L'EFFET DU TYPE D'HORIZON, DE LA DENSITÉ DES RACINES VIVANTES ET DE L'ÉLÉVATION SUR LA NITRIFICATION DANS LES SOLS FORESTIERS

par

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L'azote (N) est l'élément minéral qui limite le plus la croissance de la végétation dans la majorité des écosystèmes forestiers et il est le quatrième en importance dans la composition chimique des plantes après le carbone (C), l'hydrogène (H) et l'oxygène (O). Dans le cycle de l'azote, l'ammonification et la nitrification sont les processus responsables de la formation de deux formes d'azote minéral : l'ammonium (NH_4^+) et le nitrate (NO_3^-). Des concentrations élevées de NO_3^- peuvent occasionner des problèmes environnementaux, par exemple l'eutrophisation des lacs, et peuvent également causer des problèmes pour la santé publique.

Les pools de NO_3^- et les taux de nitrification des sols forestiers mesurés en laboratoire ou sur le terrain sont souvent négligeables ou absents. Cependant, suite à une perturbation majeure comme la coupe totale, on mesure sur une courte période de temps, une augmentation de la disponibilité du NO_3^- que l'on appelle « assart flush ». À ce jour, plusieurs hypothèses ont tenté d'expliquer le phénomène du « assart flush » mais aucune ne fait l'unanimité. Les hypothèses proposées peuvent être divisées en trois groupes. Le premier groupe traite des différents facteurs qui régularisent le taux de nitrification. Parmi ceux-ci, on retrouve les facteurs climatiques, l'acidité du sol, la structure de la communauté microbienne et la qualité chimique de la litière. Le deuxième regroupe les facteurs qui contrôlent l'assimilation du N minéral (NH_4^+ et NO_3^-) par les plantes et l'immobilisation par les microorganismes. Enfin, le troisième groupe aborde les facteurs qui contrôlent la variabilité temporelle et spatiale de la nitrification.

Le premier objectif de ce projet de recherche est de proposer deux nouvelles variables, le type d'horizon (organique et minéral) et la densité des racines vivantes, comme facteurs qui contrôlent les pools de NO_3^-. Les racines relâchent dans le sol du C réduit, comme des exsudats, du mucigel et des sécrétions qu'on définit comme étant la rhizodéposition. Étant donné que le C disponible est un facteur déterminant dans l'immobilisation du NO_3^- par les microorganismes hétérotrophes, notre hypothèse est que les racines, via la rhizodéposition,

augmentent l'immobilisation du NO_3^-. Dans un premier temps, nous avons recueilli des données sur les taux nets de nitrification et d'ammonification provenant de 56 études pour calculer l'indice de nitrification relative (INR), qu'on définit comme étant la concentration de NO_3^- par rapport à la concentration total du N minéral (*i.e.* $NH_4^+ + NO_3^-$). Les résultats de cette revue de la littérature démontrent que le INR est plus élevé dans l'horizon minéral que dans l'horizon organique. Dans l'horizon minéral, le sol est mieux décomposé, plus pauvre en C-organique disponible et on retrouve une densité moins élevée de racines fines. Dans un deuxième temps, lors d'une expérience menée dans des peuplements feuillus et conifériens, nous avons éliminé les racines à l'aide de tranchées afin de mesurer l'effet des racines sur le INR et sur les indices de disponibilité de C entre l'horizon organique et minéral. Suite à l'élimination des racines, les concentrations de NO_3^- et le INR étaient significativement plus élevés en absence de racines, alors que la biomasse microbienne et la respiration de base étaient significativement plus élevées en présence de racines. Nos résultats ont démontré que la rhizodéposition par les racines augmentait l'immobilisation du NO_3^- par les microorganismes hétérotrophes. Donc, suite à une coupe forestière, la réduction de la rhizodéposition par les racines réduiraient l'immobilisation de NO_3^- par les microorganismes hétérotrophes causant ainsi des concentrations plus importantes de NO_3^-.

Le deuxième objectif de ce projet de recherche est d'évaluer si l'élévation pourrait être utilisée pour mesurer la variabilité spatiale (1) de la concentration des cations basiques échangeables, (2) de la concentration du N minéral, et (3) des propriétés microbiennes. Dans le sud-est du Québec, la déposition atmosphérique par les nuages augmente avec l'altitude. Par conséquent, cette deuxième expérience tente de déterminer si le pH, la disponibilité des nutriments, et les propriétés microbiennes du sol varient le long d'un gradient d'élévation de 250 m dans un peuplement uniforme d'érables à sucre. Les résultats ont montré que les concentrations de Ca et de Mg échangeables, le pH et le INR diminuaient avec l'altitude alors que le quotient métabolique (qCO_2) et la minéralisation anaérobique (ANMR) étaient plus élevés à haute altitude. Premièrement, une diminution dans les concentrations de Ca et de Mg échangeables peut mener à des déséquilibres nutritionnels et à une baisse dans la

fertilité du peuplement. Deuxièmement, une baisse du INR et une augmentation du ANMR avec l'altitude suggèrent qu'une population microbienne limitée en azote peut agir comme puit pour l'azote atmosphérique (NO_3^- et NH_4^+) déposé par les nuages. Troisièmement, la déposition par les nuages de précipitations acides peut occasionner un stress environnemental supplémentaire sur la communauté microbienne et par conséquent augmenter la respiration spécifique (qCO_2). Donc, ces résultats suggèrent que l'altitude peut effectivement nous aider à mieux comprendre la variation spatiale et les interactions entre les propriétés microbiennes et les cycles des nutriments.

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INTRODUCTION GÉNÉRALE

Dans les écosystèmes forestiers, la croissance végétale est le plus souvent limitée par l'azote (N). Cet élément est le quatrième en importance dans la composition des plantes après le carbone (C), l'hydrogène (H) et l'oxygène (O) (Paul et Clark, 1996). Bien que la concentration de l'azote dans l'atmosphère est de 79 % (Kimmins, 1997), cet immense réservoir est inaccessible pour la plupart des organismes du sol. Seuls mycorhizes et bactéries fixatrices sont capables d'utiliser l'azote atmosphérique (N_2) pour leur croissance et le maintien de leur métabolisme. Donc, en milieu naturel, l'azote devient disponible pour les plantes grâce à la décomposition de la matière organique. Lorsque les microorganismes décomposent la matière organique à l'aide d'enzymes, l'azote est libéré sous forme d'azote organique dissous (AOD) et peut être alors utilisé par les plantes, les champignons et les autres organismes décomposeurs pour leur croissance et le maintien de leur métabolisme. Cependant, la majorité de l'azote absorbé par les plantes se trouve sous forme minérale (NH_4^+ et NO_3^-). Ces deux formes minérales sont produites par la minéralisation qui comprend deux processus : l'ammonification et la nitrification. Lorsque l'AOD est en concentration insuffisante pour combler les besoins de la croissance microbienne, l'azote minéral est absorbé par les microorganismes (immobilisation). Par contre, lorsque les microorganismes sont limités en C, ils métabolisent l'AOD. Ils utilisent le C et sécrète le NH_4^+ dans le sol (ammonification). Une partie de ce NH_4^+ est oxydé en NO_3^- (nitrification). Pour ces deux processus, on peut mesurer les taux bruts et nets. Le taux brut indique la production totale de NH_4^+ et de NO_3^- (production + consommation), alors que le taux net représente l'accumulation nette d'azote minéral dans le sol, autant pour la minéralisation ($NH_4^+ + NO_3^-$) , l'ammonification (NH_4^+) que pour la nitrification (NO_3^-).

Bien qu'il soit nécessaire à la croissance des plantes, le processus de nitrification peut avoir des conséquences néfastes pour la santé humaine et pour les écosystèmes aquatiques. Premièrement, le NO_3^- est un ion très mobile et peut être lessivé des sols des écosystèmes terrestres pour se retrouver dans les rivières et les lacs. À des concentrations plus élevées que

10 mg N l^{-1}, le NO_3^- peut occasionner des problèmes de santé publique, comme l'anémie chez les jeunes enfants (Paul et Clark, 1996; Min. Env. et Faune, 1998). Des concentrations trop élevées en NO_3^- accélèrent l'eutrophisation des écosystèmes aquatiques. Deuxièmement, les eaux de lessivage dans les sols doivent respecter un équilibre ionique. Donc, lorsqu'un anion comme le NO_3^- est lessivé, sa charge négative doit être contrebalancée par les charges positives des cations. Par conséquent, chaque ion NO_3^- lessivé transporte des cations comme le calcium (Ca^{2+}), le magnésium (Mg^{2+}), le potassium (K^+), ou le sodium (Na^+) (le lessivage de ces cations basiques) ce qui diminue la fertilité des sols (Galloway, 1998; Gundersen et al., 1998a ; Gundersen et al., 1998b). Enfin, la nitrification a aussi comme effet de générer de l'acidité. Lorsque les ions H^+ sont libérés en solution lors de la nitrification, ils déplacent des cations basiques sur les sites d'échanges cationiques rendant ainsi ces cations plus sensibles au lessivage.

Les pools de NO_3^- sont habituellement faibles dans les forêts non perturbées, particulièrement dans les forêts conifériennes, et l'accumulation de NO_3^- est souvent négligeable ou nul lors d'incubations à court terme effectuées en laboratoire ou sur le terrain (Federer, 1983; Davidson et al., 1992a; Smith et al., 1998; Priha et Smolander, 1999). Cependant, à la suite d'une perturbation majeure comme une coupe totale, on remarque sur une courte période de temps, une augmentation de la disponibilité du NO_3^- que l'on appelle fréquemment « assart flush » (Vitousek et al., 1979; Matson et Boone, 1984; Vitousek et al., 1989; Bradley et al., 2002). Cette augmentation rapide est responsable de pertes importantes de NO_3^- par le lessivage (Aber et Melillo, 1991; Titus et al., 1998; Holmes et Zak, 1999), l'érosion (Camiré, 1995), la dénitrification (Kurtz, 1980; Startsev et al., 1998) ou la volatilisation de l'ammoniaque (NH_3) (Vitousek et Melillo, 1979; Driscoll et al., 1999).

Actuellement, plusieurs hypothèses ont été émises afin d'expliquer le phénomène du « assart flush » mais aucune ne fait l'unanimité. Les hypothèses avancées peuvent être divisées en trois groupes. Le premier groupe considère les différents facteurs qui contrôlent le taux de nitrification. Parmi ceux-ci, on retrouve les facteurs climatiques (humidité et température),

l'acidité du sol, la structure de la communauté microbienne (composition et abondance) et la qualité chimique de la litière. Le deuxième groupe comprend l'assimilation du NO_3^- par les plantes et l'immobilisation par les microorganismes. Enfin, le troisième groupe comprend la variabilité temporelle et spatiale de la nitrification.

Afin de mieux aménager la forêt et pour être en mesure d'amoindrir les effets néfastes des coupes forestières, une meilleure connaissance des cycles des éléments minéraux comme le NO_3^- est essentielle. Le premier objectif de ce projet de recherche est de proposer, en plus de celles déjà connues, deux nouvelles variables, le type d'horizon (organique et minéral) et la densité des racines vivantes, comme facteurs qui contrôlent les pools de NO_3^-. Le deuxième objectif de ce projet de recherche est de déterminer si l'altitude peut être utilisée pour mesurer la variabilité spatiale (1) de la concentration des cations basiques, (2) de la concentration de l'azote minéral (NO_3^- + NH_4^+), et (3) des propriétés microbiennes dans les sols forestiers.

En guise d'introduction, le texte qui suit donne une explication détaillée des mécanismes contrôlés par chacun de ces groupes de facteurs. Suivront les objectifs spécifiques pour chacun des chapitres de ce mémoire.

1.1. Régulation du taux de nitrification

1.1.1. Les facteurs climatiques

L'activité microbienne peut être régulée par deux facteurs micro-climatiques en autres : l'humidité et la température des sols (Sabey et al., 1959; Robertson, 1982a). Les bactéries nitrifiantes sont aérobiques obligatoires et ont donc besoin d'oxygène pour l'oxydation du NH_4^+. Un sol saturé en eau limite la diffusion de l'oxygène et inhibe la nitrification. À l'inverse, un manque d'eau inhibe la croissance microbienne et diminue le transport des éléments dans le sol (*e.g.* NH_4^+) (Paul et Clark, 1996). Quant à la température du sol, elle a

une influence directe sur les microorganismes du sol en agissant sur leur activité métabolique (et sur la dormance) et sur leur taux de mortalité. La nitrification s'effectue principalement entre +5 °C et +40 °C, mais l'optimum de croissance pour les microorganismes nitrifiants se situe entre +30 °C à +35 °C (Paul et Clark, 1996). Donc, à la suite d'une perturbation comme une coupe forestière, l'activité microbienne peut augmenter car la température et l'humidité du sol seront plus élevées (Holmes et Zak, 1999). Une baisse de l'ombrage augmentera la température alors que l'humidité du sol sera plus élevée étant donné une diminution de l'évapotranspiration.

1.1.2. L'acidité du sol et la structure de la communauté microbienne

Bien que la nitrification en sols acides soit maintenant reconnue, il reste que la nitrification et les pools de NO_3^- demeurent généralement bas ou absents dans les sols acides. Sur la base d'études en agriculture, la nitrification a longtemps été considérée comme un processus entièrement autotrophe (NH_3 utilisé comme source d'énergie) et restreint à des sols neutres ou légèrement alcalins (Rudebeck et Persson, 1998). Ces bactéries sont aérobiques obligatoires, tirent leur énergie de l'oxydation du NH_4^+ en NO_3^- et utilise le CO_2 comme source de carbone (Morrill et Dawson, 1967). Étant donné que le pH optimal de la nitrification se situe entre 6,0 et 8,0 (Tate, 1995; Paul et Clark, 1996), on en a conclu que la nitrification autotrophe était faible ou absente dans les sols à pH acide (Priha et Smolander, 1999). Pourtant, plusieurs études ont démontré la présence de nitrification dans les sols acides (Robertson, 1982b; Persson et Wirén, 1995; Priha et Smolander, 1999). Pour expliquer la présence de la nitrification en sol acide, certains chercheurs ont émis l'hypothèse que la nitrification pouvait être effectuée par des microorganismes hétérotrophes qui sont plus résistants à l'acidité (Schimel et al., 1984; Duggin et al., 1991; Pedersen et al., 1999). Les organismes nitrifiants hétérotrophes qui tirent leur énergie de la matière organique, oxydent l'azote organique et inorganique (NH_4^+) en NO_3^- (Pedersen et al., 1999). Comme nitrifiants hétérotrophes, on a identifié des champignons, considérés comme les plus efficients, ainsi que certaines bactéries (Killham, 1986; De Boer et Kowalchuk, 2001). Néanmoins, certains

scientifiques considèrent toujours la nitrification hétérotrophe comme limitée (Barraclough et Puri, 1995; De Boer et Kowalchuk, 2001) étant donné qu'on observe la nitrification autotrophe à des pH inférieurs à 4,0 (Stams et al., 1990; Pennington et Ellis, 1993). L'inactivité des bactéries autotrophes nitrifiantes à pH acide a également été associée 1) à la toxicité de l'acide nitreux (HNO_2), et 2) à la dépendance au substrat NH_3. À pH acide, le nitrite (NO_2) se retrouve principalement sous sa forme acide (HNO_2) qui est toxique et qui peut également créer des produits toxiques (De Boer et Kowalchuk, 2001). De plus, le sol est composé de nombreux microsites et est également formé d'agrégats. Le sol est très hétérogène et pour cette raison, il est possible que le pH à l'intérieur des agrégats soit plus élevé que la valeur moyenne de la solution du sol. Par conséquent, l'agrégation permettrait aux bactéries nitrifiantes autotrophes d'avoir un milieu plus basique et moins concentré en HNO_2 et expliquerait maintenant la nitrification autotrophe sous un sol plus acide (De Boer et al., 1991; McCarty, 1999). La deuxième hypothèse sur le pH se concentre sur l'équilibre chimique entre le NH_4^+ et le NH_3 qui dépend de l'acidité. Un sol plus acide maintiendrait l'équilibre $NH_4^+ \leftrightarrow NH_3$ vers la gauche, et limiterait l'activité de *Nitrosomonas sp.* (responsable de la nitrification) qui préférerait le NH_3 plutôt que le NH_4^+ comme source d'énergie (Suzuki et al., 1974; Grerup et al., 1998; McCarty, 1999). Cet équilibre expliquerait pourquoi dans certain cas, l'addition de NH_4^+ ne stimule pas le taux de nitrification net dans les sols acides (Ste-Marie et Paré, 1999). Présentement, on explique plus facilement la nitrification autotrophe dans les sols acides, mais on accepte également que la nitrification hétérotrophe existe. Par contre, les connaissances sur leur distribution respective sont encore insuffisantes. Donc, les changements dans les conditions du sol suite à une coupe forestière, peuvent modifier la distribution des microorganismes autotrophes et hétérotrophes et par conséquent augmenter les taux de nitrification ainsi que les pools de NO_3^- (Duggin et al., 1991).

1.1.3. La qualité chimique de la litière

L'activité bactérienne du sol dépend de la qualité de la litière (Vitousek et Matson, 1985; Frazer et al., 1990; Bauhus et al., 1993; Davidson et Hackler, 1994). Par exemple, la litière des conifères est plus récalcitrante à la décomposition que celle des feuillus (Voigt, 1965; Taylor et al., 1989; Aber et al., 1990). Deux indices sont communément utilisés pour évaluer la qualité chimique de la litière. Le premier est le ratio lignine : N. Chez les plantes, on retrouve la lignine principalement dans le bois, les branches et les feuilles. On observe généralement une bonne corrélation négative entre le ratio lignine : N et le taux de minéralisation (Melillo et al., 1982; Scott et Binkley, 1997; Fisher et Binkley, 2000), bien que dans certains cas, le ratio lignine : N peut être également un mauvais indice de minéralisation (Thomas et Prescott, 2000). Chez les conifères, la lignine peut représenter entre 25 et 35 % du poids de la plante (Tate, 1995) et le ratio lignine : N est habituellement plus élevé chez les conifères que chez les feuillus (Ferrari, 1999; Giardina, 2001). La lignine a une structure moléculaire très complexe, et elle est récalcitrante à la dégradation enzymatique (Camiré, 1995). Donc, plus cet indice est élevé, plus le taux de décomposition est lent diminuant ainsi la libération d'AOD. Cet accès limité à l'AOD restreint la croissance des bactéries. Donc, lorsque les microorganismes sont limités en AOD, ils absorbent l'azote minéral (NH_4^+ ou NO_3^-) du sol. Le deuxième indice utilisé pour mesurer la qualité de la litière est le ratio C : N. Les microorganismes ont un ratio C : N entre 5 : 1 et 8 : 1 (Paul et Clark, 1996). Les microorganismes hétérotrophes ont une efficacité d'assimilation d'environ 40 % et nécessite un ratio de 25 : 1 pour combler leur besoin en azote (Paul et Clark, 1996). Lorsque la matière organique a un ratio plus élevé que 25 pour 1, les microorganismes immobilisent l'azote minéral pour combler leurs besoins en azote. Par exemple, l'immobilisation de l'azote par les microorganismes serait plus élevée dans les peuplements conifériens que feuillus car la litière des conifères a généralement un ratio C : N plus élevé que celle des feuillus (Vitousek et al., 1982; Trofymow et al., 1995; Fassnacht et Gower, 1999; Silver et Miya, 2001). À l'inverse, lorsque le ratio de la matière organique est inférieur à celui de 25 : 1, les microorganismes sécrètent du NH_4^+. Par conséquent, que le NH_4^+ soit immobilisé ou sécrété dans le sol, cela a une effet sur le taux de nitrification.

