Université du Québec en Abitibi-Témiscamingue

UTILISATION D'AMENDEMENTS DE SOL POUR RESTAURER LA PRODUCTIVITÉ DE SITES MAL RÉGÉNÉRÉS APRÈS COUPE EN FORÊT BORÉALE MIXTE

Thèse
présentée
comme exigence partielle
du doctorat sur mesure en restauration forestière

Par
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Août 2025

REMERCIEMENTS

Il me tardait d'atteindre l'étape de la rédaction de cette partie de la thèse, qui marque la conclusion de ce long et exigeant périple. Il m'est encore difficile de prendre pleinement conscience que mon parcours doctoral touche bientôt à sa fin. Ce fut un chapitre majeur de ma vie, jalonné de moments heureux mais également de périodes plus difficiles. Au cours de ces quatre dernières années, j'ai eu l'opportunité de rencontrer de nombreuses personnes qui m'ont soutenue. À toutes celles et à ceux, je tiens à exprimer ma plus sincère gratitude, car, malgré mes efforts, mes mots ne sauraient rendre pleinement justice à leur contribution essentielle à la réussite de mon parcours.

Je tiens à remercier Benoît Lafleur qui m'a ouvert les portes de son laboratoire pour débuter ma thèse et qui m'a confié un sujet qui me passionne. Je le remercie de m'avoir fait confiance et donné l'opportunité de traverser l'Atlantique pour découvrir le Canada. À la suite du départ de Benoit Lafleur en début de ce parcours, Annie DesRochers a pris en charge la direction de ma thèse. Mes remerciements les plus sincères et chaleureux vont à Annie, qui, malgré un début de thèse tumultueux, m'a accueillie au sein de son équipe, où, dès les premiers instants, je me suis sentie pleinement à ma place. Annie incarne pour moi l'image de la scientifique, de la professeure ambitieuse, bienveillante et humaine. Merci, Annie, de m'avoir toujours encouragée à aller de l'avant et pour le soutien constant que tu m'as offert. Tu n'as jamais hésité à souligner mes efforts, et cela a été d'une importance capitale pour moi.

Je tiens également à exprimer ma profonde gratitude à Vincent Poirier, mon co-directeur de thèse, qui a pris le relais après le départ de mon premier co-directeur. Vincent m'a chaleureusement accueillie dans son laboratoire pendant neuf mois, période durant laquelle j'ai pu réaliser mes analyses. Sa supervision a été exceptionnelle, et il a toujours fait preuve d'une grande générosité en matière de temps, de soutien et de conseils.

Merci à Vincent, ainsi qu'à Annie, pour nos rencontres régulières, toujours riches en échanges stimulants et en conseils pertinents, qui ont grandement contribué à faire progresser mon travail. Annie et Vincent m'ont redonné confiance dans ma carrière académique et ont ravivé mon désir de poursuivre dans cette voie. Travailler à leurs côtés, dans un cadre bienveillant et stimulant, a été une expérience des plus enrichissantes. Je leur suis profondément reconnaissante pour leur encadrement exceptionnel.

Mes remerciements s'adressent également aux partenaires financiers de ce projet. Je tiens d'abord à exprimer ma gratitude au Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), par le biais de la subvention attribuée à Annie DesRochers (#IRCPJ547921-18), ainsi qu'aux partenaires industriels, Chantiers Chibougamau, West Fraser, Agnico Eagle, et à la Chaire en aménagement forestier durable UQAT-UQAM, dont le soutien financier a rendu cette recherche possible. Je remercie également la Fondation J.A. DeSève ainsi que la Fondation de l'Université du Québec en Abitibi-Témiscamingue (UQAT) pour l'octroi de la bourse de soutien au dépôt initial de la thèse.

J'adresse ensuite mes remerciements à l'équipe de la Forêt d'enseignement et de recherche du lac Duparquet (FERLD), en particulier Claude-Michel Bouchard, Marie Robin et Yvan Poirier, pour leur accompagnement précieux lors de ma saison de terrain à la station de recherche. Je souhaite également remercier chaleureusement l'équipe de l'Institut de recherche en agriculture et agroalimentaire (IRAA) et du Centre de l'UQAT du Témiscamingue à Notre-Dame-du-Nord pour leur accueil et leur soutien tout au long de mon séjour au laboratoire. Enfin, je tiens à exprimer ma reconnaissance à l'équipe du Centre de foresterie des Laurentides, Service canadien des forêts, pour la réalisation des analyses complémentaires en laboratoire.

Je souhaite également exprimer ma gratitude aux membres de mon comité d'encadrement et d'évaluation, David Paré et Alison Munson, pour leur accompagnement tout au long des différentes étapes de cette thèse. Je les remercie sincèrement pour la qualité de leurs conseils et de leurs recommandations, qui ont grandement contribué à l'amélioration de nos articles scientifiques. Je remercie également les membres du jury qui ont accepté d'évaluer cette thèse : Valentina Buttò, qui a présidé le jury, et Patrick Faubert et Simon Bilodeau-Gauthier, qui ont agi en tant qu'évaluateurs externes. Leurs commentaires constructifs, leurs questions stimulantes et leurs suggestions pertinentes ont nourri ma réflexion et m'ont permis de pousser plus loin certaines analyses et interprétations. Je leur suis reconnaissante pour la qualité de leurs échanges et pour l'attention qu'ils ont portée à mon travail.

La réalisation d'une thèse ne saurait aboutir sans le soutien d'une équipe administrative. Je tiens à exprimer ma profonde reconnaissance envers Danièle Laporte, véritable pilier du département, dont la bienveillance, le sourire et les mots toujours encourageants ont su, à maintes reprises, apporter réconfort et sérénité. Mes remerciements s'adressent également à Marie-Hélène Longpré, pour son aide précieuse et ses encouragements constants, ainsi qu'à Frédérike Bédard, commis aux études, dont l'efficacité et la disponibilité en fin de parcours ont été grandement appréciées. Je souhaite également remercier François Rousseu et Stéphane Daigle, du Centre d'étude de la forêt (CEF), ainsi que Nicole Fenton pour leurs conseils avisés en statistiques, qui ont été déterminants dans l'analyse de mes résultats. Ma gratitude va également à Valentina Buttò, pour sa confiance et pour m'avoir offert l'opportunité d'explorer le métier d'enseignante à ses côtés. Son accompagnement m'a permis de m'épanouir pleinement dans mon rôle d'auxiliaire d'enseignement.

Je souhaite aussi souligner l'apport précieux des retraites d'écriture dirigées ENCRÉ de l'UQAT, dont le cadre structurant et l'accompagnement bienveillant ont rendu ma rédaction plus stimulante et productive. Enfin, je n'oublie pas Marie-Pier Pilon et Mélodie Rheault, dont la présence et le soutien ont grandement contribué à mon équilibre et à mon bien-être tout au long de cette aventure doctorale.

Je ne saurais oublier toutes les personnes qui m'ont apporté leur aide, tant sur le terrain qu'au laboratoire. Je tiens à exprimer ma profonde gratitude envers Abigail Leavens, pour son soutien indéfectible tout au long des longues journées passées sur le terrain et en laboratoire, et pour être restée à mes côtés jusqu'à la dernière aiguille d'épinette. Je remercie également Marion Noualhaguet pour son aide précieuse sur le terrain, ainsi que toutes celles et ceux qui, le temps d'une journée ou davantage, ont partagé avec moi une placette de cette aventure de terrain. Mes remerciements les plus sincères vont également à mon amie Mialintsoa Aroniaina Randriamananjara, pour son aide précieuse en statistiques, et bien plus encore.

Je ne saurais non plus passer sous silence le rôle essentiel de mes ami·e·s, sans qui la vie en région éloignée n'aurait jamais été aussi douce, riche en rires et en souvenirs inoubliables. Mes remerciements les plus sincères s'adressent à « la gang, le noyau, et le pépin ». Mon expérience en Abitibi-Témiscamingue n'aurait assurément pas eu la même saveur sans vous : Alex, Audrey, Colin, Dan, Éléonore, Hector, Pénélope, Samuel et Xavier. Merci pour tous les doux moments, comme les plus fous, à sillonner les sentiers de l'Abitibi, à pagayer sur les rivières du Témiscamingue, à dormir sous la belle étoile, à célébrer la vie au bord de l'eau, et pour votre patience lors de mes nombreuses tentatives de pêche infructueuses. Merci d'avoir été ma famille loin de la maison. Je conserverai précieusement chacun de ces souvenirs, gravés à jamais dans mon cœur. Une pensée particulière à mes collègues et ami·e·s de l'Institut de recherche sur les forêts (IRF) : Aro, Bandana, Enriqué, Jeri, Jonathan, Laima, Rémi et bien d'autres, pour leur bonne humeur contagieuse, leur soutien, et les échanges stimulants qui ont enrichi mon expérience.

Je remercie évidemment mon amie pour la vie, Asmae, qui vit elle aussi ce parcours doctoral à l'autre bout du monde et qui a toujours su comprendre les hauts, les bas, et les imprévus, qu'ils soient liés à la thèse ou simplement à la vie. Merci pour toutes ces heures passées à m'écouter, merci pour les voyages, merci pour les rêves, et pour tout le reste.

Enfin, je tiens à exprimer toute ma gratitude envers ma famille. Un immense merci à mes parents et mon petit frère, dont le soutien indéfectible, les encouragements et la confiance inébranlable m'ont permis d'avancer et de croire en mes capacités, même dans les moments de doute. Je leur dois une part essentielle de ce parcours. Je remercie également l'ensemble de ma grande famille, dont les encouragements et la bienveillance, malgré la distance, m'ont toujours accompagnée, notamment lors de mes présentations orales.

DÉDICACE

À mes parents, pour leur soutien indéfectible et pour leur amour incommensurable,

إلى والديّ، لدعمهما الثابت وحبهما اللامحدود

À mon petit frère, pour qu'il n'oublie jamais de croire en ses rêves,

إلى أخي الصغير، ليظل مؤمناً بأحلامه دوماً

À mes deux grand-mères, qui n'ont eu la chance de s'asseoir que peu de temps sur les bancs de l'école, et de qui pourtant j'ai tant appris,

إلى جدتيَّ، اللتين لم تتح لهما فرصة الجلوس على مقاعد المدرسة سوى لفترة قصيرة، ومع ذلك تعلمت منهما الكثير

À toutes les femmes de ma famille, pour leur force, leur courage et leur persévérance.

إلى جميع نساء عائلتي، لقوتهن وشجاعتهن ومثابرتهن

AVANT-PROPOS

Cette thèse a été rédigée sous forme de thèse par articles. Elle se compose de cinq chapitres : le chapitre 1 présente une introduction générale qui présente le contexte de l'étude, précise les problématiques et les principales questions de recherche qui ont motivé ce travail. Il définit également les objectifs et les hypothèses propres à chacun des chapitres, et décrit la zone d'étude. Les chapitres 2, 3 et 4 correspondent chacun à un article scientifique rédigé en anglais. Enfin, le chapitre 5 propose une conclusion générale qui synthétise les principaux résultats, formule des recommandations, expose les limites de l'étude et propose des perspectives de recherche. Le chapitre 2 a été publié dans la revue *Canadian Journal of Forest Research* en janvier 2025. Le chapitre 3, soumis à la revue *Forest Ecology and Management* en février 2025, fait actuellement l'objet d'une demande de révisions avant son acceptation finale pour publication, et le chapitre 4 a été soumis à la revue *New Forests* en avril 2025.

