LES CAUSES ET LES CONSÉQUENCES DE LA MIXITÉ ENTRE LE PEUPLIER FAUX-TREMBLE ET LE PIN GRIS EN FORÊT BORÉALE : UN REGARD SUR LES PROPRIÉTÉS ÉDAPHIQUES

par

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Le 18 mai 2011

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SOMMAIRE

Les peuplements mixtes (formés à la fois de feuillus et de conifères) font partie de la dynamique naturelle de la forêt boréale québécoise. Toutefois, les pratiques forestières au Québec ont eu comme conséquences de séparer les essences incluses dans ces peuplements. Hors, de récentes études suggèrent que la gestion forestière des peuplements mixtes pourrait procurer des avantages tant économiques, qu'écologiques. Cependant, nous connaissons encore mal la dynamique naturelle menant à la formation de peuplements mixtes d'essences pionnières telles que le peuplier et le pin gris et encore moins les conséquences qu'une telle mixité peut avoir sur les propriétés physico-chimiques et biologiques du sol.

Cette thèse de doctorat a, comme principal objectif, de mieux comprendre les causes et les conséquences souterraines de la mixité forestière entre le peuplier faux-tremble et le pin gris dans la forêt boréale abitibienne. En premier lieu j'évalue l'hypothèse que la fertilité du matériau parental détermine l'occurrence des peuplements mixtes de peuplier et de pin gris. Un recensement des peuplements mixtes dans le nord-ouest de l'Abitibi ainsi qu'une expérience contrôlant la fertilité du sol ont permis de confirmer cette hypothèse. En ce sens, les peuplements mixtes de peuplier et de pin gris sont exclusifs aux dépôts argileux plus riches que les dépôts sableux tels le till. En second lieu, j'évalue les conséquences de la mixité forestière sur les propriétés édaphiques, notamment, la composition et la stabilité des communautés microbiennes du sol. Ainsi, je suppose que la plus grande diversité végétale des peuplements mixtes favorise la stabilité de la biomasse des communautés microbiennes qui y sont associées. J'ai donc mesuré trois indices de stabilité de la biomasse microbienne soient : la résistance, la résilience et la tolérance. Mes résultats indiquent dans un premier temps que les communautés microbiennes des peuplements mixtes sont plus résistantes que celles des peuplements purs et, dans un deuxième temps, que la tolérance des communautés microbiennes des peuplements mixtes est assurée dans une plus grande diversité de conditions par opposition aux communautés microbiennes provenant des peuplements purs. Quant à la résilience, cet indice était plus fortement déterminé par la fertilité du matériau parental que par la composition végétale. En troisième et dernier lieu, j'explore les conséquences souterraines de frontières abruptes entre les peuplements purs de peuplier et de pin gris. Même si dans de tels cas, il n'y a pas de mixité forestière, je présente des évidences que de tels écotones constituent des écosystèmes uniques en ce qui a trait à leurs propriétés souterraines et que le peuplier, par la dispersion de sa litière, possède une plus forte influence que le pin gris sur ces propriétés, notamment, la composition des communautés microbiennes.

Les résultats et les conclusions découlant de ce projet de doctorat permettront, dans un premier temps de mieux comprendre la dynamique naturelle de la forêt boréale, et dans un second temps, de comprendre les conséquences souterraines de l'hétérogénéité du paysage de la forêt boréale. Finalement, ces résultats pourraient justifier le développement de pratiques sylvicoles préservant la diversité du paysage forestier québécois.

Mots clés : Peuplier faux-tremble, pin gris, peuplement mixte, communauté microbienne, propriétés édaphiques, forêt boréale, biodiversité

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TABLE DES MATIÈRES

LISTE DES TABLEAUX

CHAPITE 1

Tableaux tirés de Royer-Tardif et Bradley (For. Ecol. Manag. à soumettre)

CHAPITRE 2

Tableaux tirés de Royer-Tardif et al. (Soil Biol. Biochem. 42 : 813-821)

LISTE DES FIGURES

CHAPITE 1

CHAPITRE 2

CHAPITRE 3

INTRODUCTION

Les activités humaines ont longtemps exploité, et exploitent toujours, les écosystèmes naturels aux dépends de leur intégrité écologique, ce qui se solde actuellement par une extinction massive des espèces faunique et floristiques à l'échelle planétaire. Il est estimé que cette perte de biodiversité s'accomplit à un taux 1000 fois plus rapide que lors des précédentes extinctions massives ayant ponctué l'histoire de la terre (May, 2011). Cette situation représente une préoccupation majeure pour les écologistes, et ce, pour deux raisons. D'une part, nous comprenons encore mal les facteurs déterminant les niveaux de biodiversité observés tant à l'échelle globale que locale. Certes, plusieurs variables explicatives ont été identifiées, telles que la productivité et la superficie des écosystèmes, mais les mécanismes les reliant à la biodiversité sont encore insuffisamment compris (Currie, 1991; Rosenzweig, 1995; Partel *et al.*, 2010). D'autre part, nous commençons à peine à comprendre le rôle de la biodiversité dans le fonctionnement des écosystèmes. En ce sens, plusieurs études depuis les deux dernières décennies ont observé une diminution de la performance et de la stabilité des écosystèmes soumis à une perte de biodiversité (Eisenhauer *et al.*, 2010; Loreau *et al.*, 2001; Naeem *et al.*, 1994; Quijas *et al.*, 2010; Tilman, 1999).

La forêt boréale québécoise n'échappe pas à la tendance mondiale de perte de biodiversité. L'exploitation forestière industrielle combinée aux courtes révolutions des coupes a modifié profondément le paysage du sud de la forêt boréale en causant l'homogénéisation en âge et en composition des peuplements forestiers (Drapeau *et al.*, 2000; Laquerre, 2007). Dans cette forêt, la dynamique forestière est naturellement gérée par la récurrence des feux de forêt et des épidémies de tordeuse des bourgeons d'épinette (Bergeron, 2000). L'action conjointe de ces deux perturbations favorise le développement d'une mosaïque forestière composée de peuplements purs de résineux et de feuillus, mais également de peuplements mixtes. Ces derniers comprennent à la fois des essences feuillues intolérantes à l'ombre, autrefois peu recherchées par l'industrie forestière, et des conifères possédant une plus forte valeur commerciale (Bergeron et Harvey, 1997). Toutefois, les pratiques forestières telles que les plantations, le débroussaillage ou les éclaircies pré-commerciales, ont eu tendance à ségréguer ces peuplements menant soit à la formation de peuplements monospécifiques de feuillus ou de résineux, diminuant ainsi la diversité du sud de la forêt boréale (Bergeron et Harvey, 1997; MacPherson *et al.*, 2001; Man et Lieffers, 1999).

Aujourd'hui, la recherche forestière au Québec connaît un intérêt grandissant envers les peuplements mixtes pour trois raisons. Premièrement, depuis les années 1990, les essences décidues intolérantes, jadis éliminées des peuplements mixtes, sont de plus en plus recherchées (Légaré *et al.*, 2005) en raison des nouveaux procédés élaborés afin de traiter leurs fibres (Man et Lieffers, 1999). Deuxièmement, le film *L'erreur boréale* de Richard Desjardins et Robert Monderie (1999) ainsi que le rapport de la Commission Coulombe (Coulombe *et al.*, 2004) ont stimulé les réflexions de la population québécoise quant à l'importance de la biodiversité dans la forêt boréale (Asselin, 2007). Troisièmement, l'industrie forestière au Québec connaît la pire crise économique de son histoire, ce qui suscite des craintes quant à la certification de nos pratiques forestières pour la vente de nos produits sur les marchés internationaux (Asselin, 2007; Coulombe *et al.*, 2004).

À l'heure actuelle, le ministère des ressources naturelles et de la faune du Québec (MRNF) élabore sa future stratégie d'aménagement durable des forêts (SADF) dans laquelle les questions d'intégrité écologique et de biodiversité forestière seront adressées (MRNF, 2010b). Les pratiques sylvicoles devront désormais émuler les processus naturels régissant la forêt boréale afin d'en assurer, à long terme, l'intégrité écologique et la résilience, mais également les bénéfices sociaux et économiques que les québécois(es) en retirent. De telles pratiques sont désignées sous le terme d' « aménagement écosystémique » (Gauthier *et al.*, 2008). Toutefois, nous sommes loin de comprendre parfaitement l'ensemble des processus naturels de la forêt boréale et certaines questions demeurent sans réponse, en particulier en ce qui a trait aux peuplements mixtes. Ces questions rejoignent les deux grands enjeux de la biodiversité à l'échelle mondiale, à savoir: 1) quels sont les facteurs menant à la formation de peuplements mixtes? et 2) quelles sont les conséquences économiques et écologiques de la mixité forestière?

1) L'origine des peuplements mixtes.

Dans le sud de la forêt boréale, les essences feuillues intolérantes à l'ombre, principalement le peuplier faux-tremble (*Populus tremuloides* Michx) et le bouleau à papier (*Betula papyrifera* Marsh.), sont les premières à s'établir suite à une perturbation majeure comme un feu ou une coupe forestière et dominent la canopée pendant les 100 premières années (Bergeron, 2000). À un stade plus avancé, la mortalité de cette première cohorte de feuillus provoque des ouvertures dans la canopée, ce qui favorise l'émergence d'une seconde cohorte de feuillus intolérants, mais également la croissance des conifères tolérants à l'ombre tels que le sapin baumier (*Abies balsamea* (L.) Mill.), l'épinette blanche (*Picea glauca* (Moench) Voss) et l'épinette noire (*Picea mariana* [Mill.] BSP). Cette succession forestière mène donc, en des âges intermédiaires (100-200 ans), à des peuplements mixtes (Bergeron et Harvey, 1997; Bergeron, 2000). Avec le temps, la régénération des feuillus intolérants se fait de plus en plus rare et les conifères finissent par dominer le peuplement si aucune perturbation majeure ne vient réinitialiser la succession forestière.

Des peuplements mixtes peuvent également survenir en début de succession, car certaines espèces de conifères, dont le pin gris (*Pinus banksiana* Lamb.), sont intolérantes à l'ombre et s'établissent rapidement suite à une perturbation (Rudolph et Laidly, 1990). De tels peuplements mixtes se forment fréquemment entre le pin gris et le peuplier faux-tremble, où l'on observe une codominance de ces deux essences étant donné leur taux de croissance similaire (Longpré *et al.*, 1994). Toutefois, la formation de peuplements mixtes de peuplier et de pin gris n'est pas systématique et ne semble pas gouvernée par la dispersion de ces deux espèces. En effet, ces dernières peuvent soit coexister sous la forme de peuplements mixtes ou bien former des peuplements monospécifiques adjacents avec une parfaite exclusion d'une ou l'autre des espèces de chaque côté d'une frontière distincte (Ste-Marie *et al.*, 2007). Ainsi, il apparaît que la dynamique forestière mène à la formation de peuplements mixtes de peuplier et de pin gris dans certains cas seulement. Connaître les conditions dans lesquelles de tels peuplements mixtes se développent pourrait permettre d'appliquer une gestion réellement basée sur la dynamique naturelle des forêts, i.e. qui favorise la mixité dans les conditions où elle survient naturellement.

Plusieurs études réalisées à une échelle continentale ont démontré que la richesse spécifique des arbres était significativement corrélée à la productivité primaire (Adams et Woodward, 1989; Currie et Paquin, 1987; Francis et Currie, 1998; Storch *et al.*, 2005). Puisque les peuplements mixtes représentent un niveau de diversité supérieur à celui des peuplements purs, il est possible qu'ils soient associés à des conditions favorisant la productivité primaire. À une échelle continentale, cette productivité est fortement liée à des variables climatiques telles que la température ou les précipitations (Currie, 1991). À une échelle plus fine, toutefois, la productivité est plutôt déterminée par la fertilité du sol, elle-même reliée à la texture et la composition du matériau parental (Béland et Bergeron, 1996; Hamel *et al.*, 2004; Paré *et al.*, 2001).

Dans le sud de la forêt boréale abitibienne, on retrouve le peuplier et le pin gris sur deux types de matériaux parentaux, soient le till et l'argile (Longpré *et al.*, 1994; Ste-Marie *et al.*, 2007). Ces matériaux sont un héritage de l'époque glacière qu'a connue le nord-ouest du Québec il y a plus de 10 000 ans (Vincent et Hardy, 1979). Le till est un matériau de débris rocheux non trié, déposé par le retrait des glaciers et possédant une texture grossière. Par contraste, l'argile est composé de sédiments fins provenant des lacs proglaciaires Barlow et Ojibway formés à la marge des glaciers continentaux pendant leur fonte (entre 11500 et 7900 ans AP; Vincent et Hardy, 1979). Étant donné leurs natures contrastantes, le till et l'argile diffèrent dans leur fertilité. Les sols se développant sur argile sont rapportés comme étant plus fertiles que ceux se développant sur till, puisque la fine texture de l'argile lui procure un plus grand pouvoir de rétention de l'eau et des nutriments (Béland et Bergeron, 1996; Paré *et al.*, 2001). De plus, contrairement au till, l'argile est riche en calcium, ce qui permet de tamponner l'acidité du sol et favorise l'activité microbienne ainsi que la minéralisation de nutriments tels que l'azote (Lamarche *et al.*, 2004; Ste-Marie *et al.*, 2007). Par conséquent, il est possible que la fertilité du matériau parental détermine l'occurrence des peuplements mixtes de peuplier et de pin gris.

2) Les conséquences de la mixité forestière

Il a été suggéré que les peuplements mixtes pouvaient procurer certains avantages à l'industrie forestière tout en ajoutant une valeur écologique à la forêt boréale (Bergeron et Harvey, 1997). Puisque les essences forestières diffèrent dans leur utilisation des ressources, telles que la lumière ou les nutriments, les peuplements mixtes pourraient assurer une plus grande productivité que les peuplements purs, car ils mèneraient à une utilisation plus complète de ces ressources (Man et Lieffers, 1999). Ainsi, la majorité des études réalisées dans les peuplements mixtes ont comparé leurs rendements (DHP, hauteur, volume et croissance) avec ceux des peuplements purs sans toutefois considérer l'influence des peuplements mixtes sur les processus édaphiques. Hors, on observe généralement une boucle de rétroaction entre les composantes aériennes et souterraines des écosystèmes qui est sous-jacente à leur productivité et leur stabilité (Bartelt-Ryser *et al.*, 2005; Wardle, 2002). Les prochains paragraphes décrivent quelles peuvent être les conséquences souterraines d'une telle boucle de rétroaction dans le cas des peuplements mixtes de peuplier et de pin gris.

Interactions entre les composantes aériennes et souterraines des peuplements mixtes.

Les fonctions édaphiques, telles que la décomposition de la litière et la minéralisation des nutriments, sont régulées par les composantes végétales, microbiennes et physico-chimiques du sol selon deux voies d'interactions étroitement reliées (Figure 1). La première considère l'influence des communautés végétales sur les propriétés physico-chimiques du sol et les conséquences sur les fonctions édaphiques (voie #1). Par exemple, dans des conditions similaires, le sol des peupleraies possède un pH plus élevé et un ratio C:N plus faible que celui des pinèdes (Alban, 1982; Ste-Marie *et al.*, 2007). Ces caractéristiques semblent induites par des différences dans la qualité chimique de la litière, aérienne ou souterraine. En ce sens, les aiguilles du pin gris ont une durée de vie de plusieurs années, par opposition au feuillage annuel du peuplier (Aber et Melillo, 2001). Cette longévité est assurée en partie par la présence de composés structurels, tel que la lignine, dont la décomposition requiert des enzymes spécifiques et mène à la formation d'acides organiques acidifiant le sol (Chapin *et al.*, 2002).

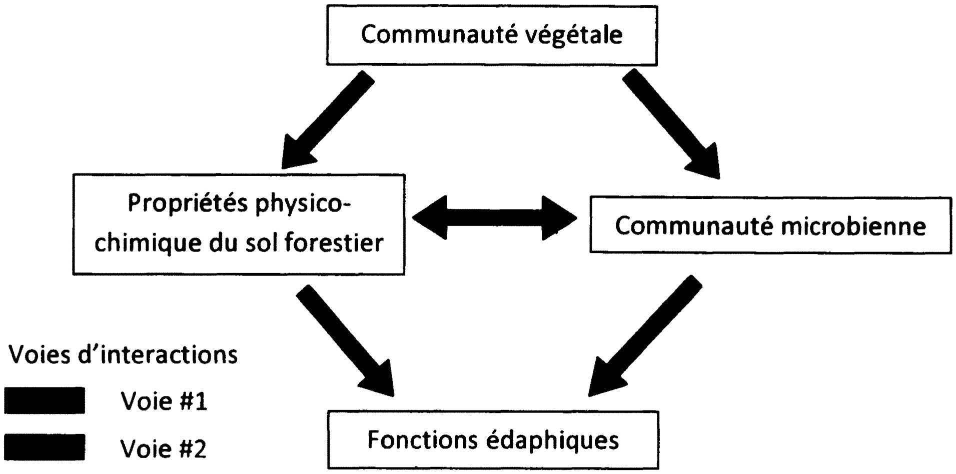

Figure 1 : Voies d'interactions entre les composantes végétale, microbienne et physico-chimique du sol déterminant les fonctions édaphiques

De plus, comparativement à celle du pin gris, la litière du peuplier est plus riche en calcium, ce qui permet de tamponner l'acidité du sol (Alban, 1982). La litière du peuplier contient également une plus forte proportion de composés labiles que celle du pin gris, ce qui favorise la décomposition de la litière (Taylor et Parkinson, 1988) et mène à un plus faible ratio C:N dans le sol (Gower *et al.*, 2000; Ste-Marie *et al.*, 2007). Par conséquent, il a été démontré que la présence de peuplier en association avec des conifères sous forme de peuplements mixtes pouvait augmenter le pH du sol et accélérer les processus édaphiques de décomposition et de minéralisation de la litière (Longpré *et al.*, 1994; Légaré *et al.*, 2005; Laganière *et al.*, 2009).

D'un autre côté, les communautés végétales peuvent influencer les fonctions édaphiques par l'intermédiaire des communautés microbiennes du sol (Figure 1 : voie #2) puisque ces dernières assurent près de 90% de la décomposition de la matière organique (Swift *et al.*, 1979). Étant donné que la base de la chaîne alimentaire microbienne provient de la litière et des exsudats d'origine végétale et que les espèces végétales modifient différemment l'environnement microbien, la composition des communautés microbiennes est intimement reliée à celle des communautés végétales (Lamarche *et al.*, 2007; Saetre et Bååth, 2000; White *et al.*, 2005). Par exemple, en entretenant un sol acide, le pin gris devrait favoriser la prédominance des champignons relativement aux bactéries puisque ces dernières tolèrent peu l'acidité (Rousk *et al.*, 2010). Hors, une communauté microbienne basée sur une biomasse fongique ralentit les cycles biogéochimiques du sol en favorisant l'immobilisation des nutriments (Wardle, 2002) alors qu'une prédominance de bactéries est reconnue pour accélérer le recyclage des nutriments puisque ces dernières sont la cible de nombreux prédateurs (Clarholm, 2002; Wardle, 2002). De plus, les champignons et les bactéries assurent des fonctions différentes dans la décomposition de la matière organique. Plusieurs bactéries sont des organismes zymogènes, i.e. qui utilisent les molécules rapidement assimilables, tels les hydrates de carbone et les acides aminés (Maier *et al.*, 2000; Paul et Clark, 1996). À l'opposé, les champignons possèdent des enzymes spécialisés dans la dégradation de la cellulose et de la lignine, des polymères plus difficiles à dégrader, et peuvent donc être considérés comme autochtones (Chapin *et al.*, 2002; Paul et Clark, 1996). Cette classification est toutefois grossière, puisque certaines bactéries, dont les actinomycètes, peuvent dégrader la lignine (Sylvia *et al.*, 1999) alors que certains champignons comme les zygomycètes, dégradent des composés labiles (Paul et Clark, 1996). Néanmoins, de telles différences impliquent que la composition des communautés microbienne influence, dans une certaine mesure, les fonctions édaphiques (Fraterrigo *et al.*, 2006; McGuire et Treseder, 2010). Ainsi, Strickland *et al.* (2009) ont démontré que des communautés microbiennes provenant de trois habitats distincts (une prairie, une pinède et des buissons de rhododendron) dégradaient à des vitesses différentes les litières provenant de ces trois habitats et que les combinaisons litière-microbes d'origine naturelle étaient les plus performantes. En forêt boréale, Ste-Marie et Paré (1999) ont démontré que les sols de pin gris présentaient des taux de nitrification très faibles comparé aux sols de peuplier. Ceci semblait être causé par l'absence de bactéries nitrifiantes puisque l'addition d'une faible quantité de sol de peuplier augmentait significativement la nitrification des sols de pin gris.

La combinaison de peuplier et de pin gris sous forme de peuplements mixtes implique que les communautés microbiennes y sont soumises à deux influences opposées déterminant leur composition et leurs fonctions. L'influence d'un arbre sur l'environnement édaphique est estimée décroître plus l'on s'éloigne de son tronc (Saetre & Bååth, 2000). Ainsi, la composition des communautés microbiennes dans les peuplements mixtes devrait varier en fonction de la répartition spatiale des arbres de chaque espèce. Toutefois, il est possible que certaines essences possèdent un rayon d'action plus large que d'autres (Saetre & Bååth, 2000) ou encore qu'une essence particulière modifie de façon plus marquée certaines conditions importantes pour la composition des communautés microbiennes telles que la disponibilité de l'azote (Selmants *et al.*, 2005) ou l'identité des espèces végétales de sous-bois (Hannam *et al.*, 2006). Déterminer le rayon d'action de chaque espèce en peuplements mixtes requiert un échantillonnage intensif du sol forestier de même que des analyses statistiques complexes de dépendance spatiale (Kembel et Dale, 2006; Saetre, 1999; Saetre et Bååth, 2000). Comme il a été mentionné précédemment, la dynamique forestière entre le peuplier faux-tremble et le pin gris forme naturellement des frontières abruptes entre les peuplements purs des deux espèces. De tels peuplements pourraient fournir un dispositif expérimental dans lequel il serait aisé d'estimer la contribution respective de chaque espèce sur les propriétés physico-chimiques ainsi que les communautés microbiennes du sol.