Les plantes peuvent aussi influencer la nitrification par des substances secondaires qui inhiberaient la nitrification dans les sols forestiers. Les études les plus citées sont celles de Rice et Pancholy (1972; 1973; 1974) qui ont postulé que la végétation au stade climacique inhibait la nitrification en libérant des composés phénoliques qui retardaient l'oxydation de NH_4^+. Une étude plus récente de White (1986) propose qu'un peuplement de pin ponderosa (*Pinus ponderosa)* inhiberait la nitrification en libérant des terpènes. Ces composés secondaires produits par les plantes ont été divisés en deux catégories (Horner et al., 1988). D'abord, les complexes monomériques dans lesquels on retrouve les terpènes, les furanocoumarins, les acides phénoliques, les phenylpropanoïdes et les flavonoïdes. Dans la deuxième classe, on distingue les complexes polymériques comme les tannins et la lignine. Malgré des résultats prometteurs (Olson et Reiners, 1983; Ward et al., 1997), plusieurs chercheurs ont tenté de discréditer la théorie des substances inhibitrices (Attiwill et Adams, 1993; Bremner et McCarty, 1993) alors que d'autres la retiennent comme une suggestion alternative (Stevenson et Cole, 1999). Chez les opposants, on reproche un manque de connaissances sur les processus chimiques de l'allélopathie et, on affirme que par des digestions, des extractions et des concentrations appropriées, toutes les espèces végétales pouvaient présenter un phénomène d'allélopathie (Fisher et al., 1994). L'argument majeur pour les opposants de l'explication allélopathique, demeure que les expériences testant l'inhibition allélopathique de la nitrification devraient être faites avec des concentrations retrouvées naturellement dans le sol (Bremner et McCarty, 1993). Néanmoins, les partisans de l'inhibition chimique expliquent l'augmentation de la concentration de NO_3^- dans le sol à la suite d'une coupe forestière, par la réduction de la végétation et de la diminution des substances inhibitrices émises par les plantes.

1.2. Immobilisation par les microorganismes et assimilation de l'azote par les plantes

Le NH_4^+ est assimilé par les bactéries nitrifiantes autotrophes, les racines et les microorganismes hétérotrophes. La disponibilité de NH_4^+ dans le sol est le facteur qui limite le plus le taux de nitrification (Jones et Richards, 1977; Robertson, 1982a; Davidson et

Hackler, 1994). La quantité de NH_4^+ dans le sol doit être suffisante pour permettre aux bactéries nitrifiantes autotrophes de rivaliser avec les autres organismes du sol. Pour ces bactéries nitrifiantes, le NH_4^+ constitue la seule source d'énergie. Donc, l'une des hypothèses suggérées pour expliquer l'absence de NO_3^- dans le sol, est la compétition pour l'utilisation de NH_4^+ entre les microorganismes hétérotrophes, les racines et les bactéries nitrifiantes autotrophes. Pendant longtemps, ces bactéries furent considérées comme de faibles compétitrices pour le NH_4^+ face aux racines et aux microorganismes hétérotrophes (Jones et Richards, 1977; Verhagen et al., 1995; Bauhus et al., 1996; Johannisson et al., 1999). Des études ont démontré la supériorité des microorganismes hétérotrophes sur les bactéries nitrifiantes autotrophes pour le NH_4^+, particulièrement en présence de litière de plantes ayant un ratio C : N relativement élevé (Kaye et Hart, 1997; Näsholm et al., 1998). Persson et Wirén (1995) ont démontré l'avantage compétitif des racines sur les bactéries nitrifiantes pour l'assimilation de NH_4^+. Ils ont observé une forte influence de la profondeur du sol sur le potentiel de nitrification des nitrifiants, c'est-à-dire de leur habilité à former du NO_3^- en absence de racines. Cependant, durant la dernière décennie, des chercheurs ont démontré que dans certains cas les bactéries nitrifiantes autotrophes n'étaient pas toujours de faibles compétitrices (Davidson et al., 1990b; Attiwill et Adams, 1993; Hart et al., 1994). Ces bactéries seraient aussi bonnes compétitrices que les microorganismes hétérotrophes pour l'obtention de NH_4^+ lorsque la population d'hétérotrophes est stagnante ou à la baisse (Jones et Richard, 1977; Hart et al., 1994; Bradley, 2001). Finalement, suite à une coupe forestière, la réduction de l'immobilisation du NH_4^+ par les microorganismes et une baisse dans l'assimilation du NH_4^+ par les racines, augmenteraient la disponibilité du NH_4^+ pour les bactéries nitrifiantes.

L'azote minéral est habituellement assimilé par les plantes sous forme de NO_3^- ou de NH_4^+. Certaines espèces forestières préfèrent le NO_3^- alors que plusieurs conifères et les éricacées assimilent surtout le NH_4^+ (Kronzucker et al., 1997). Contrairement aux plantes, certains chercheurs ont pris pour acquis que les communautés microbiennes préféraient le NH_4^+ comme source d'azote et que l'immobilisation du NO_3^- était minimal (Myrold et Tiedje,

1986). Alors, on a assumé pendant longtemps que le NH_4^+ était la source principale d'azote minéral pour les microorganismes et que l'assimilation du NO_3^- par ces microorganismes était faible. Mais des études récentes ont démontré que les communautés microbiennes avaient la capacité d'assimiler une quantité importante de NO_3^- (Davidson et al., 1992a; Hart et al., 1994; Stark et Hart, 1997). La plupart des microorganismes sont hétérotrophes, donc l'immobilisation du NO_3^- dépend de la disponibilité du C. Suite à une coupe forestière, l'apport de matière organique est réduit de façon importante. Une baisse dans la disponibilité du C réduit pour les microorganismes hétérotrophes diminuerait l'immobilisation du NO_3^- par la biomasse microbienne (Stark et Hart, 1997).

Bien que l'azote organique dissout (AOD) ne soit généralement pas assimilé par les plantes, la compétition pour cette forme d'azote peut influencer la concentration de NO_3^- dans le sol. En effet, l'AOD peut remplacer le NO_3^- comme source d'azote mobile dans les sols des forêts boréales. Plusieurs plantes comme les éricacées, ainsi que des mycorhizes de types éricoides et les ectomycorhizes seraient supérieures aux endomycorhizes et aux plantes non mycorhizées pour utiliser l'AOD comme source principale d'azote dans des milieux stressés et froids (Näsholm et al., 1998). L'utilisation de l'AOD comme source d'éléments nutritifs à la place du NO_3^- réduirait la transformation de l'azote organique en NH_4^+ (Smith et al., 1998). Dans un milieu limité en azote minéral, il peut alors survenir une compétition entre les plantes et les microorganismes hétérotrophes pour l'assimilation de l'AOD. Les microorganismes seraient probablement supérieurs aux plantes pour l'assimilation de l'AOD et les plantes auraient accès uniquement à l'azote organique lorsque les microorganismes hétérotrophes ne sont plus limités en azote (Kaye et Hart, 1997).

1.3. Variabilité temporelle et spatiale de la nitrification

Les taux de transformation de l'azote dans les sols forestiers sont très variables. La variabilité peut être spatiale, c'est-à-dire entre des échantillons adjacents, ou bien temporelle, c'est-à-dire entre différentes dates d'échantillonnage pour un même site. Cette variabilité est

importante écologiquement et reflète bien l'échelle temporelle et spatiale dans laquelle les facteurs qui contrôlent la nitrification fluctuent. Par exemple, des études effectuées en montagne, ont montré des différences significatives avec l'altitude pour le pH, l'azote minéral et la biomasse microbienne (Hendershot, 1992; Bohlen et al., 2001). La variation dans les conditions climatiques influencent énormément la minéralisation et la nitrification. Par exemple, de fortes pluies après une période de sécheresse peut causer des pertes importantes de NO_3^- par lessivage (Aber et Melillo, 1991; Titus et al., 1998; Holmes et Zak, 1999). En ne tenant pas compte de ces variations temporelles et spatiales, l'échantillonnage du sol peut être fait de façon inadéquate et l'interprétation des résultats peut être biaisée. Parmi ces erreurs, on retrouve une mauvaise décision quant à la durée de l'étude et le nombre d'échantillons de sol à récolter. Une seule prise d'échantillons dans la saison ou un nombre insuffisant d'échantillons par campagne d'échantillonnage peut sous-estimer ou surestimer la concentration de NO_3^- présent dans le sol (Morrill et Dawson, 1967; Bauhus et al., 1993; Ehrenfeld et al., 1997, Tietema, 1998). Enfin, comme deuxième type d'erreur possible, échantillonner un seul des horizons du sol (organique ou minéral). Une absence de NO_3^- dans un des horizons n'indique pas obligatoirement l'absence totale de NO_3^- dans le profil du sol échantillonné.

1.4. Objectifs spécifiques

Le travail de recherche présenté dans ce mémoire est divisé en deux parties. Le premier chapitre propose deux nouvelles variables comme facteurs qui affectent les pools de NO_3^- dans les sols forestiers : le type de qualité d'humus (organique et minéral) et la densité des racines vivantes. Nous voulions démontrer que les racines augmentaient l'immobilisation du NO_3^- par les microorganismes hétérotrophes et que cette immobilisation était plus élevée dans l'horizon organique où la densité des racines fines est plus élevée. Les racines assimilent le NO_3^- mais fournissent également un apport important de C réduit (exsudats, mucigel, sécrétions) aux microorganismes hétérotrophes. Dans le deuxième chapitre, nous voulions démontrer que l'élévation pouvait être utilisée pour mesurer la variabilité spatiale

(1) des concentrations de l'azote minéral, (2) des cations échangeables basiques, et (3) des propriétés microbiennes. Nous avons utilisé un gradient en altitude, car la déposition atmosphérique par les nuages augmente avec l'altitude.

RÉSULTATS ET DISCUSSION

Les résultats et discussion des travaux de recherche sont présentés sous forme de publications. Cette section comporte deux chapitres. Les publications seront précédées d'une brève introduction.

CHAPITRE 1

AUGMENTATION À COURT TERME DE LA NITRIFICATION RELATIVE DANS LES SOLS FORESTIERS DUE À L'ÉLIMINATION DES RACINES

Publication 1. Short-term increases in relative nitrification rates due to trenching in contrasting soil horizons across a range of deciduous and coniferous forest communities. *Soil Biology and Biochemistry (à soumettre)*

Afin de bien aménager la forêt et pour être en mesure de bien gérer les opérations forestières, il est essentiel d'avoir une bonne connaissance des cycles des éléments nutritifs tel le NO_3^-. Comme expliqué en introduction, plusieurs facteurs contrôlent la nitrification et les pools de NO_3^-. Par conséquent, trouver un processus qui lierait ensemble les facteurs qui contrôlent le cycle du NO_3^- et qui pourrait être généralisé à l'ensemble des peuplements représente un défi important. Donc, notre hypothèse de recherche est que le type d'horizon et la densité des racines vivantes, deux variables mesurables sur le terrain, contrôlent les pools de NO_3^-. Nous proposons que les racines fournissent un apport important de C réduit aux microorganismes hétérotrophes et stimulent l'immobilisation du NO_3^-. De plus, l'immobilisation du NO_3^- sera plus importante dans l'horizon organique que minéral car la densité des racines fines est plus élevée dans l'horizon organique.

Cette étude est importante car elle est la première à démontrer clairement que les racines, en relâchant dans le sol du C réduit, augmentent l'immobilisation du NO_3^- par les microorganismes hétérotrophes. Ces résultats démontrent également l'importance des racines et de la rhizodéposition dans le contrôle du cycle du NO_3^-, ainsi que l'importance de leur rôle dans les pertes de NO_3^- suite aux coupes forestières.

Short-term increases in relative nitrification rates due to trenching in contrasting soil horizons across a range of deciduous and coniferous forest communities

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Abstract

We defined *relative* nitrification index (*i.e.* RNI) as the ratio of [NO_3^--N : Total mineral-N]. An extensive literature review allowed us to establish that RNI rates in forest soils were lower in forest floor horizons than in surface mineral soil. This phenomenon typically gets ascribed to lower pH values or higher nitrification inhibitors in forest floor, however, we hypothesised that it may largely be due to higher microbial immobilisation of NO_3^- because of higher available-C concentrations conferred by a higher concentration of fine roots in the forest floor. Trenching should therefore result in fine-root die-off and a marked increase in RNI rates in the forest floor relative to surface mineral soil. In the summer 1999, three trench plots were established in each of nine sites representing a wide range of conifer and deciduous stands found in southwestern, Québec (45°,26' North, 71°,41' West). At four different dates in summer 2000 (May, June, August, October), soil samples were collected in the forest floor and surface mineral soil in each of the 27 trench plots and in an area adjacent to each trench plot. Samples were immediately extracted and analysed for mineral-N in order to calculate RNI. In order to distinguish between the effect of lower NO_3^- assimilation by trees and the effect of lower soil available-C on RN, subsamples were incubated *in situ* using buried bags, as well as in the laboratory. Laboratory incubations lasted 6 months during which RNI from each subsample was calculated periodically. Laboratory incubations were also accompanied by measurements of soil available-C (basal respiration, microbial biomass, metabolic quotient) based on soil respirometry. Results confirmed our hypothesis that trenching significantly increases RNI due to lower soil available-C mainly in the forest floor horizon, and that this effect increases as the growing season progresses. Thus, a measure of forest floor depth relative to humus enriched surface mineral soils, and a measure of live fine root density could be used as calibration parameters for representing soil NO_3^- dynamics in forest ecosystems.

Keywords: nitrification, roots, trenching, soil horizon, trench plots, microbial dynamics.

1. Introduction

Forest management is facilitated by knowledge of processes controlling the cycling of important plant nutrients, such as soil NO_3^-. These processes can then be represented within simulation models specifically developed to synthesize the complexity of important biogeochemical cycles into realistic management decision support tools (Kimmins et al., 1999). Simulating the cycling of soil NO_3^- is particularly difficult because many factors, such as litter quality, soil pH, microbial community structure, soil moisture, NH_4^+ availability, root and microbial uptake processes, concurrently affect soil NO_3^- status. Identifying some patterns and processes controlling NO_3^- cycling that can be generalised across a broad range of forest types represents, therefore, a useful challenge.

As part of a greater study designed to implement the representation of soil N cycling within the forest growth and yield model DRYADES (Mailly *et al.*, 2000), we hypothesized that that the form of humus and the density of live roots, two variables that could be measured in the field, controlled soil NO_3^- cycling in a predictable manner. Forest humus forms, which combine the effects of soil pH, microbial community structure and other biochemical factors responsible for NO_3^- cycling, can be divided into two broad categories, namely, (a) partly decomposed, well lignified, organic forest floor material, and (b) amorphous, well humified, organic matter assimilated into surface mineral soil horizons. Although the chemical quality of forest floor material varies across forest types, thick forest floors (so-called *mor* humus) are generally associated with a lower nitrification rates than soils exempt of forest floors (so-called *mull* humus) (Killham, 1994; Wilson et al., 2001). Since forest soil profiles often contain both an organic forest floor layer and a humus rich surface mineral soil horizon, it should be verified whether a clear pattern in nitrification potential exists between these two contrasting soil horizons across a broad range of forest types. Live roots, on the other hand, can control soil moisture, NH_4^+ availability to nitrifying organisms, and NO_3^- immobilisation by vegetation and microbes. On this latter point, the allocation of energy yielding substrates to heterotrophic soil microorganisms via root exudations, mucigel production, secretions, and fine-root turnover (referred to collectively as rhizodeposition) can represent up to 60 % of

photosynthetically assimilated C (Norton et al., 1990; Grayston et al., 1996). Since available C is a major determinant of microbial immobilisation of NO_3^- (Hart et al., 1994), natural and anthropogenic forest disturbance resulting in a temporary loss of rhizodeposition could, therefore, contribute significantly to higher net nitrification rates on disturbed sites.

The few studies that have focused on both humus forms and roots have shown significant interactions of these two factors in controlling soil mineral N dynamics. Thus, prior to this study, we hypothesized that the presence of live roots would reduce net nitrification more so in organic forest floors than in mineral soil layers, for two reasons. Firstly, because NH_4^+ availability to nitrifiers is important for net nitrification (Fraser et al., 1990; Priha et Smolander, 1999) and the presence of live roots has been shown to reduce NH_4^+ production in forest floors but to increase NH_4^+ production in mineral soil horizons (Parmelee et al., 1993; Bradley and Fyles, 1995; Ehrenfeld et al., 1997). Secondly, because forest floors contain a higher biomass of physiologically active fine roots than mineral soil horizons, most of which derives from the dominant tree vegetation, (Ewel et al., 1987; Pietikäinen et al., 1999). Thus, plant uptake as well as rhizodeposition rates resulting in higher microbial immobilisation of NO_3^-, should be higher in forest floors than in mineral soil horizons.

We report on a study designed to compare the nitrification potential of forest floors and surface mineral soil horizons across a broad range of forest sites. In order for these comparisons to remain unbiased by the NH_4^+ supplying capacity of each sample, we compared the relative nitrification index (RNI), that is, the ratio of soil NO_3^- concentration relative to total mineral N (*i.e.* $NH_4^+ + NO_3^-$) concentration (Robertson, 1982b). We first conducted an extensive review of the existing literature to compare RNI values of organic forest floor and mineral soil horizons occurring in various stand types. This was followed by a trench plot study to further examine the effect of roots on RNI values and on indices of available C in forest floor and mineral soil horizons across nine contrasting forest types. The incentive behind our study was to determine the potential use of humus form and live root density as robust variables for the simulation of soil NO_3^- cycling in the model DRYADES.

2. Materials and methods

2.1. Literature review

Net nitrification and ammonification data were gleaned from 56 published studies and one unpublished report, in order to calculate the relative nitrification index (RNI = NO_3^- ÷ [NO_3^- + NH_4^+]) across a wide range of conifer and hardwood ecosystems. The criterion for selecting these studies was that they all presented data for both forest floor and mineral soil horizons at individual sites and on individual sampling dates, and that total mineral N concentrations in both horizons were well above detection limits of the instrumentation used. Within each study, there often was more than one study site or sampling date, such that a total of three hundred and three comparisons of RNI were made between forest floor and mineral soil horizons. The nature of the sampling varied across studies, some data being *in situ* concentrations of NO_3^- and NH_4^+ while others reporting net accumulation rates of mineral N following laboratory incubations.