Bien que j'aie rédigé cette thèse, elle est le fruit d'un travail collaboratif avec ma directrice de recherche, Annie DesRochers, et mon co-directeur, Vincent Poirier. Ce projet a bénéficié du soutien financier de la Chaire de recherche industrielle CRSNG en sylviculture et production de bois (*#IRCPJ54721-18*), dont Annie DesRochers est la titulaire, ainsi que la Fondation J.A. DeSève et Fondation de l'UQAT pour l'attribution de la bourse de soutien au dépôt de thèse doctorale.

En tant que première auteure, j'ai rédigé les premières versions des chapitres 2, 3 et 4, et les co-auteurs ont participé à leur révision et ont approuvé la version finale pour publication. Ce travail a été réalisé en collaboration avec Alison Munson (*Université Laval*) pour les chapitres 2, 3, et avec David Paré (*Ressources naturelles Canada*) pour les chapitres 2 et 4.

La répartition des contributions des co-auteurs est la suivante : Annie DesRochers a assuré l'acquisition du financement, la gestion et la coordination du projet. Elle a également contribué à la conceptualisation des idées de recherche, à l'élaboration de la méthodologie, à la validation des résultats, à la supervision scientifique et à la révision des manuscrits des chapitres 2, 3 et 4, ainsi qu'à la mise à disposition des ressources, du matériel et des outils nécessaires à l'analyse. Vincent Poirier a participé à la conceptualisation des idées de recherche, au développement de la méthodologie, à la fourniture des ressources, du matériel et des outils d'analyse, à la supervision scientifique, à la validation des résultats, à la visualisation et présentation des données, et à la révision des manuscrits des chapitres 2, 3 et 4. Alison Munson a contribué à l'élaboration de la méthodologie, à la validation des résultats et à la révision des manuscrits des chapitres 2 et 3. David Paré a pris part au développement de la méthodologie, à la validation des résultats et à la révision des manuscrits des chapitres 2 et 4

Par ailleurs, le jeu de données du chapitre 3 a été enrichi par l'intégration de données issues des bases TOPIC et TRY. L'ensemble des références citées dans chacun des chapitres figure à la fin de ce manuscrit, accompagné du matériel complémentaire correspondant à chaque chapitre.

Chapitre 2 :¸ Hiba Merzouki, Vincent Poirier, Alison Munson, David Paré, and Annie DesRochers. 2025. Impact of single and combined soil amendments on the growth and foliar nutrients of white spruce *(Picea glauca)* on a poorly regenerated logged site. *Canadian Journal of Forest Research*. 55: 1-15. https://doi.org/10.1139/cjfr-2024-0195

Chapitre 3 : Merzouki, H., Poirier, V., Munson, A., & Desrochers, A. (2025). Soil amendments alter understory vegetation composition and functional diversity in poorly regenerated logging sites in Quebec, Canada. *Forest Ecology and Management*. (en révision)

Chapitre 4 : Merzouki, H., Poirier, V., D., Pare, D., & Desrochers, A. (2025). Interactions between soil amendments shape nutrient availability in boreal forests. *New Forests.* (en révision)

Les présentations lors de conférences liées à cette thèse sont listées comme suit :

Présentations orales :

Merzouki H., Poirier V. Munson A. & DesRochers A. (2025). Les amendements de sol modifient la composition et la diversité fonctionnelle de la végétation de sous-bois dans des sites mal régénérés après coupe au Québec, Canada. Présentation orale, 61ème conférence annuelle de l'association botanique du Canada, St-John's (Canada). Juin 2025.

Merzouki H., Poirier V., Munson A. & DesRochers A. (2025). Les amendements de sol modifient la composition et la diversité fonctionnelle de la végétation de sous-bois dans des sites mal régénérés après coupe au Québec, Canada. Présentation orale, 18ème colloque Du CEF, Rimouski (Québec). Mai 2025.

Merzouki H., Poirier V., Munson A., Paré D. & DesRochers A. (2024). L'utilisation d'amendements de sol pour restaurer ou améliorer la productivité de sites mal régénérés après coupe en forêt boréale mixte. Présentation orale, 26ème colloque de la Chaire UQAT-UQAM en Aménagement Forestier Durable (AFD), Val d'Or (Québec). Décembre 2024.

Merzouki H., Poirier V., Munson A., Paré D. & DesRochers A. (2024). Impact of single and combined soil amendments on the growth and foliar nutrients of white spruce (*Picea glauca*) on a poorly regenerated logged site. Oral presentaion, SER 2024 North American Conference, Vancouver (Canada). November 2024.

Merzouki H., Poirier V., Munson M., Paré D. & DesRochers A. (2024). L'utilisation d'amendements de sol pour restaurer ou améliorer la productivité de sites mal régénérés après coupe en forêt boréale mixte. Présentation orale, conférencière principale niveau doctorat, 4ème rencontre annuelle du Laboratoire international de recherche sur les forêts froides, Ifrane (Maroc). Octobre 2024.

Merzouki H., Poirier V. & DesRochers A. (2024). L'utilisation d'amendements de sol pour restaurer ou améliorer la productivité de sites mal régénérés après coupe en forêt boréale mixte. Présentation orale, 17ème colloque Du CEF, Gatineau (Québec). Mai 2024.

Présentations par affiche :

Merzouki H., Poirier V. & DesRochers A. (2023). Donner un coup de « pousse » à la forêt boréale mixte en utilisant des amendements de sol. Poster, 25ème colloque de la Chaire UQAT-UQAM en Aménagement Forestier Durable (AFD), Rouyn-Noranda (Québec). Décembre 2023. DOI: http://dx.doi.org/10.13140/RG.2.2.32709.83680

Merzouki H., Poirier V. & DesRochers A. (2021). Utilisation d'amendements de sol pour restaurer la productivité des sites dégradés en forêt boréale mixe. Poster, 23ème colloque de la Chaire UQAT UQAM en Aménagement Forestier Durable (AFD), Amos (Québec). Décembre 2021. DOI: http://dx.doi.org/10.13140/RG.2.2.27017.98408

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A	Cendres de bois (wood ash)
Al	Aluminium
AM	Cendres de bois-fumier (wood ash-manure)
B	Biochar
BA	Biochar-cendres de bois (biochar-wood ash)
BAM	Biochar-cendres de bois-fumier (biochar-wood ash-manure)
BM	Biochar-fumier (biochar-manure)
Bo	Bore
C	Carbone
Ca	Calcium
$CaCl_2$	Chlorure de calcium
CEC	Capacité d’échange cationique
C/N	Ratio carbone : azote
CPRS	Coupe avec protection de la régénération et des sols
CTL	Témoin (control)
Cu	Cuivre
Exch	Échangeable
Fe	Fer

FERLD	Forêt d'enseignement et de recherche du lac Duparquet
FIA	Analyse par injection en flux
HCL	Acide chlorhydrique
ICP	Plasma à couplage inductif
K	Potassium
LDMC	Teneur en matière sèche foliaire (leaf dry matter content)
LNC	Contenu en azote foliaire (leaf nitrogen concentration)
M	Fumier (manure)
Mg	Magnésium
Mn	Manganèse
N	Azote
Na	Sodium
N_{min}	Azote minéral
N_{min}/N_{tot}	Ratio Azote minéral : azote total
$N.NH_4^+$	Ammonium
$N.NO_3^-$	Nitrate
N_{tot}	Azote total
P	Phosphore

PCA	Analyse en composantes principales (principal component analysis)
PCoA	Analyse des coordonnées principales (principal coordinates analysis)
RDA	Analyse de la redondance (redundancy analysis)
SLA	Surface foliaire spécifique (specific leaf area)
SRL	Longueur spécifique des racines (specific root length)
TOPIC	Traits of plants in Canada
TRY	Plant trait database
Zn	Zinc

LISTE DES SYMBOLES ET DES UNITÉS

cm	Centimètre
cm^2	Centimètre carré
cmolc	Centimole de charge
dpi	Points par pouce (dots per inch)
g	Gramme
h	Heure
ha	Hectare
kg	Kilogramme
m	Mètre
M	Molaire
mm	Millimètre
mg	Milligramme
Mg	Mégagramme
w/	Avec (with)
w/o	Sans (without)
%	Pourcentage
°C	Degré celsius

RÉSUMÉ

L'un des défis majeurs en sylviculture est d'assurer la productivité des forêts boréales mixtes aménagées, particulièrement après une coupe totale. La régénération naturelle peut être entravée par des conditions édaphiques altérées, une disponibilité réduite en nutriments essentiels à la croissance des arbres, ainsi qu'une forte compétition par la végétation de sous-bois. Dans l'objectif de restaurer ou améliorer la productivité des sols forestiers mal régénérés, cette thèse explore l'utilisation des amendements de sol comme un outil de restauration forestière. Les amendements de sol sont largement utilisés en agriculture, et leur valorisation dans le secteur forestier suscite un intérêt croissant. Cependant, leur application reste encore limitée et peu documentée, notamment lorsqu'ils sont utilisés en combinaison de deux ou trois amendements. La plupart des études se sont concentrées sur leurs effets individuels sur les propriétés physico-chimiques des sols, tandis que leurs impacts sur la nutrition foliaire des semis et la diversité taxonomique et fonctionnelle de la végétation de sous-bois demeurent peu explorés.

Trois types d'amendements [biochar (2,6 Mg ha^{-1}), cendres de bois (7 Mg ha^{-1}) et fumier (105 Mg ha^{-1})] ont été appliqués seuls ou en combinaison de deux et trois amendements, et leurs effets ont été évalués après deux saisons de croissance en utilisant un dispositif expérimental en blocs aléatoires complets. Dans le deuxième chapitre, nous avons examiné l'effet des amendements sur la croissance d'une plantation de semis d'épinette blanche (*Picea glauca*) ainsi que leur nutrition foliaire. Dans le troisième chapitre, nous avons évalué leurs effets sur la composition taxonomique et la diversité fonctionnelle de la végétation de sous-bois. Dans le quatrième chapitre, nous avons exploré les effets sur les propriétés chimiques du sol.

Nos résultats ont montré que le fumier a significativement amélioré la croissance des semis par rapport aux traitements sans fumier, tout en augmentant les concentrations foliaires en azote et en phosphore. Le biochar et les cendres de bois ne se sont pas avérés efficaces pour améliorer la croissance des semis. Toutefois, leur application a permis d'améliorer la nutrition foliaire en macronutriments essentiels à la croissance (N, P, K, et Ca), alors que le biochar a réduit la concentration foliaire en aluminium.