La biodiversité dans le sol des peuplements mixtes.

En plus de contrôler la composition des communautés microbiennes, une plus grande diversité végétale fournit généralement une plus grande diversité de substrats, ce qui peut augmenter la diversité des communautés microbiennes du sol (Bartelt-Ryser *et al.*, 2005). C'est le cas, par exemple, des champignons ectomychoriziens, dont la diversité est fortement corrélée à celle de leurs hôtes arborescents (Kernaghan *et al.*, 2003). En retour, il a été suggéré que la diversité des communautés microbiennes pouvait affecter le rendement ou la stabilité des fonctions qu'elles assurent (Giller *et al.*, 1997). Par exemple, dans l'optique où les microorganismes diffèrent dans leur susceptibilité aux perturbations environnementales (Allison et Martiny, 2008), une plus grande diversité d'espèces microbiennes impliquerait une plus grande diversité de réponses face à ces perturbations. Une communauté plus diversifiée aurait donc plus de chances de contenir des microorganismes pouvant survivre aux nouvelles conditions et qui pourraient compenser pour ceux défavorisés, ce qui constituerait une forme d'assurance biologique (Yachi et Loreau, 1999). De cette façon, la diversité augmenterait la stabilité des communautés microbiennes, ainsi que celle de leurs fonctions, lorsque confrontées à des changements environnementaux (Girvan *et al.*, 2005; Naeem et Li, 1997). Un tel avantage pourrait s'avérer crucial pour le maintient de la productivité des sols de la forêt boréale face aux coupes forestières, aux pluies acides, ou encore à la déposition de métaux lourds issus des activités minières. Toutefois, la relation entre la diversité et la stabilité microbienne est encore fortement débattue. Puisque la diversité des microorganismes du sol est évaluée à plusieurs milliers d'espèces par gramme de sol (Torsvik et Øvreås, 2002), certains microbiologistes argumentent que la redondance fonctionnelle, i.e. le nombre d'espèces assurant une même fonction, est tellement élevée que la diversité n'a que peu ou pas d'importance sur la stabilité des communautés microbiennes (Finlay *et al.*, 1997). De plus, les études sur le sujet sont relativement peu nombreuses et souvent contradictoires et aucune n'a encore été menée dans des peuplements forestiers mixtes. Ce manque de connaissances est explicable pour trois raisons. 1) le terme « stabilité » possède plusieurs composantes, 2) les facteurs déterminant la stabilité microbienne sont nombreux et souvent inter reliés et 3) l'étude des communautés microbiennes a longtemps été limitée par des difficultés techniques.

Premièrement, je définie la stabilité des microorganismes comme étant leur capacité à défier un changement. Cette forme de stabilité possède trois principales composantes : la résistance, la résilience et la tolérance. La résistance et la résilience se mesurent face à une perturbation, c'est-à-dire : un événement discret dans le temps et qui modifie les conditions environnementales d'un écosystème (Diaz et Cabido, 2001; Orwin et Wardle, 2004). La résistance se définie comme la capacité d'un écosystème à conserver sa composition spécifique ou à maintenir ses fonctions (e.g. biomasse totale, respiration, minéralisation de l'azote) face à une perturbation. La résilience est le taux de recouvrement de ces fonctions suite à une perturbation. La tolérance, quant à elle, est la capacité à résister à un stress environnemental, c'est-à-dire : un événement apportant des changements permanents dans les conditions environnementales d'un écosystème, tels que les pluies acides, ou toute autre contamination.

Deuxièmement, plusieurs autres facteurs biotiques ou abiotiques peuvent déterminer la stabilité des communautés microbiennes. Tout d'abord, la composition des communautés microbiennes peut avoir plus d'importance sur leur stabilité que la diversité au sens stricte, puisque les microorganismes à croissance lente sont généralement plus résistants, mais moins résilients que ceux à croissance plus rapide (Orwin et Wardle, 2006). Ensuite, la productivité d'un écosystème peut déterminer la quantité de ressources disponibles pour les mécanismes de défense ou de croissance des microorganismes et ainsi déterminer leur stabilité (DeAngelis *et al.*, 1989; Loreau, 1994). Hors, la productivité d'un écosystème est souvent reliée à sa biodiversité, de sorte que les liens entre productivité, diversité et stabilité sont souvent bi-directionnels et non linéaires (Worm et Duffy, 2003). Finalement, la qualité des ressources disponibles peut également déterminer la stabilité microbienne. Ainsi, les sols limités en C favoriseraient la résistance et la résilience des communautés microbiennes comparativement à ceux limités en N (Orwin et Wardle, 2006).

Troisièmement, le sol est un environnement physiquement complexe et hétérogène et les méthodes employées pour étudier les microorganismes ont longtemps reposées sur leur culture en laboratoire (Kirk *et al.*, 2004). Hors, on estime à moins de 1% la proportion des microorganismes pouvant être cultivés sur des médiums artificiels (Hill *et al.*, 2000; Torsvik et Øvreås, 2002). Ce n'est que depuis une vingtaine d'années que l'on peut étudier l'ensemble de la diversité microbienne grâce à de nouvelles techniques dites moléculaires (Hill *et al.*, 2000). À défaut de pouvoir utiliser une classification taxonomique, ces techniques, utilisent la diversité de certaines molécules cellulaires comme indice de diversité microbienne. Les molécules les plus couramment employées sont l'ADN, l'ARN et les acides gras membranaires (Cavigelli *et al.*, 1995; Ramsey *et al.*, 2006). Ces acides gras, en particulier ceux des phospholipides, sont rapidement dégradés suivant la mort cellulaire et représentent uniquement la biomasse microbienne vivante (Drenovsky *et al.*, 2004; Zelles, 1999). Malgré le fait que les techniques basées sur l'ADN ou l'ARN sont plus sophistiquées, coûteuses et souvent plus fastidieuses que celles basées sur les acides gras, il a été démontré que ces dernières pouvaient atteindre un pouvoir de discrimination des communautés microbiennes qui était égal voire même supérieur à celui obtenu avec les premières (Ramsey *et al.*, 2006).

Objectifs et hypothèses

Cette thèse de doctorat comporte deux principaux objectifs : 1) comprendre les conditions menant à la formation des peuplements mixtes de peuplier et de pin gris et 2) identifier les conséquences de cette mixité sur les propriétés physico chimiques et biologiques du sol ainsi que la composition, la diversité et la stabilité des communautés microbiennes du sol.

Afin de répondre au premier objectif, le premier chapitre de cette thèse est basé sur deux expériences visant à évaluer le potentiel de la fertilité du matériau parental comme facteur menant à la mixité forestière. Suivant la théorie exposée dans la première partie de cette introduction, je pose l'hypothèse que les peuplements mixtes sont exclusifs aux dépôts argileux, alors que sur le till, l'exclusion entre les deux essences survient, un résultat de la compétition interspécifique. Ainsi, la première expérience de ce chapitre se base sur un recensement des peuplements mixtes de peuplier et de pin gris dans le nord-ouest de l'Abitibi alors que la deuxième expérience évalue les conséquences d'une fertilisation sur la dynamique de jeunes peuplements mixtes de peuplier-pin gris se développant sur till.

Le second objectif de cette thèse est adressé dans les deuxième et troisième chapitres. Ainis, le second chapitre de cette thèse évalue les conséquences souterraines de la mixité sur la stabilité des communautés microbiennes du sol. En ce sens, j'apporte l'hypothèse que la plus grande diversité végétale dans les peuplements mixtes induit une plus grande diversité microbienne, ce qui augmente la stabilité (résistance, résilience et tolérance) de la biomasse microbienne lorsque confronté à une perturbation (sécheresse) ou à des stress (acidité et contamination au cuivre). Par opposition, le troisième et dernier chapitre de cette thèse tente d'évaluer les conséquences souterraines de l'absence de mixité, i.e. lorsqu'il y a formation de peuplements purs adjacents. La présence de frontières abruptes entre ces peuplements permet de mesurer, de part et d'autre de cette frontière, le rayon d'influence de chaque espèce sur les propriétés du sol. Je pose l'hypothèse que c'est le peuplier qui possède la plus forte influence sur les propriétés édaphiques et que son rayon d'influence est plus large que celui du pin gris puisque la litière feuillue est plus facilement transportée par le vent. Je suggère également que même si la frontière dans la composition de ces peuplements est abrupte, on retrouve une zone de mixité dans les propriétés édaphiques qui fait de ces écotones, des écosystèmes uniques.

CHAPITRE 1

LA FERTILITÉ DU SOL CONTRÔLE LA COEXISTENCE DU PIN GRIS ET DU PEUPLIER FAUX-TREMBLE

Référence: Royer-Tardif, S., Bradley, R.L. Evidence that soil fertility controls the mixing of jack pine with trembling aspen. (Accepté pour publication dans Forest Ecol. Manag.)

La relation entre la productivité des écosystèmes et la diversité des espèces qu'on y retrouve est connue depuis fort longtemps (Hutchinson, 1959). Malgré ce fait, il n'y a encore aucun consensus sur la forme de cette relation et encore moins sur les mécanismes pouvant en être la cause (Gillman et Wright, 2006; Mittelbach *et al.*, 2001; Whittaker *et al.*, 2003). À petite échelle (locale) cette relation semble unimodale atteignant un maximum à des niveaux de productivité intermédiaires alors qu'à large échelle (continentale) cette relation semble linéaire et positive (Chase et Leibold, 2002). Néanmoins, pour la diversité arborescente, cette relation semble positive et linéaire (Adams et Woodward, 1989; Currie et Paquin, 1987; Francis et Currie, 1998; Storch *et al.*, 2005). Ces études, toutefois, se sont limitées à une échelle continentale. Ainsi, malgré les apparentes différences de diversité entre les peuplements forestiers et la fertilité des matériaux parentaux, personne n'a encore fait le lien entre l'occurrence des peuplements mixtes et la productivité d'un site. Le manuscrit présenté dans ce chapitre se base sur un recensement des peuplements mixtes de peuplier et de pin gris dans un secteur de l'Abitibi afin de tester l'hypothèse que les peuplements mixtes de peuplier et de pin gris se retrouvent exclusivement sur les dépôts argileux alors que sur till, ces deux espèces s'excluent mutuellement. De plus, ce chapitre présente les résultats d'une expérience de fertilisation dans de jeunes peuplements mixtes sur till établie en vue de mieux comprendre la réponse de chaque espèce à une fertilisation ainsi que la dynamique de ces jeunes peuplements. Les résultats de ce chapitre peuvent être utiles pour la gestion forestière, puisqu'il serait possible à l'aide d'une simple carte éco-forestière de déterminer la nature du matériau parental et donc, la possibilité de mixité forestière. De cette façon, on pourrait maintenir la biodiversité dans les conditions où on la retrouve tout en favorisant une sylviculture plus intensive (fertilisation et/ou débroussaillage) axée sur les espèces à fort rendement économique dans les milieux où la mixité forestière est absente.

J'ai effectué le recensement des peuplements mixtes sur le territoire abitibien ainsi que la collecte des informations cartographiques avec l'aide de Sylvain Chouinard de chez Norbord à l'usine de La Sarre. L'expérience de fertilisation et de débroussaillage a été initiée par mon directeur, le Dr. Robert Bradley, en mai 2003. De 2004 à 2008, je me suis chargé d'appliquer les traitements sylvicoles, de récolter les échantillons sur le terrain, d'analyser les échantillons en laboratoire, de gérer les banques de données et de performer les analyses statistiques. J'ai effectué la rédaction du manuscrit avec l'aide du Dr. Bradley.

Abstract

Jack pine and trembling aspen are boreal tree species that are found growing either in naturally regenerated mono-specific stands, or in mixed-wood stands. We conducted both a field survey and a manipulative field study to test the productivity-diversity hypothesis, which predicts that mixed-wood stands are more likely to occur on fertile soils, or following fertilization. We surveyed 44 mixed-wood stands and found 43 of these occurring on fertile clay deposits, and only one occurring on a nutrient poor till deposit. By contrast, the area surveyed comprised 45% clay and 55% till deposits. In a second study, we conducted a five year fertilization and brushing trial in a recently burned area dominated by jack pine saplings with patches of regenerating trembling aspen. Fertilization without brushing improved the growth and recruitment of aspen stems, but had no effect on jack pine growth and recruitment. Fertilization + brushing increased the growth of jack pine. Brushing the aspen, with or without fertilization, resulted in higher recruitment of jack pine. We conclude that soil fertility controls the mixing of jack pine with trembling aspen, that fertilization increases the encroachment of aspen into areas formerly dominated by jack pine, and that brushing along with fertilization is necessary to promote jack pine growth.

Keywords: Trembling aspen (*Populus tremuloides* Michx.); Jack pine (*Pinus banksiana* Lamb.); Mixed-wood stands; Geologic parent material; Fertilization and brushing

1. Introduction

Jack pine (*Pinus banksiana* Lamb.) is a pioneer tree species of economic importance in Eastern Canada, reaping financial returns of 10,000–30,000 \$ ha^{-1} (Tong et al., 2005) to the forest industry. In the Abitibi region of Quebec (Canada), jack pine can be found growing either in naturally regenerated mono-specific stands, or in mixed-wood stands along with trembling aspen (*Populus tremuloides* Michx.), a deciduous pioneer tree species (Photo 1).

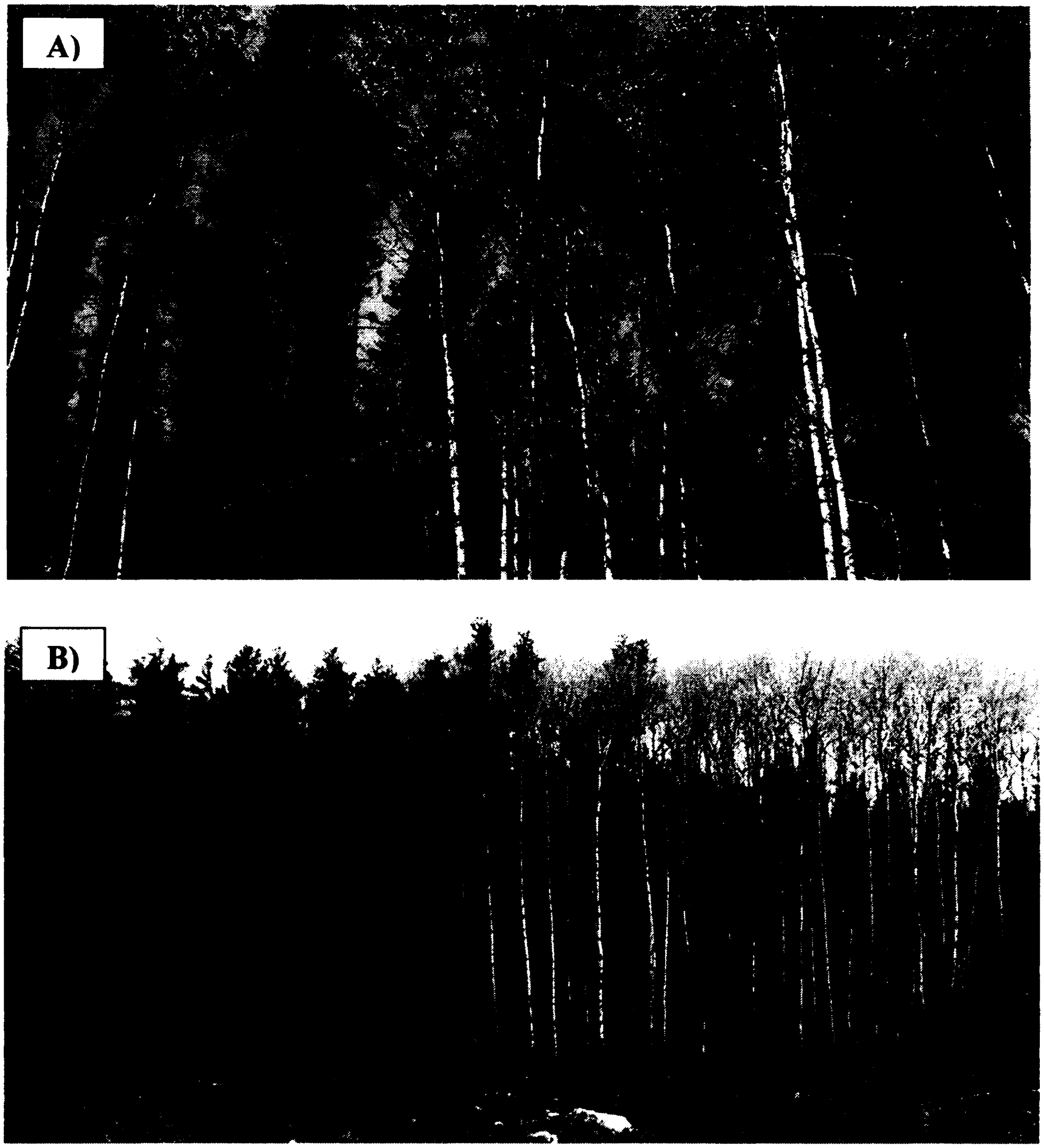

Photo 1. An example of (A) an aspen:jack pine mixed-wood stand and (B) two adjacent mono-specific stands of each species. In frame (B), a black spruce sub-canopy can be seen growing under both jack pine and aspen.

There is some debate as to the ecological and economic benefits of jack pine–aspen mixed-wood stands. A first argument is that aspen growing in mixtures with boreal conifers may increase the overall productivity of the stand (Man and Lieffers, 1999), although data is lacking to validate this claim. Even if stand productivity was to increase due to mixing, aspen is harvested for chipboard manufacturing such that its value is only about 35% that of jack pine and other boreal conifers (Mathey et al., 2009). A second argument is that jack pine–aspen mixed-wood stands comprise a unique combination of soil properties and understory vegetation, which may be linked to an increase in the stability of soil microbial biomass (Royer-Tardif et al., 2010). This issue is debatable as well, given that sharp compositional boundaries that occur between mono-specific stands of aspen and jack pine create relatively wide (i.e. 24 m) functional ecotones that are equally as unique in their soil properties as are mixed-wood stands (Royer-Tardif and Bradley, In Review). From a strictly silvicultural standpoint, jack pine–aspen mixed-wood stands are less practical than mono-specific stands, because logs need to be sorted after felling, and because most mills are specialized in only one type of wood transformation technology. There are thus theoretical as well as practical reasons for understanding how certain landscape features may promote jack pine–aspen mixed-wood stands, or lead to species segregating as mono-specific stands.

From an ecological perspective, mixed-wood stands are more diverse (i.e. higher α-diversity) than mono-specific stands. Among the different hypotheses that have been raised to explain spatial variations in α-diversity, the productivity-diversity hypothesis is one that has been thoroughly explored (Pärtel et al., 2010). This hypothesis predicts that the number of co-occurring species increases with the amount of usable energy that can be apportioned among individual species (Hutchinson, 1959; Brown, 1981; Currie, 1991). Accordingly, several broad continental-scale studies have found that tree species richness increases monotonically with ecosystem productivity (Currie and Paquin, 1987; Adams and Woodward, 1989; Francis and Currie, 1998). It can be argued, however, that the probability of observing diverse mixed-wood stands increases with the size of the regional species pool (i.e. species richness). For example, the province of Québec (Canada) covers approximately 2,000 km along its north-south axis, and there is a corresponding correlation between high species richness and high α-

diversity in the warmer southern regions, and low species richness and low α-diversity in the colder northern regions. Here, we argue that the productivity-diversity hypothesis may also explain variations in α-diversity on a smaller regional scale, where the species pool and climate do not vary across nearby plant communities. In this case, energy flow and productivity are mainly determined by edaphic variables. The Abitibi region provides a good setting to test this hypothesis, because soils are mainly formed over two contrasting geologic parent materials, fine textured glacio-lacustrine clay and coarse-textured glacial till deposits (Rompré and Carrier, 1997). Both jack pine and aspen are found growing on each of these parent materials. Clay deposits are more productive than till deposits (Béland and Bergeron, 1996; Ste-Marie et al., 2007) because of higher water retention, pH and nutrient availability (Lamarche et al., 2004). Hence, in accordance with the productivity-diversity hypothesis, we predicted that jack pine–aspen mixed-wood stands would more likely occur on clay than on till deposits at any given latitude within their range (Fig. 1).

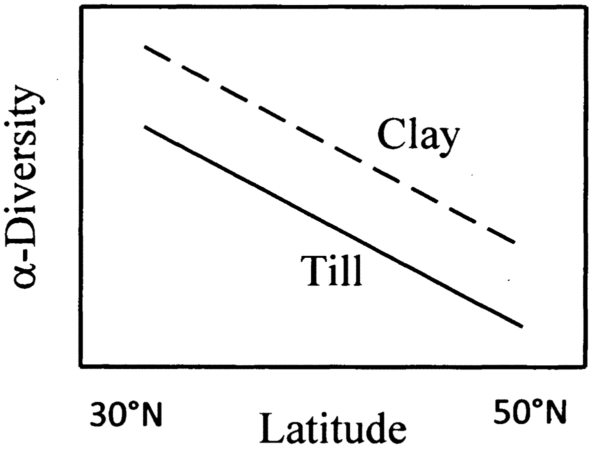

Figure 1. Theoretical relationship between latitude and species α-diversity whereby parent material (clay vs. till) controls the ability for aspen and jack pine to co-exist as mixed-wood stands.