2.2 Study sites and trenching

Our study was conducted in nine forest communities in the Eastern Townships region of southwestern Québec, near the city of Sherbrooke, Canada (45°,26' North, 71°,41' West). Mean annual precipitation in the area is 1109 mm of which approximately a quarter falls as snow, mean annual temperature is 4.1 °C, and the average elevation is 238 m above sea level. The nine sites were chosen so as to provide the zonal range of coniferous and deciduous vegetation. A description of the forest community, age-class, mean height of dominant trees, slope and drainage class of each site was obtained from recent site description sheets provided by the Domtar paper products company (Table 1).

During the summer of 1999, trenches were dug 1 m deep around three 1 m^2 plots located at each site. Roots crossing each trench were severed and a double plastic sheeting was installed

to prevent subsequent root ingrowth. Trenches were then back-filled with soil and all understory vegetation within trench plots was clipped at the ground surface. Repeated clipping at each sampling date (see below) prevented the establishment of vegetation in the trench plots and ensured a soil with substantially fewer living roots.

2.3. General soil properties

In late-June 2000, two bulk samples of forest floor F-layer and surface mineral soil horizon (0-15 cm) were collected from each of the nine study sites and returned to the laboratory for characterisation. Organic C content was estimated based on loss by ignition (20 h @ 550 °C) in a muffle furnace and assuming conversion factors of 1.8 and 2.5 for forest floors and mineral horizons, respectively. The particle-size distribution of combusted samples was determined using a Bouyoucos hydrometer, and textural classes were based on the Canadian Soil Classification System (Soil Classification Working Group, 1998). Another set of soil subsamples was dried at 65 °C and digested in sulfuric acid – hydrogen peroxide. Digests were analysed for total-N by colorimetry (nitroprusside – salycilate) using a Technicon Auto-analyser (Pulse Instrumentation, Saskatoon). A third set of subsamples was air-dried (35 °C), extracted in Bray-1 reagent (Kuo, 1996), and the extracts were analysed for available-P by colorimetry (ammonium molybdate antimonium tartrate). A fourth set of fresh subsamples (15-20 g) was extracted in 100 ml of 1.0 N NH_4OAc solution and extracts were analysed for exchangeable K, Na, Ca and Mg using a Analyst-100 Atomic Absorption Spectrometer (Perkin Elmer, Connecticut). Results of these preliminary soil tests are given in Table 1.
Soil temperature, moisture and pH were measured on seven, four and three occasions respectively, between May and October 2000, in both forest floor and mineral horizons (10 cm depth) of trench plots and surrounding soil. The pH measurements were in aqueous suspensions (soil:water = 1:2.5 and 1:10 respectively), and 90 min were allowed for equilibration time.

2.4. Laboratory incubations

Laboratory incubations were performed one year following trench establishment (*i.e.* summer 2000) on three sampling dates (mid-May, late-June, and late-August). Soil samples (*ca.* 600 g fresh weight) were collected at two different depths (forest floor F-layer and 0-15 cm mineral soil), both inside and within a 1 m radius outside each of the 27 trench plots. The one hundred and eight soil samples collected at each sampling date were immediately placed under ice packs and brought to the laboratory in coolers. Each sample was coarse-sieved through a 5 mm mesh to remove roots and coarse debris, a subsample was analysed for moisture content, and the rest stored at 4 °C until analysed (within 1 wk).

At each sampling date, each soil sample was divided into three portions. The first portion was analysed immediately (t = 0) for mineral N concentrations, anaerobic N mineralization rates (ANMR), and indices of available C (each described below). Second and third portions were weighed (forest floor = 120 g, mineral soil = 170 g fresh wt) directly into 500 ml Mason jars, covered with polyethylene film to delay moisture losses and permit gas exchanges, and incubated three and six months (t = 3 and 6 mo) respectively. Incubation temperature was set constant at 22 °C and jars were periodically weighed and initial moisture contents restored using a fine-mist spray. Following the 3 and 6 mo incubations, the soil in each jar was analysed for mineral N, ANMR, and available C in like manner as t = 0 samples.

Mineral N was determined by extracting 15-20 g (fresh wt) soil subsamples using 150 ml of 1.0 *N* KCl solution. Solutions were shaken for 1 h on a reciprocal shaker, filtered through Whatman No. 5 cellulose filter disks, and the filtrates analysed colorimetrically for NH_4^+ (nitroprusside – salycilate) and NO_3^- (Cd reduction) concentrations using a Technicon Auto-analyser (Pulse Instrumentation, Saskatoon).

ANMR was determined by weighing *ca.* 5 g (fresh wt.) of soil into 45 ml snap-cap bottles, adding 40 ml deionized water, sealing and incubating at 30 ^{0}C for 14 days (Waring and Bremner, 1964). Bottles were then shaken and the contents transferred to 250 ml Erlenmeyer flasks. Each bottle was rinsed with 40 ml of 2 *N* KCl solution to bring the final concentration

of extractant in each flask to 1 *N* KCl. Flasks were shaken for 1 h, filtered and analysed for NH_4^+-N as previously described.

Indices of available C were derived from soil respirometry and included measurements of basal respiration rate (BR) and microbial biomass (MB). BR was determined by weighing *ca.* 5 and 20 g of F-layer and mineral soil respectively (dry wt. equiv.) into 57 ml gas sampling jars, allowing 1 wk for soils to condition to room temperature, flushing the headspace with ambient air for 5 min, sealing jars with air-tight lids equipped with rubber septa, and sampling aliquots of air in the headspace with a needle and syringe after 12 h. Air samples were analysed for CO_2 concentrations using a model CP-2002 P Micro-GC (Chrompack, Middelburg) equipped with a *TCD*, with He as carrier gas. Room temperature was noted during each measurement, and ambient CO_2 concentration was measured several times each day. For each sample, ambient CO_2 concentration was subtracted from sampled CO_2 concentration and the difference was adjusted according to Ideal Gas Laws and centered at 22 °C using $Q_{10} = 2$. MB was determined by substrate induced respirometry (*SIR*) (Anderson and Domsch, 1978). Approximately 10 g of forest floor and 30 g of mineral soil (dry wt. equiv.) were weighed into 500 ml plastic containers and amended with ground and sieved (65 μm) glucose (1000 μg C g^{-1} soil) (Bradley et al., 2000). The amendments were applied as 250 mg mixtures with talc and dispersed throughout the soil samples using a kitchen handmixer with one beater. Following amendment, soil subsamples were transferred into 114 ml gas sampling jars and left uncovered for 100 min to reach optimum *SIR* rates (Anderson and Domsch, 1978). Subsamples were then flushed for 5 min with ambient air, sealed for 30 min, and headspace air was analysed for CO_2 concentration using the GC (as described above). *SIR* rates were converted to MB using equations derived by Anderson and Domsch (1978).

2.5 Buried bags

Net *in situ* ammonification and nitrification rates were measured inside and outside each of the twenty-seven trench plots, in both forest floor and mineral horizons, using the buried bag incubation method (Eno, 1960). The assay consisted of three trials concurrent with laboratory

incubations. At each trial, fresh soil samples (forest floor = 60 g, mineral soil = 100 g fresh wt.) were weighed with a field scale, placed in polyethylene bags (200 cm^2), returned to the hole in the ground that had been left by the sampling procedure, and left to incubate *in situ* for 3 weeks. Bags were then collected, placed over ice and returned to the laboratory to be analysed for NO_3^- and NH_4^+ concentrations (as previously described). Initial mineral N concentrations (*i.e.* t = 0 samples from laboratory incubations) were subtracted from final mineral N concentrations in buried bags, and average net ammonification and nitrification rates of each treatment were calculated.

2.7. Statistical analyses

Given the small size of trench plots relative to the spatial heterogeneity of the vegetation within each site, the twenty-seven trench plots were treated as independent samples each representing a unique soil profile. The main effects of sampling date (*i.e.* date) and incubation time (*i.e.* time) on mineral N cycling and indices of available C were tested sequentially by a series of one-way ANOVA's. Within each sampling date, the effects of incubation time, soil horizon (*i.e.* horizon) and soil trenching (*i.e.* roots), as well as the effects of horizon x roots interactions, on mineral N cycling and indices of available C were tested by three-way ANOVA. Significantly different means were separated using Duncan's multiple range test ($P<0.05$). All statistical tests were performed with the SAS statistical package (SAS, 1998).

3. Results

3.1 RNI values gleaned from the literature

Table 2 summarises two hundred and twenty-three comparisons of RNI values in forest floor *versus* mineral soil horizons, that were gleaned from thirty six published plus one unpublished studies. These studies measured *in situ* NO_3^- and NH_4^+ concentrations by direct

extraction. In one hundred and forty-eight cases, RNI in the forest floor was lower than in the mineral horizon, and these comparisons were denoted by the symbol '<'. In eleven cases, RNI was approximately equal in both horizons and these comparisons were denoted by the symbol "=". In thirty-eight cases, NO_3^- was not detected in neither horizon (*i.e.* RNI = 0) and these comparisons were also denoted by the symbol "=". In only twenty-six cases, RNI in the forest floor was higher than in the mineral soil horizon, and these comparisons were denoted by the symbol ">".

Likewise, Table 3 summarizes eighty comparisons of RNI values in forest floors *versus* mineral soil horizons, that were gleaned from twenty published studies. In contrast with values shown in Table 2, these studies measured NO_3^- and NH_4^+ pools that had accumulated in soil samples following different periods of incubation. In fifty-five cases, RNI in the forest floor was lower than in the mineral soil horizon. In fifteen cases, NO_3^- was not detected in neither horizon (*i.e.* denoted by the symbol "="). In ten cases, RNI in the forest floor was higher than in the mineral soil horizon.

In summary, 88 % of the three hundred and three comparisons gleaned from fifty-seven independent studies showed RNI values that were either equal or higher in the mineral soil horizon than in the forest floor.

3.2 Seasonal changes in temperature, moisture and pH

Average soil temperatures during summer 2000, ranged from ca. 6-8 °C in mid-May and late-October, to ca. 15-17 °C between July 18th and August 31st (Fig. 1.a). Soil temperatures were constantly 1-2 °C higher in forest floors than in mineral soil horizons. Average gravimetric soil moisture content was fairly constant throughout the growing season, and ca. 4x higher in forest floors than in mineral soil horizons (Fig. 1.b). Average soil pH, which ranged from 4.0 to 4.7, was significantly lower ($P < 0.001$) in mid-May than in late-June or late-August (Fig. 1.c). Average soil pH was approximately 0.2 unit higher in mineral soil horizons than in forest floors.

3.3 Mineral N cycling and indices of available C

Figure 2 shows a significant increase of *in situ* NO_3^- and NH_4^+ pools as well as RNI values in trench plots compared to surrounding soil as the season progressed. *In situ* NO_3^- and NH_4^+ pools were significantly higher in forest floor than in mineral soil horizons. At each sampling date, there were no significant differences in RNI values between each horizon.

Table 4 summarizes the main effects of sampling date and incubation time on mineral N cycling and indices of available C during laboratory incubations. Pooled across incubation times, soil horizons and trenching treatments, the mean NO_3^- concentration, RNI, ANMR and MB increased as the season progressed, and were statistically higher in late-August than in the two previous sampling dates. Although sampling date did not have a significant effect on mean values of NH_4^+ concentration or BR, these two variables also increased as the season progressed. Pooled across sampling dates, soil horizons and trenching treatments, there were significant increases in mean NO_3^- and NH_4^+ concentrations, RNI and ANMR, and significant decreases in mean MB, as the incubations progressed. The mean value of BR was statistically higher at t = 3 mo than at t = 0 and 6 mo.

Table 5 summarizes results of three-way ANOVAs testing the effects of incubation time, soil horizon, roots, and horizon x roots interactions on mineral N cycling and indices of available C, within each sampling date. Incubation time had a significant effect on all variables at each sampling date similar to the main "time" effects reported in Table 4. The effect of soil horizon on each variable was also statistically significant at each sampling date. The effect of trenching on RNI, BR and MB was statistically significant in late-June, as was the effect of trenching on NO_3^- concentrations, RNI and MB in late-August. There were significant horizon x roots interactions controlling BR and MB in late-June and NO_3^- concentrations in late-August. Also shown in Table 5 are results of two-way ANOVAs testing the effects of horizon, roots and horizon x roots interactions on NO_3^- and NH_4^+ production in buried bags. Horizon had a significant effect on both mineral N forms at each date, except on NH_4^+ production in mid-May, whereas roots and horizon x roots interactions only had a significant effect on NO_3^- concentrations in late-August.

More specifically, figures 3, 4 and 5 show how each of these variables evolved within each horizon x root combination at each sampling date. NO_3^- concentrations increased in all horizons during incubations, but the increase was two orders of magnitude greater in forest floors than in mineral horizons (Fig. 3.a, b, c). In late-August, NO_3^- concentrations in forest floors were statistically higher in trench plots than in surrounding soils at t = 3 and 6 mo (Fig. 3.c). NH_4^+ concentrations increased mainly in forest floors during incubations, and were two orders of magnitude greater than in mineral horizons (Fig. 3.d, e, f). RNI in both horizons generally increased after three months incubation and stabilised thereafter (Fig. 3.g, h, i). At each sampling date, RNI values were statistically higher in mineral horizons than in forest floors after 3 and 6 mo incubation. In late-June and late-August, RNI values within each horizon were statistically higher in trench plots than in surrounding soils (Fig. 3.h, i), although the relative increase in RNI due to trenching was higher in forest floors than in mineral soil horizons. ANMR increased mainly in forest floors during incubations and were two orders of magnitude greater than in mineral horizons (Fig. 3.j, k, l). Results from *in situ* buried bag incubations revealed significantly higher NO_3^- and NH_4^+ production rates in forest floors than in mineral horizons for most dates (Fig. 4). In late-August, net *in situ* NO_3^- production in forest floors was significantly higher in trench plots than in surrounding soils. BR measurements were generally one order of magnitude higher in forest floors than in mineral horizons (Fig. 5.a, b, c). In late-June, BR was statistically higher in surrounding soils than in trench plots (Fig. 5.b). MB decreased significantly in forest floors during incubations, but remained one order of magnitude greater than in mineral horizons (Fig. 5.d, e, f). In both late-June and late-August, MB was higher in surrounding soils than in trench plots (Fig. 5. e, f).

4. Discussion

Our study showed significant short-term increases in soil NO_3^-, NH_4^+ and RNI due to sampling date, soil horizon as well as trenching, across a range of forest types. Our trench plot experiment failed to show significantly higher *in situ* RNI values in mineral soil horizons

compared to forest floors (*i.e.* Fig. 2), however, a trend emerging from Table 2 did corroborate this hypothesis. It can be argued that this trend resulted mainly from NO_3^- leaching or plant uptake from the forest floor, since NO_3^- is a mobile anion. For this reason, long-term laboratory incubations were useful because they resulted in the accumulation of mineral N forms to concentrations several orders of magnitude above *in situ* concentrations, while preventing N losses. Long-term laboratory incubations allowed, therefore, measurement of potential net nitrification and ammonification rates and comparison of RNI values of different horizons and trenching treatments based solely on the chemical quality of humus, and removed possible confounding effects of NO_3^- leaching or plant uptake. During the incubations, significantly higher RNI values evolved in mineral soil horizons than in forest floors, thereby corroborating one of our main hypotheses as well as the trend emerging from Table 3.

Analysed collectively, our data allowed the development of hypotheses regarding the possible roles of microclimate, plant uptake, soil acidity, C availability to heterotrophic microorganisms and NH_4^+ availability to nitrifiers, and how these factors possibly interact to control soil NO_3^- dynamics.

4.1 Soil temperature and moisture

Fraser *et al.* (1990) and Holmes and Zak (1999) have alluded to the importance of higher soil temperatures in stimulating microbial activity, thereby increasing NH_4^+ availability to nitrifying organisms. Their studies compared, however, soil temperature of various silvicultural treatments and were not focused, as we were, on seasonal effects. General increases in NO_3^- and NH_4^+ production, RNI and MB during laboratory incubations, as well as in NO_3^- production in buried bags, were concordant with increases in soil temperature over the three sampling dates (Julian days 135, 175 and 245). Soil temperature cannot be dismissed, therefore, as a possible factor controlling seasonal variations in NO_3^- cycling, although it would be tenuous to establish a causal relationship issued from a correlation based on only three sampling dates. Moreover, intensive studies in forests of southern

Québec have shown no correlation between seasonal temperature gradients and soil N mineralization rates (Côté *et al.*, 1998).

Soil moisture in both horizons did not decrease markedly during the middle of summer, as usually occurs in southern Québec (Côté *et al.*, 1998), but this may be due to the exceptionally cool, humid and cloudy conditions experienced in the summer of 2000 (Environment Canada, 2001). Average seasonal gravimetric moisture content was greater in forest floors (*ca.* 150 %) than in mineral horizons (*ca.* 35 %) due to higher organic matter content of the former, but neither horizon at any of the sites was subjected to anaerobiosis that would have reduced nitrification during the sampling period.

We expected that a loss of plant uptake would cause average soil moisture content of trench plots to be significantly higher than that of surrounding soils (Fisher and Gosz, 1986; Hart and Sollins, 1998), but this did not occur (data not shown), perhaps because of the exceptional humid warm climatic conditions of summer 2000. We conclude, therefore, that soil moisture was not important in controlling *date*, *horizon* or *root* effects on soil N cycling and microbial dynamics in our study.

4.2 Soil acidity

Soil pH varied according to sampling date and soil horizon, but not according to trenching treatment (data not shown). The higher soil acidity in mid-May compared to late June and late-August, could be due to a springtime release of organic acids from the previous summer's litter cohort. Likewise, the higher acidity of forest floors compared to mineral soils could result from higher concentrations of soluble organic acids in the forest floor, and to the buffering capacity of some soil minerals. Ste-Marie and Paré (1999) showed, through experimental manipulation of forest floor pH, that soil acidity can significantly reduce nitrification. Based on previous work by Suzuki (1974), they proposed that increases in soil pH result in a shift of NH_4^+ to NH_3, and that NH_3 is a preferred substrate for nitrifying

bacteria. It is therefore possible that the lower RNI values measured in springtime or in forest floors were controlled, in part, by higher soil acidity.

4.3 Plant uptake

Preferential plant uptake of one mineral N form should theoretically lead to higher concentrations of the other mineral N form in soil, and vice versa. In order for RNI values to be constantly lower in forest floors than in mineral horizons, preferential uptake of NO_3^- would constantly have to be higher in the former. This seems unlikely and there is no evidence from the literature that preferential plant uptake of NH_4^+ or NO_3^- differs significantly across horizons.