Par ailleurs, le fumier a significativement augmenté l'indice de diversité de Shannon de la végétation de sous-bois et a favorisé l'établissement des graminées et des légumineuses, caractérisées par une stratégie d'acquisition rapide des ressources et une forte compétition. La diversité fonctionnelle était la plus élevée avec le fumier et la plus faible dans les traitements sans fumier. En revanche, le biochar et les cendres de bois n'ont pas significativement modifié la diversité taxonomique de la végétation de sous-bois, bien que ces amendements aient favorisé l'installation d'espèces

forestières et rudérales composées d'herbacées et d'arbustes ligneux caractéristiques des perturbations forestières. De plus, les cendres de bois ont augmenté la concentration foliaire en azote par rapport aux traitements sans cendres.

En ce qui concerne le sol, le biochar n'a pas modifié les teneurs en carbone et azote totaux, mais a réduit la concentration en aluminium et la capacité d'échange cationique (CEC), tout en augmentant la concentration en manganèse. La combinaison du biochar et du fumier a augmenté le magnésium échangeable. Les cendres de bois ont réduit l'acidité du sol, et ont augmenté le rapport C/N et la teneur en phosphore, mais ont également augmenté l'aluminium et réduit l'azote total lorsqu'elles étaient combinées au fumier. Bien que les cendres de bois aient augmenté la CEC en absence du fumier, leur co-application avec biochar et fumier a entraîné une diminution de la CEC. Le fumier a réduit les teneurs en carbone et azote totaux, ainsi que plusieurs macro- et micronutriments (K_{exch}, Ca_{exch}, Mg_{exch}, Mn, Al, Na), mais a amélioré la disponibilité de l'azote.

Cette thèse met en évidence le rôle clé du fumier comme source d'azote et de phosphore pour la croissance des semis, tout en soulignant l'intérêt des combinaisons d'amendements pour améliorer la nutrition et la croissance des semis en forêt boréale mixte. Ces résultats illustrent également l'importance d'une approche combinant taxonomie et traits fonctionnels pour mieux comprendre les effets des amendements sur la diversité taxonomique et fonctionnelle des communautés végétales de sous-bois. Enfin, cette étude met en lumière les interactions complexes entre les amendements et leur influence sur la fertilité des sols mal régénérés, renforçant ainsi le potentiel des combinaisons d'amendements pour améliorer la productivité des sols forestiers.

Dans l'ensemble, cette recherche démontre que l'utilisation des amendements de sol est efficace pour améliorer la croissance des semis, augmenter la diversité taxonomique et fonctionnelle de la végétation de sous-bois, et modifier les propriétés chimiques du sol. Ces résultats offrent des perspectives intéressantes pour la restauration des forêts boréales mixtes mal régénérées et proposent des pistes de solutions directement applicables pour un aménagement forestier durable des plantations forestières.

Mots-clés : amendement, biochar, cendre de bois, fumier, croissance, nutrition foliaire, végétation de sous-bois, indice de diversité, trait fonctionnel, traits agrégés, sol minéral, épinette blanche, forêt boréale mixte

Keywords: soil amendments, biochar, wood ash, manure, growth, foliar nutrition, diversity indices, functional traits, community-weighted mean, mineral soil, white spruce, understory vegetation, boreal mixed forest

1. INTRODUCTION GÉNÉRALE

1.1 Mise en contexte

Depuis le début du 19ème siècle, les forêts boréales de l'Est du Canada font l'objet d'une exploitation commerciale forestière en raison d'un besoin grandissant en ressources forestières (Drushka & Society, 2003). Les coupes totales sont pratiquées depuis des décennies au Canada, et leurs effets sur la fertilité des sols forestiers ont fait l'objet de plusieurs études (Bélanger et al., 2003; Kishchuk et al., 2014; Maynard et al., 2014; Powers et al., 2005; Thiffault et al., 2011; Thiffault et al., 2008; Thiffault et al., 2006). Bien que les coupes totales soient de moins en moins pratiquées et remplacées par des coupes avec protection de la régénération et des sols (CPRS), les coupes forestières engendrent un changement important dans les conditions microclimatiques en comparaison avec les conditions avant la coupe. Elles exposent le sol à des niveaux de lumière élevés, ce qui offre des conditions propices à l'installation d'une végétation intolérante à l'ombre, telle que l'érable à épis (*Acer spicatum*) et le noisetier à long bec (*Corylus cornuta*) dans les forêts boréales mixtes (Archambault et al., 1998; Laflèche et al., 2000). Ces espèces peuvent envahir rapidement les parterres de coupe et créer de la compétition avec les jeunes semis d'essences forestières pour les nutriments du sol et la lumière, et ainsi inhiber leur croissance et compromettre le processus de régénération (Jobidon, 2000; Thiffault et al., 2015). De plus, les coupes totales n'éliminent pas l'épaisse couche organique de mousses typique des forêts boréales, qui peut constituer une barrière à la germination et l'installation du nouveau peuplement (Bouchard, 2009). Il peut parfois résulter de ces conditions post-récolte un échec ou un retard de la régénération naturelle ainsi qu'une perte ou une diminution de la productivité forestière (Binkley & Fisher, 2020; Doucet, 1988), particulièrement lorsque l'utilisation d'herbicides est prohibée en sylviculture (Thiffault & Roy, 2011). À partir de ce contexte, il est essentiel de mettre en place une démarche de restauration forestière afin de remettre en productivité les sites forestiers mal régénérés après les coupes totales.

La restauration forestière est le processus visant à rétablir la structure, la composition et les fonctions écologiques d'un écosystème forestier dégradé (Lamb, 2015). La restauration forestière peut avoir différents objectifs, selon le niveau de dégradation du site, le temps et l'investissement financier disponibles (Chazdon, 2008). L'amélioration de la fertilité des sols, la production de biomasse et la gestion de la compétition par la végétation de sous-bois peuvent être des motifs pertinents pour la restauration forestière (Ciccarese et al., 2012). Il est courant de réaliser une intervention mécanique par scarifiage afin d'exploser le sol minéral et de replanter les sites forestiers après les coupes, en raison d'une régénération naturelle insuffisante ou de l'absence de l'espèce forestière recherchée. Dans le contexte de cette étude, les amendements de sol peuvent être utilisés comme un outil de restauration forestière complémentaire, afin d'accélérer l'établissement des semis plantés sur un site mal régénéré après coupe totale dans un contexte de compétition importante par la végétation de sous-bois. Nous allons présenter un état des connaissances sur les travaux réalisés concernant ces amendements en milieu forestier boréal, afin de faire le point sur les avancées scientifiques actuelles et identifier les limites ayant motivé notre étude.

1.2 Les amendements de sol

Au cours des dernières décennies, les amendements ont fait l'objet d'une grande attention en tant que moyens d'augmenter les rendements des cultures dans les systèmes agricoles (Hébert, 2015; Joseph et al., 2021), et leur utilisation dans un contexte forestier est grandissante (Smethurst, 2010). Trois amendements de sol ont été sélectionnés pour faire l'objet de cette étude : le biochar, les cendres de bois, et le fumier. Les deux premiers amendements sont des matières résiduelles fertilisantes (MRF) : il s'agit des résidus industriels ou municipaux utilisés pour entretenir ou corriger la nutrition des végétaux et les propriétés physico-chimiques des sols (Gouvernement du Québec, 2012). Plus récemment, le biochar et les cendres de bois ont été des amendements d'intérêt pour améliorer la régénération dans les forêts boréales canadiennes (Bieser & Thomas, 2019), tandis que le fumier a rarement été appliqué dans ce contexte (Han et al., 2016). Des quantités massives de résidus sont générés par les secteurs agricole et forestier. Au Canada, 180 millions de tonnes d'effluents d'élevage (Statistics Canada, 2006) et 21 millions de tonnes anhydres de résidus d'exploitation forestière (Paré, 2020) ont été produites chaque année.

L'utilisation de sous-produits pour la fertilisation des sols peut réduire les déchets et les coûts d'enfouissement, et contribuer à améliorer la qualité des sols (Muscolo et al., 2021). Les sols pourraient bénéficier de l'apport de matière organique des amendements, alors que les engrais chimiques se limitent à l’ajout des nutriments directement disponibles pour les plantes (Larney & Angers, 2012).

1.2.1 Le biochar

Issu d’un processus de pyrolyse en l’absence ou sous présence restreinte d’O_2, le biochar est produit à partir de différents types de biomasse (Lehmann et al., 2009). Cette variabilité des matières premières et des conditions de pyrolyse (température de chauffe) engendre une diversité des propriétés physiques, chimiques et de la teneur en nutriments biologiques. Certains auteurs parlent ainsi de "biochars" plutôt que d'un biochar unique (Chan & Xu, 2009). Le biochar est un amendement récalcitrant et riche en carbone (C), capable de séquestrer ce dernier dans le sol pendant plus d’un siècle (Lehmann et al., 2006; Lehmann & Joseph, 2015). Il contient une concentration importante de macronutriments tels que le phosphore (P), le calcium (Ca), le magnésium (Mg) et le potassium (K), mais est pauvre en azote (N) (Ippolito et al., 2015). Peu d'études ont été menées sur le biochar en milieux forestiers. Néanmoins, certaines études ont montré que les semis d'arbres répondent de façon neutre, favorable ou négative à l’application du biochar (Palviainen et al., 2020; Pluchon et al., 2014; Robertson et al., 2012; Thomas & Gale, 2015). Une augmentation du pH, de la capacité d'échange cationique (CEC) et des concentrations en cations échangeables (Ca_{exch}, Mg_{exch} et K_{exch}) a été observée, en plus d’un enrichissement du sol en C et N totaux, ainsi qu’une augmentation du ratio C/N (Robertson et al., 2012). L’apport direct des nutriments par le biochar, l’augmentation de la CEC, la rétention des nutriments et de l'eau, la réduction du lessivage (Atkinson et al., 2010) et l'adsorption des sels (Thomas, 2013) et des phénols (Wardle et al., 1998) sont des mécanismes qui jouent un rôle clé dans l'augmentation de la productivité des peuplements forestiers après un amendement au biochar. Toutefois, les effets du biochar sur la croissance des semis en forêt boréale varient selon les contextes. Par exemple, Pluchon et al. (2014) et Gundale et al. (2016) ont rapporté des effets neutres ou positifs, tandis que Bieser and Thomas (2019) ont observé une croissance négative des semis d'épinette blanche, attribuée à une contamination du sol par des métaux lourds contenus dans le biochar. Par ailleurs, le biochar étant naturellement pauvre en azote, il devrait être combiné à une source complémentaire d'azote pour optimiser la restauration forestière (Thomas & Gale, 2015). En effet, le biochar permet de retenir l'azote dans le sol et de prévenir son lessivage (Joseph et al., 2021; Shi et al., 2020). Lorsqu'il est apporté avec une source d'azote, ce mélange permet d'améliorer la croissance des semis par rapport à l'utilisation d'un fertilisant azoté seul (Robertson et al., 2012).