Industrial logging has altered the forest landscape of the Abitibi region, causing an increase in the area occupied by aspen and a concomitant decrease in coniferous species (Harvey and Bergeron, 1989; Laquerre, 2007; Laquerre et al., 2009). This is likely due to timber rotations being shorter than the average natural fire-disturbance regime (Cyr et al., 2009), which causes an increase of early-seral deciduous species such as aspen in areas previously occupied by late-seral coniferous species such as black spruce (*Picea mariana* (Mill.) BSP). These studies have not specified, however, whether an increase in aspen over the landscape can also be due to an encroachment of aspen onto areas previously dominated by jack pine. Given that both jack pine and aspen are early-seral species, this type of encroachment would not likely result in an immediate coniferous-to-deciduous stand replacement, but rather in a transition to jack pine–aspen mixed-wood stands. In accordance with our first hypothesis that predicted a prevalence of mixed-wood stands on clay rather than on till deposits, we posit that the encroachment of aspen into areas previously dominated by jack pine stands will be more prevalent on clay than on till.

Because of its high nutrient use efficiency and tolerance to drought, jack pine grows well on coarse-textured till and sandy deposits. Jack pine is thus well suited to impart economic value to otherwise unproductive soils (Rudolph and Laidly, 1990). Studies have shown, however, that jack pine growth on till will nevertheless respond positively to N-based fertilizers (Newton and Amponsah, 2006). Because fertilization is expensive, it is important to determine its effectiveness in the presence of competing species. For example, would fertilization on till emulate the higher fertility found on clay deposits and thus promote the encroachment of aspen onto naturally regenerating jack pine stands and lead to the formation of jack pine-aspen mixed-wood stands? Such being the case would require that fertilization be accompanied by a brushing treatment to remove hardwood competition if the goal is to promote jack pine growth. From another perspective, a fertilization within young mixed-wood stands on till could increase the strength of interspecific competition what may highlight the mechanisms by which species exclusion occurs over till deposits.

We report on two independent but related studies on jack pine–aspen stand dynamics in the Abitibi region. The first study was designed to answer the fundamental question of whether mixed-wood stands are more prevalent on clay than on till deposits. The second study addressed the successional implications of fertilizing and/or brushing competing aspen stems in regenerating jack pine stands occurring on till.

2. Material and Methods

Both studies were performed in the portion of the Abitibi region that lies within the black spruce–feather moss bioclimatic domain (ca. 48° N, 79° W), according to the hierarchical classification system used by Québec's Ministry of Natural Resources (Thibault and Carrier, 1983). The nearest weather station, near the Town of La Sarre (48° 46' N; 79° 13' W), reports a mean annual temperature and precipitation of 0.7°C and 889.8 mm respectively (Environment Canada, 2008). The most common disturbances are wildfire and spruce budworm outbreaks, but clearcut logging has been more prevalent over the past century (Bergeron, 2000).

2.1. Study 1 – Occurrence of mixed-wood stands

2.1.1. Roadside survey

Polygons designated as "Pe-Pg" on forest cover maps of the Abitibi region, refer to areas where aspen and jack pine are co-dominant. In a majority of cases, visual inspections of these forests reveal a series of adjacent mono-specific stands rather than homogenous mixed-wood stands. For this reason, an extensive survey within areas designated as "Pe-Pg" was performed in summers 2004 and 2008, in order to locate true jack pine–aspen mixed-wood stands along primary and secondary roads as well as some logging roads. We selected only naturally regenerated homogeneous mixed-wood stands covering more than 0.5 ha and displaying approximately equal proportions (40-60 %) of aspen and jack pine. For each selected stand, we removed the humus layer and dug three pits to identify the geologic parent material (clay or till) by hand texturing.

2.1.2. Statistical analyses

Using ArcGIS software and high resolution digital soil maps obtained from the Quebec Ministry of Natural Resources (MRNFQ), we estimated the proportion of clay and till within 100 m margins on both sides of each road that was surveyed. A chi-square test was used to evaluate if the proportion of mixed-wood stands found on till and clay was significantly different from the proportion of clay and till deposits over the area that was surveyed.

2.2. Study 2 – Fertilizer response of jack pine in the presence or absence of aspen

2.2.1. Study area and experimental design

The trial was established in spring 2003 near the town of Val-Paradis (49°10'N, 79°17'W), within a 12,540 ha area that had burned by wildfire in 1997. Three sites, located approximately 500 m apart, were selected within a zone that had previously been dominated by a mature jack pine stand occurring on a sandy till deposit. The ground was covered with regenerating jack pine saplings, but the three experimental sites were established in patches that also included aspen saplings in approximately equal density as jack pine (ca. 5,000 stems ha^{-1}). A Latin square of four experimental plots, each measuring 100 m^2, was established at each site. Four treatments were assigned to plots at each site: (1) inorganic fertilizer (10-30-10) applied in the spring of each year (2003–2008 inclusively) at a rate of 20 kg N, 26.2 kg P and 16.6 kg K ha^{-1} y^{-1}; (2) handheld mechanical removal of aspen and all deciduous competition (brushing); (3) combined fertilization + brushing; (4) non-treated control. Plot boundaries were trenched to 40 cm to minimize fertilizer uptake by roots of trees occurring on non-fertilized plots.

2.2.2. Diagnosis of nutrient limitations

Before budburst in May 2004, five twigs bearing 1 year old needles were collected from each of five randomly selected jack pine saplings within each plot, and oven-dried at 65°C for 48 h. For each tree, 250 needles were randomly selected and weighed. These were ball-milled and a 200 mg subsample was digested in a H_2SO_4/H_2O_2 solution. Total N and P were then analysed colorimetrically using a Technicon AutoAnalyser (Pulse Instrumentation, Saskatoon, Canada) according to protocols described by Mulvaney (1996) and by Bernhardt and Wilhelms (1967). Digests were further analysed for total K and Ca concentrations using an AAnalyst-100 atomic absorption spectrometer (Perkin Elmer Corporation, Norwalk, USA). Needle nutrient content was calculated as the product of nutrient concentration and needle mass. For each block, the average needle mass, nutrient content and nutrient concentration in fertilized and/or brushed treatment plots were reported as a percentage of these values measured in the control treatment plot. Based on these relative values, diagnostic vector analysis (Haase and Rose, 1995; Imo and Timmer, 1998) was used to assess the nutrient status of jack pine saplings on till.

2.2.3. Forest floor properties

In May 2005, before applying fertilizer for that year, five samples of forest floor material were collected from each plot with a 10 cm dia. metal core. These samples were pooled to give one bulk sample per plot, passed through a 5 mm sieve to remove roots and coarse debris, transferred into plastic bags and transported to the laboratory in coolers with ice-packs. Field moist subsamples (10 g dry wt. equiv.) were extracted with 1.0 N KCl solution and respectively analysed for NH_4^+-N and NO_3^--N concentrations by the Berthelot and the Griess-Illosway reaction methods (Mulvaney, 1996). NH_4^+-N and NO_3^--N concentrations were determined in the same way following a 30 d aerobic incubation (22°C), in order to assess net ammonification and net nitrification rates (i.e. after subtracting initial concentrations). Basal respiration (BR) was determined by weighing field moist subsamples (10 g dry wt equiv.) in 126 mL gas sampling jars and measuring CO_2 production in the headspace after 4 h using a model CP-2002 P Micro-GC (Chrompack, Middelburg, Netherlands). Microbial biomass (MB) was estimated by substrate induced respiration (Anderson and Domsch,1978) following the addition of glucose-talc mixtures (Bradley and Fyles, 1995). Metabolic quotient (qCO_2) was calculated as the ratio of BR over MB. The remaining forest floor material was oven-dried (65°C for 48h) and a 5 g (dry wt. equiv.) subsample was mixed with deionized water (1:5) to assess pH. Total C and N contents were determined from 150 mg ground subsamples using a Vario Macro CN Analyser (Elementar GmbH, Hanau, Germany). A 200 mg subsample was digested in H_2SO_4/H_2O_2 solution and analysed for total P, K and Ca as previously described.

2.2.4. Tree height and biomass

In May 2008, we measured height and diameter at breast height (DBH) of 10 randomly selected jack pine saplings from each plot, and of 10 randomly selected aspen saplings from the non-brushed plots. Only trees with DBH >2 cm were considered. These data were then used to estimate stem, crown and total biomass of each species using allometric equations developed by Lambert et al. (2005). Stem density for each species was also recorded by counting every stem within each plot.

2.2.5. Statistical analyses

Mixed-effects ANOVA was used to test the effects of fertilization, brushing and their interaction (i.e. fixed factors) on needle nutrient concentrations, forest floor properties, tree height and biomass, while considering blocks as random factors. When necessary, data were log-transformed to meet assumptions of ANOVA. A rank transformation (Conover and Iman, 1981) was performed on forest floor NO_3^- concentrations, as well as on nitrification rates, because no transformation could remove the skewness in the distribution of these variables. Differences among treatment means were explored using Tukey's HSD test. Single degree of freedom orthogonal contrasts were used to test a priori hypotheses regarding the combined effects of fertilization + brushing on jack pine growth and recruitment. All statistical analyses were performed with R software (v.2.10.1; The R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Occurrence of mixed-wood stands

Our roadside survey identified 44 jack pine–aspen mixed-wood stands, 43 of which occurred on clay and only one on till. Over the surveyed area (i.e., 100 m on either side of each travelled road), clay accounted for 35 % and till for 43 % of the geologic parent material. The remaining area (22 %) comprised organic deposits, rocky outcrops and wetlands. This area was removed from our analysis and the remaining area thus comprised 45 % clay and 55 % till deposits. Under the null hypothesis, the occurrence of mixed-wood stands is neutral with respect to geologic parent material and we thus expect to find 20 stands on clay and 24 on till. The difference between observed and expected frequencies was, therefore, highly significant ($\chi^2_1=48.48$, $P<0.0001$).

3.2. Fertilizer response of jack pine in the presence or absence of aspen

Treatments had no significant effect on forest floor pH, total nutrient concentrations, or respirometry measurements (Table 1).

Table 1
Mean values of forest floor parameters measured in 2005 for each treatment (n=12). Values in parentheses are standard error (n=12). BR=Basal respiration; MB=Microbial biomass; *q*CO2=Metabolic quotient.

pH (water)	4.05 (0.11)
C (%)	38.38 (3.37)
N (%)	1.64 (0.19)
P (mg g^{-1})	0.38 (0.09)
K (mg g^{-1})	1.78 (1.07)
Ca (mg g^{-1})	5.08 (0.58)
BR (µg CO_2-C g^{-1} h^{-1})	4.21 (0.88)
MB (mg C_{mic} g^{-1})	1.87 (0.29)
*q*CO2 (µg CO_2-C mg C_{mic}^{-1} h^{-1})	2.26 (0.19)

Fertilization resulted in significantly higher NH_4^+ ($F_{1,6}$=13.47, P=0.010) and NO_3^- ($F_{1,6}$=7.60, P=0.033) concentrations, as well as higher net nitrification rates ($F_{1,6}$=15.75, P=0.007) (Fig. 2).

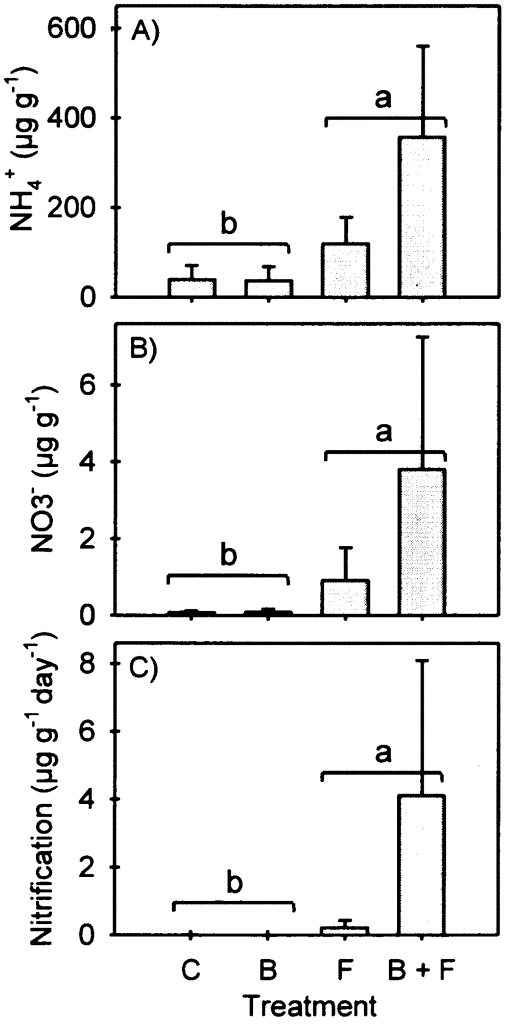

Figure 2. Mean initial A) NH_4^+-N and B) NO_3^--N concentrations as well as potential C) nitrification rates for the four different treatments: Control (C), Brushed (B), Fertilized (F) and Brushed + Fertilized (B + F). Vertical lines = 1 S.E. (n=3); different lower-case letters indicate a significant fertilization effect.

Orthogonal contrasts showed that these three variables were significantly higher ($P < 0.05$) in fertilized + brushed plots than in the other three treatment plots. Fertilization increased jack pine needle mass ($F_{1,55}=56.63$, $P<0.0001$), needle N concentration ($F_{1,55}=9.57$, $P=0.003$), as well as needle N ($F_{1,55}=58.34$, $P<0.0001$), needle P ($F_{1,54}=56.53$, $P<0.0001$) and needle K ($F_{1,44}=4.75$, $P=0.035$) content (Fig. 3). These results indicate that only soil N content is limiting jack pine growth over till deposits (Imo and Timmer, 1998)

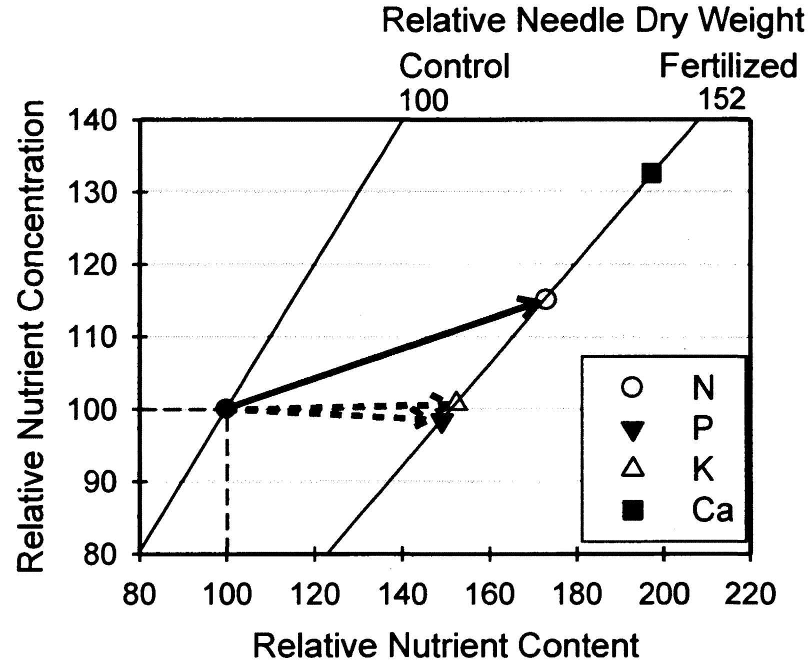

Figure 3. Shifts in jack pine needle nutrient content and concentration, and in needle dry weight, due to first year fertilization. Values are expressed as percentages relative to control plots. Since brushing had no effect on these response variables, "Fertilized" refers to the pooled values of fertilized and brushed + fertilized plots, whereas "Control" refers to the pooled values of control and brushed plots. Dashed arrows indicate significant shifts in nutrient content; solid arrows indicate significant shifts in both nutrient content and concentration.

In the non-brushed plots, aspen was taller than jack pine ($F_{1,114}$=24.61, P<0.0001), however jack pine had larger DBH ($F_{1,114}$=7.56, P<0.0071) and biomass (stem : $F_{1,114}$=8.83, P=0.0036; crown : $F_{1,114}$=28.03, P=0.0001; total : $F_{1,114}$=13.94, P=0.0003) than aspen (Table 2).

Table 2
Mean tree height, biomass and density for each species within the four treatments. Data were collected on summer 2008. Values in parentheses are standard error (n=10; except for density where n=3). Samples with different letters are significantly different. No interaction between treatments was significant.

	Treatment			
	Control	Brushed	Fertilized	Brushed + Fertilized
Aspen				
Height (m)	3.95 (0.11)	-	4.27 (0.17)	-
DBH (cm)	2.83 (0.11) b		3.44 (0.19) a	
Aboveground biomass (kg)				
Stem	0.65 (0.07) b	-	1.12 (0.17) a	-
Crown	0.28 (0.02) b	-	0.45 (0.05) a	-
Total	0.93 (0.09) b	-	1.57 (0.22) a	-
Density (tree 100 m^{-2})	64.11 (24.25) b	-	74.32 (26.01) a	-
Jack Pine				
Height (m)	3.43 (0.10)	3.37 (0.11)	3.58 (0.13)	3.50 (0.11)
DBH (cm)	3.57 (0.23)	3.67 (0.23)	3.78 (0.24)	4.36 (0.32)
Aboveground biomass (kg)				
Stem	1.17 (0.18)	1.20 (0.16)	1.36 (0.19)	1.73 (0.26)
Crown	0.69 (0.12)	0.74 (0.11)	0.77 (0.11)	1.18 (0.20)
Total	1.87 (0.30)	1.94 (0.26)	2.13 (0.30)	2.91 (0.46)
Density (tree 100 m^{-2})	45.21 (12.20)	64.26 (21.22)	43.94 (2.59)	70.61 (22.57)

Fertilization increased aspen DBH ($F_{1,56}$=7.23, P=0.0094), biomass (stem : $F_{1,56}$=5.88, P=0.019; crown : $F_{1,56}$=7.85, P=0.007; total :$F_{1,56}$=6.47, P=0.014) and stem density ($F_{1,2}$=30.53, P=0.031), as well as aspen:jack pine biomass ratios ($F_{1,8}$=6.58, P=0.033) (Fig. 4). Jack pine DBH ($F_{1,114}$=3.04, P=0.084) and biomass ($F_{1,114}$=3.00 P=0.086) were higher in fertilized plots, but these main effects were not statistically significant. Orthogonal contrasts showed, however, that jack pine DBH, crown and total biomass were all significantly higher ($P<0.05$) in the fertilized + brushed treatment than in the other three treatments. Brushing (i.e., main effect) resulted in higher ($F_{1,2}=1.41$, $P=0.047$) jack pine stem density.

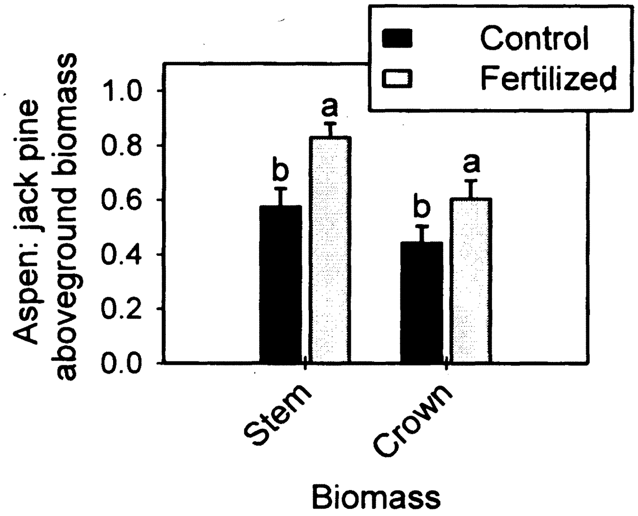

Figure 4. The effect of fertilization on aspen:jack pine crown and stem biomass ratios. Error bars correspond to standard error over the three blocks. Vertical lines = 1 S.E. (n=3); different lower-case letters indicate a significant fertilization effect.

4. Discussion

According to Rosenzweig and Abramsky (1993), the word "productivity" is synonymous to "the rate at which energy flows through an ecosystem", and so we use these terms interchangeably.

There is theoretical as well as empirical support for the notion that environmental energy availability promotes faster speciation and higher species richness (see review by Evans and Gaston, 2005) thus resulting in broad scale positive diversity-productivity relationships. By confirming that jack pine–aspen mixed-wood stands occurring within a small region are significantly more prevalent on clay than on till deposits, our study suggest that usable energy also promotes the local co-existence of species. Clay deposits are more nutrient rich and they retain water better than do till deposits, which makes them more productive (Béland and Bergeron, 1996; Ste-Marie et al., 2007). The more productive clay may allow species to co-exist by providing the minimal supply of resources for each species to sustain itself (Yee and Juliano, 2007).

The fact that fertilization increased needle P and K content without increasing needle P and K concentrations is a sign that the supply of these two nutrients on till deposits is sufficient for jack pine (Haase and Rose, 1995). On the other hand, fertilization indicated that jack pine growing over till deposits is N-deficient because increased needle N concentrations in fertilized plots were associated to an increase of needle mass, which is a good predictor of future biomass increment in coniferous species (Haase and Rose, 1995). Thus, from a silvicultural standpoint, one would be justified to fertilize jack pine saplings on till, in order to obtain optimal growth rates. Our study showed, however, that fertilization will benefit aspen more so than jack pine when these two species are growing in proximity to each other. The specific root length (SRL; root length per unit dry mass) of aspen may be three times higher than that of jack pine (Comas and Eissenstat, 2009). SRL is correlated to root growth rate (Eissenstat, 1991), which explains how aspen may preempt the acquisition of fertilizer nutrients. Fertilization that is meant to increase jack pine recruitment and growth should, therefore, only be undertaken in combination with a brushing treatment.