In our study, trenching increased *in situ* concentrations of NO_3^- and NH_4^+ in both horizons, but RNI values also increased due to trenching (Fig. 2). If the rate of plant assimilation was the only potential fate of mineral N altered by trenching, we would have to conclude that most stands were preferentially taking up NO_3^-. While it is true that some trees, such as poplars, discriminate against soil NH_4^+, others, such as spruces, discriminate against soil NO_3^- (Kronzucker et al., 1997). Hence, across a wide range of forest types, RNI values cannot consistently increase after to trenching.

Another possible explanation for the positive effect of trenching on RNI values, which involves the role of plant uptake, is based on the common assumption that plants compete with soil microbial communities for soil mineral N (Kaye and Hart, 1997). Given their small genome, many bacterial species do not carry the genes for NO_3^- assimilation (Lin and Stewart, 1998), and several studies have suggested that most herbs and trees compete better for NO_3^- than for NH_4^+, even when the latter is their preferred N form (Jackson et al., 1989; Norton and Firestone, 1996). Under this scenario, trenching should consistently result in higher RNI values across a range of forest types.

4.4 Labile C and NH_4^+ availability

The chemical quality of SOM can be partitioned in terms of its nutritional value and its energy yield. Based on Liebig's law of the minimum, heterotrophic microorganisms are, therefore, said to be N limited when SOM is at a C:N ratio above 30:1, and mainly C limited when SOM is below this critical value (Kaye and Hart, 1997). In our study, C:N ratios of all horizons at all sites were ≤ 30 and heterotrophic microorganisms were theoretically C-limited (Kaye and Hart, 1997) rather than N-limited. SOM quality in this study was therefore synonymous to C availability.

Our study showed a decrease in available C during laboratory incubations. An increase in mean BR between t = 0 and t = 3 mo was likely due to a conditioning of soil samples to an incubation temperature *ca.* 5-10 °C higher than *in situ* conditions, rather than to an increase in available C. The depletion in available C substrates is reflected by the decrease in BR between t = 3 and 6 mo, in spite of a constant incubation temperature. This was further confirmed by significant decreases in mean MB, perhaps a more reliable estimate of available C (Bradley and Fyles, 1995), during the incubations.

BR and MB in mineral horizons were only a fraction of those in forest floors because of the lower organic matter content of the former. The fact that MB in forest floor samples declined precipitously during incubations compared to MB in mineral horizons indicates a different chemical quality of organic matter in each horizon. High quality soil organic matter is characterised by high microbial activity and decay rates that decline rapidly whereas low quality organic matter is characterised by constant MB and slow decay rates (Melillo *et al.*, 1989). Forest floor OM is less decomposed than mineral soil OM and, therefore, comprise a pool of more labile organic compounds.

Trenching also resulted in lower indices of available C compared to surrounding soils. Norton et al. (1990) showed that metabolically active fine roots are responsible for rhizodepositing up to one third of recently fixed plant C. Since fine root activity is generally much higher in forest floors than in mineral horizons (Ewel et al., 1997; Finér *et al.*, 1997; Pietikäinen *et al.*, 1999), we expected a greater reduction of BR and MB due to trenching in

forest floors compared to mineral horizons. This outcome occurred mainly in late-June, as illustrated by significant *horizon* x *root* interactions controlling BR and MB, perhaps because of the seasonal periodicity of fine-root growth (Côté *et al.*, 1998).

Differences in NO_3^- and NH_4^+ accumulation rates as well as RNI values due to incubation time, horizon and roots can theoretically be explained by differences in labile C. Low available C results in low microbial immobilization rates. The availability of NH_4^+ thus increases and, in turn, stimulates nitrification rates (Fraser et al., 1990; Holmes and Zak, 1999). Although this model appears applicable for explaining trenching effects on *in situ* mineral N pools as well as time and horizon effects on mineral N pools during laboratory incubations, there are shortcomings to its overall applicability. For example, reductions in available C due to trenching did not produce significantly higher NH_4^+ pools during incubations whereas trenching did cause NO_3^- pools to increase. The model is equally poor at justifying why lower available C does not reduce NO_3^- and NH_4^+ immobilization rates equally. An alternative model that would explain higher RNI values due to trenching is one that links both the effects of lower available C and higher NH_4^+ pools as two factors contributing in tandem to higher NO_3^- immobilization rates. Hart *et al.* (1994) showed that lower available C can be important in controlling NO_3^- immobilization and net nitrification rates, independently from NH_4^+ supply. Building on this concept, we hypothesize that lower available C decreases microbial N demand leading to higher NH_4^+ concentrations which reduce the rate of NO_3^- assimilation relative to that of NH_4^+. This is because of the higher energy required for assimilatory NO_3^- reduction (Lin and Stewart, 1998). Using the isotope dilution technique, Bradley (2001) showed that increasing NH_4^+ pool size resulted in a marked decrease of gross NO_3^- immobilization rates, more so than in an increase of gross NO_3^- production rates. Hence, a decrease in available C coupled to high NH_4^+ pools should result in proportionately higher microbial immobilization of NH_4^+, the preferred microbial N source, and, by implication, higher RNI values.

4.5 Generalized versus local concepts

Since our data were pooled across contrasting stands, significant seasonal effects as well as significant effects of soil horizon (*i.e.* humus form) and trenching (*i.e.* live root density) on *in situ* soil NO_3^- pools, potential nitrification rates, RNI and indices of available C can be generalized for most forest types across the Eastern Townships of Quebec and similar forest types in other parts of the world. By plotting the incubation data from both horizons on the same scale, the effect of trenching on potential nitrification in the mineral horizon was blurred graphically (*i.e.* Fig.3a, b, c), but it made it possible to appreciate how potential NO_3^- production and the effect of trenching are much greater in the forest floor than in the mineral soil. This potential for forest floors in the Eastern Townships of Quebec to nitrify contrasts sharply with several studies performed in some old-growth conifer forests on the Pacific West Coast that showed very little net nitrification during long-term incubations and insignificant NO_3^- leaching following major forest disturbance (Feller, 2000; Bradley et al., 2000; Bradley, 2001). Although there is a need to find generalized concepts that can be applied across a broad range of sites, we believe there is a danger in extrapolating nitrification data beyond the regional scale.

Tables 2 and 3 suggest that the trend towards higher RNI values in mineral soil horizons, compared to forest floors, spans a broader geographical scale than the Eastern Townships of Québec. Although 88 % of tabulated RNI values in mineral soil horizons were greater or equal to those in corresponding forest floors, it would be useful to our understanding of soil NO_3^- dynamics to discern trends among the 12 % of comparisons that showed an opposite direction. It may be worth noting that seventeen of the twenty-six contrary cases (*i.e.* $RNI_{\text{forest floor}} > RNI_{\text{mineral soil}}$) listed in Table 2 were found in pine stands and four others in young plantations. Six of the ten contrary cases listed in Table 3 were found in pioneer aspen or birch stands and three others in young plantations. Hence, there may be combinations of factors found either in pine stands or in juvenile forests that would exceptionally predispose the forest floor toward higher RNI values than mineral soil horizons.

4.6 Significance of the study

The practice of clearcutting is no longer allowed in the Eastern Townships, and has been replaced by small strip-cutting and shelterwood harvesting. One of the tenets of these partial cutting methods is that maintaining some degree of canopy cover increases the resilience of the ecosystem. Our data have shown, however, that a very local disturbance underneath a mature forest canopy, that would result in root death, can have a significant short-term effect on net nitrification and RNI, especially in the forest floor. This may, in turn, trigger changes to ecosystem dynamics by reducing site N capital through NO_3^- leaching and by affecting the competitive abilities within the plant community (Kronzucker et al., 1997).

Because ecosystems are complex, forest simulation models should strive to represent observable features, such as humus forms and root density, which implicitly represent a subset of processes that are important in controlling the dynamics of key nutrients such as N. In order for these observable features to be robust within our models, the combined effects of the processes that they implicitly represent must differ predictably across forest types. Our study tends to confirm that RNI values are generally higher in mineral soil horizons than in organic forest floors, and that loss of live-root function increases RNI values equally in both mineral soil horizons and forest floor layers. Thus, a measure of forest floor depth relative to humus enriched surface mineral soils, and a measure of live fine root density could be used as calibration parameters for representing soil NO_3^- dynamics in forest ecosystems.

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Table 1. Site and soil descriptions for nine forest communities; abbreviations for dominant tree species are: Ms = Sugar maple; By = Yellow birch; Aw = White ash; He = Eastern hemlock; Mr = Red maple; Ba = American beech; Sw = White spruce; Fb = Balsam fir; Pr = Red pine; Ce = Eastern white cedar; At = Trembling aspen; Le = Eastern larch; abbreviations for textural classes are: SL = Sandy loam; LS = Loamy sand; S = Sand; SiL = Silt loam. Within soil description, first row describe forest floor while second row describe mineral soil horizon.

	Deciduous sites			Coniferous sites					
	I	II	III	IV	V	VI	VII	VIII	IX
Site description									
Forest communities	Ms, By	Ms, Aw, Ba	Mr, Ms, Ba	Sw	He	Fb	Pr	Ce, Fb, At	Le, Sw
Age	80-100 yrs	40-60 yrs	40-60 yrs	40 yrs	90 yrs	50 yrs	30 yrs	40-60 yrs	40-60 yrs
Height	22 m +	17-22 m	17-22 m	12-17 m	22 m +	12-17 m	17-22 m	12-17 m	12-17 m
Slope	very mild	mild	flat	flat	very mild	flat	flat	flat	mild
Drainage	well	well	well	well	well	imperfect	well	imperfect	imperfect
Soil description									
Textural class	SL	LS	LS	SL	SL	S	LS	SiL	S
pH	3.7	3.9	4.2	5.2	4.0	3.7	4.4	5.9	4.8
	4.1	4.2	4.7	4.8	4.1	4.4	4.4	6.5	5.0
Organic C (mg g^{-1})	199.8	246.9	257.3	121.1	380.8	315.9	178.9	223.3	55.9
	26.6	33.1	36.5	38.1	34.0	46.8	29.4	15.6	19.0
Total N (mg g^{-1})	7.2	10.1	10.7	4.0	14.7	11.9	7.0	9.0	3.9
	1.0	1.4	1.3	1.5	1.2	1.7	1.8	0.9	1.4

(suite table 1)

C : N ratio	27.8	24.4	24.0	30.3	25.9	26.6	25.6	24.8	14.3
	26.6	23.6	28.1	25.4	28.3	27.5	16.3	17.3	13.6
Extractable P ($\mu g\ g^{-1}$)	11.5	12.6	11.9	7.3	14.7	8.2	15.1	39.7	2.5
	0.4	0.4	0.5	0.8	4.0	1.1	0.8	8.8	0.5
Exchangeable Ca^{2+} ($mg\ g^{-1}$)	0.8	2.6	3.1	3.2	1.8	0.8	0.7	7.4	1.8
($\mu g\ g^{-1}$)	58.3	154.8	368.5	480.1	59.2	35.3	12.7	893.5	238.5
Exchangeable Mg^{2+} ($\mu g\ g^{-1}$)	151.7	879.4	576.4	577.8	330.8	224.3	42.9	751.5	146.8
	13.1	29.9	51.7	158.2	13.6	21.8	4.8	69.9	25.3
Exchangeable K^{+} ($\mu g\ g^{-1}$)	111.3	155.6	125.5	323.0	174.5	198.8	164.4	135.0	115.7
	29.9	25.9	18.2	120.6	18.4	21.4	14.8	21.3	13.8
Exchangeable Na^{+} ($\mu g\ g^{-1}$)	8.1	20.3	16.4	17.1	29.9	20.5	17.2	19.9	10.5
	4.4	4.9	4.5	17.4	5.6	5.1	4.8	6.0	5.4

Table 2. Comparison of relative nitrification index (RNI) of forest floor *versus* mineral soil horizons in various stand types. RNI was calculated with *in situ* NO_3^- and NH_4^+ concentrations. Comparisons within studies with more than one site or sampling date may be denoted by multiple symbols ("<", "=", ">").

	Forest communities	Forest Floor RNI		Mineral RNI	Location	Source
1	Spruce (three sites)	0.08 – 0.38	<	0.17 – 0.63	Sweden	*Popovic, 1967*
2	Spruce (five sites)	0.02 – 0.14	<	0.07 – 0.40	Sweden	*Popovic, 1971a*
3	Spruce (twelve dates: May 1967- Nov. 1968)	0.15 - 0.67	<=>	0.08 – 0.50	Sweden	*Popovic, 1971b*
4	I-Beechwood (2 sites)	0.10 – 0.11	<	0.19 – 0.20	Belgium	*Van Praag and Weissen, 1973*
	II-Spruce	0.05	>	0.03		
5	I-Pine (two soil types)	0.01	<=>	0.00 - 0.07	Japan	*Ohta and Kumada, 1978*
	II-Deciduous broad-leaf tree (three soil types)	0.01 - 0.04	<	0.07 – 0.15		
	III-Cypress (nine soil types)	0.00 – 0.58	<=	0.00 – 0.80		
	IV-Cedar (six soil types)	0.09 – 0.69	<=>	0.11 – 0.95		
	V-Larch (two soil types)	0.01 – 0.02	<=	0.02 - 0.14		
	VI-Evergreen broad-leaf trees (three soil types)	0.01 – 0.03	<=	0.00 - 0.50		
6	Douglas fir (two soil types)	0.05 – 0.08	<=	0.08	Seattle	*Johnson, 1979*
7	I-Maple-Beech	0.12	<	0.27	Indiana	*Vitousek et al., 1982*
	II-Oak	0.04	<	0.09	Indiana	
	III-Shortleaf pine	0.05	<	0.12	Indiana	
	IV-Oak-Pine	0.02	<	0.15	New England	
	V-Red pine	0.01	<	0.07	New England	
	VI-Oak-red pine	0.03	<	0.06	New England	
	VII-Northern hardwood	0.08	<	0.19	New England	
	VIII-Balsam fir	0.04	<	0.08	New England	
	IX-Ponderosa pine	0.05	>	0.03	New Mexico	
	X-Mixed conifer	0.04	>	0.02	New Mexico	
	XI-Aspen	0.03	>	0.01	New Mexico	
	XII-Spruce-subalpine fir	0.01	<	0.02	New Mexico	
	XIII-Coastal hemlock	0.01	<	0.27	Pacific Northwest	
	XIV-Alder	0.23	>	0.19	Pacific Northwest	

(suite table 2)

	Forest communities	Forest Floor RNI		Mineral RNI	Location	Source
	XV-Douglas fir	0.03	<	0.04	Pacific Northwest	*Vitousek et al., 1982*
	XVI-Douglas fir	0.02	<	0.07	Pacific Northwest	(suite)
	XVII-Pacific silver fir	0.01	<	0.02	Pacific Northwest	
8	I-Douglas fir (rich site : two dates: July 1976 – Jan. 1977)	0.05 – 0.11	<	0.12 – 0.77	Washington	*Vogt and Edmonds, 1982*
	II-Douglas fir (poor site : two dates: July 1976 – Jan. 1977)	0.01	<	0.06 – 0.07		
9	I-Fir-Spruce	0.00	=	0.00	Maine	*Federer, 1983*
	II-Birch-Beech	0.00	=	0.00	New Hampshire	
	III-Oak-Beech	0.00	=	0.00	New Hampshire	
	IV-Oak	0.01	=	0.00	Connecticut	
10	Balsam fir	0.04	<	0.15	New Hampshire	*Olson and Reiners, 1983*
11	Pine-Aspen	0.18	<	0.31	Ontario	*Hendrickson et al., 1985*
12	Oak-Beech stand (two plots)	0.15 – 0.25	<	0.33 – 0.41	Netherlands	*Tietema and Verstraten, 1988*
13	Conifers (seven sites; mean annual)	0.00 – 0.01	=	0.00 – 0.01	Oregon	*Myrold et al., 1989*
14	Black spruce	0.09	>	0.04	Alaska	*Van Cleve et al., 1990*
15	Oak-Beech	0.15	<	0.52	Netherlands	*Tietema and Verstraten, 1991*
16	Old-growth conifers (seven dates: Nov. 1986 – Sept. 1987)*	0.06 – 0.36	<	0.18 – 0.47	Sierra Nevada	*Davidson et al., 1992*
17	Douglas fir	0.11	>	0.07	Netherlands	*De Boer et al., 1992*
18	I-Douglas fir-Pine	0.04	>	0.00	Netherlands	*Tietema et al., 1992*
	II-Oak	0.08	<	0.20		
	III-Douglas fir	0.11	<	0.30		
	IV-Oak-Beech	0.11	<	0.40		
19	I-Red pine (twelve dates: May 1988 – Oct. 1990)*	0.00	<=	0.00 – 0.17	Massachusetts	*Aber et al., 1993*
	II-Hardwood (twelve dates: May 1988 – Oct. 1990)*	0.00	<=	0.00 – 0.56		
20	Western redcedar (four dates: Sept. 1987 – March 1989)*	0.00 – 0.41	<=	0.00 – 0.50	Oregon	*Turner et al., 1993*
	Douglas fir (four dates: Sept. 1987 – March 1989)*	0.01 – 0.50	<	0.57 – 0.71		
	Western hemlock (four dates: Sept. 1987 – March 1989)*	0.00 – 0.28	<=	0.00 – 0.80		
21	Hardwood (three dates: spring 1991 - spring 1992)*	0.00 - 0.08	=	0.00 – 0.08	New Hampshire	*Christ at al., 1995*

(suite table 2)

	Forest communities	Forest Floor RNI		Mineral RNI	Location	Source
22	I-Douglas fir plantation (nine dates: May 1992 – Apr. 1993)	0.13 – 0.33	<	0.26 – 0.90	Netherlands	*Koopmans et al., 1995*
	II-Scots pine plantation (nine dates: May 1992 – April 1993)*	0.08 – 0.25	<=>	0.08 – 0.23	Netherlands	
23	I-Scots pine *	0.01	<	0.07	Sweden	*Nohrstedt et al., 1996*
	II-Scots pine-Norway spruce *	0.14	<	0.31		
24	I-Spruce-Aspen (rich stand : two plots)	0.07 – 0.08	<	0.13 – 0.19	Alberta	*Schmidt et al., 1996*
	II-Spruce-Aspen (poor site : two plots)	0.06 – 0.07	<	0.09 – 0.12		
25	Pitch pine (three dates: May 1991 – June 1992)	0.00 – 0.04	=>	0.00 – 0.02	New Jersey	*Ehrenfeld et al., 1997*
26	I-Pine plantation (four years: 1988 – 1993)*	0.00	<=	0.00 – 0.14	New England	*Magill et al., 1997*
	II-Hardwood (four years: 1988 – 1993)*	0.00	<=	0.00 – 0.05		
27	I-Scots pine plantation	0.00	=	0.00	France	*Degrange et al., 1998*
	II-Scots pine plantation	0.17	=	0.17		
28	Ponderosa pine (two dates: May 1995 – Nov. 1995)	0.02 – 0.05	<	0.06 – 0.22	Arizona	*Kaye and Hart, 1998*
29	Norway spruce (three sites)	0.00 – 0.06	<	0.07 – 0.10	Sweden	*Rudebeck and Persson, 1998*
30	Sub-boreal spruce (three age-classes: 14 – 140 years)	0.02 – 0.24	<	0.23 – 0.51	British Columbia	*Driscoll et al., 1999*
31	I-Upland Hardwood (five dates: July 1995 – June 1996) *	0.00 – 0.05	<	0.11 – 0.25	New York	*Ohrui et al., 1999*
	II-Conifers (five dates: July 1995 – June 1996)	0.00	<=	0.00 – 0.02		
	III-Forested wetland (five dates: July 1995 – June 1996)	0.00	<	0.10 – 0.38		
32	I-Pine (2 sites)	0.00 - 0.05	<=	0.00 - 0.15	Finland	*Priha and Smolander, 1999*
	II-Spruce (2 sites)	0.00	=	0.00		
	III-Birch (2 sites)	0.00	=	0.00		
33	Scots pine plantation	0.07	<	0.21	Netherlands	*Laverman et al., 2000a*
34	Scots pine plantation	0.06	<	0.20	Netherlands	*Laverman et al., 2000b*
35	Hardwood	0.00	=	0.00	Massachusetts	*Magill and Aber, 2000*
36	I-Hardwood - 775 m alt. (three dates: Oct. 1995 – Oct. 1996)	0.29 – 0.55	<>	0.06 – 0.63	New Hampshire	*Excerpted from data used by*
	II-Hardwood - 685 m alt. (three dates: Oct. 1995 – Oct. 1996)	0.24 – 0.45	<>	0.02 – 0.49		*Bohlen et al., 2001*
	III-Hardwood - 585 m alt. (three dates: Oct. 1995 – Oct. 1996)	0.28 – 0.59	<>	0.03 – 0.71		
	IV-Hardwood - 525 m alt. (three dates: Oct. 1995 – Oct. 1996)	0.06 – 0.23	<>	0.00 – 0.41		
37	Conifers (six dates: July 1999 – Sept. 2000)	0.00 – 0.21	<=>	0.01 – 0.15	British Columbia	*Hannam, unpublished*

* Graphic approximation

Table 3. Comparison of relative nitrification index (RNI) of forest floor *versus* mineral soil horizons across various forest types. RNI was calculated with NO_3^- and NH_4^+ pools that had accumulated in soil samples following different periods of incubation. Comparisons within studies with more than one site or sampling date may be denoted by multiple symbols ("<", "=", and ">").

