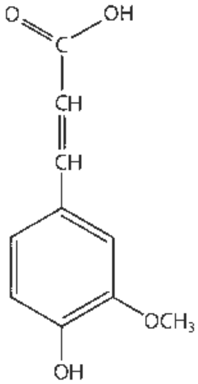
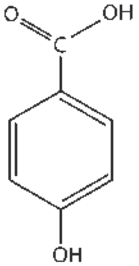
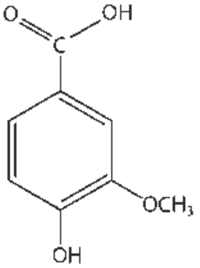
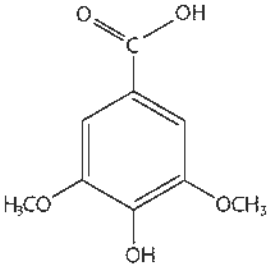
Finalement, les données empiriques récoltées ici, de même que les connaissances apportées sur la dynamique du bois mort, notamment sa décomposition, contribueront à l'amélioration des modèles du C, comme le modèle CBM-CFS, permettant d'améliorer les prédictions des flux de C en forêt boréale canadienne. Des inventaires à plus long terme après coupes partielles et totales permettraient de tester si les coupes partielles favoriseraient la production de bois mort de résineux, et si après coupes totales, la production de bois mort récupérerait et la couverture morte serait altérée.

APPENDICES

Appendix A. Possible assignments of signals in the ^{13}C NMR spectra (from Baldock et al., 1992; Knicker and Lüdermann, 1995; Almendros et al., 2000). Values in parenthesis correspond to chemical shift range (ppm).

Region	**Assignment**
1) Alkyl (0-50)	Methyl groups bound to carbon (13-17). Acetate (21). Methylene groups in aliphatic rings and chains (fatty acids, amino acids, cutin, waxes and resins) (30-32).
2) Methoxyl (50-59)	Methoxyl groups in lignins and hemicelluloses (56-57), C-N of some amino acids (45-65).
3) *O*-alkyl (59-93)	C-2 to C-5 of hexoses (72-73), C-6 of some polysaccharides (62), C-N of some amino acids (45-65), higher alcohols, aliphatic part of lignin structures.
4) Di-*O*-alkyl (93-110)	Di-O-alkyl C, anomeric carbon (C-1) of carbohydrates (103-105), C-2 and C-6 of syringyl units, quaternary aromatic carbons in tannins (105).
5) Aromatic (110-142)	Aromatic C-H and C-C in guaiacyl units (C-2 and C-6) and in non-hydrolysable tannins, olefinic carbons.
6) Phenolic (142-166)	Aromatic C-O (phenolic) and C-N in lignins and hydrolysable tannins.
7) Carbonyl (166-230)	Carboxylic acid, amide, and ester C in lipids, proteins, hydrolysable tannins, degraded lignins, hemicellulose and resin acids(172-176). Aldehyde and ketone C in lignins (198-200).

Appendix B. Lignin monomers extracted by alkaline CuO oxidation: vanillyl phenols, syringyl phenols, p-hydroxy phenols and cinnamyl phenols.

p-Hydroxyl phenols	Vanillyl phenols	Syringyl phenols	Cinnamyl phenols
 *p*-Hydroxybenzaldehyde	 Vanillin	 Syringaldehyde	 *p*-Coumaric acid
 *p*-Hydroxyacetophenone	 Acetovanillone	 Acetosyringone	 Ferulic acid
 *p*-Hydroxybenzoic acid	 Vanillic acid	 Syringic acid	

Appendix C. Integration values of the major C-types (% of Total Area) in the ^{13}C NMR spectra of original and decayed foliar litters and wood blocks.