SRL is also a measure of a plant's investment in absorbing structures. Aspen is adapted, therefore, to acquire larger amounts of nutrients in comparison to jack pine. Aspen's higher nutrient absorption was reflected, for example, by the higher soil mineral N remaining in "fertilized + brushed" plots, compared to plots that were only fertilized. Conversely, aspen growing on till is not likely to compete very well against jack pine in these nutrient poor conditions. Fertilization essentially emulates the effect of clay deposits, by allowing aspen to establish and sustain itself in the presence of jack pine, thereby creating mixed-wood conditions. It is, however, uncertain whether this condition can persist over the long-term, as various studies have reported a decrease in species richness with fertilization (e.g. DiTommaso and Aarssen, 1989; Rajaniemi, 2002). Thus, some have argued that the "true" productivity-diversity relationship may be unimodal, in other words "hump-shaped" (e.g., Mittelbach et al. 2001; Rosenzweig 1995), whereby fertilization supplies abnormally high amounts of nutrients

(Gough et al. 2000) and reduces resource heterogeneity, both of which lead to competitive exclusion of some species (Tilman, 1982; Rajaniemi, 2003). As aspen reproduces mainly by root suckering, compared to jack pine that reproduces from post-fire seed dispersal, fertilization is likely to result in the progressive encroachment of aspen onto stands previously dominated by jack pine.

In summary, our study showed that soil fertility determines the ability for jack pine and aspen to co-exist. Species co-existence along natural soil fertility gradients appear to respond according to the productivity-diversity hypothesis. Increasing soil nutrient supply on till deposits through fertilization may lead, however, to the encroachment of aspen into areas formerly dominated by jack pine.

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CHAPITRE 2

ÉVIDENCES QUE LA DIVERSITÉ DES PLANTES ET LA PRODUCTIVITÉ D'UN SITE PROCURENT UNE PLUS GRANDE STABILITÉ À LA BIOMASSE MICROBIENNE DE LA COUCHE MORTE

Référence: Royer-Tardif, S., Bradley, R.L., Parsons W.F.J. (2010). Evidence that plant diversity and site productivity confer stability to forest floor microbial biomass. Soil Biol. Biochem. *42:* 813-821.

Même si les fondements théoriques de l'association entre la biodiversité et la stabilité des écosystèmes ont été élaborés depuis plus d'un demi-sciècle (Elton, 1958; MacArthur, 1955), il s'agit d'un domaine encore fortement débattu. Ceci est en partie causé par un manque de données empiriques (Hooper *et al.*, 2005), en particulier, en ce qui a trait aux communautés microbiennes du sol. Le présent chapitre constitue une des rares études établissant un lien de causalité entre la diversité végétale et le fonctionnement des communautés microbiennes du sol et l'unique étude, à notre connaissance, ayant étudié cette relation dans un écosystème forestier. Plus spécifiquement, nous avons testé l'hypothèse que la plus grande diversité végétale dans les peuplements mixtes était associée à une plus forte stabilité de la biomasse microbienne. Ici, nous définissons la stabilité selon trois composantes : la résistance, la résilience et la tolérance. La résistance est l'inverse de la quantité de changement dans la biomasse microbienne suite à une perturbation, i.e. un événement modifiant les conditions environnementales de façon ponctuelle. La résilience correspond au taux de recouvrement de la biomasse microbienne suite à la fin de cette perturbation. La tolérance détermine la quantité de changement dans la biomasse microbienne face à un stress, i.e. une caractéristique de l'environnement exerçant une action constante sur les communautés microbiennes. Les résultats de notre étude proposent donc que 1) les communautés microbiennes des peuplements mixtes sont plus résistantes que celles des peuplements purs 2) la mixité forestière permet d'assurer une forte tolérance dans une plus grande diversité de conditions environnementales et 3) la résilience des communautés microbiennes est plus fortement déterminée par la fertilité du matériau parental que par la composition végétale. Finalement, l'analyse des acides gras microbiens, employée dans ce chapitre, a permis d'explorer de façon plus concrète les relations entre la composition des peuplements (pur vs mixte), la composition des communautés microbiennes et leur stabilité.

J'ai élaboré le dispositif expérimental ainsi que développé les tests de résistance, résilience et tolérance de la biomasse microbienne. Je me suis chargé de la récolte des données sur le terrain, de leur analyse en laboratoire, de la gestion des données et des analyses statistiques. Les stagiaires M. Dufresne et M. Bergeron m'ont respectivement aidé dans la récolte de données sur le terrain et dans les analyses de laboratoire. La rédaction du manuscrit a été réalisée avec la grande collaboration de mon directeur, Dr. Robert Bradley ainsi que le Dr. William F.J. Parsons qui a révisé une version préliminaire de cet article en plus d'y apporter des réflexions majeures quand à la présentation des résultats.

Abstract

The ability of soil microbial communities to withstand punctual disturbance or chronic stress is important for the stability of ecosystem processes. Factors controlling microbial community composition or soil resource availability should be regarded as potential determinants of this stability. Here, we explored the effects of three stand types (jack pine, aspen and mixed-wood) and two geologic parent materials (clay and till), on the stability of the microbial biomass in the forest floor. We hypothesised that microbial communities in mixed-wood stands or on the clay soil would show greater resistance to, and resilience from, a dry-wet disturbance, and a higher tolerance to incremental additions of HCl or Cu, than microbial communities in mono-specific stands or on the till soil. We also surveyed the understory vegetation, and measured chemical properties and microbial phospholipid fatty acid profiles in the forest floor, so as to gain insights into the factors regulating microbial stability. Microbial resistance to disturbance was found to be higher in mixed-wood than in mono-specific stands. Microbial communities from mixed-wood stands also showed a high tolerance to HCl and Cu stress over both geologic parent materials, as opposed to those in mono-specific stands that showed a high tolerance to stress on only one type of parent material. Some forest floor properties in mixed-wood stands (e.g. Ca on clay, mineralisable N and C:N ratio on till) were more similar to the more productive aspen, than to jack pine stands. Other properties (understory plant communities, pH, actinomycete and arbuscular mycorrhizae) of mixed-wood stands were transitional between those in aspen and jack pine stands, suggesting that both tree species contribute in structuring the forest floor microbial pool in mixed-wood stands. We put forward that this may provide a more diverse capability to resist disturbance and tolerate stress than in mono-specific stands. We found no effect of stand type on microbial resilience to disturbance, but resilience was higher on clay than on till plots. This could be due to a higher fungal:bacterial ratio on till plots, as slower fungal growth rates may hinder resilience, or to lower carbon and nutrient availability limiting the growth rate of resistant microbial cells. We conclude that plant diversity and site productivity are important drivers of forest floor microbial stability in the southern boreal forest of eastern Canada.

(*Keywords*: Disturbance and stress; Forest floor; Geologic parent material; Microbial stability; *Pinus banksiana*; PLFA; *Populus tremuloides*.)

1. Introduction

Microbial communities are important components of soil food webs that regulate the cycling of materials, energy and nutrients. Their ability to withstand punctual disturbance or chronic stress is, therefore, likely to be repercussive on the stability of important ecosystem processes (de Ruiter et al., 2002). Attempts to describe the factors controlling soil microbial stability have failed, however, to reach a consensus. In theory, an increase in the number of functionally equivalent genotypes within a community should increase the probability of occurrence of resistant populations that compensate for the loss of those vulnerable to disturbance and stress (Yachi and Loreau 1999). Accordingly, several studies have shown positive diversity–stability relationships among microbial communities (e.g. Naeem and Li 1997; Briones and Raskin 2003; Girvan et al. 2005; Ptacnik et al. 2008). Conversely, Finlay et al. (1997) have argued that microbial diversity is of little importance because most microbial taxa are ubiquitous, such that all likely bacterial functions can be maintained in a given environment. Empirical support for this view was given by Wertz et al. (2007), who failed to show the existence of a soil microbial diversity–stability relationship after artificially reducing microbial diversity using serial dilutions. A possible explanation for these divergent results is that soil microbial stability may not be solely affected by microbial species richness, but also by specific components of the microbial community (Griffiths et al., 2004). Factors controlling either microbial diversity or microbial community composition should, therefore, be regarded as potential determinants of soil microbial stability.

Besides community composition, the availability of resources is another factor that likely affects soil microbial stability. Some theoretical models predict an increase in community resilience with higher nutrient availability (DeAngelis et al. 1989). Likewise, community stability may be linked to the number and length of energy flow pathways (Moore et al. 1993), hence to its potential productivity. Productivity is, however, inextricably related to diversity, such that productivity-stability relationships are rarely evoked without referring to diversity as well (e.g. Johnson et al., 1996). It is increasingly acknowledged, however, that the relationships between these three ecosystem components (productivity – diversity – stability) are bi-directional and non-linear (Worm and Duffy, 2003), making it difficult to predict the outcome of higher resource supply on soil microbial stability. For example, Orwin and Wardle (2005) obtained idiosyncratic results, showing an increase of microbial resistance in C-limited soils, concomitant with an increase in microbial resilience in soils with higher N supply.

Most studies on soil microbial stability have been performed under controlled conditions where microbial diversity was manipulated through soil dilutions (e.g. Wertz et al., 2007), biocidal agents (Griffiths et al., 2004) or fixed rhizosphere effects (e.g., Wardle and Nicholson, 1996; Orwin and Wardle, 2005). By and large, these have failed to show clear trends between productivity, bacterial diversity and stability. It is possible that experimental factors imposed as such do not allow time for microbial communities to condition to their environment, as they might over the long term in undisturbed natural ecosystems. Under field conditions, two obvious factors, plant diversity and geologic parent material, come to mind as probable determinants of soil microbial stability. Plant diversity exerts a control on soil microbial community structure by increasing the diversity of litter and rhizodeposition products (Bartelt-Ryser et al. 2005), as well as the number of mycorrhizal hosts (DeBellis et al., 2006; Kernaghan et al., 2003). In a recent field study, Lacombe et al. (2009) showed higher microbial ß-diversity (i.e. the spatial variability in microbial community composition) in agroforestry systems that combined widely-spaced tree rows and a soybean intercrop, than in adjacent fields planted in soybean monoculture. Their study also found higher microbial tolerance to Cu contamination in the agroforestry system compared to the monoculture, providing evidence that increasing plant diversity in species-poor agro-ecosystems results in greater microbial stability. Plant diversity is also regarded as a driver for ecosystem productivity (Tilman et al., 1996), which may also improve microbial stability. Geologic parent material, on the other hand, controls site nutrient capital, including base cations which control soil pH, as well as CEC and drainage. Hence, geologic parent material may exert a long-term influence on microbial community structure and soil resources, each of which may control microbial stability.

We report on a study where forest floor samples were collected in mono-specific and mixed-wood stands of jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.), occurring on both clay and till deposits in the southern boreal forest of Eastern Canada. Previous studies in this region have shown that these stand types and geologic parent materials are associated to distinct understory communities (Légaré et al., 2001), their soils differ significantly in chemical and biochemical characteristics (Ste-Marie and Paré, 1999), and their forest floors harbour distinct microbial communities with distinct carbon source utilization patterns (Lamarche et al., 2007). There is also evidence that boreal mixed-wood stands may be more productive than mono-specific stands (Man and Lieffers, 1999; Légaré et al., 2004), and that stands occurring on clay develop forest floors that are less acidic and more nutrient rich than those occurring on till (Lamarche et al., 2004). This led us to predict that microbial biomass in mixed-wood stands (Hypothesis 1) and on clay plots (Hypothesis 2) would be more resistant and resilient to disturbance (dry-wet cycle), and/or more tolerant of chemical stress (Cu or acidity), than those in mono-specific stands or to those on till plots. At the same time, we compared understory vegetation, forest floor chemistry, as well as microbial community structure in order to provide additional insights into the factors controlling forest floor microbial stability.

2. Material And Methods

2.1. Study area and experimental design

The study area is located in the Abitibi region of Québec, Canada (ca. 48°N, 79°W), and comprises a mosaic of thick glacio-lacustrine clay and undifferentiated glacial till deposits. This mosaic of geologic parent materials, combined with frequent forest disturbance (mainly wildfire and harvesting), has created a heterogeneous landscape composed of pure and mixed-wood stands dominated by deciduous species such as trembling aspen and paper birch (*Betula* *papyrifera* Marsh.), and by coniferous species such as jack pine, black spruce (*Picea mariana* [Mill.] BSP), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and eastern white cedar (*Thuja occidentalis* L.). Average annual precipitation and temperature are respectively 890 mm and 0.8 °C (Environment Canada, 2008).

In May 2006, we identified 10 different sites (five on clay, five on till), each comprising naturally occurring trembling aspen, jack pine and mixed-wood (i.e. trembling aspen + jack pine) stands. According to logging records, forest cover maps and visual observations, the three stand types within each site were similar in slope (0 to 5%) and drainage (well to moderately-well drained). Stand density (650 to 1690 stems ha^{-1}) and stand age (35 to 76 y) varied between sites, but this variation did not coincide with stand type nor with geologic parent material. A 14 m dia. (i.e. 154 m^2) circular plot was established in 28 of the 30 stands. Because mixed-wood stands occurring on till were found on only three sites, this stand type was approximated on the other two till sites by the area comprised within a 30 m-long by 5 m-wide strip established along an abrupt natural boundary separating aspen and jack pine stands. Each of the two species in mixed-wood stands accounted for 40% to 60% of total basal area, based on trees with a diameter at breast height (DBH) > 5 cm. The understory vegetation (0-30 cm) in each plot was estimated by noting all species occurring within 10 cm diameter circular quadrats (28 per plot) established at 1 m intervals along two perpendicular transects (Daget and Poissonet 1971). For the two rectangular plots, this survey was done along a single 30 m transect. For each plot, understory species richness was measured as the number of species observed, and relative frequency as the percentage of quadrats where each species occurred. From these, we calculated the Shannon diversity index (H') and species richness for each plot.

2.2. Forest floor sampling and analyses

In June 2006, 10 forest floor samples were collected from the F horizon (Soil Classification Working Group, 1998) in each plot and bulked into a single sample per plot. Each bulked sample was then passed through a 4 mm metal mesh, and approximately 1 kg (dry wt equiv.) of the sieved material was transferred into a plastic bag. The bags were placed under ice packs in coolers, and transported to Université de Sherbrooke where they were stored at 4°C. A field-moist aliquot (~100 g) of each sample was kept separately frozen at -20°C for subsequent phospholipid fatty acid (PLFA) analyses, as described below.

Mineralisable N was measured as the (NH_4^+ + NO_3^-) concentration following a 30 d aerobic incubation. We weighed 10 g (dry wt. equiv.) subsamples of field-moist forest floor material into Mason jars, covered these with a polyethylene film to prevent desiccation and allow gas exchange, and incubated these at 25 °C. After incubation, mineral N was extracted with 50 mL of 1 N KCl solution, shaken for 1 h and filtered through Whatman No. 5 cellulose filter discs. Filtrates were analysed colorimetrically for NH_4^+ and NO_3^- on a Technicon AutoAnalyser (Pulse Instrumentation, Saskatoon, SK, Canada), via the Berthelot (nitropusside, salicylate, hypochlorite) and Griess–Ilosvay (sulphanilamide-N-(1-naphthyl)-ethylenediamine) reactions (Mulvaney 1996). Oven-dried (65 °C) forest floor material was ground in a ball mill, and total C and N were determined from a 150 mg subsample using a Vario Macro CN Analyzer (Elementar GmbH, Hanau, Germany). Bulk pH was measured in slurries containing 5 g of oven-dried material and 25 mL of deionised water. Another 500 mg of oven-dried material was digested in a H_2SO_4/H_2O_2 solution and analysed for total base cations (Ca, Mg, K and Na) using an AAnalyst-100 atomic absorption spectrometer (Perkin Elmer Corporation, Norwalk, USA).

2.3. Microbial community structure

Microbial community structure in each bulk sample was determined by phospholipid fatty acid (PLFA) analysis, using the procedure described by Hamel et al. (2006). Fatty acid (FA) concentrations were estimated from the detection of methylated 19:0 FA (Sigma Aldrich, St.-Louis, MO), introduced as an internal standard. Concentrated FA extracts were dissolved in hexane and injected in a HP 6890 gas chromatograph equipped with a flame ionisation detector (300°C), a 30-m Restek Rtx-1 column, and He as carrier gas. Microbial community structure was based on the FA nomenclature proposed by Ratledge and Wilkinson (1988).

Peaks of interest were identified based on retention times using 41 FA standards (Supelco Bacterial Acid Methyl Ester Mix 47080-U, Sigma-Aldrich). The abundance of these FAs was estimated from the area under each peak relative to the area below the 19:0 peak, calibrated according to a standard curve made from 19:0 FA standards. The FA 18:2ω6c was ascribed to fungal biomass (Frostegard and Baath 1996). Total bacterial biomass was calculated as the sum of Gram+ (FAs i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 10me16:0, 10me18:0, br17:0, br18:0) and Gram- (FAs cy17:0, cy19:0, 16:1ω7c, 16:1ω7t, 16:1ω9, 18:1ω7) bacteria, plus FA 17:0 (Ratledge and Wilkinson 1988; Zelles 1999; Harwood and Russell 1984). FAs 16:1w5 and 10Me18:0 were respectively ascribed to arbuscular mycorrhizal fungi (AMF) (Madan et al. 2002) and to actinomycetes (Frostegard et al. 1993). The trans:cis ratio, used as an index of microbial nutritional stress, was approximated by the ratio of FAs 16:1w7t and 16:1w7c (Guckert et al. 1986).

2.4. Microbial stability

Three components of microbial stability were measured in each forest floor sample, namely resistance and resilience to disturbance, and tolerance to stress. The first two of these components were assessed according to the protocol described by Orwin and Wardle (2004). Briefly, disturbance consisted of drying 100 g of field-moist forest floor material for 72 h at 40 °C, then rewetting the material to its previous moisture content. Microbial biomass was measured by substrate-induced respiration (SIR; Anderson and Domsch, 1978) in triplicate 5 g (dry wt. equiv.) subsamples before disturbance, immediately after re-wetting, as well as 24 h and 48 h after rewetting. Microbial biomass was simultaneously measured in three control subsamples that had not been disturbed. Resistance and resilience were determined as follows:

$$\text{Resistance} = 1 - |2 D_0| \bullet |C_0 + D_0|^{-1} \qquad [1]$$

$$\text{Resilience} = |2 D_0| \bullet |D_X + D_0|^{-1} - 1 \qquad [2]$$

where C_0 is microbial biomass in the control immediately after rewetting, D_0 is the difference between C_0 and microbial biomass in the disturbed soil immediately after rewetting, and D_X is analogous to D_0 measured 24 h or 48 h after rewetting (Orwin and Wardle, 2004).

Tolerance was assessed in each forest floor sample according to the protocol described by Lacombe et al. (2009). Briefly, duplicate field-moist subsamples (5 g dry wt. equiv.) were treated with 5 mL of one of 12 aqueous solutions containing different concentrations (0-0.6 $mol \cdot l^{-1}$) of a heavy metal (Cu) contaminant. The 24 subsamples were left to incubate at room temperature for 7 d after which microbial biomass was determined by SIR. The entire procedure was repeated, this time substituting the Cu solutions by 12 HCl solutions of different concentrations (0–2.25 N). These two contaminants (Cu and HCl) were chosen because of their relevance to the study area, where copper mines and smelters are sources of Cu and acid deposition. For each forest floor sample, microbial biomass was plotted as a function of Cu or HCl concentrations, and these relationships were fitted to a decreasing exponential function using SAS (SAS Institute, Cary, NC) statistical software :

$$C_{mic} = (IC_{mic}) \bullet e^{-k[Cont]} \qquad [3]$$

where C_{mic} is microbial carbon at a given contaminant concentration [Cont], IC_{mic} is microbial carbon at [Cont] = 0 (i.e., Y-intercept), e is the base of the natural logarithm, and k is a first-order decay rate constant. Tolerance was thus calculated as follows:

$$\text{Tolerance} = 2k_{max} - k_{x} \qquad [4]$$

where k_{max} is the highest decay rate among all subsamples and k_{x} is the decay rate of sample X.

2.5. Statistical analyses

The effects of stand type, geologic parent material and their interaction, on soil properties and microbial stability were tested using mixed-effects ANOVA models, with stand type and parent material as fixed factors and site as a random factor. Prior to analyses, normality and equality of variance were verified for each variable using Shapiro's and Levene's tests. All data deviating from normality or homoscedasticity were transformed (log or square-root) to meet assumptions of ANOVA. Main effects and pairwise comparisons were tested at the 0.05 confidence level. When an interaction was significant, simple main effects and pair-wise comparisons were tested at the 0.01 confidence level, to conserve a family-wise error rate of

0.05. ANOVAs were performed using the MIXED procedure, whereas pair-wise comparisons were performed using the LSMEANS procedure, in SAS statistical software (SAS Institute, Cary, NC). Relationships between individual soil properties and indices of microbial stability were explored by linear regression.

Principal component analysis (PCA) were used to ordinate plots according to PLFA profiles. To ordinate plots according to the understory vegetation, we used correspondence analysis (CA) because an "arch effect" was detected using PCA. Plant species present in less than 10% of the plots were removed from the analysis. Because PLFA and vegetation data included many zero values, these data were Hellinger-transformed (Legendre and Gallagher, 2001) prior to analyses. PCA and CA were carried out using CANOCO version 4.53 software (ter Braak and Smilauer, 2002). DISTLM v.5 statistical software (Anderson 2001, 2004a), a non-parametric permutation-based multivariate procedure, was used to test for differences among stand types and between parent materials based on PLFA profiles and understory plant communities. In order to compare the relative importance of each stand type, or of each parent material, in determining plant and microbial community composition, we applied PERMDISP (Anderson, 2001, 2004b), a multivariate analogue of Levene's test of dispersion, to test the equality of variance in vegetation or PLFA data.

3. Results

3.1. Forest floor properties

Forest floor pH was highest in aspen and lowest in jack pine stands ($F_{2,16} = 35.06$, $P<0.001$), whereas pH ($F_{1,16} = 30.45$, $P<0.001$), microbial biomass ($F_{1,16} = 6.16$, $P<0.05$), total K ($F_{1,16} = 15.88$, $P<0.001$) and Mg ($F_{1,16} = 32.38$, $P<0.001$) were higher on clay than on till (Table 1). ANOVAs also revealed significant interactions between stand type and parent material in controlling mineralisable N ($F_{2,16} = 3.95$, $P<0.05$), total Ca ($F_{2,16} = 5.47$, $P<0.05$) and C/N ratio ($F_{2,16} = 3.77$, $P<0.05$). More specifically, there was no significant difference in mineralisable

Table 1

Significant effects of stand type, parent material, and their interaction on forest floor properties; lower-case letters indicate significant (*P*<0.05) differences within each cluster (n = 5); numbers in parentheses = 1 SE.