	Forest communities	Forest floor RNI		Mineral RNI	Location	Source
1	I-Fir-Spruce	0.00	<	0.20	Maine	*Federer, 1983*
	II-Birch-Beech	0.00	<	0.59	New Hampshire	
	III-Oak-Beech	0.00	<	0.04	New Hampshire	
	IV-Oak	0.00	<	0.28	Connecticut	
2	Pinus-Aspen	0.01	<	0.05	Ontario	*Hendrickson et al., 1985*
3	I-Ponderosa pine (five dates: Jan. 1979 - May 1980)	0.00 - 0.02	<	0.08 - 0.85	New Mexico	*Gosz and White, 1986*
	II-Mixed-conifer (five dates: Jan. 1979 - May 1980)	0.00 - 0.84	<	0.76 - 0.94		
	III-Aspen (three dates: May 1979 - Oct. 1979)	0.14 - 0.88	<>	0.18 - 0.85		
	IV-Spruce-Fir (four dates: June 1979 - July 1980)	0.00	=	0.00		
4	Oak-Beech (two dates: 1985 - 1987)	0.43 - 0.58	<	0.84 - 1.11	Netherlands	*Tietema and Verstraten, 1991*
5	Douglas fir	0.23	>	0.14	Netherlands	*De Boer et al., 1992*
6	I-Red pine (two dates: 1988 and 1990)	0.04 - 0.12	<	0.28 - 0.62	Massachusetts	*Aber et al., 1993*
	II-Hardwood stand (two dates: 1988 and 1990)	0.00	=	0.00		
7	I-Western redcedar	0.14	<	0.52	Oregon	*Turner et al., 1993*
	II-Douglas fir	0.49	<	0.74		
	III-Western hemlock	0.07	<	0.49		
8	I-Douglas fir plantation	0.34	<	0.50	Netherlands	*Koopmans et al., 1995*
	II-Scots pine plantation	0.19	>	0.10		
9	Norway spruce (nine sites)	0.00 - 0.91	<	0.38 - 1.84	Sweden and Denmark	*Persson and Wirén, 1995*
10	Beech stand (two dates: June and Dec., 1999)	0.28 - 0.47	<	0.89 - 1.60	Germany	*Bauhus et al., 1996*
11	I-Aspen stand (four age-classes: 29 - 123 years)*	0.00 - 1.38	=>	0.00 - 0.02	Quebec	*Paré and Bergeron, 1996*
	II-Birch stand (three age-classes: 29 - 123 years)*	0.00 - 0.47	=>	0.00 - 0.01		
	III-Spruce stand (three age-classes: 29 - 123 years)*	0.00 - 0.05	=>	0.00 - 0.01		

(suite table 3)

	Forest communities	Forest floor RNI		Mineral RNI	Location	Source
12	Pitch pine (three dates: May 1991 - June 1992)*	0.00 - 0.81	<=>	0.00 - 0.02	New Jersey	*Ehrenfeld et al., 1997*
13	I-Pine plantation (4 years: 1988 - 1993)*	0.04 - 0.12	<	0.24 - 0.61	New England	*Magill et al., 1997*
	II-Hardwood stand (4 years: 1988 - 1993)*	0.00	<=	0.00 - 0.05		
14	Conifer forest (field and laboratory incubations)	0.06 - 0.08	<	0.41 - 0.51	British Columbia	*Prescott, 1997*
15	I-Scots pine plantation	0.20	<	0.22	France	*Degrange et al., 1998*
	II-Scots pine plantation (high atmospheric pollution)	0.14	>	0.10		
16	Ponderosa pine*	0.33	<	0.48	Arizona	*Kaye and Hart, 1998*
17	Norway spruce (three sites)	0.00 - 0.01	<	0.13 - 0.39	Sweden	*Rudebeck and Persson, 1998*
18	Pine plantation (two soil types)	0.25 - 0.84	<	0.95 - 0.97	New Zealand	*Scott et al., 1998*
19	I-Upland hardwood	0.10	<	0.37	New York	*Ohrui et al., 1999*
	II-Conifer stand	0.00	<	0.05		
	III-Forested wetland	0.01	<	0.54		
20	Scots pine	0.05	<	0.11	Netherlands	*Laverman et al., 2000b*

* Graphic approximation

Table 4. Main effects of sampling date (*i.e.* Date) and time of incubation (*i.e.* Time) on NO_3^- and NH_4^+ concentrations, on relative nitrification index (*i.e.* RNI), basal respiration rate, microbial biomass, and anaerobic mineralization (*i.e.* ANMR) during aerobic laboratory incubations; results from one-way ANOVAs are summarised as $*P<0.05$, $**P<0.01$ and $***P<0.001$; values represent pooled means; different lower-case letters within each line designate significant differences ($P<0.05$, Duncan's Multiple Range Test). Data from site-VIII were excluded from analyses for date = mid-May. NA= Non available

Date	mid-May	late-June	late-August
** NO_3^- ($\mu g\ NO_3^-N\ g^{-1}$)	73.1 b	95.3 b	127.7 a
NH_4^+ ($\mu g\ NH_4^+N\ g^{-1}$)	130.7 a	147.7 a	179.2 a
* RNI (unitless)	0.47 b	0.50 ab	0.56 a
* ANMR (mg N g^{-1})	0.20 b	0.24 ab	0.29 a
** Buried bag NO_3^- ($\mu g\ NO_3^-N\ g^{-1}\ d^{-1}$)	0.25 b	0.86 a	1.02 a
Buried bag NH_4^+ ($\mu g\ NH_4^+N\ g^{-1}\ d^{-1}$)	0.24 a	0.83 a	0.67 a
Basal respiration ($\mu g\ CO_2C\ g^{-1}\ h^{-1}$)	1.6 a	1.5 a	1.8 a
* Microbial biomass (mg $C_{mic}\ g^{-1}$)	0.61 b	0.68 ab	0.75 a
Time	t= 0	t= 3 mo	t= 6 mo
*** NO_3^- ($\mu g\ NO_3^-N\ g^{-1}$)	8.0 c	116.1 b	173.1 a
*** NH_4^+ ($\mu g\ NH_4^+N\ g^{-1}$)	26.4 c	166.4 b	265.6 a
*** RNI (unitless)	0.28 b	0.62 a	0.63 a
*** ANMR (mg N g^{-1})	0.14 b	0.27 a	0.33 a
Buried bag NO_3^- ($\mu g\ NO_3^-N\ g^{-1}\ d^{-1}$)	NA	NA	NA
Buried bag NH_4^+ ($\mu g\ NH_4^+N\ g^{-1}\ d^{-1}$)	NA	NA	NA
** Basal respiration ($\mu g\ CO_2C\ g^{-1}\ h^{-1}$)	1.4 b	2.0 a	1.4 b
*** Microbial biomass (mg $C_{mic}\ g^{-1}$)	0.91 a	0.64 b	0.49 c

Table 5. Results of three-way ANOVAs testing the effects of time of incubation (*i.e.* time) and two experimental factors (*i.e.* Horizon and Roots) on soil NO_3^- and NH_4^+ concentrations, relative nitrification index (*i.e.* RNI), anaerobic mineralization during aerobic incubations, buried bag NO_3^- and NH_4^+ concentrations, basal respiration rate, and microbial biomass; Data from site-VIII were excluded from analyses for date = mid-May. NA= Non available.

	Time		Horizon		Roots		Horizon*Root	
	F-value	Prob.>F	F-value	Prob.>F	F-value	Prob.>F	F-value	Prob.>F
Date = mid-May								
NO_3^-	32.8	< 0.001	68.7	< 0.001	0.1	0.779	0.2	0.679
NH_4^+	28.6	< 0.001	122.1	< 0.001	0.1	0.831	< 0.1	0.864
RNI	49.1	< 0.001	37.1	< 0.001	1.2	0.269	< 0.1	0.843
ANMR	13.2	< 0.001	159.8	< 0.001	1.0	0.315	0.8	0.374
Buried bag NO_3^-	NA	NA	9.9	0.002	< 0.1	0.908	< 0.1	0.945
Buried bag NH_4^+	NA	NA	2.5	0.121	0.9	0.359	0.7	0.405
Basal respiration	3.1	0.045	236.1	< 0.001	< 0.1	0.920	0.2	0.673
Microbial biomass	21.2	< 0.001	395.8	< 0.001	2.2	0.142	0.9	0.340
Date = late-June								
NO_3^-	46.2	< 0.001	86.8	< 0.001	0.8	0.374	0.5	0.501
NH_4^+	32.4	< 0.001	132.7	< 0.001	0.2	0.653	0.1	0.722
RNI	71.7	< 0.001	77.6	< 0.001	10.9	0.001	0.5	0.502
ANMR	7.6	< 0.001	177.7	< 0.001	1.3	0.261	2.6	0.107
Buried bag NO_3^-	NA	NA	20.7	< 0.001	1.0	0.317	1.0	0.324
Buried bag NH_4^+	NA	NA	3.9	0.051	0.3	0.561	0.4	0.512
Basal respiration	5.5	0.004	106.3	< 0.001	5.4	0.021	4.3	0.039
Microbial biomass	14.5	< 0.001	707.2	< 0.001	14.1	< 0.001	4.0	0.047

(suite table 5)

Date = late-August								
NO_3^-	42.5	< 0.001	122.6	< 0.001	18.0	< 0.001	14.3	< 0.001
NH_4^+	25.9	< 0.001	128.6	< 0.001	0.9	0.347	1.0	0.310
RNI	40.9	< 0.001	74.0	< 0.001	42.7	< 0.001	0.3	0.580
ANMR	9.7	< 0.001	178.7	< 0.001	< 0.1	0.876	0.1	0.736
Buried bag NO_3^-	NA	NA	22.6	< 0.001	9.5	0.003	8.7	0.004
Buried bag NH_4^+	NA	NA	15.2	< 0.001	0.4	0.516	0.3	0.618
Basal respiration	7.9	0.005	196.4	< 0.001	< 0.1	0.877	0.4	0.550
Microbial biomass	41.9	0.001	486.5	< 0.001	5.8	0.017	0.5	0.496

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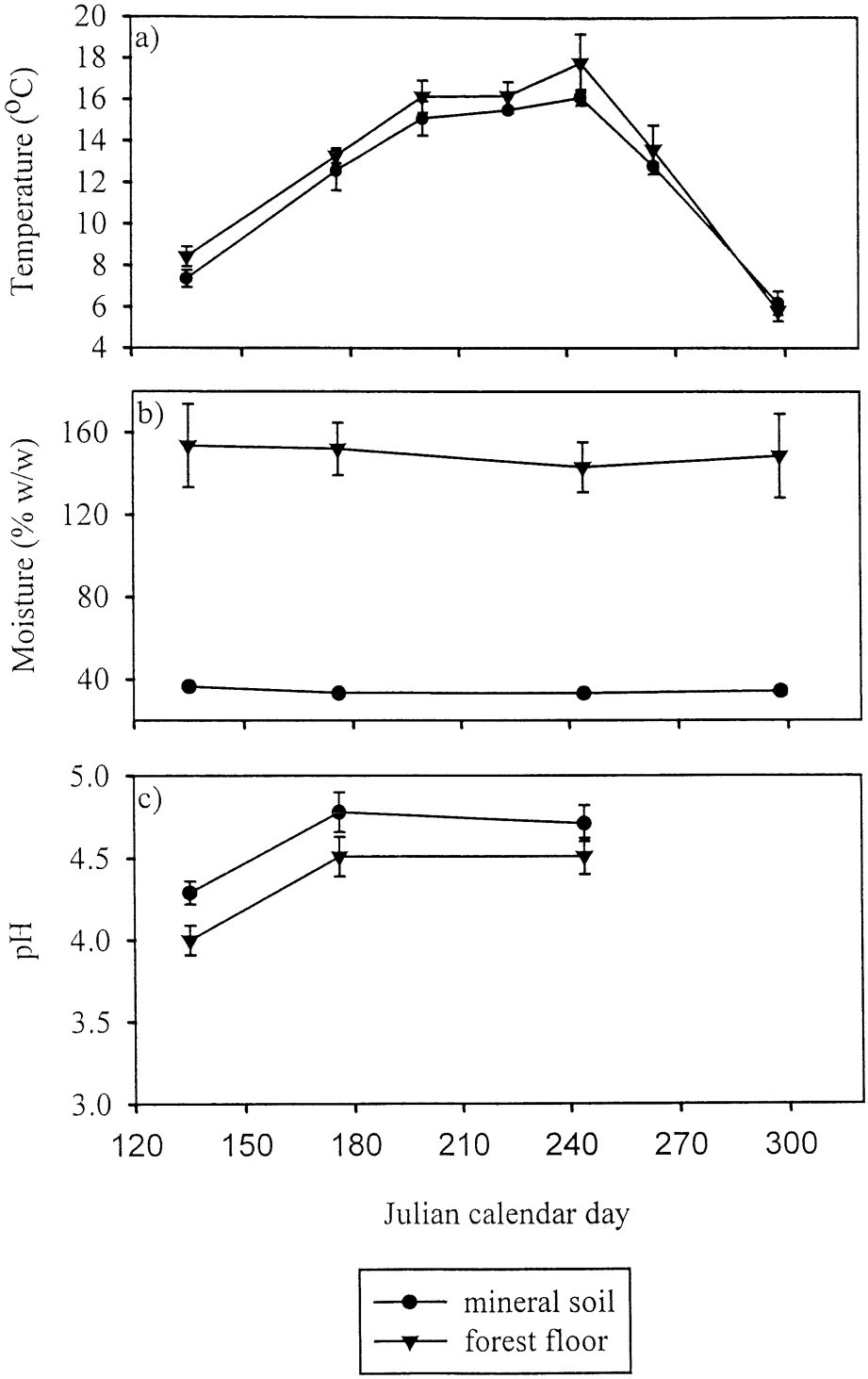

Figure 1. Soil temperature (a), soil moisture content (b), and soil pH (c) in forest floor and mineral soil horizons in nine forest communities (n = 27). Error bars refer to standard error.

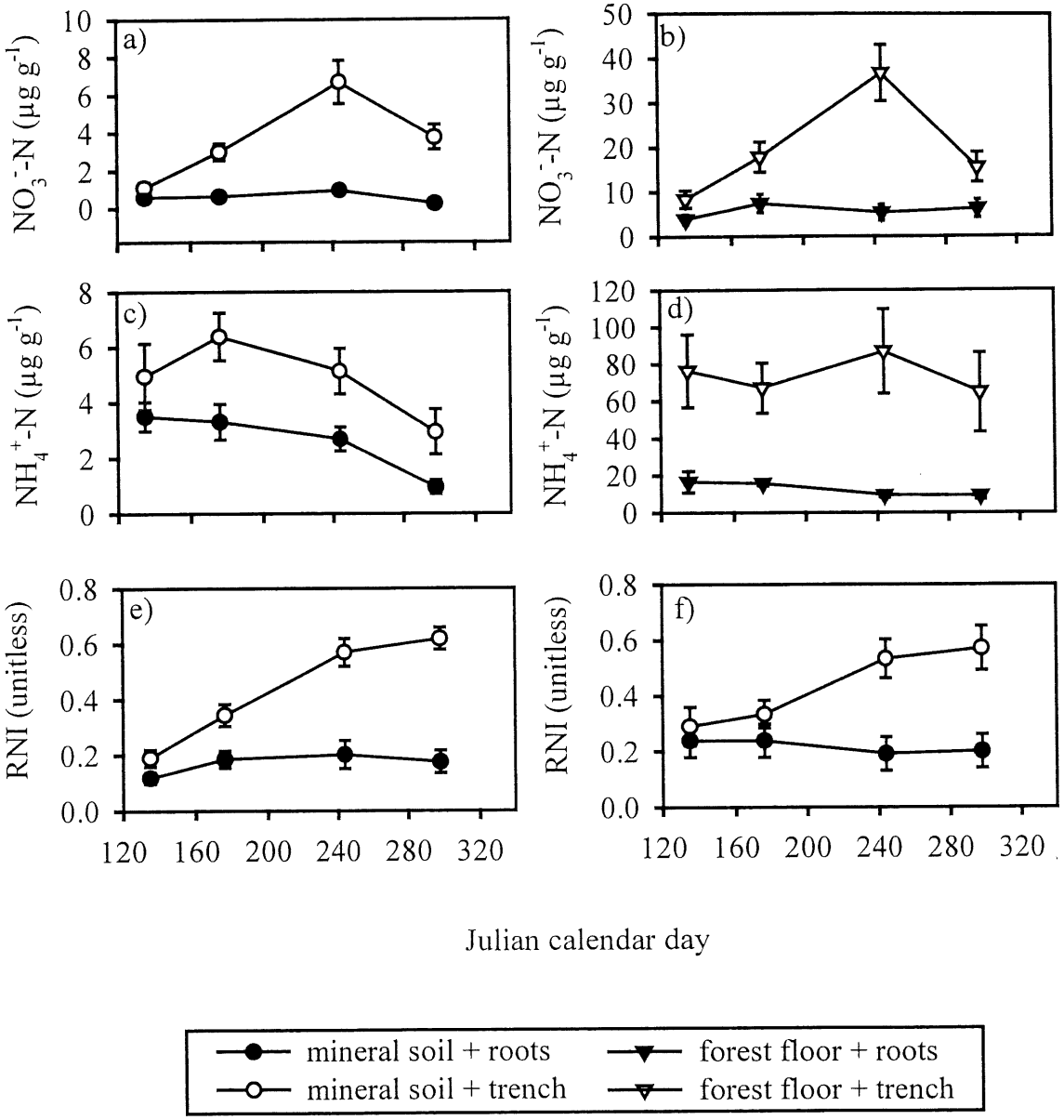

Figure 2. *In situ* concentrations of NO_3^-- N, NH_4^+-N, and relative nitrification index (RNI) values in trench plots and surrounding soils during summer 2001 (mid-May, late-June, late-August and late-October) in forest floor and mineral soil horizons (n = 27). Mean RNI is calculated from 27 ratios. Error bars refer to standard error.