1.2.2 Les cendres de bois

Au Québec, environ 300 000 tonnes de cendres issues de la biomasse forestière sont produites chaque année (base humique), dont seulement la moitié est recyclée, principalement en agriculture, tandis que le reste est valorisé pour la végétalisation de sites dégradés, la fabrication de terreaux ou le compostage, ou encore enfoui (Hébert & Breton, 2008). Les cendres de bois sont des substances riches en minéraux (Ca, Mg, K, Na, P) nécessaires à la croissance des arbres, à l'exception du N qui se volatilise sous de fortes températures lors du processus de combustion (Brais et al., 2015). Dans les sols forestiers, il en résulte un effet de chaulage équivalent à la moitié de celui de la chaux calcique, i.e. $CaCO_3$ (Augusto et al., 2008) ainsi qu'une augmentation de la concentration en cations échangeables (Ca_{exch}, Mg_{exch} et K_{exch}) (Arvidsson & Lundkvist, 2003; Ingerslev et al., 2014; Kahl et al., 1996; Saarsalmi et al., 2001) et du taux de minéralisation nette de l'N (Brais et al., 2015). Cela est dû à la diminution de l'acidité qui entraine une activité microbienne plus importante (Jokinen et al., 2006), favorisant la minéralisation de l'N (Bååth & Arnebrant, 1993; Mahmood et al., 2003; Perkiömäki & Fritze, 2002). Les cendres de bois peuvent toutefois être une source de contamination par les métaux lourds et les dioxines. Néanmoins, l'augmentation du pH du sol permet de réduire la solubilité et la biodisponibilité des métaux (Augusto et al., 2008; Dimitriou et al., 2006). L'effet des cendres de bois sur la croissance des arbres varie en fonction de l'espèce et de la taille de l'arbre, des conditions initiales du sol et du temps écoulé depuis l'application (Reid & Watmough, 2014). Des résultats favorables ont été observés à moyen (6-16 ans) et long terme (16-50 ans) sur des sols organiques acides après épandage de cendres de bois

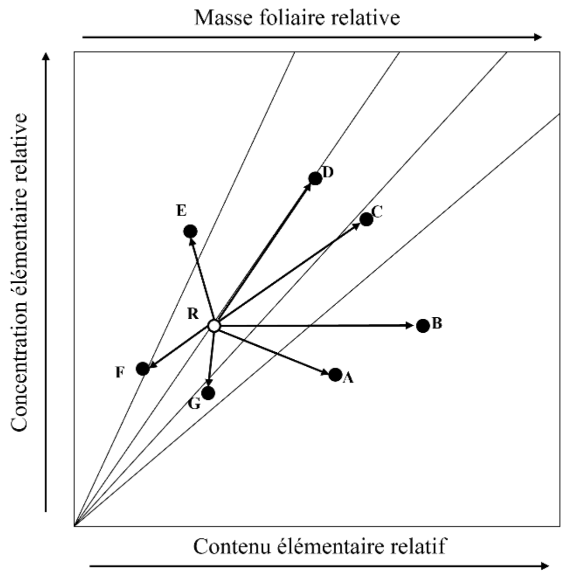
(Augusto et al., 2008). Toutefois, sur des sols très acides, une augmentation du pH pourrait entraîner le lessivage de l'aluminium (Al) et du fer (Fe) (Pitman, 2006). Dans les sols minéraux, la croissance des arbres est majoritairement conditionnée par l'azote (Jacobson, 2003; Jacobson et al., 2014; Saarsalmi et al., 2004). Cependant, chez l'épinette noire (*Picea mariana*), une dose de 8 Mg ha^{-1} de cendres a réduit la croissance de 30 % comparativement au témoin, et l'ajout d'azote n'a pas compensé cet effet après cinq ans (Brais et al., 2015). Cette réduction pourrait être liée à une contamination par les métaux ou à une compétition accrue avec la végétation favorisée par les cendres (Emilson et al., 2020). De même, une réponse négative des semis d'épinette blanche a été rapportée trois ans après l'apport de cendres, probablement en raison de la toxicité causée par les métaux (Bieser & Thomas, 2019). Toutefois, dans certains contextes, un apport en cendres a amélioré significativement la croissance des semis, comme pour le bouleau blanc (*Betula pendula*) sur un sol tourbeux pauvre en nutriments, où hauteur et diamètre du collet ont été stimulés (Mandre et al., 2010).

1.2.3 Le fumier

Largement utilisé en milieu agricole, le fumier a été produit à raison de 0,5 million de tonnes par jour au Canada en 2006, marquant une augmentation de 16 % depuis 1981 (Statistics Canada, 2006). Bien que son application en milieu forestier soit encore peu répandue, les quelques études menées suggèrent un fort potentiel pour l'amélioration de la fertilité des sols et la croissance des arbres. Riche en azote et en phosphore, le fumier a favorisé le stockage du carbone dans le sol forestier (Lafleur et al., 2012). Son application a permis d'augmenter le taux de matière organique et de favoriser la formation de macroagrégats (250–1000 µm), un effet non observé avec les fertilisants minéraux (Aoyama et al., 1999). Les recherches ont montré que l'apport de fumier stimule la croissance des arbres, accroît leur biomasse et le volume de leurs tiges (Lafleur et al., 2012). Il a amélioré également la fertilité des sols en réduisant leur acidité et en augmentant la concentration en N, P, et en cations majeurs (Ca_{exch}, Mg_{exch}, K_{exch}) (Han et al., 2016). De plus, il a contribué à la diminution des concentrations en aluminium (Al) et en manganèse (Mn) sur les sols acides (Benke et al., 2010).

1.3 L'analyse vectorielle de la nutrition foliaire

Alors que l'effet des amendements est souvent étudié en analysant les propriétés physico-chimiques du sol, notre étude explore également leur impact sur les nutriments foliaires. Les analyses foliaires renseignent sur les nutriments absorbés par les plantes et sont étroitement liées à leur croissance. Chez les semis, la concentration en nutriments dans les feuilles reflète bien celle de l'ensemble de la plante en raison de leur petite taille et de leur rôle clé dans la photosynthèse (Timmer, 1991). Les analyses foliaires permettent de mesurer la concentration des nutriments (g kg^{-1}) dans les feuilles, et le contenu absolu (g $aiguille^{-1}$) de ces nutriments peut être calculé à partir de la masse de la matière sèche des feuilles (g), afin d'évaluer l'absorption ou l'accumulation des nutriments dans la plante. L'analyse vectorielle (Salifu & Timmer, 2001; Timmer, 1991) combine ces trois paramètres sur une représentation graphique (Figure 1), attribuant une valeur constante de 100 au témoin et rapportant les valeurs des nutriments et de la masse sèche relativement au témoin. Cette analyse permet d'interpréter la direction nutritionnelle des semis amendés, en comparaison avec ceux n'ayant pas reçu de fertilisation. En effet, les arbres ne peuvent croître de façon optimale en cas de carence de certains nutriments essentiels à leur développement, en particulier l'azote. Lorsque ces éléments sont disponibles et absorbés par la plante, celle-ci croit, ce qui correspond au vecteur C où les trois variables (concentration, contenu et masse sèche) augmentent en réponse au traitement apporté. En revanche, lorsque les nutriments dépassent les besoins de la plante, ils peuvent s'accumuler dans le feuillage, entraînant potentiellement une toxicité, ce qui correspond aux vecteurs E ou F. Entre ces deux états, la plante peut se retrouver en état de consommation de luxe. Dans ce cas, bien que la concentration et le contenu en nutriments augmentent, la croissance reste stable, ce qui est représenté par le vecteur D. Cette analyse permet également de dissimuler d'autres directions nutritionnelles, à savoir la dilution (A), la suffisance (B) et l'appauvrissement (G).



Direction du vecteur	Changement foliaire :			Interprétation
	Masse	Concentration	Contenu	
A	(+)	(-)	(+)	Dilution
B	(+)	0	(+)	Suffisance
C	(+)	(+)	(+)	Carence
D	0	(+)	(+)	Consommation de luxe
E	(-)	(++)	(+) or (-)	Excès
F	(-)	(-)	(-)	Excès
G	0 or (+)	(-)	(-)	Appauvrissement

(+) : Augmentation, (-) : Diminution, 0 : Aucun changement

Figure 1 Cadre pour l'interprétation nutritionnelle foliaire des changements directionnels entre les traitements selon la masse, le contenu et la concentration foliaires. Reproduit de Thiffault et al. (2006).

1.4 Les enjeux de la compétition par la végétation de sous-bois

Les plantes vasculaires représentent une partie considérable de la diversité mondiale et comptent environ 1000 espèces dans la forêt boréale, dont seulement 2 % sont des arbres (De Grandpré et al., 2014). Les arbres ont longtemps été la cible principale des recherches, car ils constituent les plantes d'intérêt en termes de productivité forestière et de gain économique. Bien que l'on pourrait négliger la contribution de la végétation de sous-bois en raison de sa hauteur, biomasse et productivité primaire nette aérienne modestes par rapport à celles des arbres, l'ensemble de cette végétation participe étroitement au fonctionnement écologique des écosystèmes qu'elle domine, en maintenant une dynamique au sein de la forêt boréale (Nilsson & Wardle, 2005). Elle va donc interagir avec le cycle des nutriments, participer à la décomposition de la litière, retourner au sol une quantité considérable de nutriments et aller jusqu'à impacter les espèces régénérantes dans la succession de la forêt boréale (Hart & Chen, 2006).

La végétation de sous-bois peut poser un défi à la régénération naturelle des arbres (Archambault et al., 1998; Laflèche et al., 2000) et limiter la croissance des semis replantés en raison de la compétition pour les ressources telles que la lumière, l'eau et les nutriments (Jobidon, 2000). Cet effet peut devenir davantage problématique en cas de fertilisation des sols, qui peut profiter davantage à la végétation de sous-bois au détriment des arbres ciblés, voire favoriser la présence d'espèces non indigènes (Buss et al., 2018). La végétation de sous-bois, par sa capacité à croître et à se reproduire de façon plus importante et plus rapide, est souvent favorisée par rapport aux plants de conifères (Shropshire et al., 2001). Shepard (1997) a relevé une réduction de la croissance des semis d'épinettes noires et une diminution dans la concentration foliaire en N suite à un apport de cendres de bois et de boues de papeterie riches en N. La végétation herbacée, souvent plus exigeante en nutriments que les plants de conifères nouvellement reboisés, aurait absorbé les nutriments apportés par ces MRF (Shepard, 1997). Un autre exemple de compétition entre des semis d'épinette blanche et le framboisier (*Rubus idaeus*) s'est produit trois ans après un amendement au biochar, ce qui a eu un effet neutre sur la croissance des arbres au profit de l'accroissement en couverture de la végétation de compétition citée (Bieser & Thomas, 2019). Le calamagrostis du Canada (*Calamagrostis canadensis*) exerce aussi une forte compétition sur l'épinette blanche, car il envahit grandement les parterres de coupes totales grâce à son rhizome (Lieffers et al., 1993). De plus, la capacité de cette espèce nitrophile à puiser les deux formes de N minéral (NH_4^+ et NO_3^-) au début d'une succession dans la forêt boréale est quatre fois supérieure à celle des semis reboisés d'épinette blanche (Hangs et al., 2003).