	Main effects					
	Stand type			Parent material		
	Aspen	Jack pine	Mixed-wood	Clay	Till	
pH (water)	5.03 (0.28) a	4.05 (0.16) c	4.61 (0.25) b	4.96 (0.26) a	4.16 (0.19) b	
Microbial biomass (mg C_{mic} g^{-1})	NS			6.97 (0.54) a	5.12 (0.52) b	
K_{total} (mg/g soil)	NS			2.82 (0.46) a	1.57 (0.20) b	
Mg_{total} (mg/g soil)	NS			1.21 (0.25) a	0.50 (0.06) b	
	Interaction effects					
	Stand type within clay			Stand type within till		
	Aspen	Jack pine	Mixed-wood	Aspen	Jack pine	Mixed-wood
Mineralisable N (mg g^{-1})	0.59 (0.15) a	0.45 (0.18) a	0.49 (0.16) a	0.59 (0.13) a	0.02 (0.01) b	0.48 (0.08) a
Ca_{total} (mg g^{-1})	11.31 (0.74) a	5.2 (0.48) b	12.13 (0.57) a	8.36 (1.16) a	3.79 (0.54) c	5.83 (0.44) b
C/N ratio	19.73 (1.31) b	25.62 (2.29) a	22.15 (1.03) ab	21.18 (1.30) b	30.89 (2.29) a	21.80 (0.96) b

N among stand types on clay, whereas mineralisable N on till was higher in aspen and mixed-wood stands than in jack pine stands ($F_{2,16} = 11.89$, P<0.001). Total Ca on clay was higher in aspen and mixed-wood stands than in jack pine stands ($F_{2,16} = 32.67$, P<0.001), whereas total Ca on till was higher in aspen stands only ($F_{2,16} = 16.18$, P<0.001). The C/N ratio on clay was higher in jack pine than in aspen stands ($F_{2,16} = 11.19$, P<0.001), whereas the C/N ratio on till was higher in jack pine than in both aspen and mixed-wood stands ($F_{2,16}=29.83$, P<0.001).

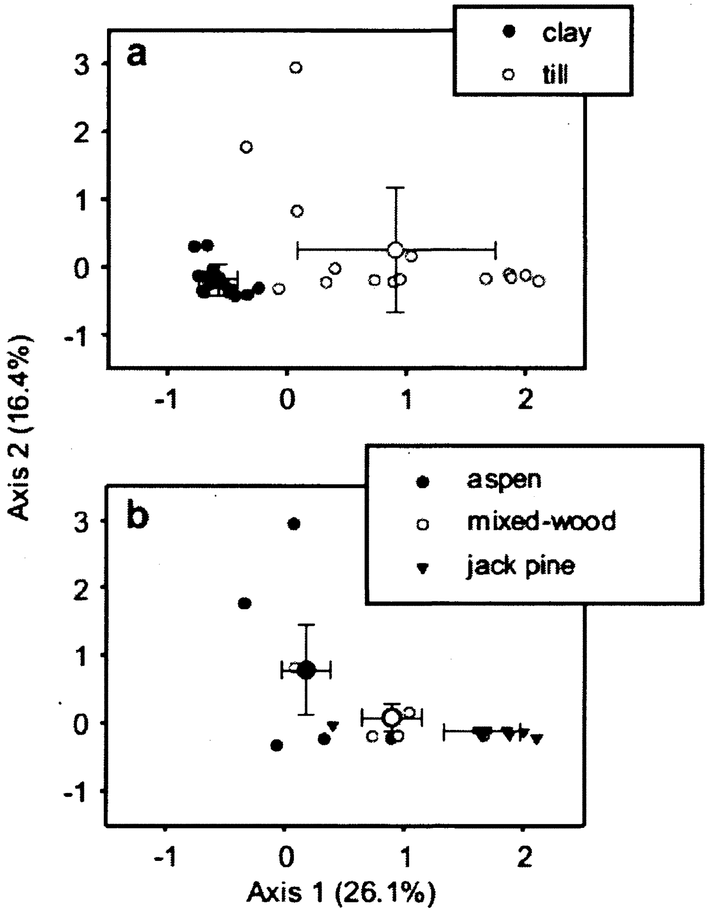

Figure 1. Ordination biplots generated from correspondence analysis (CA) of the understory vegetation. Frame (a) distinguishes stands according to parent material, whereas frame (b) distinguishes plots according to stand type on till. Small symbols are individual plot positions whereas large symbols with error bars represent centroids and standard deviations. The proportion of variance explained by each of the first two principal components is indicated in parentheses.

3.2 Understory vegetation

Results of CA based on the understory vegetation showed a segregation of clay and till plots along Axis 1, which accounted for 26% of the total variation (Fig. 1a), and this difference in understory plant communities was confirmed as significant (pseudo-$F_{1,24}$ = 7.45, P<0.001) with DISTLM. Among species with the highest factor loadings, *Gaultheria procumbens* L., *Kalmia angustifolia* L. and *Vaccinium angustifolium* Ait. correlated positively with Axis 1, whereas *Carex* spp. and *Lonicera canadensis* Bartr. correlated negatively with Axis 1. PERMDISP revealed a greater variability of the understory vegetation on till than on clay ($F_{1,24}$ = 71.40, P<0.001). On till, CA based on the understory vegetation showed mixed-wood stands ordinating between those of aspen and jack pine stands (Fig. 1b). DISTLM confirmed that the understory vegetation in aspen and jack pine stands were significantly different on till plots only (pseudo-$F_{1,24}$ = 4.03, P<0.001).

ANOVAs revealed a significant interaction between stand type and parent material regulating understory plant species diversity ($F_{2,16}$ = 9.93, P<0.01) and richness ($F_{2,16}$ = 6.06, P<0.05). More precisely, species diversity (t = 4.23, P<0.001) and richness (t = 5.29, P<0.001) were higher in aspen than in jack pine stands on till plots only (Table 2). For both jack pine and mixed-wood stands, species diversity and richness were higher on clay than on till (P<0.001 for all comparisons).

Table 2

Effect of stand type on Shannon's diversity index and species richness of the understory plant community; lower-case letters indicate significant (P<0.01) differences within each row (n = 5); numbers in parentheses = 1 SE.

		Aspen	Jack pine	Mixed-wood
Clay	Shannon H'	2.02 (0.11) a	2.08 (0.16) a	2.22 (0.16) a
	Richness	12 (2) a	13 (2) a	14 (2) a
Till	Shannon H'	1.83 (0.33) a	1.01 (0.49) b	1.58 (0.20) ab
	Richness	11 (3) a	4 (8) b	7 (2) ab

3.3. Microbial community structure

Results of PCA based on PLFA profiles showed a segregation of clay and till plots along Axis 1 (Fig. 2a), and a segregation of stand types along axes 1 and 2 (Fig. 2b), which together accounted for 62 % of the variation in the data set.

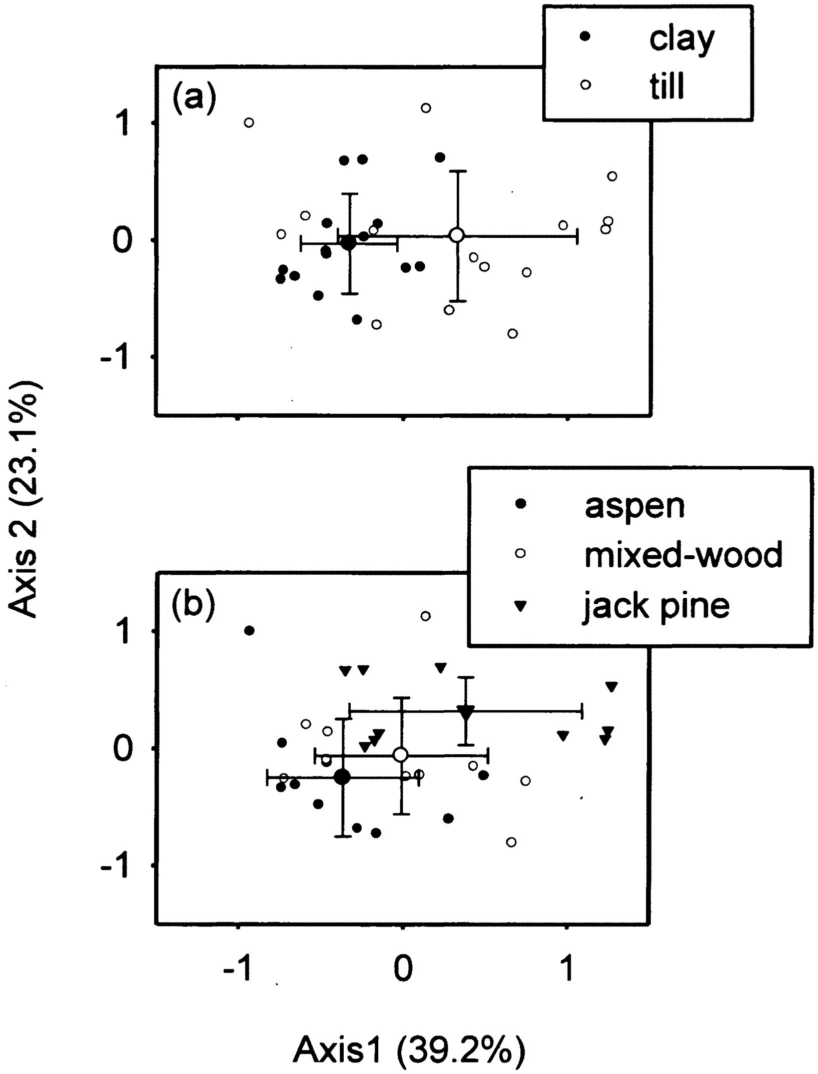

Figure 2. Ordination biplots generated from principal component analysis (PCA) of 41 soil fatty acids (PLFAs). Frame (a) distinguishes stands according to parent material, whereas frame (b) distinguishes plots according to stand type. Small symbols are individual plot positions whereas large symbols with error bars represent centroids and standard deviations.

The proportion of variance explained by each of the first two principal components is indicated in parentheses.

DISTLM confirmed that PLFA profiles in clay plots were distinct from those in till plots (pseudo-$F_{1,24} = 4.63$, $P<0.001$), and that those in jack pine were distinct from those in aspen (pseudo-$F_{1,24} = 6.54$, $P<0.001$) and mixed-wood stands (pseudo-$F_{1,24} = 2.74$ $P<0.05$). FAs with the highest factor loadings on PCA Axis 1 were the fungal-specific 18:2ω6c (positive correlation), bacterial-specific 18:1ω7, i17:0 and 16:1ω9 (negative correlations), and the AMF-specific 16:1ω5 (negative correlation) (Table 3). Four of the microbial FAs (22:0, 24:0, 19:0, 20:0) with the highest factor loadings on PCA Axis 2 are also found in plants (Zelles, 1999), whereas the fifth FA (20:1) is not reported in the literature as being specific to soil microbial communities.

Table 3

FAs with the highest factor loading along the first two principal components (PCA).

	Fatty acid	Loading
PC 1	18:1ω7	-1.50
	i17:0	-1.49
	18:2ω6c	1.41
	16:1ω9	-1.37
	16:1ω5	-1.34
PC 2	22:0	1.94
	24:0	1.87
	19:0	1.58
	20:0	1.55
	20:1	-1.26

We found a significant interaction ($F_{2,16} = 6.68$, $P<0.01$) between stand type and parent material in controlling the fungal:bacterial ratio (Fig. 3a). On till only, this ratio was significantly higher in jack pine than in mixed-wood and aspen stands. There was a marginal effect ($F_{1,24}$ = 3.91, P=0.06) of parent material (clay < till) on the trans:cis ratio (Fig. 3b). Actinomycetes and AMF were highest in aspen and lowest in jack pine stands ($F_{2,16}$ = 24.32, P<0.001 and $F_{2,16}$ = 23.73, P<0.001, respectively), and both were higher in clay than in till plots ($F_{1,16}$= 10.13, P<0.01 and $F_{1,16}$= 6.47, P<0.05, respectively) (Fig. 3c, d).

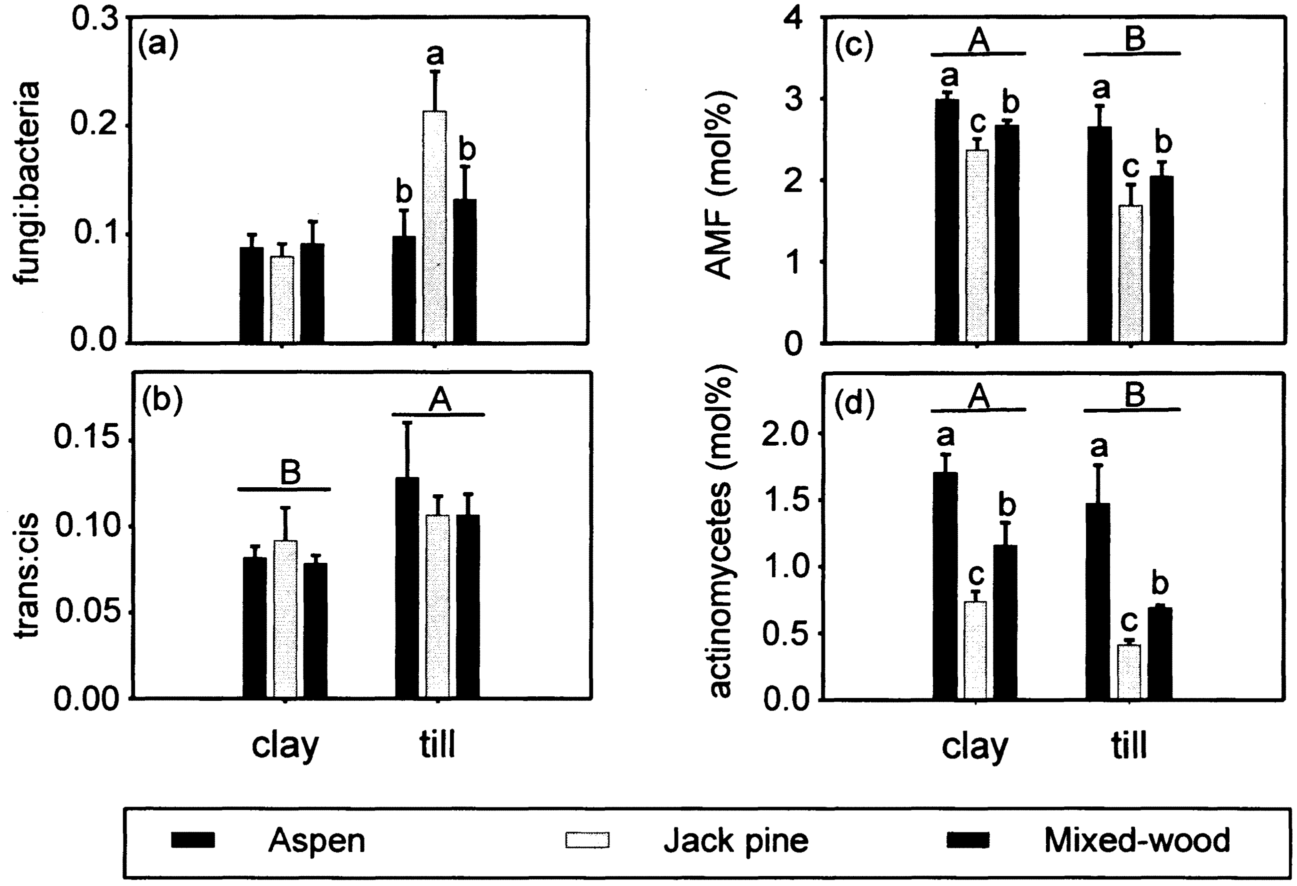

Figure 3. Fatty acid abundances expressed as mol %, or ratio of mol %, for (a) fungal/bacterial ratio, (b) trans/cis ratio, (c) arbuscular mycorhiza, and (d) actinomycetes. Lower-case letters indicate significant differences between stand types within a given parent material, whereas upper-case letters indicate significant differences between parent materials over all stand types. Vertical bars represent standard errors.

3.4. Microbial stability

.Resistance was significantly higher in mixed-wood than in single species stands ($F_{2,16} = 4.29$, $P<0.05$) (Fig. 4a). Resilience (24 h after disturbance) was higher in clay than in till plots ($F_{1,16} = 6.45$, $P<0.05$) (Fig. 4b). There were significant interactions between stand type and parent material in controlling tolerance to Cu ($F_{2,16} = 4.63$, $P<0.05$) and to HCl ($F_{2,16} = 9.57$, $P<0.01$). In each case, microbial communities from aspen stands were

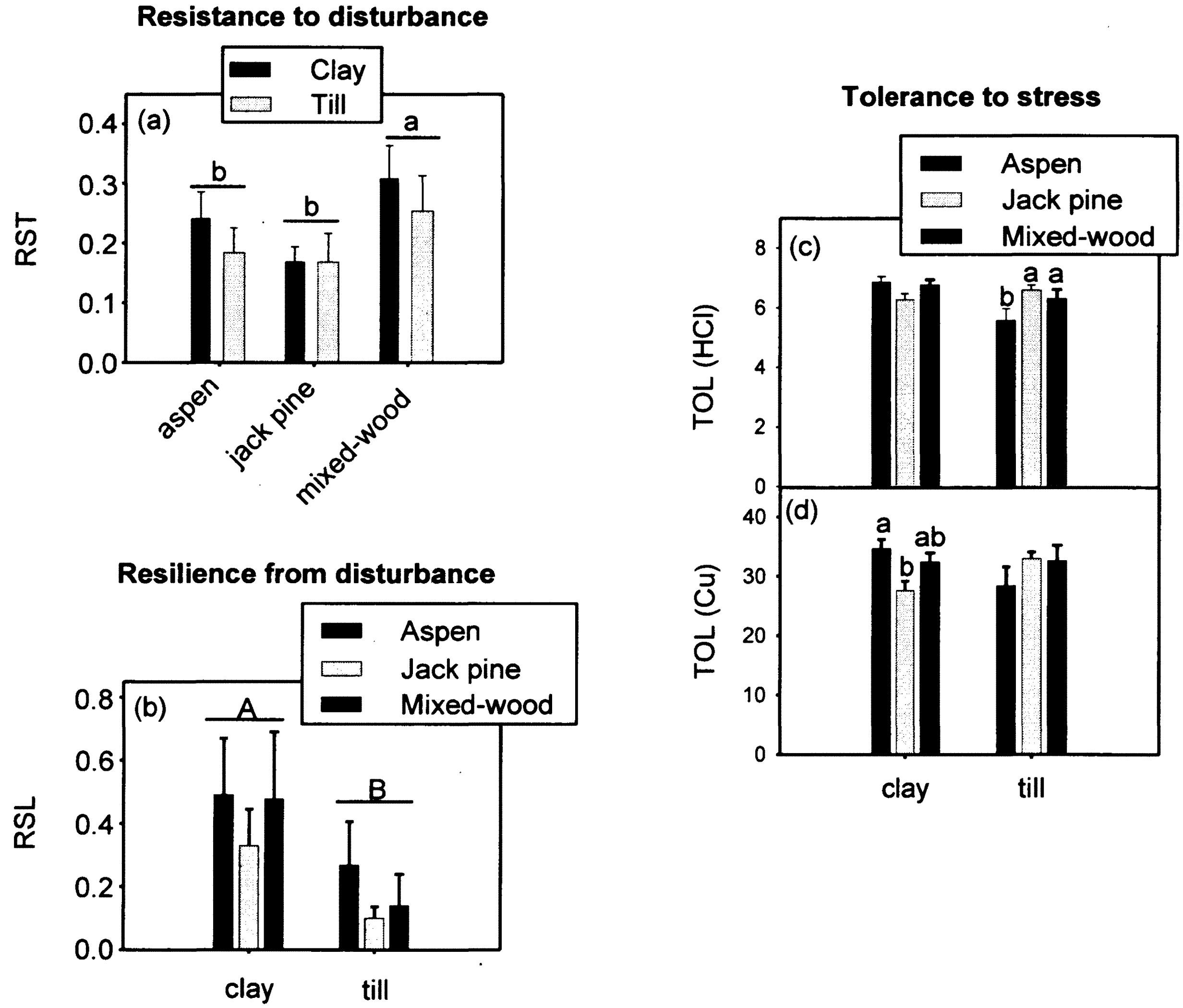

Fig. 4. Effect of stand type and parent material on (a) microbial resistance to wet-dry disturbance, (b) microbial resilience 24 h following wet-dry disturbance, and (c, d) tolerance to HCl and Cu stress. Lower-case letters indicate significant differences between stand types, whereas upper-case letters indicate significant differences between parent materials. Vertical bars represent standard errors.

most tolerant on clay, and those from jack pine stands were most tolerant on till (Fig. 1c, d). The effect of stand type on tolerance to Cu was, however, only significant on clay ($F_{2,16}$ = 3.59, P=0.05), whereas the effect of stand type on tolerance to HCl was only significant on till ($F_{2,16}$ = 8.09, P<0.01). In mixed-wood stands, tolerance to Cu and to HCl were as high as in aspen stands on clay, and as high as in jack pine stands on till. Tolerance to both Cu and HCl were positively correlated to soil pH on clay, and negatively correlated to soil pH on till (Fig. 5a, b).