Litter type	Time of decay (years)	**Alkyl (0-46 ppm)**	**Methoxyl (46-58 ppm)**	***O*-alkyl (58-93 ppm)**	**Di-*O*-alkyl (93-111 ppm)**	**Aromatic (111-142 ppm)**	**Phenolic (142-166 ppm)**	**Carbonyl (166-222 ppm)**
Aspen leaves	0	24.61 (1.61)	3.67 (0.06)	43.49 (0.49)	10.44 (0.24)	6.89 (0.36)	4.29 (0.27)	6.60 (0.22)
	1	28.47 (1.09)	4.92 (0.26)	37.89 (1.81)	9.08 (0.4)	7.88 (0.42)	4.33 (0.26)	7.44 (0.49)
	3	25.40 (3.08)	6.47 (0.19)	35.40 (2.06)	8.62 (0.63)	9.65 (0.32)	5.05 (0.41)	9.42 (0.34)
	6	23.36 (2.05)	7.02 (0.08)	37.12 (1.22)	8.79 (0.55)	9.99 (0.13)	4.89 (0.45)	8.82 (0.23)
Spruce needles	0	15.91 (0.23)	3.91 (0.25)	52.06 (0.32)	10.34 (0.07)	9.03 (0.16)	4.59 (0.20)	4.16 (0.31)
	1	19.69 (0.18)	4.48 (0.12)	46.99 (0.66)	9.69 (0.15)	9.41 (0.39)	4.49 (0.14)	5.25 (0.32)
	6	20.69 (0.85)	6.22 (0.43)	39.76 (0.34)	8.50 (0.20)	11.74 (0.51)	5.52 (0.26)	7.58 (0.40)
Fir needles	0	31.53 (0.23)	4.56 (0.05)	38.66 (0.04)	7.39 (0.08)	7.83 (0.04)	4.31 (0.05)	5.72 (0.08)
	1	34.23 (0.49)	5.82 (0.25)	32.84 (0.44)	6.60 (0.05)	9.45 (0.44)	4.52 (0.12)	6.55 (0.33)
	5	29.53 (0.53)	6.70 (0.22)	33.91 (0.41)	6.82 (0.09)	10.02 (0.43)	4.38 (0.27)	8.63 (0.33)
Aspen wood	0	6.57 (0.57)	5.97 (0.26)	62.92 (0.74)	14.15 (0.15)	4.83 (0.35)	2.63 (0.17)	2.95 (0.20)
	1	6.58 (0.45)	6.25 (0.23)	63.84 (0.96)	14.15 (0.17)	4.29 (0.40)	2.37 (0.24)	2.52 (0.31)
	3	8.11 (0.85)	7.39 (0.70)	59.00 (2.85)	13.35 (0.32)	5.68 (1.01)	3.20 (0.52)	3.25 (0.63)
	6	9.36 (1.14)	7.33 (1.04)	56.62 (3.63)	12.96 (0.49)	6.49 (1.04)	3.46 (0.57)	3.77 (0.45)
Spruce wood	0	4.67 (0.11)	6.06 (0.05)	61.93 (0.43)	11.72 (0.07)	9.62 (0.28)	4.10 (0.17)	1.91 (0.11)
	1	5.01 (0.45)	6.13 (0.06)	62.03 (0.28)	11.69 (0.09)	9.43 (0.16)	3.82 (0.09)	1.88 (0.15)
	6	6.15 (1.07)	6.44 (0.50)	59.87 (1.33)	11.29 (0.36)	9.92 (0.38)	3.99 (0.28)	2.36 (0.32)
Fir wood	0	4.81 (0.33)	6.63 (0.18)	60.34 (1.06)	11.24 (0.25)	10.47 (0.56)	4.43 (0.24)	2.08 (0.21)
	1	4.84 (0.41)	6.64 (0.12)	60.64 (0.32)	11.29 (0.14)	10.38 (0.21)	4.37 (0.16)	1.84 (0.08)
	5	5.26 (1.12)	7.20 (1.32)	56.36 (6.82)	10.53 (1.41)	12.57 (3.36)	5.40 (1.76)	2.67 (0.68)

Note: Mean values (n = 3) and standard deviations (in parentheses).

Appendice D : Description des quatre types de peuplements, où les études de cette thèse ont été réalisées

Type peuplement	**Pin gris**	**Tremble (ASPEN)**	**Mixte (MIXED)**	**Suranné (OLD)**
Année du dernier feu	1923	1923	1910	1760
Surface terrière (m^2/ha)	33.4	43.9	42.3	18.6
Composition en espèces (% de surface terrière)				
Peuplier faux-tremble	3.3	92.4	79.9	3.6
Peuplier baumier	0	1.6	0.2	1.4
Bouleau à papier	6.8	2.6	1.8	56.4
Pin gris	80.1	0.4	0	0
Épinette blanche	2.1	2.0	9.8	27.6
Épinette noire	3.3	0.2	4.4	0.6
Sapin baumier	4.5	0.9	3.9	10.4

Appendice E : Description des peuplements, où les chicots de la chronoséquence ont été échantillonnés

Type peuplement	**Pin gris**	**Tremble**	**Bouleau**	**Tremble**	**Mixte**	**Suranné**	**Suranné**	**Total**
Description des peuplements								
Feu	1923	1923	1923	1916	1870	1797	1760	
Nombre parcelles (400 m^2)	3	4	4	1	1	1	2	
Nombre de chicots échantillonnés par espèce et par type de peuplement								
Peuplier faux-tremble		13		4	3			20
Bouleau à papier	2	4	6			1	7	20
Pin gris	19	2						21
Sapin baumier	1	5	7			1	9	23
Nombre total de chicots								84

Appendice F : Types de peuplements, où les billes de la chronoséquence ont été échantillonnées

Type peuplement	**Pin gris**	**Tremble**	**Mixte**	**Suranné**	**Total**
Nombre de billes échantillonnées par espèce et par type de peuplement					
Peuplier faux-tremble		28	13		41
Bouleau à papier		12	1	11	24
Pin gris	12	20	1	5	38
Épinette spp.		4	16	5	25
Sapin baumier		1	8	27	36
Nombre total de billes					164

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