Dans cette thèse, l'étude de la végétation de sous-bois a pour but de s'assurer que la réponse aux amendements de cette végétation ne nuise pas à la croissance des semis ciblés, mais aussi de comprendre comment les amendements façonnent la diversité et la composition de la communauté végétale de sous-bois. Pour cela, deux approches ont été empruntées. Nous nous sommes intéressés à l'aspect taxonomique de la végétation de sous-bois, ainsi qu'à sa composante fonctionnelle (Carnus et al., 2006). D'une part, l'approche taxonomique traite de la diversité des espèces à travers le calcul de divers indices de diversité (Pitkänen, 1998). D'autre part, l'approche fonctionnelle permet d'aller au-delà de cette description taxonomique pour expliquer le fonctionnement de l'écosystème (Díaz & Cabido, 2001). Combiner les approches taxonomiques et fonctionnelles pour étudier les communautés végétales représente une approche complémentaire et globale pour étudier les changements induits par les amendements de sol sur cette strate de l'écosystème forestier.

1.5 Les traits fonctionnels

Selon Violle et al. « un trait est toute caractéristique morphologique, physiologique ou phénologique mesurable à l'échelle de l'individu […] sans référence à l'espèce, à l'environnement ou à tout autre niveau d'organisation » (2007, p. 884). Les traits fonctionnels permettent d'expliquer le niveau de performance de l'individu, car ils reflètent la capacité des plantes à acquérir les ressources, à croitre, à être compétitives et à subsister (Li & Bao, 2015). Une large diversité existe entre les espèces de la végétation de sous-bois selon leurs traits fonctionnels : il s'agit de la diversité fonctionnelle (Díaz & Cabido, 2001; Violle et al., 2007).

Les perturbations naturelles ou anthropiques façonnent la diversité fonctionnelle des écosystèmes. Les traits fonctionnels sont le résultat d'un filtrage environnemental, et seuls les organismes possédant des traits requis sont capables de subsister, persister et dominer dans la communauté végétale (Garnier et al., 2016). Les traits fonctionnels ont fait l'objet de plusieurs études selon le gradient environnemental de disponibilité des nutriments, et sont étroitement liés aux ressources disponibles dans le sol (Lavorel et al., 2007). Une attention particulière a été portée aux traits relatifs à la croissance, à la hauteur maximale ainsi qu'aux feuilles des plantes [surface foliaire spécifique (SLA), concentration en azote des feuilles (LNC) et teneur en matière sèche des feuilles (LDMC)], car ce sont des traits facilement mesurables, en termes de temps et de coût. Ils sont également essentiels pour évaluer la diversité fonctionnelle des plantes et suivre les changements le long des gradients environnementaux, tels que la fertilisation des sols, ainsi que la réponse des traits aux perturbations (Lavorel et al., 2007). Par exemple, une augmentation des nutriments peut entraîner une élévation de la hauteur maximale, de la SLA et de la LNC, tout en réduisant le LDMC (Garnier et al., 2016). La théorie de Grime (1998) avance que les caractéristiques d'un écosystème sont déterminées par les traits fonctionnels des espèces dominantes, soit celles qui représentent plus de 80 % de la couverture totale au sein de la communauté (Garnier et al., 2004), et c'est cette dimension qui a été considérée dans le cadre de cette thèse. En outre, nous avons mesuré les traits par espèce, mais également par communauté, en calculant les traits agrégés, soit les moyennes des valeurs de traits pondérées selon la proportion des espèces dans les différentes communautés (Garnier et al., 2004; Grime, 1998).

1.6 Questions de recherche

Les amendements constituent une approche prometteuse pour améliorer la fertilité des sols et favoriser la croissance des semis en restauration forestière. Toutefois, la littérature scientifique présente des lacunes quant à leurs effets, en particulier ceux du fumier, dans les écosystèmes forestiers boréaux. De plus, lorsqu'ils sont appliqués en milieu forestier, ces amendements sont généralement étudiés de manière individuelle. Cette étude vise à combler ces lacunes en explorant les effets d'un apport combiné des amendements, afin d'évaluer leur potentiel synergique sur la restauration des sols. Les études existantes se concentrent principalement sur les effets des amendements sur les sols, tandis que notre recherche s'intéresse également aux nutriments foliaires, qui fournissent des informations plus directes sur les nutriments disponibles aux arbres et permettent d'interpréter leur direction nutritionnelle. En outre, notre étude vise à explorer les effets des amendements sur la diversité de la végétation de sous-bois ainsi que sur les traits fonctionnels des communautés végétales, des aspects souvent sous-étudiés dans le cadre des recherches actuelles.

Ainsi, notre étude offre une perspective globale en intégrant les trois composantes clés des écosystèmes forestiers : le sol, l'arbre et la végétation de sous-bois. En explorant les effets des amendements sur chacune de ces composantes, nous cherchons à obtenir une compréhension complète des interactions écologiques et des impacts potentiels sur la restauration des écosystèmes forestiers.

Dans cette thèse, nous cherchons à répondre aux questions suivantes : Quels sont les effets des amendements, individuellement et en combinaison, sur la croissance des semis, leur nutrition foliaire ainsi que les propriétés physico-chimiques des sols ? Comment les amendements impactent-ils la composition de la communauté végétale de sous-bois ainsi que sa diversité fonctionnelle ? Est-ce que les amendements ne profitent-ils pas plus à la végétation de compétition plutôt qu'aux semis d'épinette blanche, considérant que c'est une espèce plus conservatrice à croissance lente ? Quels sont les indices taxonomiques et les traits fonctionnels qui sont favorisés ou défavorisés par les amendements ? Et enfin, est-ce que les amendements sont réellement efficaces pour restaurer la productivité forestière de sites mal régénérés après coupe ?

1.7 Objectifs et hypothèses

L'objectif général de cette thèse consistait à déterminer en forêt boréale mixte l'effet des amendements, i.e. biochar, cendres de bois et fumier, individuellement et en combinaison, pour restaurer ou améliorer la productivité forestière des plantations d'épinette blanche dans un site mal régénéré à la suite d'une coupe totale. Pour cela, nous nous sommes concentrés sur trois composantes de l'écosystème forestier : les arbres à travers leur croissance et leur nutrition foliaire, le sol selon ses propriétés physiques et chimiques, et enfin la végétation de sous-bois à travers la diversité taxonomique ainsi que la diversité fonctionnelle de la communauté des plantes vasculaires. Cet objectif général a été décuplé en trois objectifs spécifiques dont chacun a fait l'objet d'un chapitre de thèse :

Le chapitre 2 avait pour objectif d'évaluer (1) si l'application des amendements pouvait améliorer la croissance des semis d'épinette blanche (*Picea glauca*) à court terme, et

(2) si les amendements de sol augmentaient les nutriments foliaires et la surface foliaire spécifique (SLA), ce qui pourrait avoir un effet positif sur la croissance à plus long terme. Nous avons émis l'hypothèse selon laquelle l'application de chaque amendement augmenterait les concentrations foliaires des nutriments relativement aux propriétés des amendements, en raison de l'apport direct des nutriments au sol et de l'amélioration de leur disponibilité grâce à l'effet de chaulage. Cependant, nous ne nous attendions pas à une augmentation de la croissance des semis, de la disponibilité des éléments nutritifs et de la SLA dans le cas d'une application individuelle ou combinée des cendres de bois et du biochar, en raison d'un manque d'azote. D'autre part, nous avions prévu que l'azote et le phosphore provenant du fumier augmenteraient la croissance des semis, la SLA et la nutrition foliaire.

Le chapitre 3 visait à examiner l’effet de l’application des amendements sur la végétation de sous-bois à travers (1) la diversité et la composition de la communauté, et (2) les traits fonctionnels au niveau de l’espèce et de la communauté, ainsi que la diversité fonctionnelle. Nous avons émis l'hypothèse qu'après deux saisons de croissance, les amendements du sol modifieraient la composition de la communauté et les indices de diversité de la végétation de sous-bois, et changeraient les traits fonctionnels en raison des changements dans les éléments nutritifs du sol après les traitements. Plus précisément, notre première hypothèse était que les traitements contenant du fumier augmenteraient la diversité et favoriseraient l'établissement des graminées ainsi que l'introduction d'espèces non indigènes (plantes agricoles) par rapport aux traitements sans fumier. Le fumier devrait également augmenter la hauteur maximale et les traits d'acquisition (augmentation de la SLA et de la LNC et diminution de la LDMC) parce qu'il est riche en azote. Comme deuxième hypothèse, nous ne nous attendions pas à des changements majeurs dans la composition des communautés ou dans les indices de diversité après l'application de cendres de bois, car les changements dans la composition des communautés ont tendance à se produire à plus long terme (Moilanen et al., 2002). Cependant, nous nous attendions à une augmentation de la LNC, comme observé dans le chapitre 2 pour les semis d'épinette blanche cultivés sous les cendres de bois par rapport aux traitements sans cendres. Notre troisième hypothèse stipulait que la décomposition lente du biochar et son application à la surface du sol auraient des effets similaires à ceux des traitements de contrôle, favorisant ainsi les espèces rudérales, avec une tendance à la diminution de la diversité, sans effet sur les traits fonctionnels.

Le chapitre 4 avait pour objectif d'explorer l'effet des amendements sur les propriétés chimiques du sol afin de déterminer leurs avantages potentiels pour la qualité du sol et les écosystèmes forestiers. Le sol est une composante fondamentale qui régit la productivité forestière. Ses propriétés physiques, chimiques et biologiques sont étroitement reliées à la rétention, l'absorption et le transport des éléments nutritifs (Schoenholtz et al., 2000). Nous avons émis l'hypothèse que l'application d'amendements augmenterait le pH du sol, mais que les cendres de bois auraient l'effet le plus important en raison de leur teneur élevée en carbonates. Le biochar augmenterait le carbone total du sol, et le fumier augmenterait l'azote total du sol de manière substantielle par rapport aux autres amendements. Nous nous attendions à ce que les cendres de bois augmentent les concentrations des macronutriments disponibles (P_{avail}, K_{exch}, Ca_{exch} et Mg_{exch}) et la capacité d'échange cationique, en raison de l'important effet de chaulage. Nous nous attendions aussi à ce que les cendres de bois réduisent les concentrations d'aluminium échangeable en raison de leur capacité à diminuer la biodisponibilité des métaux.