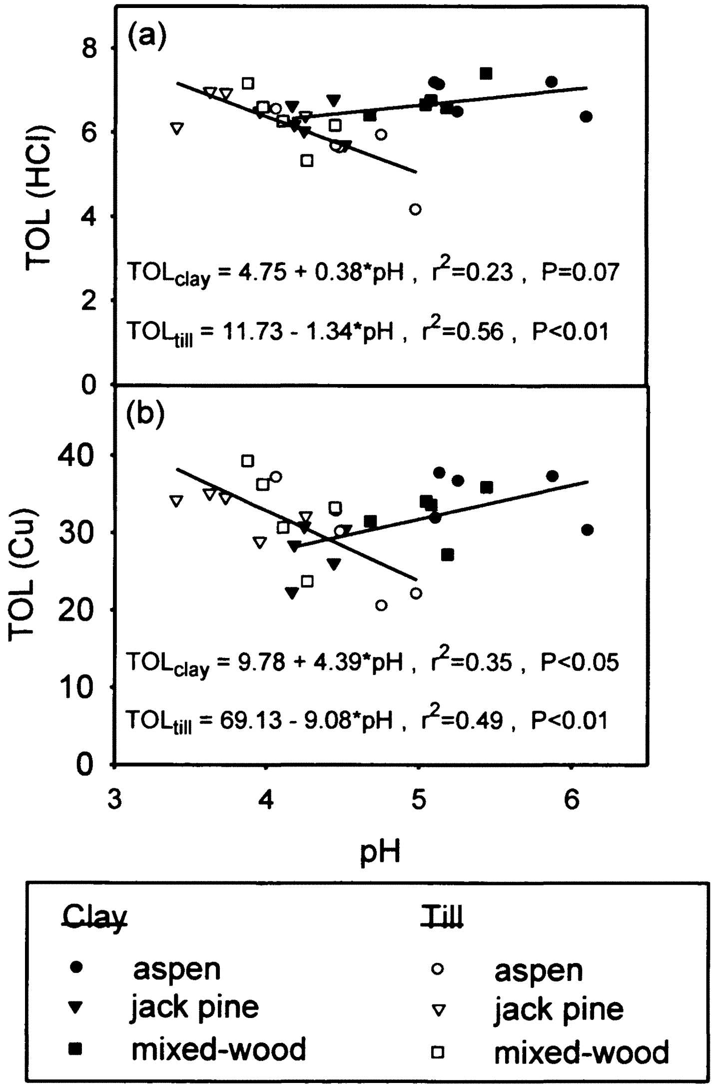

Fig. 5. Linear regression analysis of microbial tolerance to (a) HCl and (b) Cu stress, as a function of initial forest floor pH.

4. Discussion

4.1. Higher microbial resistance in mixed-wood stands

In accordance with our first hypothesis, we found higher microbial resistance to disturbance in mixed-wood than in mono-specific stands of aspen or jack pine. This may be a consequence of a greater diversity of forest floor resources brought about by the mixture of two contrasting tree species, each contributing different litter and rhizodeposition products (DeBellis et al. 2006). In a recent litterbag study, Keith et al. (2008) showed that litter species diversity increases the stability of decomposer communities. The diversity of forest floor resources may also come about via the understory litter, which may also affect microbial community composition (Hannam et al. 2006). Mixed-wood stands maintained understory species diversity and richness comparable to those in aspen stands. Although these understory communities comprise a small proportion of the standing biomass, their high turnover rates and high nutrient contents imply that they produce a substantial proportion of litterfall nutrients (Nilsson and Wardle, 2005). For example, Perala and Alban (1982) found that the understory vegetation in 40-y-old trembling aspen and jack pine stands, returned 6–19 % and 5–13 % of total annual litterfall biomass, corresponding to 14–36 % and 13–37 % of total litterfall nitrogen. Perhaps more important than species diversity and richness *per se*, understory communities in mixed-wood stands comprised plant species common to each mono-specific stands, thus increasing functional attributes of the plant litter. In keeping with Walker's "redundancy hypothesis" (Walker, 1992), we put forward that resource diversity in mixed-wood stands could increase microbial diversity and, by implication, the number of resistant microbial taxa.

Alternatively, higher microbial resistance may have resulted from higher net primary productivity in boreal mixed-wood stands. For example, our data showed that mixed-wood stands exhibited some forest floor properties that were more similar to aspen than to jack pine stands (i.e. Ca on clay, mineralisable N and C:N ratio on till), which would make them more productive. Aspen is known to cycle large amounts of Ca compared to jack pine (Alban, 1982), and clay deposits in Abitibi are known to contain more available Ca than till deposits (Lamarche et al., 2004). The fact that mixed-wood plots on clay, with aspen only comprising ~50% of total basal area, cycled Ca at approximately the same concentrations as plots with 100% aspen, suggests positive resource partitioning due to low Ca demand by jack pine. With respect to N mineralisation rates on till, jack pine stands harboured ericaceous plants, such as *Kalmia angustifolia*, that were nearly absent in mixed-wood stands. These shrubs are known to produce large quantities of condensed tannins that reduce N mineralization, by forming stable complexes with soil protein (Joanisse et al., 2009). With respect to C:N ratios on till, we can only speculate as to why these were lower in mixed-wood than in jack pine stands. Perhaps aspen litter can synergize the decomposition of jack pine litter (Fyles and Fyles, 1993), or perhaps mixed-wood stands create positive feedback between N mineralisation rates in the forest floor and litter-N concentrations. Both of these mechanisms would lead to a lower C:N ratio. Regardless of the underlying explanations, higher Ca concentrations and N mineralisation rates, and lower C:N ratios, are consistent with reports that aspen grown in mixtures can improve stand productivity beyond what can be predicted from growth rates of mono-specific stands (Man and Lieffers, 1999; Légaré et al., 2004). Accordingly, it was suggested that productivity and nutrient availability may improve soil microbial stability (DeAngelis et al., 1989; Moore et al., 1993), which is consistent with the higher resistance values we observed in mixed-wood stands.

4.2. Higher microbial resilience in clay plots

In accordance with our second hypothesis, we noted that microbial resilience was higher in clay than in till plots. PCA revealed that till plots were positively correlated to fungal FAs, and negatively correlated to some bacterial FAs. It is expected that fungi will thrive in the more acidic till plots, and bacteria in the higher pH clay plots (Matthies et al., 1997). Because resilience is implicitly related to growth rates, and because most fungi have slower potential growth rates than bacteria (Cooke and Whipps, 1993), resilience should be lower in plots where fungi:bacteria ratios are higher.

Alternatively, resilience may not be limited by potential microbial growth rates per se, as these are rarely achieved in nature (Maier et al., 2000). Rather, resilience values may reflect the relative limitation of carbon and nutrients within each type of parent material. Lower microbial biomass on till is indicative of lower available C supply (Bradley and Fyles, 1995). Given that a wet-dry disturbance should increase the maintenance energy costs of soil microorganisms (Tobor-Kaplon et al., 2005), resilience should consequently be lower on till than on clay. Likewise, nutritional stress could limit the growth rate of resistant bacterial cells. There are clear indications that nutrients are more limiting on till than on clay plots. Firstly, forest floors on till had lower concentrations of base cations (K, Mg, Ca) than forest floors on clay. In addition, understory plant diversity was lower and more variable in till plots, consistent with reports that few plant species can co-exist in acidic soils with low base cation concentrations (Roem and Berendse, 2000). Likewise, results of CA revealed strong positive correlations between till plots and ericaceous shrub species (*G. procumbens*, *K. angustifolia* L. and *V. angustifolium*) that are indicative of nutrient-poor conditions. Finally, we found higher trans:cis FA ratios on till, further evidence of greater nutritional stress among microbial communities (Guckert et al., 1986).

4.3. Mixed-wood stands confer tolerance to stress on both parent materials

On till plots, tolerance was high in both jack pine and mixed-wood stands. Microbial communities in jack pine were characterised by a large fungi:bacteria ratio. Fungi have a lower surface:volume ratio than bacteria what decreases their contact with the external environment (Cooke and Whipps, 1993) and may explain why they are more tolerant to acidic conditions (Matthies et al., 1997) as well as to Cu-induced stress (Kostov and Van Cleemput, 2001). Fungi:bacteria ratios fail to explain, however, why tolerance on till was higher in mixed-wood than in aspen stands. For this observation, we are short of an explanation. On clay plots, tolerance was higher in both aspen and mixed-wood stands. Compared to jack pine stands, microbial communities in these two stand types were characterised by a greater biomass of AMF and actinomycetes. AMF fungi, especially those from the Acaulosporaceae family, are highly tolerant of soil acidity (Vosatka et al., 1999; Sharma et al., 2009).

Actinomycetes, on the other hand, have been shown to tolerate high concentrations of heavy metals such as Cu (Siñeriz et al., 2005). It may thus be reasoned that mixed-wood stands confer tolerance to stress on both parent materials by maintaining microbial communities that combine components of both aspen and jack pine stands (Fig. 2b).

Past studies in the Abitibi region have shown forest floors on clay to be less acidic than those on till (e.g. Lamarche et al., 2004). Initial soil pH may be a filter that drives the response of microbial communities to subsequent stress. For example, two theories predict opposite responses in biological stability with increasing stress. The first predicts that previously non-stressed communities will be more stable, because they have benefited from more resources to maintain their functions under subsequent stress (Bruins et al., 2000; Loreau, 2000). This appears to be the case on clay, where initial pH correlated positively with tolerance. The second theory proposes that initial exposure to stress will condition microbial communities and increase their ability to cope with further stress (Giller et al., 1998; Mertens et al., 2007). This seemed to be the case on till, where initial pH correlated negatively with tolerance.

4.4. Forest management implications

Jack pine and trembling aspen are two early-seral tree species that can naturally occur as mixed-wood stands in the southern boreal forest of Eastern Canada. Over the past 80 years, forest management practices have favoured the establishment of mono-specific stands of these two species following forest harvesting or wildfire, thereby minimising the diversity of the forest landscape. Results from our study point to the ecological value of maintaining some mixed-wood stands in this landscape. Our study also revealed that the resilience of forest floor microbial communities may be affected by geologic parent material. Given that parent material will not change over the short term, detailed soil maps could be used as tools for predicting the stability of forest floor microbial processes in the context of anthropogenic disturbance or stress.

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CHAPITRE 3

LES PROPRIÉTÉS DE LA COUCHE MORTE ÉCHANTILLONNÉE EN TRAVERS D'UNE FRONTIÈRE ABRUPTE SÉPARANT DES PEUPLEMENTS PURS DE PEUPLIER ET DE PIN GRIS DANS LE SUD DE LA FORÊT BORÉALE

Référence: Royer-Tardif, S., Bradley, R.L. Forest floor properties across sharp compositional boundaries separating trembling aspen and jack pine stands in the southern boreal forest. (Accepté pour publication dans Plant and Soil)

Nous avons vu, dans l'introduction, comment l'influence du pin gris sur les propriétés édaphiques différait de celle du peuplier. Toutefois, nous ne savons pas jusqu'à quelle distance chacune des espèces influence ces propriétés et encore moins laquelle possède la plus forte influence sur l'environnement édaphique. Comme il a été mentionné dans l'introduction, sur till, le peuplier et le pin gris tendent à former des peuplements purs adjacents séparés par une frontière très nette. Ce troisième et dernier chapitre a pour objectif d'étudier la variation des propriétés physico-chimiques du sol ainsi que la composition et l'activité microbienne le long de telles frontières. En ce sens j'ai testé l'hypothèse que le peuplier possède une plus forte influence sur les propriétés édaphiques que le pin gris dû, entre autre, à la plus grande dispersion de sa litière. Pour ce faire, j'ai employé des analyses statistiques utilisant le déplacement de fenêtres (split moving window; SMWA et moving window regression analysis; MWRA) le long de transects placés perpendiculairement à des frontières entre des peuplements purs de peuplier et de pin gris. Ces techniques sont fréquemment employées en écologie végétale (Cornelius et Reynolds, 1991; Hennenberg *et al.*, 2005), mais rarement en écologie des sols. L'utilisation de telles techniques pour évaluer les changements dans la composition des communautés microbiennes dans des transitions végétales représente une première et pourrait s'avérer utile dans d'autres études visant à établir un lien entre les diversités végétale et microbienne.

Les résultats de cette étude confirment que le peuplier possède la plus forte influence sur les variables édaphiques reliées à la qualité de sa litière aérienne ainsi que sur la composition des communautés microbiennes du sol. Toutefois, le pin gris influence également les propriétés édaphiques, notamment les taux de nitrification, probablement par le biais de son activité racinaire. Dans l'ensemble, ces résultats suggèrent que ces écotones naturels présentent une combinaison unique de propriétés édaphiques et font partie intégrante de la diversité à l'échelle du paysage. Ceci devrait être pris en considération dans les plans de gestion forestière tentant d'imiter la dynamique naturelle des forêts.

J'ai établi le dispositif expérimental, récolté les données et effectué les analyses de laboratoire pour cette étude. J'ai également suggéré l'utilisation des analyses de SMWA et de MWRA et les ai appliquées aux données récoltées. En ce sens, j'ai reçu les conseils statistiques du Dr. William F.J. Parsons. Les stagiaires M. Dufresne et R. Roy ont participé, respectivement, à la récolte de données sur le terrain et à l'analyse des données en laboratoire. Nous avons reçu l'aide du Dr. Erland Bååth pour l'analyse des acides gras phospholipidiques. La rédaction du manuscrit a été répartie entre mon directeur, le Dr. Robert Bradley et moi.

Abstract

Jack pine and trembling aspen are two early-seral boreal tree species with contrasting nutrient cycling strategies. Both species may form adjacent mono-specific stands separated by sharp compositional boundaries. We hypothesized that such a sharp change in vegetation results in wider functional ecotones that can be gauged by spatial transitions in humus forms, nutrient cycling patterns and forest floor microbial communities. These properties were thus assessed across 32 m long transects set perpendicular to sharp compositional boundaries separating four jack pine and aspen stands. Split moving window analysis (SMWA) and moving window regression analysis (MWRA) were used to locate functional boundaries and ecotones. We found a gradual transition from moder humus under aspen to mor humus under jack pine, spanning approximately 16 m across the compositional boundary. An abrupt increase in forest floor water content was observed at 3 m within jack pine stands, possibly due to aspen roots foraging for water beyond the compositional boundary. The functional boundary and associated ecotone for several forest floor properties (pH, C:N ratio, Mg, ammonification) were skewed toward jack pine stands, likely the result of a greater dispersal of aspen leaves. Low nitrification rates were measured throughout jack pine stands and up to 11 m into aspen stands, suggesting that jack pine roots might extend far within aspen stands and produce metabolites (e.g. monoterpenes) that suppress nitrification. SMWA performed on the multivariate dataset of microbial fatty acids (FAs) revealed three distinct forest floor microbial communities that were skewed toward jack pine stands. Pine-type communities were associated to fungal FAs, pine-type and transition-type communities to non-fungal eukaryotic FAs, and aspen-type communities to bacterial FAs. Taken collectively, our data delimit a 24 m wide functional ecotone straddling sharp compositional boundaries separating trembling aspen and jack pine stands. We conclude that the functional diversity of boreal landscapes, where adjacent mono-specific stands are prevalent, is related to the patchiness of the landscape.

Keywords Ecotone • Forest floor • Humus form • Phospholipid fatty acids analysis • *Pinus banksiana* • *Populus tremuloides* • Split moving window analysis

Introduction

Müller (1889) is credited for classifying humus forms as “mor”, “moder” and “mull”, which describe a gradient in the rate at which tree and understory plant litters persist and accumulate over the mineral soil surface. This gradient may result from abiotic factors such as temperature and subsoil drainage, but also from biotic factors such as plant litter chemistry and decomposer food webs (Coûteaux et al. 1995; Aerts 2006). Different humus forms are, therefore, intrinsically related to nutrient cycling strategies of dominant plant species and their attendant effects on the soil biota. Forest ecosystems comprising a diversity of stand types should, therefore, maintain a diversity of humus forms, which in turn maintain a diversity of attributes among ecosystem functions such as hydrologic cycling (Sevink et al. 1989) and carbon sequestration (Laganière et al. 2010).

In the southern boreal forest of eastern Canada, jack pine and trembling aspen are two early-seral, shade-intolerant species. Though they achieve similar growth rates (Longpré et al. 1994), they have been shown to induce dissimilar understory plant communities (Légaré et al. 2001), forest floor properties (Ste-Marie et al. 2007) and microbial communities (Royer-Tardif et al. 2010). These differences are likely to result from differences in litter quality, root properties, and light transmittance of each species. Aspen is a high nutrient and water requiring species (Gower et al. 2000) that produces leaf litter with more labile compounds (Taylor and Parkinson 1988) and base cations (Alban 1982) than jack pine needle litter. Forest floors under aspen are expected, therefore, to have a higher pH and a lower fungi:bacteria ratio than those under jack pine (Rousk et al. 2009; Wardle 2002). Conversely, jack pine litter is richer in lignin and other phenolic substances (Taylor and Parkinson 1988), which further reduce decomposition rates relative to aspen litter (Bockheim et al. 1991). Taken collectively, these differences in litter quality suggest that forest floors under jack pine will be thicker (i.e. mor humus) than under aspen (moder or mull humus), with corresponding differences in chemical and microbial properties.

When aspen and jack pine co-occur on glacial till deposits, it is commonly observed that they do not mix, but rather form adjacent mono-specific stands separated by sharp boundaries (Fig. 1) (Royer-Tardif et al. 2010; Ste-Marie et al. 2007).

Figure 1. An example of an abrupt compositional boundary between early-seral jack pine and trembling aspen stands occurring on a till deposit in the southern Abitibi region . An evenly distributed second cohort of slow-growing shade-tolerant late-seral black spruce trees can be seen growing beneath the canopies of both early-seral species.

Although these "compositional boundaries" are abrupt, it is not known how underlying forest floor properties and microbial communities respond to the sudden change in vegetation. A first possibility is that forest floor properties change as abruptly as does the vegetation (Fig. 2, Case 1). Alternatively, the effect of both tree species on a given forest

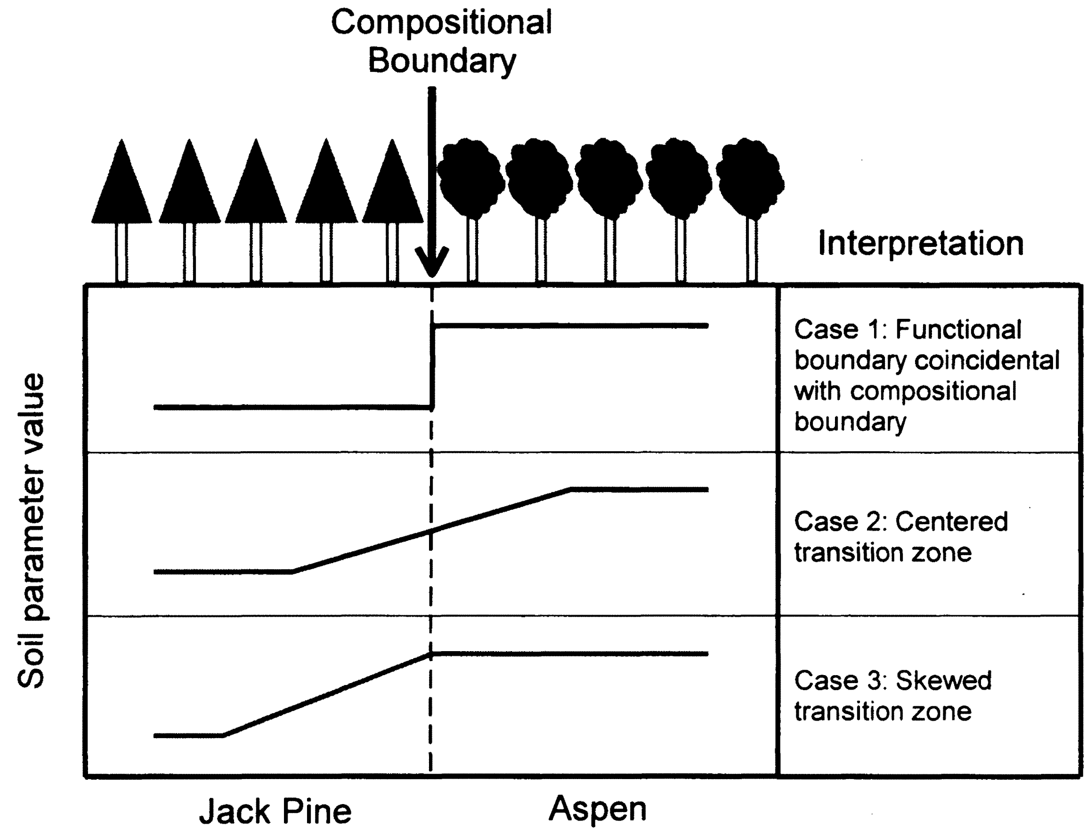

Figure 2. Hypothetical changes that may occur in the value of a given forest floor property measured across an abrupt compositional boundary.

floor property could reciprocally extend on either side of the compositional boundary, thereby creating a centered transition zone (Fig. 2, Case 2). Then again, if one of the two species has a greater range of influence on a given forest floor property, we could observe a "functional boundary" and a transition zone that are skewed relative to the compositional boundary (Fig.2, Case 3). Cases 2 and 3 would effectively result in functional ecotones with humus forms, nutrient cycling patterns and microbial communities that are distinct from those found in mono-specific stands of either species. Such being the case would imply that compositional boundaries between aspen and jack pine, as sharp as they may be, increase the diversity of ecosystem functions. Thus, the functional diversity of aspen–jack pine landscapes would be determined not only by the relative abundance of each species, but also by the extent of compositional boundaries across the landscape.

Here, we report on a study where we assessed functional boundaries and transition zones of humus forms, as well as chemical and biological properties of forest floors, across sharp compositional boundaries separating aspen and jack pine stands. We also assessed forest floor microbial community structure across these compositional boundaries, and related these to the measured physico-chemical properties. Since deciduous litter has, in general, a greater range of dispersion than conifer needles (Ferrari and Sugita 1996), we hypothesized that forest floor ecotones would be skewed within jack pine stands. Our objective was to provide information on the nature, position and width of forest floor ecotones that could be used to evaluate how various forest management strategies reduce or increase the functional diversity of boreal forest landscapes.