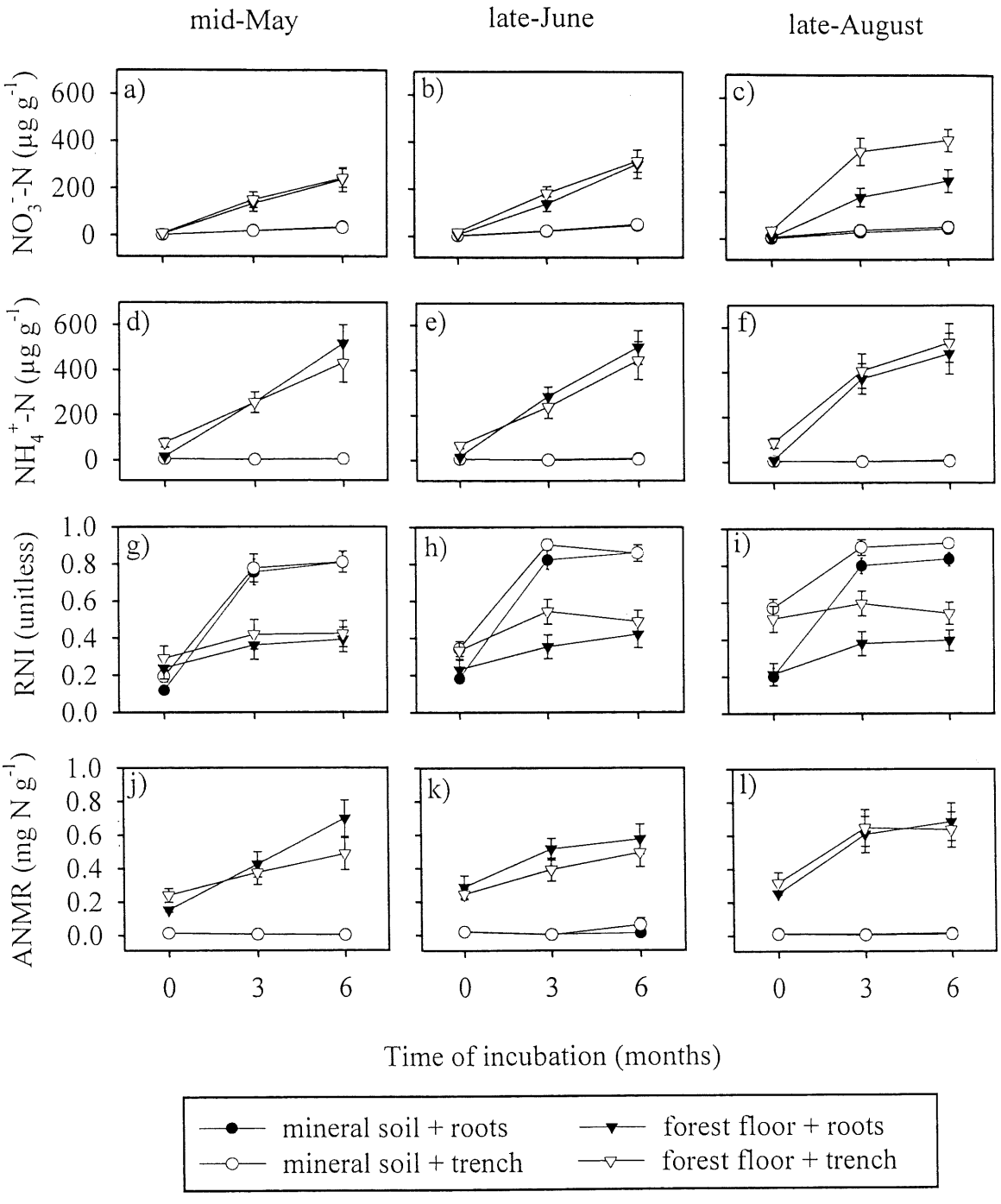

Figure 3. Nitrification, ammonification, relative nitrification index (RNI) and anaerobic N mineralization rate (ANMR) in trench plots and surrounding soils during six months laboratory incubations in forest floor and mineral soil horizons for three sampling dates (mid-May, late-June and late-August) (n = 27). Mean RNI is calculated from 27 ratios. Error bars refer to standard error.

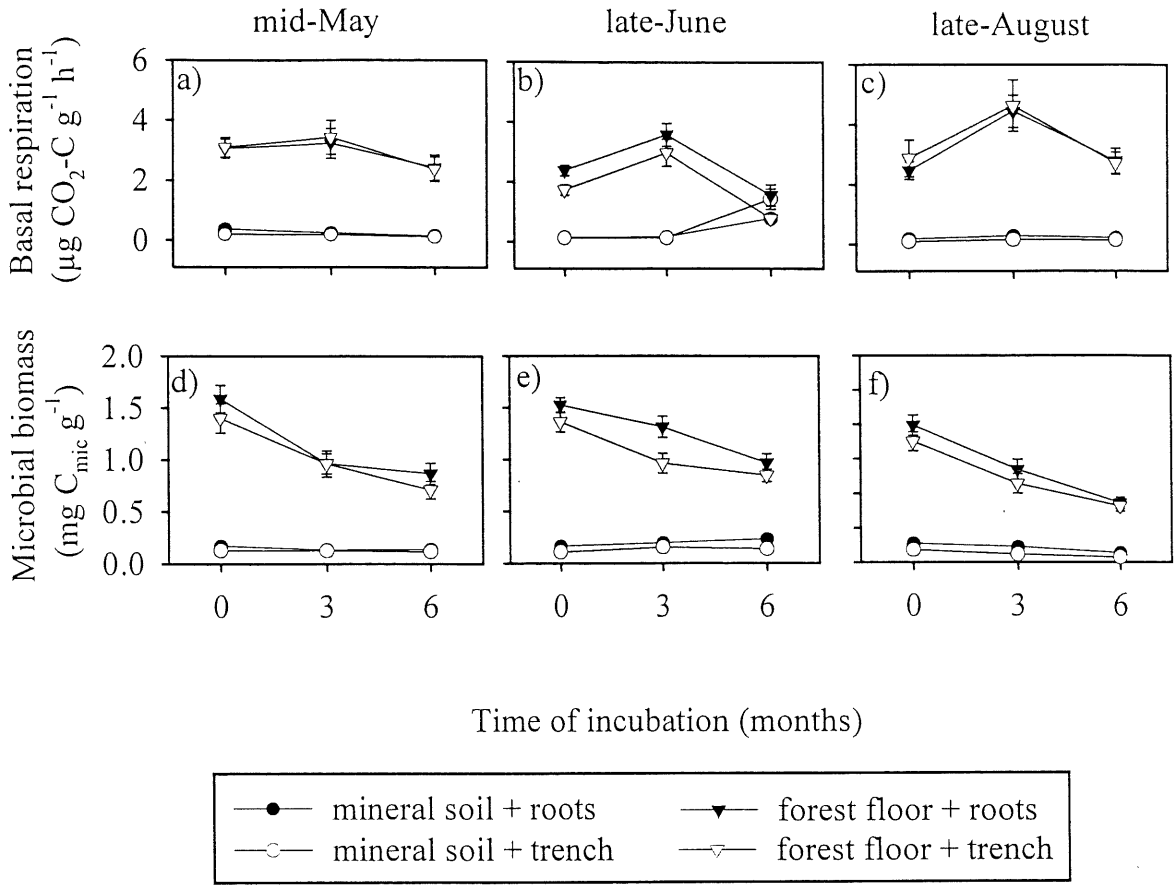

Figure 4. Basal respiration rate (BR) and microbial biomass (MB) in trench plots and surrounding soils during six months laboratory incubations in forest floor and mineral soil horizons for three sampling dates (mid-May, late-June and late-August) (n = 27). Error bars refer to standard error.

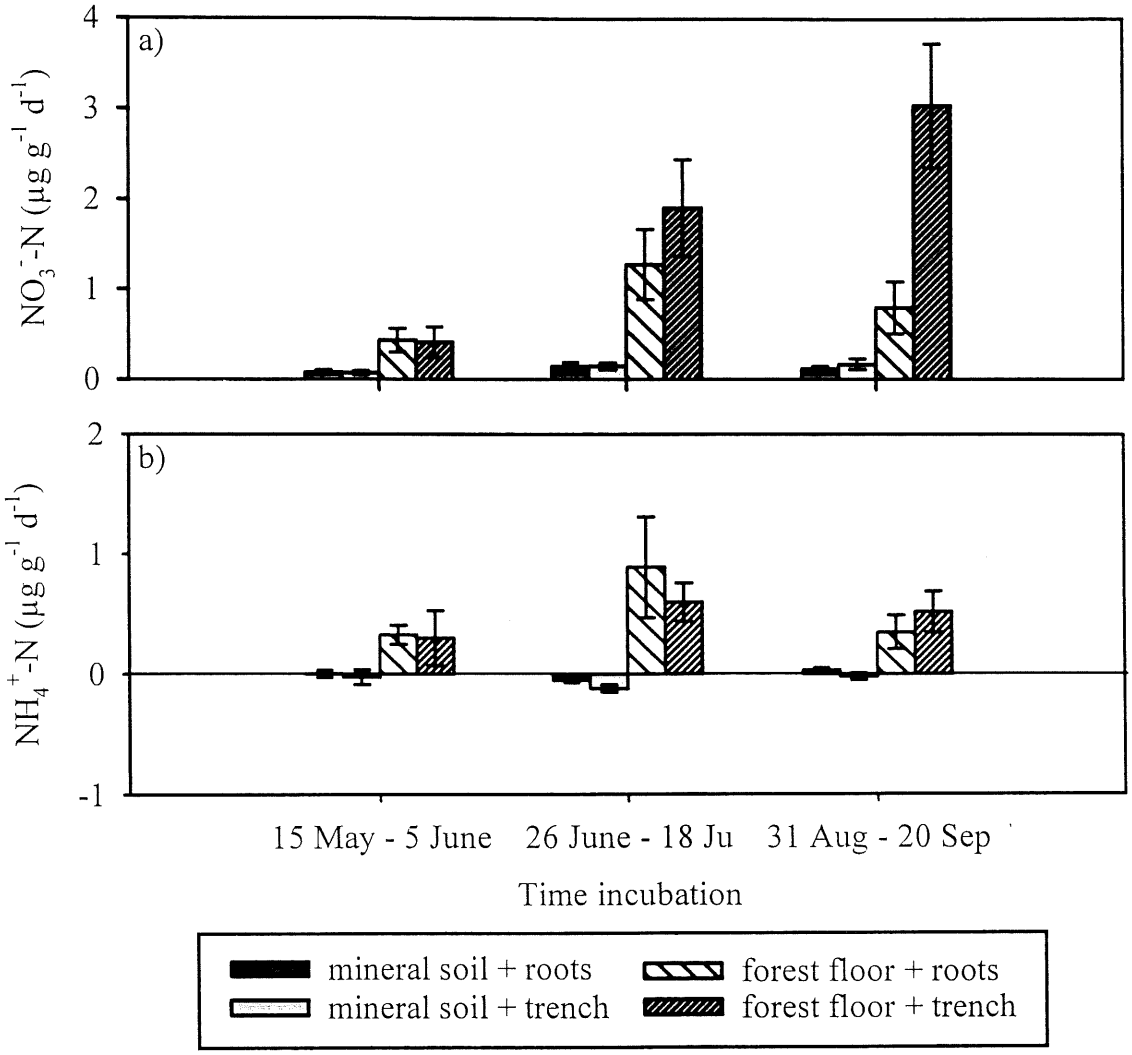

Figure 5. Nitrification and ammonification in trench plots and surrounding soils during three weeks *in situ* incubations with buried bags in forest floor and mineral soil horizons for three sampling dates (mid-May, late-June and late-August) (n = 27). Bars show mean values with standard error.

CHAPITRE 2

LA DÉPOSITION ATMOSPHÉRIQUE PAR LES NUAGES LE LONG D'UN COURT GRADIENT EN ALTITUDE POURRAIT EXPLIQUER LES CHANGEMENTS DANS LE CYCLE DES ÉLÉMENTS NUTRITIFS ET DES PROPRIÉTÉS MICROBIENNES

Publication 2. Cloud deposition may explain changes in forest floor nutrient cycling and microbial properties along a short elevation gradient. Water, Air, and Soil Pollution (À soumettre).

Dans le chapitre précédent, nous avons démontré que les racines augmentaient l'immobilisation du NO_3^- par les microorganismes hétérotrophes et que ces résultats apportent une nouvelle explication au phénomène du « assart flush ». Le type d'horizon et la densité des racines vivantes sont des variables qui influencent les pools de NO_3^-. Mais, comme expliqué dans l'introduction générale, les pools de NO_3^- sont également très dynamiques et la variabilité spatiale est très élevée dans les sols forestiers. Pour mieux comprendre les facteurs qui expliquent la variabilité spatiale des pools de NO_3^-, nous avons effectué une expérience au Mont Orford, le long d'un gradient en altitude. Très souvent, la déposition atmosphérique par les précipitations et par les nuages augmentent avec l'altitude. Par conséquent, nous voulions savoir si la déposition atmosphérique modifiait 1) la concentration des cations échangeables, (2) la concentration du N minéral, et (3) les propriétés microbiennes.

Cette étude démontre bien que l'élévation en altitude dans un peuplement uniforme peut être utilisée pour comprendre la variabilité spatiale des éléments nutritifs et des propriétés microbiennes.

Cloud deposition may explain changes in forest floor nutrient cycling and microbial properties along short elevation gradients

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Short title : Nutrient cycling along an elevation gradient

Key words : elevation gradient, cloud deposition, forest floor, nutrient cycling, N mineralization, microbial biomass

Abstract

In south-eastern Québec, cloud water deposition often increases with elevation, and it is widely accepted that this cloud water is more acidic than precipitation. A study was undertaken to determine if a 250 m elevation gradient (*i.e.* 420–665 m), along a uniform sugar-maple stand on the slope of Mount Orford, corresponded to a pH gradient in the forest floor and to predictable changes in soil nutrient availability and microbial properties. Forest floor temperature did not differ significantly across elevations, but moisture was significantly higher, whereas pH and exchangeable Ca and Mg were significantly lower, at the higher elevations. Average seasonal net nitrification rates, determined by long-term laboratory incubations, did not differ significantly across elevations, but average seasonal net ammonification rates were significantly higher at higher elevations. Basal respiration rates and microbial biomass did not differ significantly across elevations, but metabolic quotient was significantly higher at higher elevations indicating possible environmental stress on forest floor microbial communities due to cloud water deposition. Anaerobic N mineralization rates were significantly higher at higher elevations suggesting that N-limited microbial communities frequently exposed to cloud cover can be important short-term sinks for atmospheric N, thereby contributing to increase the active-N fraction of forest floors. We conclude that elevation can be used to understand the spatial variability of nutrient cycles and microbial properties within this sugar-maple dominated stand.

1. Introduction

Below 50°N latitude in Québec, wet deposition of both sulfate and nitrate can exceed 20 kg ha^{-1} yr^{-1} and the mean annual pH in precipitation is 4.35 (Min. Env. et Faune, 1996). Sigmon et al. (1989) have shown that cloud water is actually four times more acidic than bulk precipitation, and that inputs of major ions to Virginia hardwood forests from cloud water exceeded that from precipitation and contributed significantly to forest acidification. Similary, Friedland and Miller (1999) presented ten years of elemental cycling data from Whiteface Mountain, New York, which showed that cloud deposition contributed most of the

atmospheric deposition at their study area, located between 950 m and 1150 m elevation. Since cloud cover tends to increase with elevation, we can expect a clear relationship between forest acidification and elevation (Hendershot et al., 1992). For example, Lovett and Kinsman (1990) found that acid deposition to mountaintop sites in the northern Appalachian Mountains was 3–7 times greater than on nearby lowland sites (*ca.* 600–700 m gradients).

Many studies on cloud deposition have focused on quantifying element fluxes through ecosystems (*e.g.* Friedland and Miller, 1999), or on monitoring changes in physiological response of trees to cloud water (*e.g.* DeHayes et al., 1991). Few have focused on the possible effects of cloud deposition on soil nutrient availability and microbial dynamics. Foster et al. (1989) found that leaching of Ca and Mg from the soil increased as a result of acid deposition, so we could expect to find lower concentrations of the extractable form of these major base cations at higher elevations. Similarly, many studies predict (*e.g.* Ste-Marie and Paré, 1999) a decrease in net nitrification relative to net ammonification as a result of acidification, so we could expect to find lower NO_3^--to-NH_4^+ ratios at higher elevations. Soil microbial communities that are exposed to frequent acidic cloud cover may more stressed and exhibit a higher specific respiration rate (Wolters, 1991).