1.8 Méthodologie générale : zone d'étude

Le site d'étude est situé dans la Forêt d'enseignement et de recherche du lac Duparquet (FERLD) dans la région de l'Abitibi dans le nord-ouest du Québec (48°30' N, 79°22' O) (Figure 2). Le climat de la zone d'étude est continental, caractérisé par une température moyenne annuelle de 1 °C et des précipitations annuelles de 989 mm, dont 30 % tombent sous forme de neige (Environnement Canada, 2019). L'expérimentation s'est déroulée au cœur de la forêt boréale mixte dans le domaine du sapin baumier (*Abies balsamea*) - bouleau blanc (*Betula papyrifera*) (Saucier et al., 2003). Ce site d'étude était auparavant dominé par une pinède à pin gris (*Pinus banksiana*) avec peupliers faux-tremble (*Populus tremuloides*) âgés de 93 ans, et se situait sur une pente douce de 8 à 15 %. Tous les sols ont été classés comme des brunisols mélaniques. La formation de ce type de sol est le résultat des dépôts de surface glaciolacustres à texture grossière (Soil Classification Working Group, 1998). Le bas de la pente est un sol minéral argilo-limoneux modérément bien drainé, tandis que le milieu et le haut de la pente sont des sols minéraux limoneux à drainage rapide (Chapitre 2 : Tableau 1).

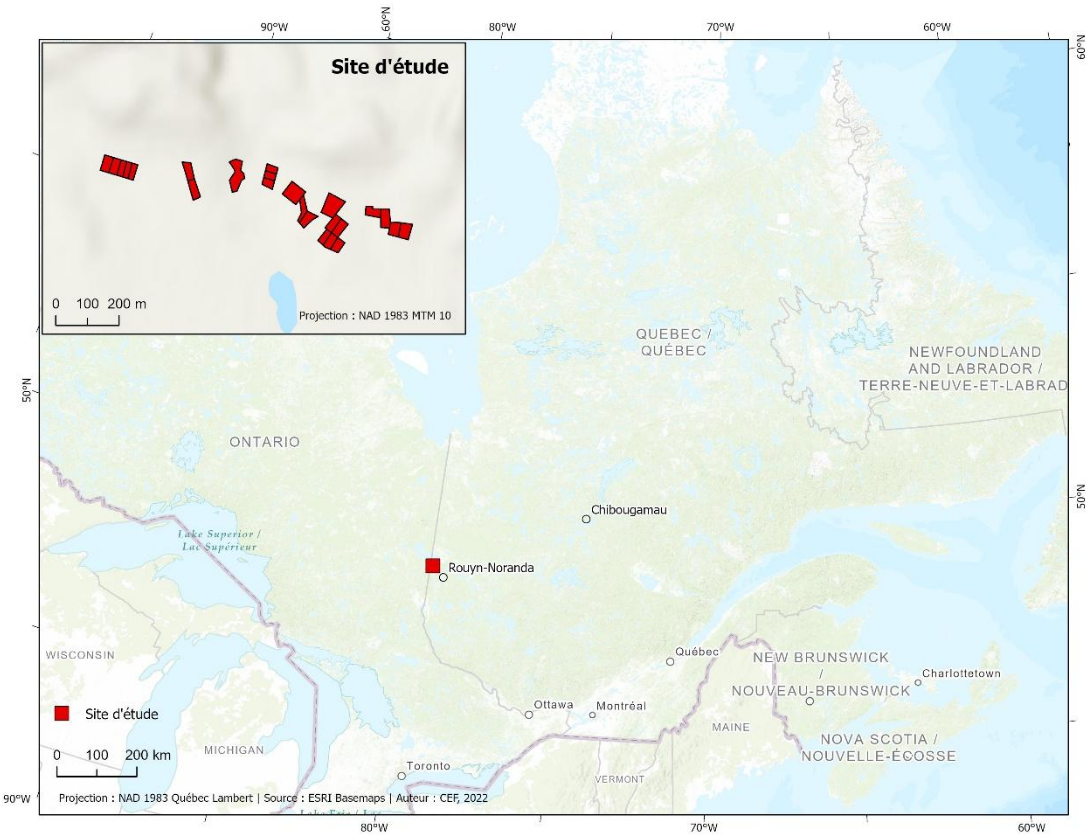
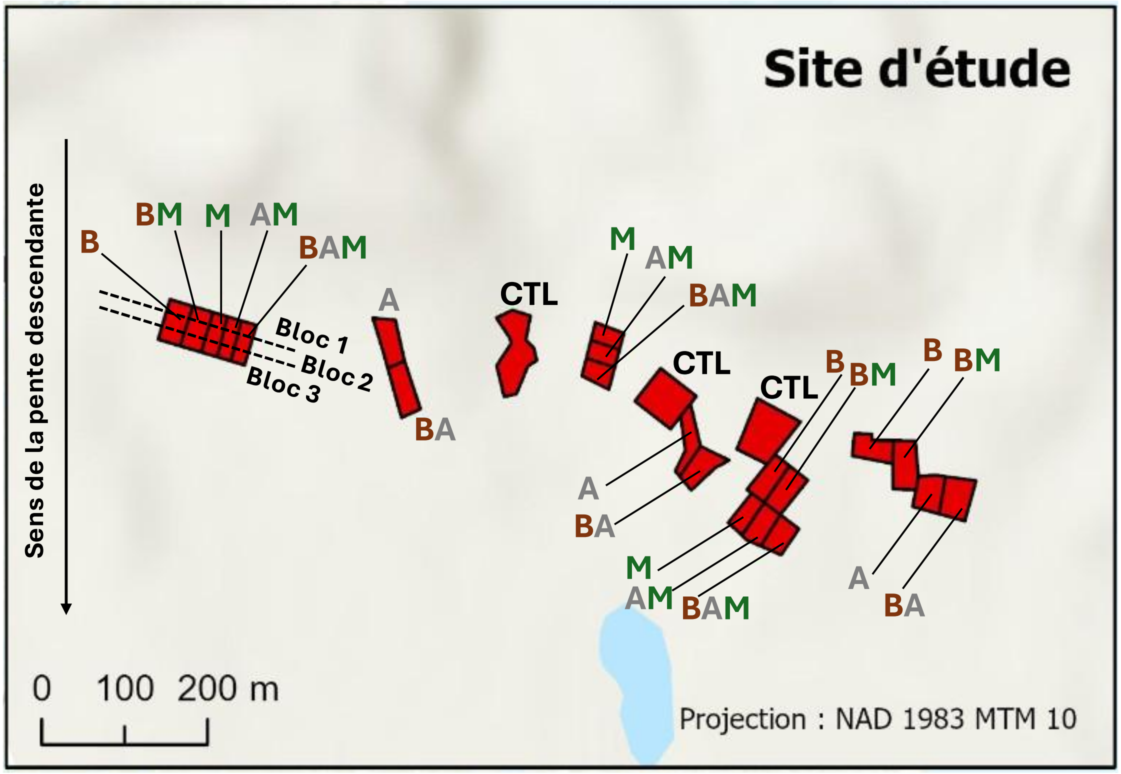


Figure 2 Localisation du site d'étude dans la province du Québec.

L'installation de l'expérimentation tire parti des sites qui ont connu un échec de régénération naturelle à la suite de la récolte forestière par coupe totale réalisée en 2016, et les résidus de coupe ont été laissés sur le site. L'absence de régénération naturelle a été observée en 2019, en raison de la compétition par la végétation de sous-bois et les conditions humides de sol au bas de la pente. L'expérience a été réalisée selon un plan en blocs aléatoires complets, avec trois blocs correspondant à un gradient longitudinal de 50 à 100 m de texture de sol et de disponibilité en eau (Figure 3). En novembre 2019, un scarifiage par décapage à l'aide d'une pelle mécanique munie d'un godet de 1 m de large a été réalisée en dessinant des placeaux de 3 m x 5 m (250 placeaux ha^{-1}). Les amendements ont été épandus mécaniquement sur la surface du sol dans chaque placeau en juin 2020 à l'aide d'une pelle mécanique munie d'un godet de 3 m de large, avant que les semis d'épinette blanche ne soient plantés en juillet 2020 pour remédier à l'absence de régénération naturelle. Chaque placeau a accueilli une moyenne de sept semis de trois ans plantés à 2 m de distance pour une densité de 1500 semis ha^{-1}. Les semis provenaient d'une pépinière provinciale et ont été produits dans des conteneurs 25-310 (25 cavités par conteneur, 310 cm^3 par cavité). Les traitements consistaient en l'application de biochar (B) (2,6 Mg ha^{-1}), de cendre de bois (A) (7 Mg ha^{-1}), de fumier (M) (105 Mg ha^{-1}), et un contrôle (sans amendement) (Chapitre 2 : Tableau 2). Ils ont été appliqués individuellement et dans une combinaison de deux et trois amendements (Chapitre 2 : Tableau 3). Les doses étaient cumulatives ; par exemple, le traitement cendre de bois-fumier (AM) consistait en 7 Mg ha^{-1} de A et 105 Mg ha^{-1} de M. Le biochar a été produit industriellement à partir de compost ligneux d'écorces anciennes, tandis que les cendres de bois proviennent de la combustion de tremble, et le fumier provenait d'une exploitation locale de bovins.



wood Ash (cendres de bois); Biochar; ConTroL (témoin); Manure (fumier)

Figure 3 Représentation du dispositif expérimental en blocs aléatoires complets, établi le long d'un gradient de texture de sol, selon une pente descendante. Les traitements comprenaient l'application d'amendements seuls, en combinaisons de deux ou trois, ainsi qu'un témoin sans amendement.

2. IMPACT OF SINGLE AND COMBINED SOIL AMENDMENTS ON THE GROWTH AND FOLIAR NUTRIENTS OF WHITE SPRUCE (*PICEA GLAUCA*) ON A POORLY REGENERATED LOGGED SITE

Ce chapitre a été publié dans la revue *Canadian Journal of Forest Research* en janvier 2025, https://doi.org/10.1139/cjfr-2024-0195.

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2.1 Résumé

Les sols des forêts boréales mixtes sont parfois sujets à des échecs de régénération après une coupe à totale, principalement en raison de la végétation de compétition et de l'altération des conditions du sol. Cette étude examine les effets de l'application de plusieurs amendements de sol pour améliorer la croissance des plantations d'épinettes blanches sur des sites forestiers mal régénérés. Le biochar (2,6 Mg ha^{-1}), les cendres de bois (7 Mg ha^{-1}) et le fumier (105 Mg ha^{-1}) ont été utilisés seuls ou en combinaison, et leurs effets sur la croissance des semis d'épinette blanche et les nutriments foliaires ont été évalués après deux saisons de croissance. Bien que le biochar et les cendres de bois aient été fréquemment utilisés, leur combinaison avec le fumier a été limitée dans les forêts boréales. En utilisant un dispositif expérimental en blocs aléatoires complets, nous avons mesuré le pH du sol, la lumière, la croissance des arbres, la surface foliaire spécifique et la nutrition foliaire. Le fumier a augmenté de manière significative la croissance des semis (+ 37 %) par rapport aux traitements sans fumier. Il a également augmenté l'azote (+ 17 %) et le phosphore (+ 14 %) foliaires. Les cendres de bois ont augmenté l'azote (+ 7 %), le phosphore (+ 15 %), le potassium (+ 19 %) et le calcium (+ 29 %) foliaires. Le biochar, sans cendres de bois, a diminué l'aluminium foliaire de 56 %. Nous concluons que le fumier représente une source importante d'azote et de phosphore pour la croissance des semis. Cette recherche met en évidence le potentiel des combinaisons d'amendements pour améliorer la croissance et la nutrition foliaire des semis dans les écosystèmes forestiers boréaux mal régénérés, par exemple lorsque l'utilisation d'herbicides est interdite.