Methods

Study area

Our study was conducted in the southern boreal forest of the Abitibi region of Québec, Canada (ca. 48° 58' N; 79° 09' W). Mean annual temperature and mean annual total precipitations are, respectively, 0.7 °C and 890 mm (Environment Canada, 2010). The jack pine and aspen stands that we sampled developed over sandy glacial till deposits, and are all well-drained, acidic and nutrient-poor in comparison with lacustrine clay deposits that are also common in this region (Royer-Tardif et al. 2010). These stands are even-aged and originated from a fire that occurred around the year 1915 (Bergeron et al. 2003). A charcoal layer is observable below the organic horizon, suggesting that the totality of the forest floor was burned.

Forest floor sampling and analysis

We selected sharp boundaries occurring between four adjacent aspen and jack pine stands located on flat terrain. A 32 m long transect was established perpendicular to, and centered on, each of these compositional boundaries. The forest floor was sampled at 2 m intervals along these transects yielding a total of 17 samples per transect, that is, eight samples on each side of the boundary and one on the boundary itself. Surface litter was manually brushed off, and the thickness of the underlying forest floor F and H horizons (Soil Classification Working Group 1998) was recorded. The F-horizon is characterized by an accumulation of fibrous partly decomposed organic matter, whereas the H-horizon is characterized by an amorphous accumulation of well decomposed organic matter in which the original structures are indiscernible. At each sampling location, both forest floor horizons were collected with a 10 cm dia. metal core, mixed and passed through a 4 mm sieve to remove roots and coarse debris. Forest floor samples were transferred into plastic bags, placed in a cooler with ice-packs and transported to our laboratory. A field moist aliquot of each sample was kept frozen (-20°C) for phospholipid fatty acid (PLFA) analysis, as described below.

Forest floor water content (WC) was determined by mass loss after drying at 65 °C (48h). Subsamples of the dried material were mixed with water (1:5) and analyzed for pH using a hydrogen electrode. Total C and N concentrations were determined from 150 mg ground subsamples using a Vario Macro CN Analyser (Elementar GmbH, Hanau, Germany). A 500 mg subsample was digested in H_2SO_4/H_2O_2 solution, and total base cations (K, Ca and Mg) were measured using an AAnalyst-100 atomic absorption spectrometer (Perkin Elmer Corporation, Norwalk, USA). Basal respiration was determined by weighing field moist subsamples (10 g dry wt equiv.) in 126 mL gas sampling jars, flushing the headspace with ambient air for 5 min, sealing jars with airtight lids equipped with rubber septa, and measuring net CO_2 production in the headspace 4 h after jars had been sealed using a model CP-2002 P Micro-GC (Chrompack, Middelburg). Microbial biomass was then estimated in each jar by substrate induced respiration following the addition of glucose (Anderson and Domsch 1978). Potential ammonification and nitrification rates were estimated as the net amount of KClextractable NH_4^+ (Berthelot reaction) and NO_3^- (Griess-Illosway reaction) produced in field-moist subsamples (10 g dry wt. equiv.) over the course of a 30 d aerobic incubation (22°C) (Mulvaney 1996).

Microbial community structure in each forest floor sample was determined by phospholipid fatty acid (PLFA) analysis, as described by Hamel et al. (2006). Briefly, fatty acids (FAs) were extracted with dichloromethane–methanol–citrate buffer solution (1:2:0.8; v/v/v), separated on a silica-gel column, methylated with a sulfuric acid-methanol solution (80°C for 10 min.), dried and subsequently dissolved in hexane prior to analysis using a HP 6890 gas chromatograph equipped with a FID (300°C), a 30-m Restek Rtx-1 column, and He as carrier gas. A known concentration of methylated 19:0 FA was used as an internal standard to quantify the concentrations of indigenous FAs. In total, 60 FAs were identified based on elution rates of a 41 FA standard (Supelco Bacterial Acid Methyl Ester Mix 47080-U, Sigma-Aldrich) and by a chromatogram published by Frostegård et al. (1993b). The molar proportion of each FA was calculated relative to the sum of molar concentrations of all 60 FAs. A total of 19 microbial FAs were identified as belonging to distinct microbial groups using the following classification: FA 18:2ω6c was ascribed to fungal biomass (Frostegård and Bååth 1996); FAs i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 10Me16:0, 10Me18:0, br17:0, br18:0 were ascribed to Gram+ bacteria; FAs cy17:0, cy19:0, 16:1ω7c, 16:1ω7t, 16:1ω9, 18:1ω7) were ascribed to Gram- bacteria; total bacterial biomass was calculated as the sum of Gram+ and Gram- bacteria, plus FA 17:0 (Harwood and Russell 1984; Ratledge and Wilkinson 1988; Zelles 1999); FAs 16:1ω5 and 10Me18:0 were respectively ascribed to arbuscular mycorrhizal fungi (AMF) (Madan et al. 2002) and to actinomycetes (Frostegård et al. 1993a). After removing rare (i.e., present in less than 25% of sampling plots) and stable (i.e. CV < 5%) FAs, we used the remaining 34 FAs for subsequent statistical analyses.

Statistical analyses

The position of forest floor functional boundaries relative to the forest compositional boundary was determined by split moving window analysis (SMWA) (Webster 1973; 1978). First, a window containing an even-number of sampling points was uniformly drawn at one end of each transect and split in two equal halves. A dissimilarity index (here Euclidean distance) was computed between the means of both halves. The window was then moved point by point along the transect and the computation was repeated at each step. The functional boundary corresponds to the position with the greatest dissimilarity value between window halves. We repeated the analysis using windows of four, six and eight sampling points and computed the z-score developed by Cornelius and Reynolds (1991), which corresponds to the weighted mean of dissimilarities calculated with different window sizes. This index is centered to zero with positive and negative values indicating dissimilarity and similarity respectively. SMWA was performed on individual forest floor variables, as well as on the multivariate microbial PLFA data set.

The statistical significance of boundaries identified with SMWA was determined by a procedure of hierarchical partitioning similar to that described by Cornelius and Reynolds (1991). Briefly, all dissimilarity peaks higher than zero were recorded, and sampling points on both sides of a given peak were treated as distinct groups. ANOVA was then used to test the significance of each grouping factor on the various forest floor variables, followed by Tukey HSD tests to identify significantly different groups of sampling points. If adjacent groups were not statistically different, the boundary separating these two groups was not considered significant. Similarly, multivariate PLFA data were analyzed by non-parametric permutation-based multivariate ANOVA using the DISTLM v.5 software (Anderson 2001; Anderson 2004) with transect as a covariate.

For each significant boundary identified with SMWA, the width and position of the associated ecotone was determined by moving window regression analysis (MWRA) (Hennenberg et al. 2005; Walker et al. 2003). This procedure computes the slope of a linear regression relating z-scores to transect position within a window drawn over five sampling points. As for SMWA, the MWRA window was moved point by point along each transect and the computation was repeated at each step. The width and position of the ecotone thus corresponds to the area bound by the highest and lowest slopes straddling the boundary.

Redundancy analysis (RDA) was used to explore relationships between microbial community composition (i.e. PLFA data) and the five forest floor chemical variables that showed significant boundaries along the transects (i.e., WC, pH, C:N ratio, total K and Mg). The biomass of specific microbial taxa (i.e., specific biomarker FAs) within groupings identified by SMWA was compared using linear mixed models, with SMWA groupings and transects respectively used as fixed and random effects factors, followed by Tukey HSD post-hoc tests.

When necessary, data were log or square-root transformed prior to analysis in order to meet ANOVA and RDA assumptions of normality and homoscedastity. All statistical computing (except DISTLIM) was performed in the software R (v.2.10.1; The R Foundation for Statistical Computing, Vienna, Austria).

Results

Forest floor properties

The forest floor F-horizon was thicker in jack pine (ca. 3.0–4.5 cm) than aspen stands (ca. 2.0 cm) with a significant ($F_{1,63}=3.18$ $P<0.0001$) boundary at 1 m within jack pine stands and an 8 m wide ecotone distributed evenly on either side of this boundary (Fig. 3A). The H-horizon showed a reverse pattern, being almost absent beyond 8 m into jack pine stands while reaching 3 cm of thickness within aspen stands (Fig. 3B). For this variable, a transition zone was delimited by two significant boundaries, one at 7 m within jack pine stands ($Z_{1,62}=6.89$, $P<0.0001$), the other at 3 m within aspen stands ($Z_{1,62}=6.29$, $P<0.0001$). Each of these boundaries was associated to a 6 m wide ecotone.

SMWA performed on a multivariate array of forest floor variables revealed non-significant boundaries justifying a separate application of SMWA to each forest floor variable. Forest floor Ca concentration followed a random pattern along the four transects such that it was impossible to find a significant boundary for this variable. A significant boundary in forest floor water content was found at 3 m within jack pine stands ($F_{1,63}$=29.02, P<0.0001) with an 8 m wide ecotone distributed evenly on either side. More specifically, forest floor water content under jack pine remained at about 200% up to 3 m from the boundary with aspen, where it abruptly decreased to about 150% from thereon (Fig. 4A).

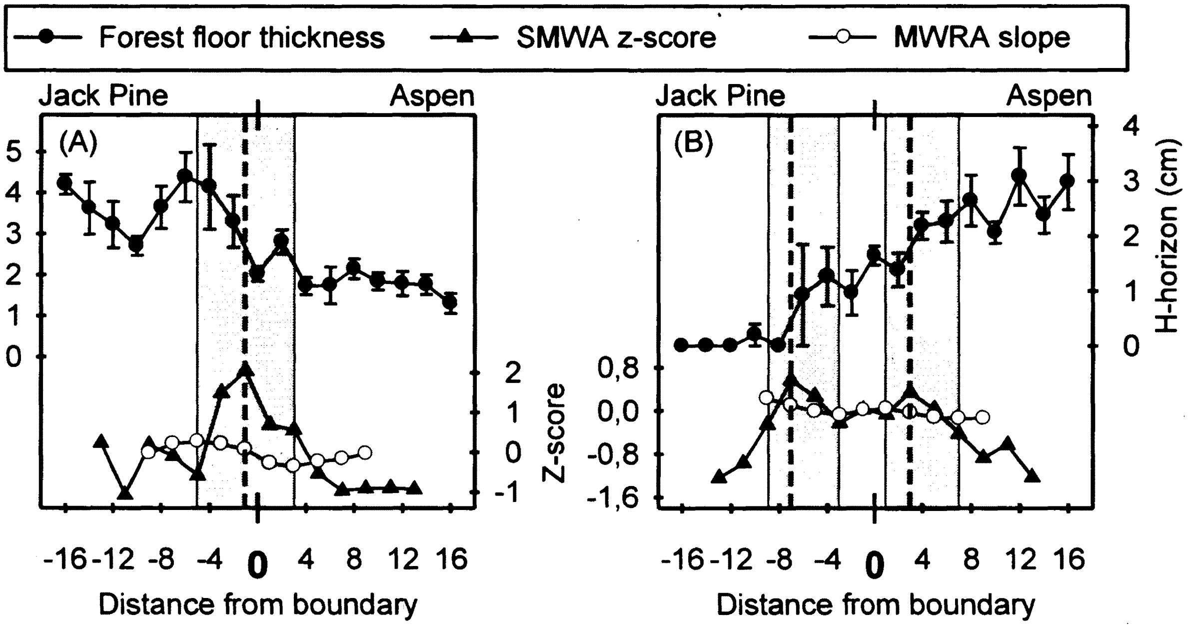

Fig. 3. Average thickness of forest floor (A) F-horizon and (B) H-horizon along transects set perpendicular to abrupt compositional boundaries between jack pine and aspen stands; error bars = 1 S.E. (n=4); dashed lines are significant functional boundaries identified by SMWA; grey areas represent ecotones determined by MWRA.

Forest floor pH increased almost monotonically from jack pine to aspen stands across the entire transect (fig 4B), whereas the opposite trend was observed for the C:N ratio (fig 4C). For these two variables, a significant boundary was found within jack pine stands at respectively 3 m and 5 m from the compositional boundary. Likewise, the ecotones for these two variables were 10 and 8 m wide and occurred mainly within jack pine stands. Significant boundaries in forest floor K ($F_{1,63}$=91.26, P<0.0001) and Mg ($F_{1,63}$=33.06, P<0.0001) concentrations were found at 1 m within jack pine stands, with higher concentrations of these base cations occurring under aspen (Fig. 4D,E). A 10 m wide ecotone in K concentrations straddled the compositional boundary, whereas a 6 m

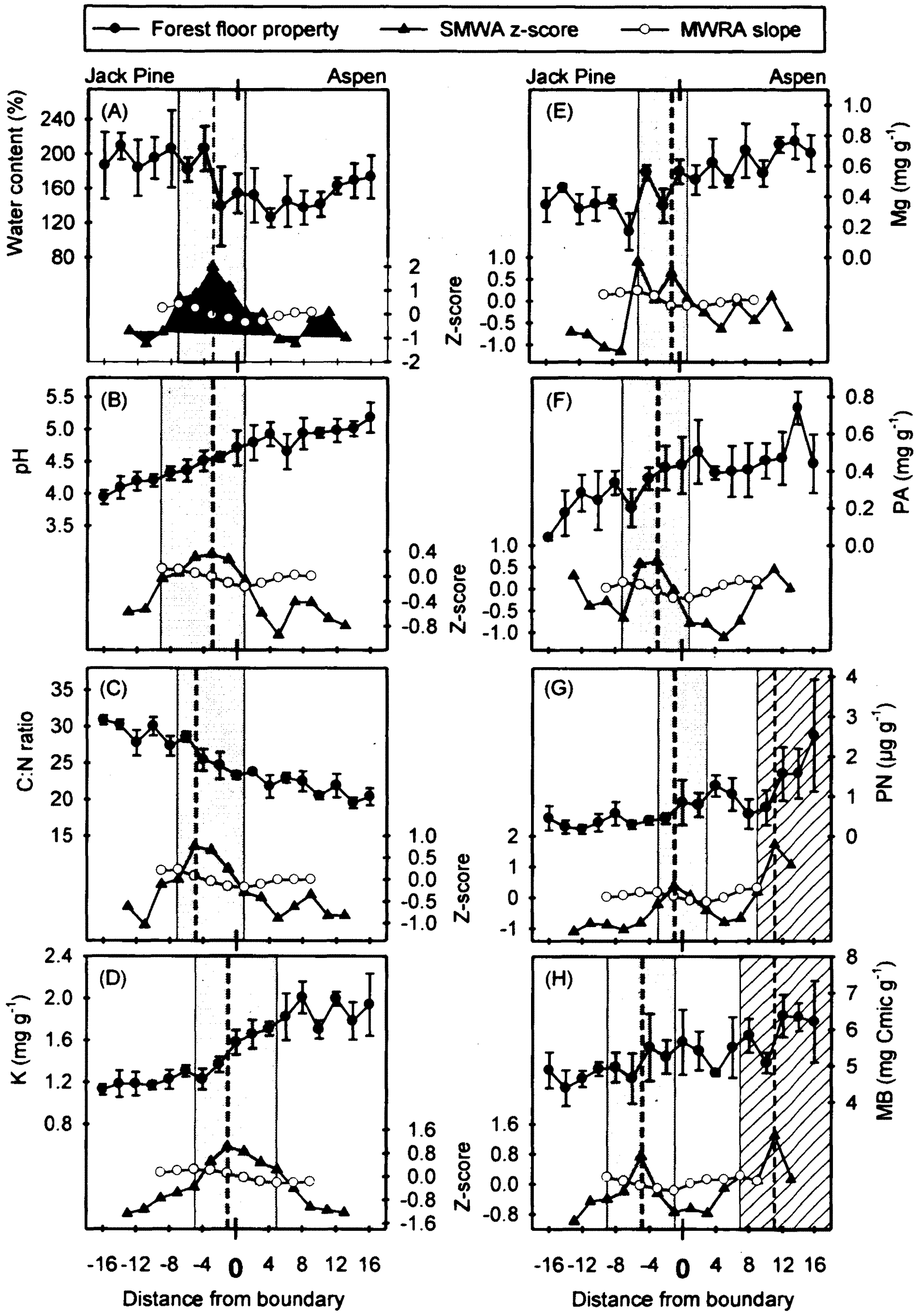

Fig 4. Average forest floor (A) water content, (B) pH, (C) C:N ratio, (D) total-K, (E) total-Mg, (F) potential nitrification, (G) potential ammonification, and (H) microbial biomass along transects set perpendicular to abrupt compositional boundaries between jack pine and aspen stands; error bars = 1 S.E. (n=4); dashed lines are significant functional boundaries identified by SMWA; grey areas represent ecotones determined by MWRA; hatched areas represent ecotones for which the external limit could not be determined by MWRA.

wide ecotone in Mg concentrations occurred mainly in jack pine stands. Potential ammonification rates were higher in aspen than in jack pine stands (Fig. 4F), with a significant boundary at 3 m within the jack pine ($F_{1,63}$=18.16, *P*=0.0001) centered within a 6 m wide ecotone. Potential nitrification rates were also higher in aspen than in jack pine stands, but in this case one significant boundary ($Z_{1,62}$=3.00, *P*=0.0069) was found near the compositional boundary while another marginally non-significant ($Z_{1,62}$=2.07, *P*=0.073) boundary was found at 11 m within the aspen stand (Fig. 4G). The first corresponding ecotone was 6 m wide and straddled the compositional boundary whereas the second ecotone began at 7 m within the aspen; the external limit of this second ecotone could not be determined because MWRA is based on a window width of five sampling points and thus cannot be computed for sampling locations beyond 9 m from the compositional boundary. Microbial biomass was higher in aspen than in jack pine stands (Fig. 4H) and two significant boundaries were once again found, one at 5 m within the jack pine stand ($Z_{1,62}$=2.35, *P*=0.048) and the other at 11 m within the aspen stand ($Z_{1,62}$=2.44, *P*=0.038). The first of these two boundaries was centered within an 8 m wide ecotone; the second boundary was associated to an ecotone with an undefined external limit due to its distance from the compositional boundary.

Microbial fatty acids composition

SMWA performed on the multivariate dataset of microbial fatty acids revealed three peaks of dissimilarity (Fig. 5) from which DISTLM software identified two significant boundaries occurring at 13 (pseudo-$F_{1,61}$=5.50, *P*=0.0008) and at 5 m (pseudo-$F_{1,61}$=11.85, *P*=0.0002) within jack pine stands. These boundaries thus discriminated three distinct microbial communities that are hereafter referred to as "pine-type" (i.e., 13 to 16 m within jack pine stands), "transition-type" (i.e., 5 to 13 m within jack pine stands), and "aspen-type" (i.e., 16 m in aspen to 5 m in jack pine stands).

RDA performed on the 34 selected FAs, and constrained by the five forest floor chemical variables, explained 28.9% of the total variation in FA composition of which 25.8% was explained by the first two axes. RDA corroborated DISTLM analysis by discriminating

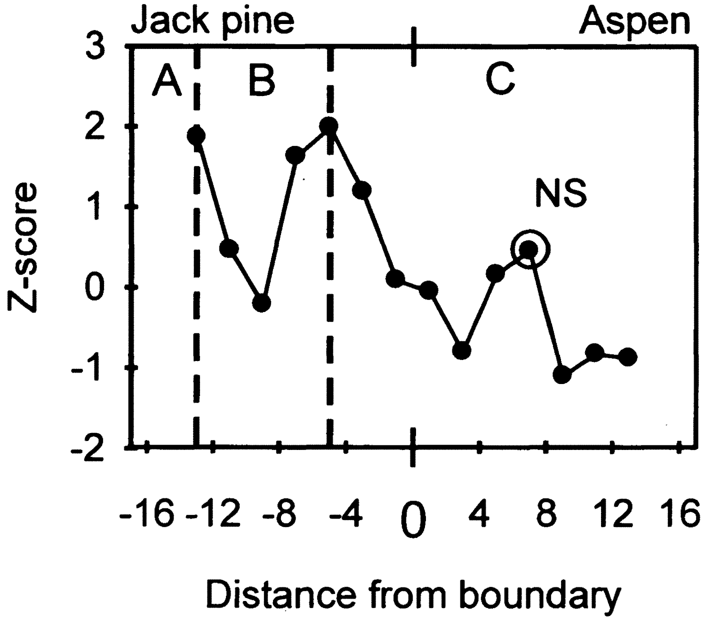

Fig. 5. Dissimilarity index (Z-score) based on microbial FA composition, computed for each sampling location by SMWA. Significant peaks of dissimilarity are identified by dashed lines and delimit three distinct microbial communities: (A) pine-type, (B) transition-type, and (C) aspen-type. A circled peak occurring at 7 m is non-significant.

the three different microbial communities separated by the two significant boundaries (Fig. 6). The first axis clearly distinguishes pine-type and transition-type from aspen-type communities, while the second axis loosely separates transition-type from pine-type communities. RDA identified seven important FAs with high loadings (i.e., scores >0.5) on both axes (Fig. 6A). Pine-type communities were associated to the fungal FA 18:2w6c, pine-type and transition-type communities to eukaryotic FAs 22:0 and 24:0, and aspen-type communities to bacterial FAs i15:0 (gram-positive), cy19:0 and 18:1w7 (gram-negative), and Me18:0 (actinomycetes). Forest floor pH, K and Mg were associated to aspen-type communities, C:N ratio to pine-type and transition-type communities, and WC was mainly associated to transition-type communities (Fig. 6B).