Garten Jr. (2000) found most indices of soil N availability in the southern Appalachian Mountains did not exhibit significant trends with elevation, but it is uncertain whether their chosen range of elevations (*ca.* 1500–2000 m) corresponded to a sharp gradient in cloud cover. In a related study, Garten Jr. et al. (2000) found significantly higher net nitrification rates, and significantly higher soil microbial activity, in valley floors than on ridges and slopes at the Walker Branch watershed, Tennessee. They did not, however, allude to any gradient in cloud cover between high and low elevation sites and mention, rather, differences in soil parent material and vegetation between sites. The confounding effects of vegetation (Knoepp and Swank, 1998), temperature (Lawrence et al., 2000) or other factors that vary with elevation and affect soil processes, present, therefore, a challenge for testing the hypothesis that elevation–cloud deposition gradients have significant effects on nutrient cycling and soil microbial properties. One way around these problems is to study an

elevation gradient, corresponding to a steep gradient in cloud cover, which is sufficiently short to maintain a uniform vegetation and temperature.

The objective of our study was to determine if elevation could be used to understand the spatial variability of cation pools, N transformations, and microbial properties in the forest floor of a uniform sugar maple dominated stand. We sampled forest floor material between 420–665 m along the north-east slope of Mount Orford, Québec. The base of Mount Orford lies at 313 m while the summit reaches 853 m above sea level. A preliminary survey using sequences of early-morning photographs, and data given by Schemenauer (1988), led us to conclude that a steep gradient in cloud cover occurred at approximately 500–550 m elevation. Forest floor material was sampled, rather than mineral soil horizons, because forest floors, and more specifically the F horizon, is the soil layer which contains the highest fine-root biomass derived from canopy trees (Pietikäinen et al., 1999), and is the zone with the highest concentration of microbial activity (Chang and Trofymow, 1996). Also, moisture deficits during the summer months corresponding to our study period would likely limit leaching of cloud water in mineral soil horizons. Hence, we assumed that changes in nutrient availability and microbial properties due to cloud deposition would occur primarily in the F-layer where they were more likely to affect tree growth.

2. Materials and methods

2.1 Study site

The research was conducted on the north-easterly face of Mont Orford, located in the Eastern Townships region of Québec, Canada (45°,26'-N, 71°,41'-W). Mean annual temperature in the area is 4.0 °C and mean annual precipitation is 1200 mm, a quarter of which falls as snow. The study was conducted between 420 and 665 m above sea level. The area is preserved and unlogged although some trees were damaged by ice storms in January 1998. Overstory vegetation over this elevation gradient is dominated by a 80-100 year-old stand of

sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Michx.), and American beech (*Fagus grandifolia* Ehrh.). Soils are well drained Humo-Ferric Podzols (Soil Classification Working Group, 1998) that have developed over bedrock and comprise a 2-5 cm forest floor (L-F layers) overlaying shallow (< 1 m) podzolised mineral layers. The slope varies between 15-30 %.

2.2. Humus sampling

Humus sampling was performed on three dates (mid-May, late-June, and late-August) during summer 2000. Sampling plots (25 m^2) were set up at four different altitudes (420, 515, 603, and 665 m) along three parallel transects placed 200 m apart. The plots were located with some discretion to maximise their similarity in terms of vegetation and micro-relief. At each sampling date, numerous samples of F-layer humus material were collected from each of the twelve plots and bulked (*ca.* 700 g fresh weight). The temperature of the humus was noted two minutes after inserting a digital thermometer down to the mineral soil surface. The twelve bulked samples were transported on ice to the Soil Ecology Laboratory of *l'Université de Sherbrooke* where they were sieved through a 5 mm mesh to remove roots and coarse debris, and stored at 4 °C until analysed (within one week). A subsample was dried at 105 °C for 24 h to determine field moisture content.

2.3. Chemical analyses

Humus pH was analysed (soil:water = 1:10) in each bulked sample at each sampling date. On the second sampling date (late-June), one extra bulked sample of F-layer humus material was collected from each plot and analysed for total N (Kjeldahl digestion), Bray-extractable P, and NH_4^+-acetate extractable cations (Ca^{2+}, Mg^{2+}, K^+, Na^+) (Suarez, 1996; Helmke and Sparks, 1996).

2.4. Laboratory incubations

At each sampling date, each of the twelve bulk humus samples were separated into three portions. The first portion (referred to as t=0) was immediately analysed for mineral-N (NH_4^+ and NO_3^-) concentrations, as described below. Second and third portions were incubated three and six months (t=3 and t=6) respectively before being analysed for mineral-N, as well as for basal respiration (BR), microbial biomass (MB), and anaerobic N mineralization rate (ANMR). The incubation procedure consisted of weighing 120 g (fresh weight) of humus into a 500 ml Mason jar, re-weighing the jar + humus, and covering the jar opening with a polyethylene film to delay moisture losses and permit gas exchanges. Incubation temperature was set constant at 22 °C. Jars were periodically weighed and initial moisture contents restored using a fine-mist spray. At the end of each incubation, two subsamples (*ca.* 10 g fresh wt) of humus from each jar were used to determine gravimetric moisture content by weight loss after 48 h in a draft oven (101 °C).

Mineral-N was extracted from 10-15 g (fresh weight) humus subsamples using 150 ml of 1.0 N KCl solution. Solutions were shaken for 1 h on a rotary shaker, filtered through Whatman No. 5 cellulose filter disks, and the filtrates analysed colorimetrically for NH_4^+-N (nitroprusside – salycilate) and NO_3^--N (Cd reduction) concentrations using a Technicon Auto-analyser (Pulse Instrumentation, Saskatoon). Net ammonification and nitrification rates were calculated by subtracting t=0 concentrations from t=3 and t=6 concentrations. Total mineralization (*i.e.* NO_3^--N + NH_4^+-N) was calculated as the sum of net ammonification and nitrification. The relative nitrification index (RNI) was calculated as the quotient of net nitrification and total mineralization.

BR was determined on 5 g (dry weight equivalent) of humus placed into a 65 ml gas sampling jar. The headspace was flushed with ambient air for 5 min, the jar was then sealed with an air-tight lid equipped with a rubber septum, and an aliquot of air in the headspace was sampled with a needle and syringe after 12 h. Air samples were analysed for CO_2 concentrations using a model CP-2002 P Micro-GC (Chrompack, Middelburg) equipped with a *TCD*, with He as carrier gas. Ambient CO_2 concentration and room temperature were noted

frequently during the trial. For each sample, ambient CO_2 concentration was subtracted from sampled CO_2 concentration and the difference was adjusted according to Ideal Gas Laws and centered at 22 °C using $Q_{10} = 2$.

MB was determined by substrate induced respiration (*SIR*) (Anderson and Domsch, 1978). The dry weight equivalent of 10 g of humus was weighed into a 500 ml plastic container and amended with ground and sieved (65 μm) glucose (1000 μg C g^{-1} soil). The amendments were applied with talc as 250 mg mixtures and dispersed throughout the humus using a kitchen handmixer with one beater. The amended humus subsamples were then transferred into 125 ml gas sampling jars and left uncovered for 100 min to reach optimum *SIR* rates. Each subsample was then flushed for 5 min with ambient air, sealed for 30 min, and headspace air was analysed for CO_2 concentration using a GC (as described above). *SIR* rates were converted to MB using equations described by Anderson and Domsch (1978). The qCO_2 of each sample was calculated as the quotient of BR and MB.

ANMR was determined by weighing 5 g (fresh wt) of humus into 45 ml snap-cap bottles, adding 40 ml deionized water, sealing and incubating (30 °C) for 14 days (Waring and Bremner, 1964). Bottles were then shaken and the contents transferred to 250 ml Erlenmeyer flasks. Each bottle was rinsed with 40 ml of 2 N KCl solution to bring the final concentration of extractant in each flask to 1 N KCl. Flasks were shaken for 1 h, filtered and analysed for NH_4^+-N as previously described.

2.5. Statistical analyses

A series of one-way ANOVA tests were used to describe the main effects of sampling date on humus temperature and moisture, of sampling date and incubation time on variables related to mineral-N cycling and indices of available-C, and of elevation on all measured variables within each sampling date. Significantly different means were separated using Duncan's multiple range test ($P < 0.05$). All statistical tests were performed with the SAS statistical package (SAS, 1998).

3. Results

3.1 Humus temperature, moisture and chemical properties

Humus temperature was significantly lower in mid-May than in late-June, and significantly lower in late-June than in late-August (Table 1). Humus temperature was not, however, significantly affected by elevation (Fig. 1a). Conversely, gravimetric humus moisture content did not differ significantly between sampling dates (Table 1), but did differ significantly between elevations (Fig. 1.b). More specifically, average seasonal moisture content of humus from the 665 m elevation was significantly higher than at the three lower elevations. Average humus pH did not differ significantly between sampling dates (Table 1), but did differ significantly between elevations (Fig. 1.c). More specifically, average humus pH at the 420 m (4.92) elevation was significantly higher than humus pH at the three higher elevations (4.17, 4.07, and 3.87). There were no significant differences in total-N or extractable-P due to elevation (Fig. 2.a, 2.b). Concentrations of exchangeable-Ca and exchangeable-Mg were significantly higher at the 420 m elevation than at the 603 m and 665 m elevations (Fig. 2.c, 2.d). Exchangeable-K^+ and exchangeable-Na^+ concentrations did not, however, differ significantly across elevations (Fig. 2.e, 2.f). The sum of positive charges held by the four major base cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) was significantly higher at 420 m elevation than at the 603 m and 665 m elevations (Fig. 2.g).

3.2. Mineral-N cycling

There were no significant differences in the average net nitrification and ammonification rates (*i.e.* values pooled across elevations and incubation times) between dates for each incubation time (Table 1). Total mineral-N (*i.e.* NH_4^+-N + NO_3^--N) produced during incubation was, however, significantly higher in late-August than in mid-May. The average RNI was significantly higher in late-August than in late-June.

Elevation did not significantly affect net nitrification at t=3 and t=6 (Fig. 3.a) when values were pooled across sampling dates. Net ammonification at t=3 and t=6 was, however, significantly lower at 420 m than at 603 m and 665 m (Fig. 3.b). Total mineral-N produced at t=3 and t=6 did not differ significantly between elevations (Fig. 3.c), but total RNI was significantly higher at 420 m than at 603 m and 665 m (Fig. 3.d).

3.3. Microbial properties

Average BR (*i.e.* pooled across elevations and incubation time) was significantly higher in late-August than in mid-May and late-June (Table 1). Likewise, MB and ANMR were significantly higher in late-August than in mid-May. Average qCO_2 was significantly lower in late-June than in mid-May and late-August.

Elevation had no significant effect on average BR and average MB (Fig. 4.a, 4.b), although these two variables were significantly higher at t=3 than at t=6. Average qCO_2, was significantly lower at 420 m than at the three higher elevations (Fig. 4.c). Average ANMR, at t=3, was significantly lower at 420 m than at the three higher elevations, whereas average ANMR, at t=6, was significantly higher at 665 m than at the three lower elevations (Fig. 3.d).

4. Discussion

4.1 Cloud deposition hypothesis

Our study showed that a small elevation gradient of less than 250 m is correlated with significant changes in forest floor nutrient cycling and microbial properties. We believe that these changes were the direct result of a gradient in cloud water deposition resulting in greater acid input to the forest floor at the higher elevations. Although we did not generate data on cloud deposition *per se*, there are numerous facts corroborating our hypothesis. Firstly, Schemenauer et al. (1988) conducted a study at Roundtop Mountain, located within

40 km of Mount Orford, and found that forests at 520 m and at 850 m elevation were under cloud cover 25 % and 37 % of the time respectively. According to the authors, this translated to approximately 50 % more precipitation at the higher altitude with an additional 77 cm yr^{-1} of fog water deposition. Secondly, the lower forest floor pH and the lower concentrations of Ca^{+2} and Mg^{+2} that we observed at the higher elevations are consistent with results of past studies that have specifically monitored soil nutrient export due to acid deposition (Foster et al., 1989). Thirdly, we observed greater forest floor moisture content at the higher elevation. Fourthly, temperature and vegetation were uniform over the short elevation gradient that we studied, which minimized the possibility of confounding the effects of these two factors with the effect of cloud deposition, on nutrient cycling and microbial properties.

4.2 Cations

Based on results of prior studies on acid deposition (*e.g.* Foster et al., 1989), we expected concentrations of exchangeable Ca and Mg to vary as a function of forest floor pH. Our results showed a drop of nearly one pH unit and approximately 80% lower exchangeable Ca and Mg between the lowest and highest elevations. In order to understand the importance of these differences, we compared our results with those of Yanai et al. (1999) who tested the hypothesis that loss of base cations from forest floors at the Hubbard Brook Experimental Forest, New Hampshire, was accelerated by acid rain. They found no evidence to show a temporal trend in the status of exchangeable Ca and Mg over the past twenty years. We conclude, therefore, that the difference in acidification due to short elevation gradients are likely greater than acid inputs from precipitation over the past twenty years.

Although Ca and Mg are not as important for tree growth rates as N and P, low base cation status in the forest floor may cause nutritional imbalances and weaken the health of the stand. For example, Arthur et al. (1999) observed decreasing Ca and Mg concentrations in forest floors with increasing elevation, which coincided with decreasing concentration of these cations in wood. It is well known that Ca influences cell membrane permeability as well as the cell's ability to tolerate drought and cold (DeHayes et al., 1991).

The fact that average pH values were similar between 515 m and 665 m elevation, whereas average exchangeable Ca and Mg concentrations continued to fall, suggests that acidification may not be entirely responsible for the base status of the forest floor. We hypothesize, however, that the low permeability of the subsoil results in subsurface lateral flow of leached nutrients down the slope where they may be intercepted by deep roots and recycled in lower stands. Thus, acid deposition increases leaching Ca and Mg whereas topography exacerbates the elevation gradient in these cations.

Ca and Mg are considered immobile nutrients in litter, where they form stable covalent bonds within plant cell walls, whereas K^+ and Na^+ are considered mobile nutrients that remain unbound within plant cells. As a result, Ca^{2+} and Mg^{2+} dissolution is mainly determined by decomposition rates (Titus and Malcolm, 1999) whereas the cycling of K^+ and Na^+ is very rapid. Once in soil solution, the divalent cations are held more strongly to exchange sites than are monovalent cations. As a result of these differences, there was no relationship between exchangeable-K^+ or exchangeable-Na^+ and pH, because these cations cycle rapidly and do not occupy an important proportion of exchange sites in soil.

4.3 N-dynamics

Significant differences in total mineralisable N value between sampling dates emphasize the fact that mineral-N cycling can vary significantly over the course of one growing season (Bradley et al., 2002). For this reason, our study included three sampling dates allowing us to estimate seasonal averages of NO_3^- and NH_4^+ cycling rates. Mineral-N cycling can also be very dynamic on a diurnal scale with *in situ* mineral-N pools changing rapidly with the occurrence of episodic events, such as rainfall, which control processes such as plant uptake, microbial flushes, N leaching and volatilisation. For this reason, we opted for long-term laboratory incubations to compare net ammonification and nitrification potentials at different elevations based solely on the chemical and microbial properties of the humus.

Many studies have reported a decrease in net nitrification due to acid input (*e.g.* Ste-Marie and Paré, 1999). This may be due to excess protons in soil solution favouring the NH_4^+ form

of N thereby reducing the activity of chemoautotrophic nitrifiers who prefer to oxydise the NH_3 form of N (Suzuki et al, 1974). Acidity may also interfere directly with some soil nitrifier populations (Paavolainen and Smolander, 1998). We therefore expected net nitrification to decrease at higher elevations, but this did not occur. The presence of acid-tolerant nitrifying fungi (*e.g.* Stroo et al., 1986) in the forest floors at our study site may explain the similarity in net nitrification rates across elevations.

Soil acidity is expected to reduce litter decomposition rates (Côté and Fyles, 1994), and decomposition rates are often related to net ammonification rates (Prescott, 1996). It would, therefore, have seemed reasonable to expect lower ammonification rates at higher elevations. Since the contrary occurred, it is possible that the greater net ammonification rates observed at higher elevations were due to accrued N inputs from cloud deposition. For example, Joslin and Wolfe (1992) found that deposition of NO_3^- and NH_4^+ was 15 % to 55 % greater in a high cloud site than a low cloud site atop the summit of Whitetop Mountain, Virginia. Similarly, Sigmon et al. (1989) found that cloud water was approximately four times more concentrated in nutrients, including NO_3^- and NH_4^+, than bulk precipitation. Microbial biomass in forest soils can be N-limited and represent a strong sink for exogenous N (Bradley et al. 2000). Thus extra N inputs from cloud deposition could have significantly enlarged the microbial-N pool in the forest floor and, by implication, the active-N fraction prone to mineralise. We conclude that lower RNI values at higher elevations occurred because of greater ammonification rates, not because of lower nitrification rates.

4.4 Microbial properties

Forest floor microbial communities are mostly heterotrophic and are assumed, therefore, to be primarily C-limited (Bradley and Fyles, 1995). BR, which is a measure of microbial C utilisation, depends on substrate quality at the time of sampling. On the other hand, MB is not related to actual C-supply, but is rather an indicator of past C supply (Bradley and Fyles, 1995). Neither of these variables were significantly different across the elevation gradient, indicating fairly uniform substrate quality and C-supply within the study area. Primary C-

limitation could be, however, a characteristic of microbial communities in mineral soil horizons more so than a characteristic of those in forest floors (Bradley and Fyles, 1996). There is a far greater disparity between the microbial C-to-N ratio (and other microbial C-to-nutrient ratios) and the C-to-N ratio of soil organic matter in the forest floor than in mineral horizons. Bradley et al. (2000) presented evidence of high N-limitation in forest floor microbial communities. Their study showed that fertiliser-N addition to forest floor humus did not significantly increase microbial biomass, but did significantly increase the gross transformation rates of N as well as net ammonification and ANMR. This is entirely consistent with our results, based on the assumption that cloud deposition at higher elevations increased the active-N fraction of forest floors.

The qCO_2, also referred to as the specific respiration rate, is a measurement of C-utilisation per unit microbial biomass. The suggestion that qCO_2 be used as an indicator of disturbance and ecosystem development, or as an index of available-C supply, has created some controversy (*e.g.* Wardle et Ghani, 1995; Bradley and Fyles, 1995). The qCO_2 remains, however, conceptually sound as an indicator of environmental stress insofar as comparisons be made between similar soils of similar history. For example, both Wolters (1991) and Anderson and Domsch (1993) have shown higher qCO_2 occurring as a result of acidification, the first using simulated acid rain on a single soil type, the second sampling a series of related European beech (*Fagus sylvatica*) stands. Increasing soil acidity can be a stress to microbial communities, and the normal physiological response to stress is an increase in the proportion of acquired-C used for maintenance purposes rather than for growth (Paul and Clark, 1996), that is, an increase in qCO_2.