Mots-clés : Biochar, Cendre de bois, Fumier, Amendement de sol, Croissance des semis, Nutrition foliaire

2.2 Abstract

Regeneration failure is occasionally encountered in the boreal mixed forest following clear-cutting, primarily due to competing vegetation and altered soil conditions. This study investigates the effects of applying several soil amendments to improve white spruce plantation growth on poorly regenerated forest sites. Biochar (2.6 Mg ha^{-1}), wood ash (7 Mg ha^{-1}), and manure (105 Mg ha^{-1}) were used alone or in combination, with effects on foliar elements and seedling growth assessed after two growing seasons. While biochar and wood ash have been frequently used, combining them with manure has been limited in boreal forests. Using a randomized complete block design, we measured soil pH, incident light, seedling growth, specific leaf area, and foliar nutrition. Manure significantly increased seedling growth (+37%) compared to treatments without it. It also increased foliar nitrogen (+17%) and phosphorus (+14%). Wood ash increased foliar nitrogen (+7%), phosphorus (+15%), potassium (+19%) and calcium (+29%). Biochar, without wood ash, decreased foliar aluminum by 56%. We conclude that manure represented an important nitrogen and phosphorus source for seedling growth. This research highlights the potential of amendment combinations for improving growth and foliar nutrition of seedlings in poorly regenerated boreal forest ecosystems, for example where herbicide use is prohibited.

Keywords: Biochar, Wood ash, Manure, Soil amendment, Seedling growth, Foliar nutrition

2.3 Introduction

Clear-cutting is widely applied in boreal forests for timber production. However, it can sometimes compromise natural regeneration (Keenan & Kimmins, 1993). Forest soils in the mixed boreal region are generally nitrogen (N) and phosphorus (P) deficient (Maynard et al., 2014). Intensive harvesting may also lead to an increase in competition by understory vegetation, which can rapidly invade the forest site, disrupt tree re-establishment and hinder tree growth due to competitive effects on light availability and soil micronutrients (Jobidon, 2000). Vegetation management through mechanical release is a high-cost approach (Homagain et al., 2011), and the use of chemical herbicides in forestry is becoming more restrictive (Thiffault & Roy, 2011). In this context where competing vegetation has caused a regeneration failure, soil amendments may offer a sustainable solution to reclaim poorly regenerated post-harvest forest sites and accelerate seedling growth in forest plantations, especially in situations where the use of herbicides is forbidden.

Massive quantities of by-products are generated by the agriculture and forestry sectors. Combining by-products with different properties to amend nutrient-deficient soil and to counter competition for nutrients could contribute to improving fertility and increasing seedling growth, yet knowledge gaps persist regarding their individual and combined impacts. Biochar is a carbon-rich soil amendment derived from pyrolyzed organic matter. It is primarily used in agriculture, but interest in using it in forestry has grown over the past decade (Bruckman & Pumpanen, 2019). Biochar contains important concentrations of macro-elements but it is nitrogen-poor (Ippolito et al., 2015). Its application generally results in long-term carbon sequestration (Lehmann et al., 2015) and increases soil pH, potentially serving as a lime substitute (Thomas & Gale, 2015). Its co-application with an N source improves N retention and seedling growth (Joseph et al., 2021; Robertson et al., 2012). However, its impact on tree growth varies, with studies showing positive (Thomas & Gale, 2015), neutral and negative effects (Joseph et al., 2021). Richard et al. (2018) attributed improved short-term growth of seedlings to increased water-holding capacity and cation exchange capacity.

In contrast to biochar, wood ash is an inorganic amendment rich in macro-nutrients which lacks nitrogen (Pitman, 2006). It serves as an efficient liming and fertilizing agent. However, it can be a source of heavy metal and dioxin contamination (Augusto et al., 2008). Wood ash effect on tree growth is variable according to tree species and size, initial soil conditions, and time since application (Reid & Watmough, 2014). Since biochar and wood ash are N-poor, they should be combined with another nitrogen source (Augusto et al., 2008; Joseph et al., 2021).

Manure is nitrogen-rich and can benefit forest soils by increasing carbon concentrations as it is a source of organic matter (Lafleur et al., 2012). Although the impact of manure on agricultural soil fertility is widely documented (Rayne & Aula, 2020), its use in a boreal forest context is scarce and only a few studies documented its effect on soil fertility and tree growth (Han et al., 2016; Lafleur et al., 2012; Larcheveque et al., 2011). Results showed that manure fertilization enhances soil pH, soil N concentrations, available P, exchangeable potassium (K), calcium (Ca), and magnesium (Mg), as well as foliar N and K, hence improving soil quality and tree growth (Han et al., 2016; Lafleur et al., 2012). However, manure may contain weed propagules (Mendonça et al., 2021), which can introduce non-native species, increasing competition for target plants (Buss et al., 2018).

A complete assessment of amendment effects should include both soil properties and foliar nutrition. Foliar nutrient analysis provides information on the nutrient status and overall plant health. Moreover, specific leaf area (SLA) serves as a good indicator of plant growth and nutrient acquisition (Garnier et al., 2016), and provides valuable insights into the physiological responses of trees to soil amendments, but few studies have assessed the impact of amendments on this functional trait. Therefore, this study represents an opportunity to investigate the individual and combined effects of soil amendments, i.e. biochar, wood ash, and manure, to improve seedling growth on a forest site four years after clearcutting. Specifically, we assessed if (1) amendment application had positive effects on white spruce (*Picea glauca*) seedling growth in the short-term, and (2) whether soil amendments increased foliar nutrients and SLA, which may have a positive effect on long-term growth. We hypothesized that the application of each amendment would enhance foliar nutrient concentrations according to amendment properties, because of direct nutrient input to the soil and improved nutrient availability through the liming effect. However, we did not expect increased seedling growth and SLA in the case of individual or combined wood ash and biochar application because of a lack of nitrogen. On the other hand, we anticipated the additional N and P from manure would increase seedling growth, SLA and foliar nutrition.

2.4 Materials and methods

2.4.1 Study site

The research took place in the Lake Duparquet Research and Teaching Forest (FERLD) located in the Abitibi area of northwestern Quebec (48°30' N, 79°22' W). The climate of the study area is continental, characterized by an average annual temperature of 1°C and yearly precipitation of 989 mm. Notably, 30% of this precipitation falls as snow (Environnement Canada, 2019). The experiment was conducted in the mixedwood boreal forest within the balsam fir (*Abies balsamea*) - white birch (*Betula papyrifera*) domain (Saucier et al., 2003). The study site was located on a slope (altitude between 69 m and 320 m) and was previously dominated by a jack pine (*Pinus banksiana*) forest with aspen (*Populus tremuloides*) aged 93 years old. The forest was clear-cut in 2016, and logging residues were left on the site. The lack of natural regeneration was observed in 2019, due to competition of ground vegetation and wetness at the bottom of the slope, which prompted the study.

The experiment was set up as a randomized complete block design, with three blocks according to a longitudinal gradient of soil texture and water availability: the bottom of the slope was a moderately well-drained clay-loam mineral soil, whereas the middle and top of the slope were a rapidly draining loam mineral soil (Tableau 1). A scarification by scraping 3 x 5 m plots using an excavator with a 1 m bucket (250 plots ha^{-1}) was carried out in November 2019. Amendments were mechanically spread on the soil surface in each plot in June 2020, before white spruce seedlings were planted in July 2020 to address the lack of natural regeneration. Each plot hosted an average of seven three-year-old seedlings planted 2 m apart (1500 seedlings ha^{-}

^{1}). Seedlings came from a provincial nursery and were produced in 25-310 containers (25 cavities per container, 310 cm^3 per cavity). Treatments consist of biochar (B) (2.6 Mg ha^{-1}), wood ash (A) (7 Mg ha^{-1}), manure (M) (105 Mg ha^{-1}), and control (no amendment) (Tableau 2). They were applied individually and in a combination of two and three amendments (Tableau 3). The doses were cumulative; for example, the wood ash-manure (AM) treatment consist of 7 Mg ha^{-1} of A and 105 Mg ha^{-1} of M. Biochar and wood ash were industrially produced from woody compost of legacy bark and aspen respectively, whereas manure was sourced from a local beef cattle farm

2.4.2 Field measurements and laboratory analyses

Fieldwork was carried out from early September to mid-October 2022. All measurements and sampling were completed at the end of the second growing season of seedlings, except for light measurements which were taken in late July 2023. Data was collected in three randomly selected plots (n = 3) for each treatment and block.

Seedling sampling and needle chemical analyses. In each plot, we measured annual growth of all seedlings, which is the length of annual shoot (season 2022). Survival (%) was measured by counting the number of live and dead seedlings. In each plot, three seedlings were randomly selected for needle sampling to form a composite sample. Current-year needles were collected for SLA and chemical analyses. Needles were put in a plastic bag with distilled water to preserve their water saturation and kept in the fridge at 2°C for a maximum of 48 hours before leaf area measurements. Needles were dried with a cotton tissue and leaf area was measured using a scanner (1200 dpi) and the Winfolia software (WinFOLIA Pro 2022, Régent Instruments Inc., Québec, QC, Canada). Foliar dry mass was measured by weighing 100 needles after being dried in the oven at 60°C for 72h. Needles were ground to 2 mm using an ultra centrifugal Mill Retsch ZM 200 Ultra (Haan, Germany) before chemical analyses. Total carbon (C) and nitrogen (N) concentrations were determined by dry combustion using a Vario MAX cube elemental analyzer (Elementar, Langenselbold, Germany). Macro- and micronutrients concentrations [phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), copper (Cu), zinc (Zn), aluminium (Al), boron (Bo)] were measured by inductively coupled plasma (ICP) using an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA) after ashing at 500°C for 2 hours and recovery in 1 M HCl following Kalra (1997). Nutrient content of the needles was measured using the dry mass of 100 needles and their nutrient concentration (content = concentration × foliar dry mass).

Soil sampling and chemical analyses. The soil was sampled 30 to 50 cm away from each of the three preselected seedlings in each plot at depths of 0-15 cm and 15-30 cm using an auger. Soil samples were then air-dried and ground to 2 mm using a Humboldt hammer mill (Dayton Electric Mfg. Co., Lake Forest, IL 60045 USA). Composite samples were formed by mixing equal weighted quantities of dried and ground soil from the three samples. Soil pH was measured in 0.01 M $CaCl_2$ solution (Hendershot et al., 2008b) and soil texture was measured using the hydrometer method (Kroetsch & Wang, 2008). Available P, exchangeable K, Ca, Mg, Mn, Al, iron (Fe), and sodium (Na) were obtained through the use of a Mehlich III extraction solution (Ziadi & Sen Tran, 2008). Subsequently, these elements were subjected to analysis using inductively coupled plasma (ICP) and an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA). The effective cation exchange capacity (CEC) was calculated by summing the exchangeable cations (K, Ca, Mg, Mn, Al, Fe, Na) (Hendershot et al., 2008a). Soil samples were analyzed for mineral nitrogen ($N.NH_4^+$, $N.NO_3^-$) by the flow injection analysis (FIA) on a Lachat QuikChem® 8500 Series 2 following Maynard et al. (2008).