Linear mixed effects ANOVA and Tukey post-hoc tests showed a higher proportion of fungal biomass in pine-type communities, compared to transition-type ($Z_{1,62}$=3.36, P=0.002) and aspen-type ($Z_{1,62}$=3.19, P=0.004) communities (Fig. 7A). Conversely,

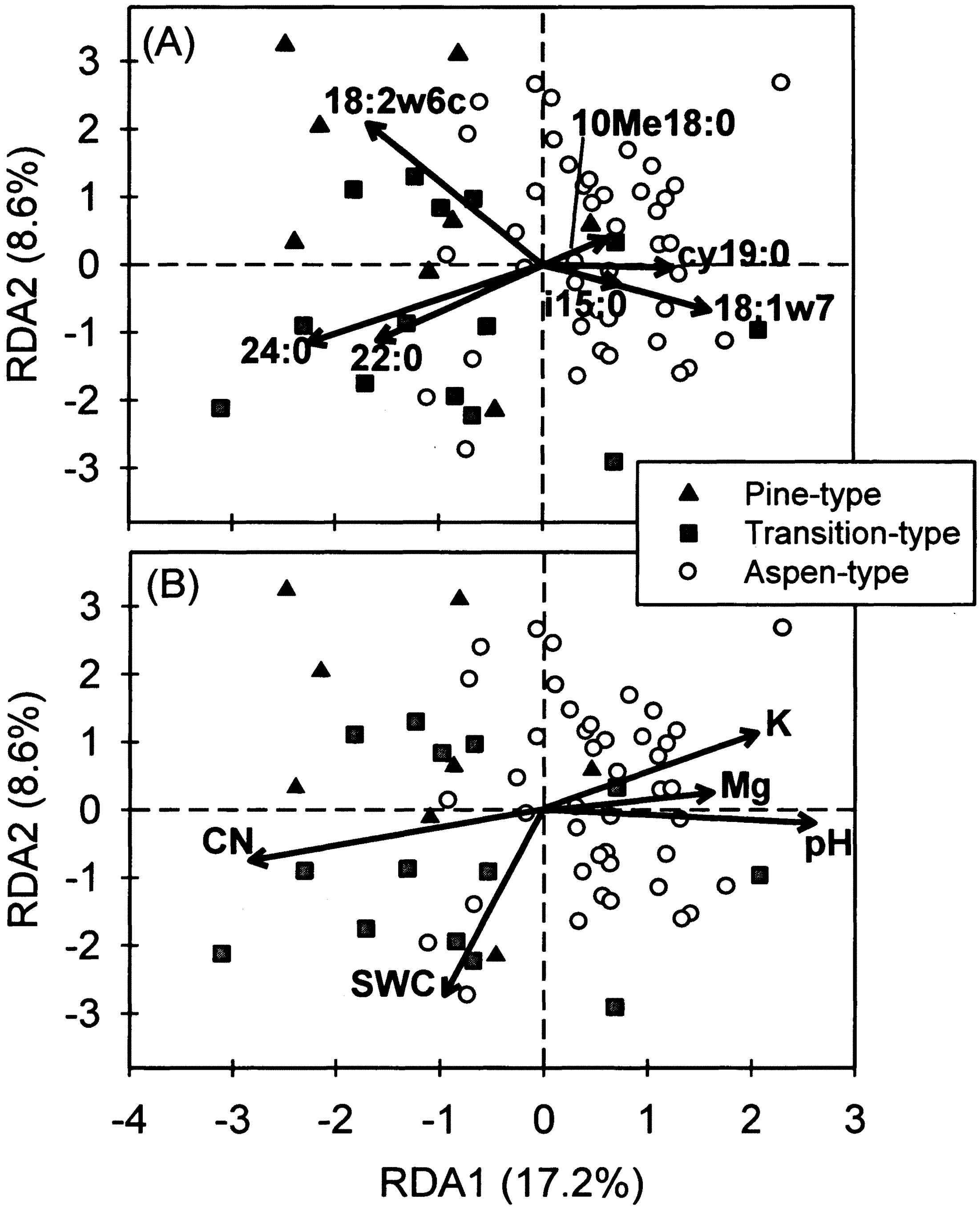

Fig. 6. RDA biplots generated from microbial FA composition and forest floor chemical properties; biplots show the relationship between sampling location and (A) seven FAs with loadings greater than 0.5, and (B) five forest floor properties. Each forest floor sample is classed as either an aspen-type, transition-type or pine-type microbial community based on its location along the transect. The proportion of total FA variation explained by the first two axes is given in parentheses.

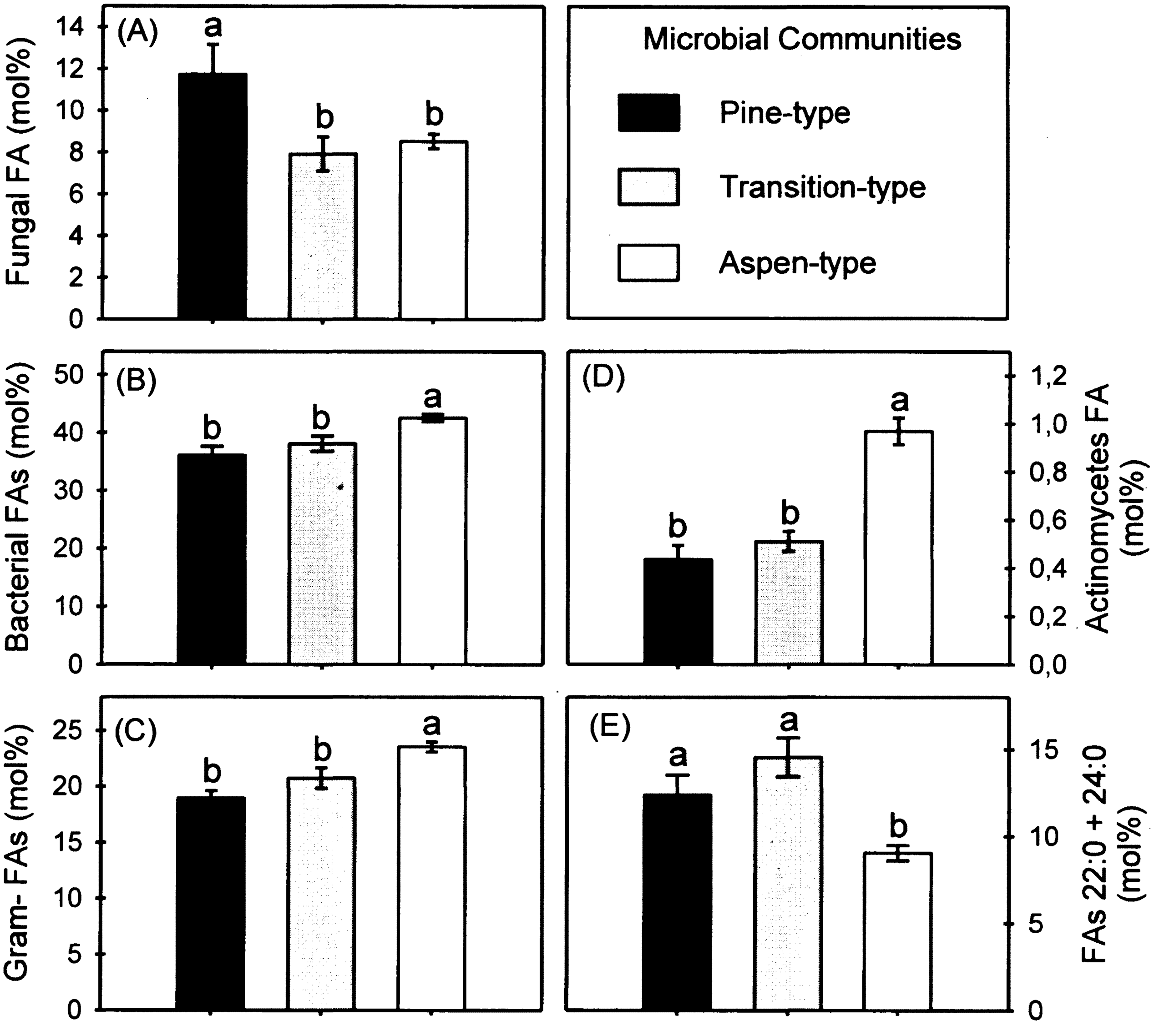

Fig. 7. Molar percentage of (A) fungi, (B) bacteria, (C) gram-negative bacteria, (D) actinomycetes, and (E) unknown eukaryotic FAs (i.e., 22:0 and 24:0) within each of the three microbial communities identified by SMWA. Different letters within each frame indicate significant differences ($P<0.05$).

higher proportions of bacterial and actinomycetal biomass were found in aspen-type communities than in pine-type ($Z_{1,62}=4.00$, $P<0.001$ and $Z_{1,62}=5.18$, $P<0.001$) and transition-type ($Z_{1,62}=3.65$, $P<0.001$ and $Z_{1,62}=5.61$, $P<0.0001$) communities (Fig. 7B and 7C). Likewise, the proportion of gram-negative bacteria was higher in aspen-type than in pine-type ($Z_{1,62}$=3.56, *P*=0.001) and transition-type ($Z_{1,62}$=4.43, *P*<0.001) communities (Fig. 7D). There thus resulted a higher fungi:bacteria ratio in pine-type than in transition-type ($Z_{1,62}$=3.06, *P*=0.006) and aspen-type ($Z_{1,62}$=3.32, *P*=0.003) communities (data not shown). Finally, a higher proportion of eukaryotic FAs 22:0 and 24:0 were found in pine-type and transition-type communities, than in aspen-type ($Z_{1,62}$=2.60, *P*=0.024 and $Z_{1,62}$=5.66, *P*<0.001) communities (Fig. 7E).

Discussion

Nutrient cycling strategies and humus forms

The changes in humus forms along our transects highlight different nutrient cycling strategies of aspen and jack pine. As expected, forest floors under aspen have a higher pH, more base cations and a lower C:N ratio than those under jack pine. These differences reflect aspen's lower nutrient use efficiency, hence a lower leaf longevity and a lower investment in structural compounds such as lignin. Given that fungi are more acid tolerant and can metabolize substrates of lower quality than bacteria (Högberg et al. 2007; Matthies et al. 1997), we should observe bacteria-based food webs under aspen, and fungi-based food-webs under jack pine. Bacteria generally grow faster and are more nutrient rich than fungi (Wardle 2002), hence we expect higher nutrient and energy cycling rates under aspen. The outcome of these distinct nutrient cycling strategies in aspen and jack pine is reflected, therefore, by the occurrence of a moder humus form (i.e. thin F-horizon and thick H-horizon) under aspen, and of a mor humus form (thick F-horizon and absence of H-horizon) under jack pine (Ponge, 2003). Our data show a transition zone of these two humus forms spanning approximately 8 m on either side of the compositional boundary.

Plausible tree litter effects

As we predicted, the functional boundary and associated ecotone for many forest floor properties were skewed toward jack pine stands. This is likely the result of a greater dispersal of aspen leaves, whose shorter life-span and higher specific surface area allows them to be wind-blown in greater quantity and over a greater distance than jack pine needles. Skewed forest floor chemical properties such as pH, C:N ratio, Mg, and potential ammonification are thus all likely related to the higher chemical quality of aspen leaf litter encroaching within jack pine stands. That the ecotone for K straddled the compositional boundary rather than being skewed is possibly due to leaf litter K occurring exclusively in ionic form (K^+), which makes it highly leachable from litter and mobile in soils (Sparks 1999).

It is more difficult to ascribe the spatial pattern in microbial biomass on aspen leaf litter dispersal, as a three-tier pattern was observed along our transects, with a significant boundary found on each side of the compositional boundary. Microbial biomass, especially bacterial biomass, is not only bottom-up regulated by litter quality, but also top-down regulated through the soil food-chain (Wardle 2002). Different faunal groups could exert different predatory pressures on lower trophic levels such as bacterial grazers. The observed spatial pattern in microbial biomass may thus reflect the compound effects of litter quality and of distinct trophic networks occurring across transects. For example, predatory beetles (carabidae and staphylinidae) are abundant in aspen stands whereas microarthropods and Enchytraeidae are more abundant under boreal conifer stands (Laganière et al. 2009).

Plausible tree root effects

The higher forest floor WC in jack pine stands may be related to differences in humus forms, as organic horizons differing in their degree of decomposition and humification may also differ in their water absorption potential (Grelewicz 1985). The abrupt transition in forest floor WC that occurred at 3 m within jack pine stands is not consistent, however, with the gradual changes in humus forms that we observed along the transects. Compared to jack pine, aspen requires more water for its growth (Légaré et al. 2005), which explains why forest floor WC was lower under aspen. It is possible that aspen roots would extend and forage for water up to

3 m within jack pine stands. By doing so, aspen roots should favour aerobic conditions thereby increasing decomposition and nutrient cycling. This is corroborated by high microbial biomass and net ammonification rates at 0–4 m within jack pine stands.

Ste-Marie and Paré (1999) found that mixing small amounts of aspen forest floor to large amounts of jack pine forest floor resulted in a disproportionate increase in nitrification rates. By contrast, we observed low nitrification throughout jack pine stands and up to 11 m into aspen stands. What sets our two studies apart is that Ste-Marie and Paré (1999) performed forest floor incubations in the absence of roots. Thus, the spatial pattern in potential nitrification rates that we observed could be related to tree root dynamics. For example, several studies have shown that volatile monoterpenes produced by conifer roots such as Norway spruce (Paavolainen et al. 1998) and ponderosa pine (White 1991) are effective at suppressing nitrification. It is plausible that similar compounds produced by jack pine roots reduce nitrification rates up to 11 m within aspen stands, as the horizontal spread of lateral roots by jack pine can be four times greater than for aspen (Strong and La Roi, 1983).

Microbial community structure

As was the case for most forest floor properties, aspen exerted a greater control over microbial community composition than jack pine. In fact, microbial community structure was the most skewed of all forest floor properties, as revealed by the presence of an 8 m-wide transition-type community entirely located within jack pine stands. Forest floor pH is generally regarded as the strongest factor determining bacterial abundance (Rousk et al. 2010), especially acid-intolerant actinomycetes (Giri et al. 2005) and gram-negative bacteria (Frostegård et al. 1993a). In our study, the proportion of these two bacterial groups in transition-type microbial communities were as low as in pine-type microbial communities, even though forest floor pH was steadily decreasing across the transects. Thus, there may have been a threshold forest floor pH (~ 4.5) corresponding to the boundary between aspen-type and transition-type microbial communities, below which these bacterial populations were strongly repressed.

Aspen will hasten forest floor nutrient cycling by producing a higher quality litter than jack pine. Given that bacteria generally grow faster and are more nutrient demanding than fungi (Cooke and Whipps 1993; Tate III 1995), aspen is therefore expected to promote bacterial biomass. Jack pine litter, on the other hand, reduces nutrient cycling rates (e.g. low N mineralization), which is consistent with its lower N demand (Alban 1982, Gower et al. 2000), and promotes a higher fungal biomass. It is curious that fungal biomass in transition-type was not higher than in aspen-type microbial communities, given the lower pH and the lower proportion of actinomycetes that otherwise antagonize fungal growth (Jayasinghe and Parkinson 2008). Rather, we found a higher proportion of long-chain saturated FAs 22:0 and 24:0 in transition-type microbial communities. These FAs, which are specific to eukaryotes cells (Zelles 1999), were not correlated to the fungal specific FA 18:2w6c. As a result, FAs 22:0 and 24:0 may represent another component of the forest floor microbial community, such as bacterial and fungal grazers, which might further explain the low proportion of both bacteria and fungi in transition-type microbial communities. Grazers such as nematodes and protozoa are often associated to high soil moisture content (Paul and Clark 1996), as was the case for transition-type microbial communities.

Ecological importance of compositional boundaries

The occurrence of sharp compositional boundaries separating mono-specific forest stands are not generally regarded as important ecotones. Our study has shown, however, that sharp compositional boundaries can in fact be associated to a relatively large transition zone in forest floor properties. For a given forest floor property, the width and position of the transition zone depend on the mechanisms by which tree species influence this property. For example, aspen had a larger influence on what we assumed to be litter-related forest floor properties within jack pine stands, including microbial FA composition. Conversely, a large lateral root spread might enable jack pine to exert control over potential nitrification far within adjacent aspen stands. Taken collectively, the position of functional boundaries and their associated ecotones delimited a 24 m wide transition zone (i.e., 13 m within jack pine to 11 m within aspen stands) in forest floor properties and microbial communities. We conclude, therefore, that sharp compositional boundaries separating mono-specific forest stands may contribute significantly to the diversity of ecological processes. Forest management strategies that aim to enhance the functional diversity of boreal landscapes, where mono-specific stands are prevalent, should focus, therefore, on preserving the patchiness of these landscapes rather than simply controlling for the proportion of each major tree species.

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CONCLUSION

Implication sylvicoles

Depuis avril 2010, le ministère des ressources naturelles et de la faune du Québec (MRNF) s'est doté de la Loi sur l'aménagement durable du territoire forestier (Loi 57) dont l'aménagement écosystémique occupe une place prépondérante (MRNF, 2010a). Un tel aménagement se doit d'inclure la gestion des peuplements mixtes de peuplier et de pin gris, puisqu'ils font partie intégrante de la diversité et de la structure naturelle de la forêt boréale. En ce sens, les résultats présentés dans cette thèse de doctorat pourraient s'avérer utiles afin de développer une gestion des coupes s'harmonisant avec les processus naturels menant à la formation de ces peuplements mixtes.

Tout d'abord, le premier chapitre de ce doctorat a permis d'identifier la fertilité du matériau parental comme facteur déterminant l'occurrence des peuplements mixtes de peuplier-pin gris. Ainsi, l'occurrence de tels peuplements est limitée aux dépôts argileux alors que sur till, la ségrégation entre les deux espèces semble prévaloir. Cette particularité pourrait favoriser différents aménagements sylvicoles dépendamment du matériau parental. Ainsi, sur argile, l'aménagement de peuplements mixtes permettrait de conserver la biodiversité et la structure naturelle de ces forêts alors que sur till, il serait possible de viser une gestion plus intensive du pin gris dont la valeur économique est supérieure à celle du peuplier. Dans ce dernier cas cependant, mes résultats suggèrent que la compétition occasionnée par le peuplier devrait être contrôlée par débroussaillage si l'objectif est d'accroître la productivité du pin gris à l'aide d'une fertilisation.

Ensuite, les résultats obtenus dans le deuxième chapitre de cette thèse ont confirmé que la stabilité des communautés microbienne était favorisée par la plus grande diversité végétale des peuplements mixtes, mais également par la fertilité du matériau parental. Hors, la stabilité des communautés microbiennes peut être un facteur important pour le maintient des fonctions édaphiques dans la forêt boréale qui est soumise à de fréquentes perturbations et stress d'origine naturelle ou anthropique tels que les feux de forêts, les épidémies, les coupes forestières, les pluies acides et, plus récemment, le réchauffement climatique. C'est pourquoi le maintient de l'intégrité et des fonctions écologiques des sols forestiers fait partie des grandes orientations de la future stratégie d'aménagement durable des forêts du MRNF (MRNF, 2010b). Selon mes résultats, cet objectif serait réalisable en préservant la biodiversité forestière au sein des peuplements mixtes.

Finalement, il a été démontré dans le troisième chapitre que même si les zones de transition entre le peuplier et le pin gris sur till peuvent être abruptes, elles constituent un écosystème différent des peuplements purs de ces deux espèces. Par conséquent, de tels écotones font partie intégrante de la biodiversité boréale et devraient être préservés dans les proportions observées naturellement. Ceci n'est possible qu'en préservant la structure hétérogène du paysage boréal tant en composition qu'en âge. Ceci serait possible en appliquant des interventions forestières de la superficie des peuplements naturels et s'échelonnant sur plusieurs dizaines d'années au sein d'un même secteur afin de recréer toutes les structures de peuplements retrouvées à l'état naturel.

Futures recherches

En plus d'améliorer notre compréhension de la dynamique forestière entre le peuplier et le pin gris et de ses implications souterraines, les travaux effectués dans cette thèse soulèvent d'autres questions. Premièrement, quel est le mécanisme menant à la ségrégation du peuplier et du pin gris sur till? Une possibilité serait que l'exclusion survient suite à l'intensification de la compétition interspécifique pour la lumière, une ressource vitale pour ces deux espèces intolérantes à l'ombre. Toutefois, ceci irait à l'encontre de la théorie, puisque l'intensité de la compétition interspécifique diminue généralement avec la fertilité d'un site (Callaway *et al.*, 2002). Toutefois, le fait que le peuplier est une espèce clonale pourrait lui permettre de maintenir une forte compétition sur till en puisant des ressources de son système racinaire parental.

Une autre question à laquelle il serait intéressant de répondre concerne la stabilité des communautés microbiennes. Dans le deuxième chapitre, nous n'avons mesuré que la tolérance de la biomasse microbienne en faisant abstraction de la composition de ces communautés. Hors, dans le cadre de mes recherches doctorales, j'ai eu la chance d'accumuler des données sur la composition des acides gras de communautés microbiennes confrontées à des stress. Ces données pourraient nous aider à comparer la réponse de la composition microbienne à celle de la biomasse microbienne. En ce sens, on pourrait s'attendre à ce qu'une augmentation de la stabilité de la biomasse soit compensée par de plus fortes variations dans la composition de ces communautés (Tilman, 1999).

Finalement, on associe généralement les stratégies d'utilisation des ressources à des groupes microbiens différents. Toutefois, ces classifications axées sur les distinctions taxonomiques contiennent de nombreuses exceptions. Par exemple, dans l'introduction de cette thèse, il a été démontré que la classification des bactéries et des champignons comme étant des organismes zymogènes et autochtones comportait certaines exceptions. En raison de ces variabilités dans les groupes taxonomiques et étant donnée l'énorme diversité microbienne, une approche visant plutôt les différences fonctionnelles entre les organismes serait plus appropriée. Ceci impliquerait de déterminer des traits fonctionnels, i.e. des traits suffisamment variables qui sont reliés directement aux fonctions microbiennes, afin qu'il soit plus aisé d'établir des liens de causalité entre la nature de ces traits fonctionnels, la composition végétale et le fonctionnement des écosystèmes.

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