ANMR is commonly used in comparative forest soil studies to indicate N availability to forest trees (Powers, 1980). Myrold (1987) showed a strong relationship between ANMR and microbial-N, thus confirming the importance of microbial-N pools within the active-N fraction of forest floors. For this reason, we presented ANMR data along with BR, MB and qCO_2 data, because ANMR conceptually represents a microbial property more so than a measurement of N cycling. We can thus presume that the greater values of ANMR at t=6, compared to t=3, are partly due to the lower MB values at t=6. The fact that MB did not

differ significantly between elevations, whereas ANMR was significantly greater at higher elevations, is strong evidence of N-limitation in forest floor microbial communities resulting in increased microbial assimilation of N arising from cloud deposition. Even if the experimental errors associated to the means in Figure 4.b (t=3) had been smaller such that the upward trend in MB along the elevation gradient had been significant, the relative increase in MB would only have been 33 % compared to the relative increase in ANMR which was 300%. Thus, the microbial biomass appears to be an important short-term sink for N deposition from cloud water.

5. Conclusion

Our study has shown that elevation can be used to understand the spatial variability of nutrient cycles and microbial properties within a sugar maple dominated stand. Given the uniformity of the experimental site in terms of vegetation and temperature, we conclude that greater cloud deposition occurring at higher elevations is a plausible explanation for these gradients. The decrease in exchangeable Ca and Mg can lead to nutrient imbalances and decrease stand health. N-limited microbial communities frequently exposed to fog and cloud cover can be important short-term sinks for atmospheric N, thereby contributing to increase the active-N fraction of forest floors. Cloud water acidity could create an environmental stress on forest floor microbial communities, thereby increasing their specific respiration rates.

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Table 1. Main effects of sampling date on physico-chemical properties, net mineralisable-N and microbial-related properties (pooled across t=3 and t=6); results from one-way ANOVAs are summarised as $*P<0.05$, $**P<0.01$ and $***P<0.001$; values represent pooled means; different lower-case letters within each line designate significant differences ($P<0.05$, Duncan's Multiple Range Test).

	mid-May	late-June	late-August
Physico-chemical properties			
***Temperature (°C)	9.4 c	14.1 b	15.7 a
Moisture (%)	216.7 a	247.1 a	253.8 a
pH	4.2 a	4.2 a	4.5 a
Mineralisable-N			
NO_3^- (μg NO_3^--N g^{-1})	298.1 a	338.5 a	435.2 a
NH_4^+ (μg NH_4^+-N g^{-1})	336.3 a	427.7 a	477.0 a
* Total mineral-N (μg N g^{-1})	634.3 b	766.3 ab	912.2 a
* RNI (unitless)	0.47 ab	0.35 b	0.52 a
Microbial properties			
** BR (μg CO_2-C g^{-1} h^{-1})	2.7 b	3.2 b	4.5 a
** MB (mg C_{mic} g^{-1})	1.2 b	1.4 ab	1.8 a
qCO_2 (μg CO_2-C mg^{-1} C_{mic} h^{-1})	2.5 a	2.2 b	2.6 a
*ANMR (mg N g^{-1})	0.54 b	0.62 ab	0.80 a

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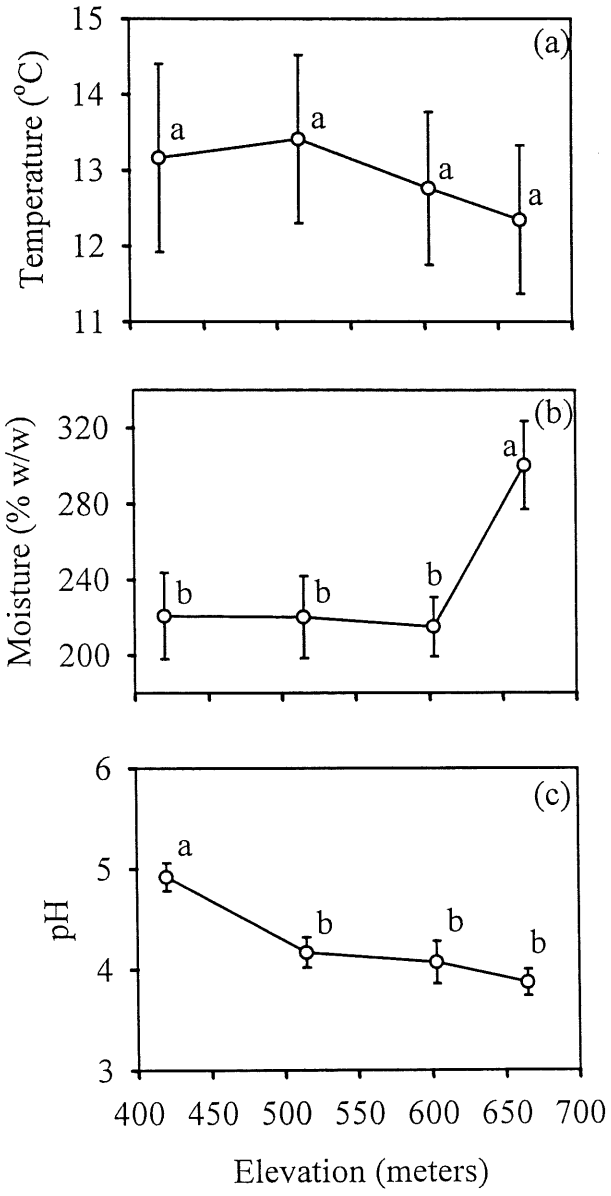

Figure 1. Soil temperature (a), soil moisture content (b), and soil pH (c) in forest floor at the Mont Orford (n = 9). Error bars refer to standard error.

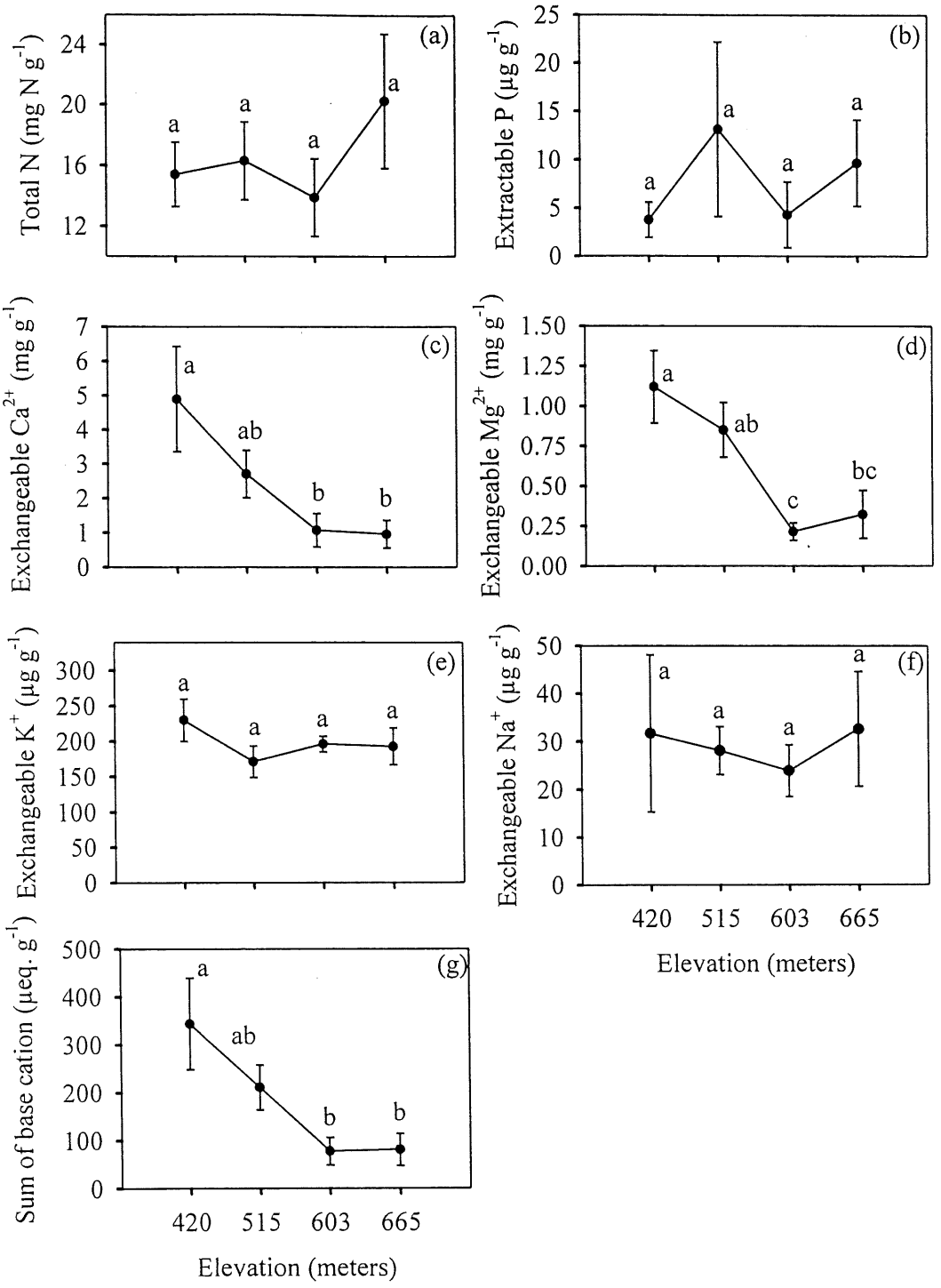

Figure 2. Concentrations of different exchangeable nutrients during summer 2000 (late-June) in forest floor (n = 3). Error bars refer to standard error.

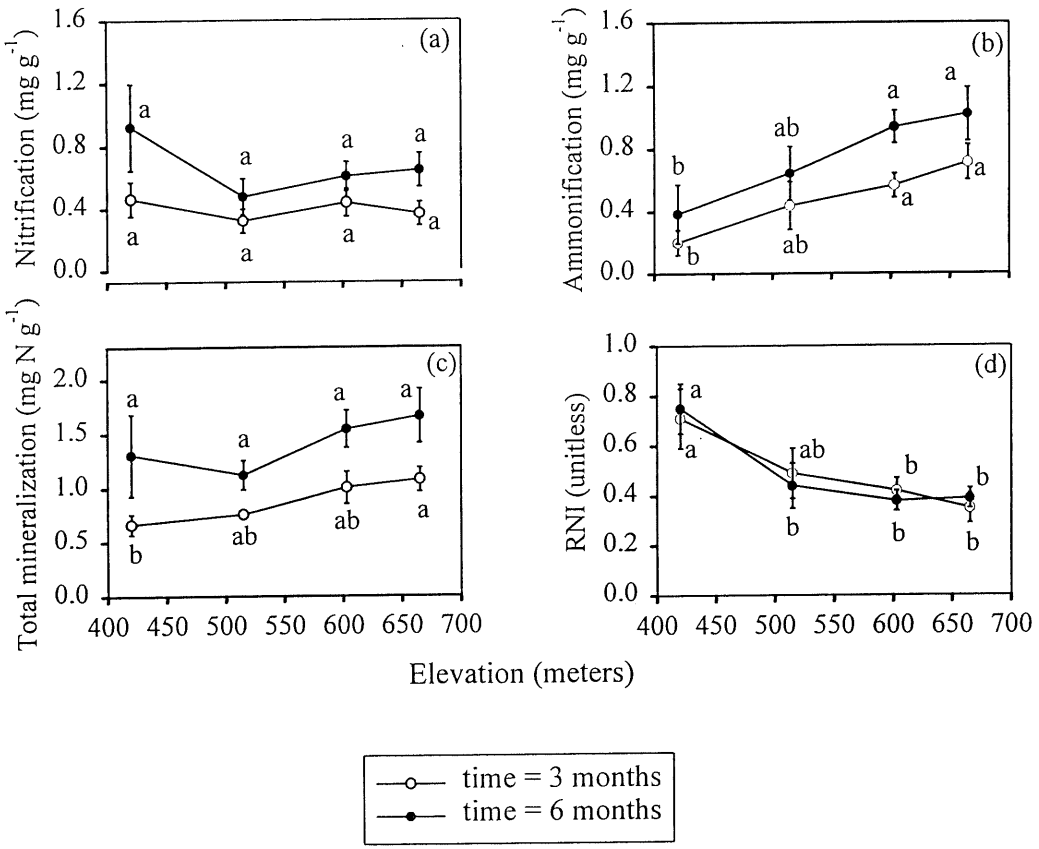

Figure 3. Nitrification (a), ammonification (b), total mineral N (c) and relative nitrification index (RNI) (d) in forest floor during three and six months laboratory for three sampling dates (mid-May, late-June and late-August) (n = 9). Mean RNI is calculated from nine ratios. Error bars refer to standard error.

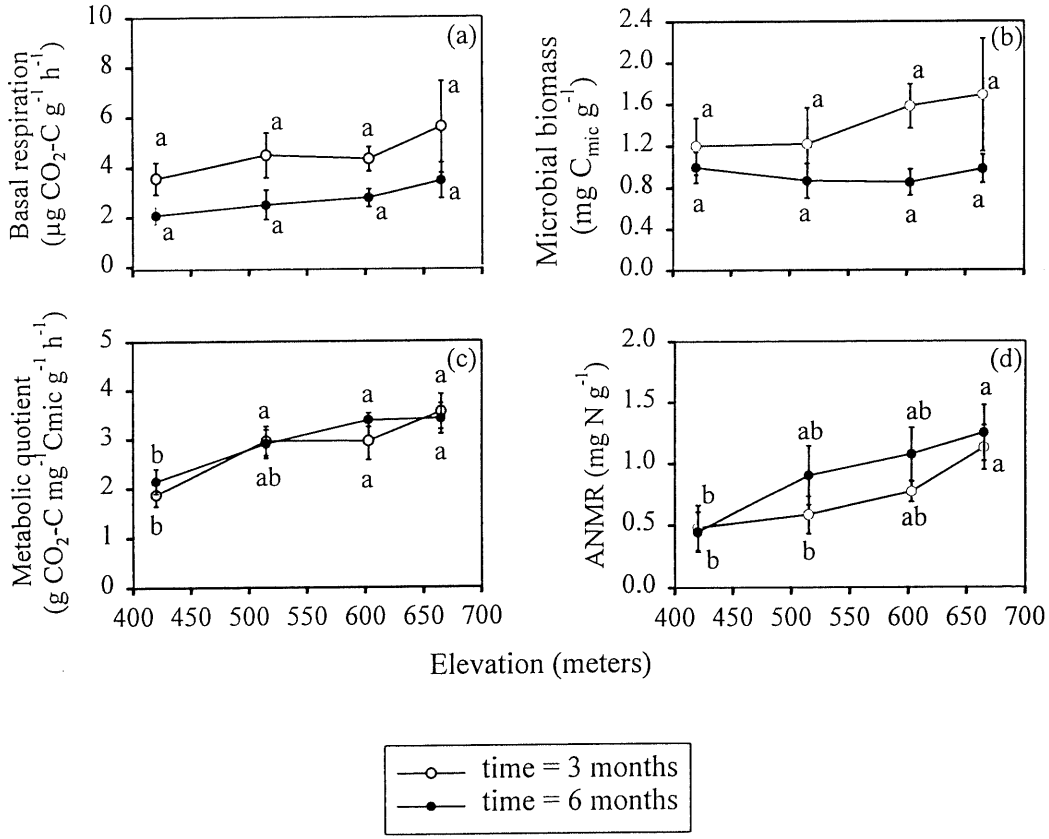

Figure 4. Basal respiration rate (BR) (a), microbial biomass (MB) (b), metabolic quotient (c) and anaerobic mineralization rate (ANMR) (d) in forest floor during three and six months laboratory incubations for three sampling dates (mid-May, late-June and late-August) (n = 9). Error bars refer to standard error.

CONCLUSION

Nos résultats démontrent que l'horizon et la densité des racines vivantes sont deux variables mesurables sur le terrain et qui contrôlent les pools de NO_3^-. En effet, les racines fournissent un apport important de C réduit aux microorganismes hétérotrophes ce qui stimule l'immobilisation du NO_3^-. En plus, l'immobilisation du NO_3^- est plus importante dans le sol organique que minéral car la densité des racines fines est plus élevée dans l'horizon organique. Éventuellement, un suivi à moyen et à long terme de l'effet de l'élimination des racines sur les concentrations de NO_3^- dans différents peuplements est également recommandable. De meilleures connaissances pourraient nous permettre de développer ou de choisir les pratiques d'exploitation forestière les plus appropriées afin de réduire les pertes de NO_3^- suite aux coupes forestières. Par exemple, doit-on pratiquer un reboisement rapide après coupe afin d'augmenter (1) l'apport de C réduit aux microorganismes hétérotrophes par les racines pour augmenter l'immobilisation du NO_3^-, et (2) l'assimilation d'azote minéral (NO_3^- et NH_4^+) par les racines ? Dans un deuxième temps, l'effet de l'élimination des racines sur les taux bruts de nitrification et d'ammonification doit être également mesuré. Ce type d'expérience pourrait nous donner un portrait sur les différences de production et de consommation du NO_3^- en présence et en absence de racines. Enfin, jumelée aux mesures des taux bruts, une expérience sur la distribution des nitrifiants autotrophes et hétérotrophes suite à l'élimination des racines serait aussi nécessaire. Cette étude nous permettrait de savoir si une baisse de la rhizodéposition occasionnée par l'élimination des racines provoquerait des changements dans la distribution des nitrifiants autotrophes et hétérotrophes.

La deuxième partie de cette recherche traitait du problème associé à la variabilité spatiale des pools de NO_3^-. Pour mieux comprendre ces variations, nous avons fait une expérience au Mont Orford le long d'un gradient d'élévation. Nos résultats montrent que le pH, le calcium, le magnésium et le INR diminuaient avec l'altitude alors que le quotient métabolique et la minéralisation anaérobique augmentaient. Étant donné que la température et le peuplement sont uniformes le long de ce gradient, nous concluons que la déposition atmosphérique par les nuages, qui est plus élevée en haute altitude, est responsable de ces gradients. Une baisse

dans les concentrations du calcium et du magnésium dans le sol peut éventuellement mener à des carences nutritionnelles et par conséquent réduire la fertilité du peuplement. De plus, les populations microbiennes limitées en azote et qui sont exposées à la déposition atmosphérique, peuvent servir de puits pour l'azote atmosphérique (NO_3^- et NH_4^+). Enfin, la déposition d'acidité par les nuages peut créer un milieu plus stressant pour les communautés microbiennes et ainsi augmenter la respiration spécifique (quotient métabolique). Ces résultats suggèrent que l'élévation peut être utilisée pour expliquer la variation spatiale dans le cycle des éléments nutritifs et dans les propriétés microbiennes. Finalement, mesurer les concentrations des éléments nutritifs de la litière au sol, et dans la biomasse végétale vivante (*i.e.* feuillage, branches et bois), en plus des éléments nutritifs du sol, pourrait nous aider à mieux comprendre les interactions entre les plantes, le cycle des éléments nutritifs et les propriétés microbiennes des sols.

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