Soil amendments were air-dried and ground to 2 mm using a Humboldt hammer mill (Dayton Electric Mfg. Co., Lake Forest, IL 60045 USA). Both soil samples and amendments total C and N were determined by dry combustion using a Vario MAX cube elemental analyzer (Elementar, Langenselbold, Germany). Total P, K, Ca, Mg, Mn, Cu, Zn, Al, Fe, molybdenum (Mo), and B were measured by inductively coupled plasma (ICP) using an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA) after ashing at 500°C for 2 hours and recovery in 1 M HCl following Kalra (1997).

Light measurements. The light was measured using a plant canopy analyzer LAI-2000 (LI-COR Inc., Lincoln, Nebr.) at 30 cm at the base of two randomly selected seedlings per plot. We also measured light in an open field adjacent to each plot as a reference. The incident light was obtained as a proportion of the light at the base of the seedling relative to the reference light.

Tableau 1 Soil properties before amendment application.

	Blocks		
	Bottom	**Middle**	**Top**
Texture			
Sand (%)	37.8 *(22.0)*	40.9 *(21.6)*	47.8 *(25.5)*
Clay (%)	31.8 *(19.3)*	25.9 *(17.3)*	24.5 *(17.9)*
Silt (%)	30.4 *(12.0)*	33.2 *(11.4)*	27.7 *(14.6)*
Chemical properties			
pH	5.0 *(0.6)*	4.5 *(0.1)*	4.4 *(0.1)*
C (g kg^{-1})	14.4 *(5.9)*	19.0 *(14.5)*	20.8 *(21.8)*
N (g kg^{-1})	0.8 *(0.2)*	1.0 *(0.4)*	1.1 *(0.7)*
Available P (mg kg^{-1})	2.3 *(0.4)*	5.6 *(3.5)*	7.9 *(7.6)*
Exchangeable K^+ (cmolc kg^{-1})	0.2 *(0.1)*	0.2 *(0.1)*	0.3 *(0.1)*
Exchangeable Ca^{2+} (cmolc kg^{-1})	5.5 *(4.2)*	3.0 *(1.5)*	5.5 *(4.1)*
Exchangeable Mg^{2+} (cmolc kg^{-1})	1.9 *(1.5)*	1.2 *(0.9)*	2.3 *(1.7)*
Exchangeable Mn^{2+} (cmolc kg^{-1})	0.1 *(0.0)*	0.1 *(0.1)*	0.1 *(0.1)*
Exchangeable Al^{3+} (cmolc kg^{-1})	16.3 *(4.5)*	16.6 *(3.9)*	15.8 *(2.1)*
Exchangeable Fe^{2+} (cmolc kg^{-1})	1.7 (*0.4)*	1.5 *(0.9)*	1.7 *(0.2)*
Exchangeable Na^+ (cmolc kg^{-1})	0.1 *(0.0)*	0.1 *(0.0)*	0.1 *(0.1)*
N.NH_4^+ (mg kg^{-1})*	1.6 *(0.8)*	3.3 *(1.4)*	4.8 *(1.9)*
N.NO_3^- (mg kg^{-1})*	0.0 *(0.0)*	0.0 *(0.0)*	0.2 *(0.6)*
CEC (cmolc kg^{-1})	25.7 *(1.96)*	22.7 *(1.7)*	25.9 *(5.44)*

Note: Data provides the mean and standard deviation *(in italics)* for each block. *Values < 0.1 were replaced by zero.

Tableau 2 Chemical properties of amendments.

Chemical properties (g kg^{-1})	**Biochar**	**Wood ash**	**Manure**
Carbon	715 *(15)*	146	194 *(10)*
Nitrogen	1.3 *(0.0)*	1	10.6 *(0.5)*
C/N	556 *(2.8)*	122	18.3 *(0.2)*
Phosphorus	0.8 *(0.1)*	4.4	1.3 *(0.0)*
Potassium	2.7 *(0.2)*	26.1	1.0 *(0.0)*
Calcium	7.0 *(0.6)*	148	5.7 *(0.1)*
Magnesium	7.2 *(0.5)*	13.4	2.6 *(0.0)*
Manganese	0.4 *(0.0)*	1.1	0.3 *(0.0)*
Copper	0.0 *(0.0)*	0.0	0.03 *(0.0)*
Zinc	0.0 *(0.0)*	0.8	0.1 *(0.0)*
Aluminium	1.3 *(0.1)*	14.9	4.1 *(0.1)*
Iron	3.8 *(0.4)*	14.7	6.1 *(0.2)*
Molybdenum	0.0 *(0.0)*	0.0	0.0 *(0.0)*
Boron	0.0 *(0.0)*	0.1	0.0 *(0.0)*

Note: Data provides the mean and standard deviation *(in italics)* for each soil amendment. Standard deviation of wood ash is lacking because data was supplied by the manufacturing company.

Tableau 3 Chemical properties of amendments according to application rate.

Chemical properties	B	A	M	BM	BA	AM	BAM
Carbon ($Mg\ ha^{-1}$)	1.9 *(0.0)*	1.0	20.4 *(1.1)*	22.2 *(1.1)*	2.9 *(0.0)*	21.4 *(1.1)*	23.3 *(1.1)*
Nitrogen ($kg\ ha^{-1}$)	3.4 *(0.1)*	8.4	1112 *(55)*	1115 *(55)*	11.8 *(0.1)*	1120 *(55)*	1124 *(55)*
Phosphorus ($kg\ ha^{-1}$)	2.0 *(0.1)*	30.8	138 *(3.2)*	140 *(3.2)*	32.8 *(0.1)*	168 *(3.2)*	170 *(3.2)*
Potassium ($kg\ ha^{-1}$)	7.0 *(0.4)*	182	108 *(3.2)*	115 *(3.2)*	189 *(0.4)*	291 *(3.2)*	298 *(3.2)*
Calcium ($kg\ ha^{-1}$)	18.2 *(1.5)*	1035	597 *(8.4)*	616 *(8.4)*	1053 *(1.5)*	1632 *(8.4)*	1650 *(8.4)*
Magnesium ($kg\ ha^{-1}$)	18.8 *(1.4)*	93.5	270 *(4.2)*	289 *(4.2)*	112 *(1.4)*	363 *(4.2)*	382 *(4.2)*
Manganese ($kg\ ha^{-1}$)	1.0 *(0.0)*	7.8	27.3 *(0.0)*	28.3 *(0.0)*	8.7 *(0.0)*	35.1 *(0.0)*	36.0 *(0.0)*
Copper ($kg\ ha^{-1}$)	0.0 *(0.0)*	0.3	1.1 *(0.0)*	1.1 *(0.0)*	0.3 *(0.0)*	1.3 *(0.0)*	1.0 *(0.0)*
Zinc ($kg\ ha^{-1}$)	0.1 *(0.0)*	5.5	7.4 *(0.0)*	7.4 *(0.0)*	5.5 *(0.0)*	12.8 *(0.0)*	13.0 *(0.0)*
Aluminium ($kg\ ha^{-1}$)	3.5 *(0.2)*	104	426 *(13.7)*	430 *(13.7)*	108 *(0.2)*	531 *(13.7)*	534 *(13.7)*
Iron ($kg\ ha^{-1}$)	10.0 *(0.9)*	103	645 *(24.2)*	655 *(24.2)*	113 *(0.9)*	748 *(24.2)*	758 *(24.2)*
Molybdenum ($kg\ ha^{-1}$)	0.0 *(0.0)*	0.0	1.1 *(0.0)*	1.1 *(0.0)*	0.0 *(0.0)*	1.1 *(0.0)*	1.0 *(0.0)*
Boron ($kg\ ha^{-1}$)	0.0 *(0.0)*	0.8	1.1 *(0.0)*	1.1 *(0.0)*	0.9 *(0.0)*	1.9 *(0.0)*	2.0 *(0.0)*

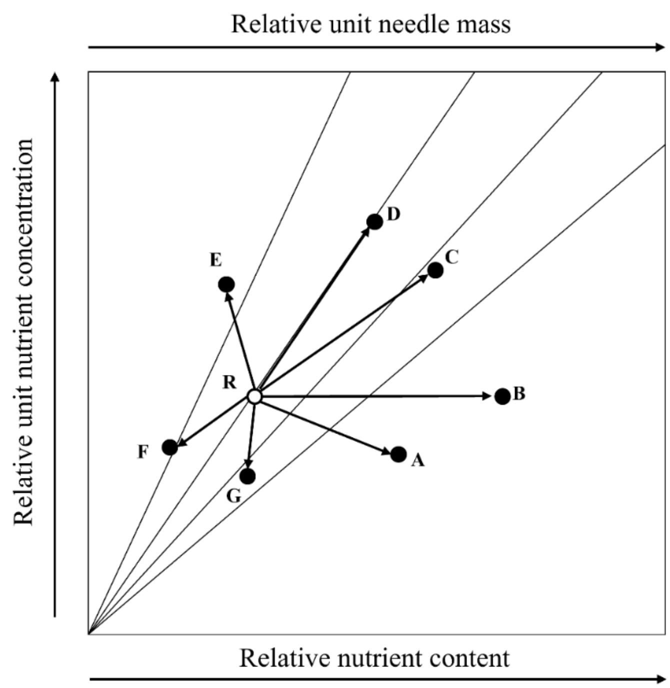
Note: Treatments correspond to biochar (B), wood ash (A), manure (M), biochar-manure (BM), biochar-wood ash (BA), wood ash manure (AM), and biochar-wood ash-manure (BAM). Data provides the mean and standard deviation *(in italics)* for each soil amendment. Standard deviation of wood ash is lacking because data was supplied by the manufacturing company.

2.5 Statistical approach

To compare the effect of each soil amendment used in the single and combined treatments, we created a binary factor of presence (1) and absence (0) of each of the three soil amendments biochar, wood ash and manure, and we considered the interaction between these three factors. We performed linear mixed models for each numerical variable separately. To estimate the parameters of the mixed model, the three interacting binary factors were set as fixed effects and block as a random effect. The plot was set as a random effect when multiple measures were taken in the plot. Pairwise post hoc multiple comparisons with Tukey's Honestly Significant Difference (Tukey HSD) test were used to assess differences between factor levels (Lenth et al., 2018).

Vector nomograms analysis was performed on foliar nutrient data to determine how seedlings responded to the presence or absence of soil amendments in treatments beyond the assessment of nutrient concentrations (Salifu & Timmer, 2001; Timmer, 1991). Nutrient concentrations, nutrient contents and foliar dry mass were used in this analysis. Nutrient data and foliar dry mass were standardized relative to the control treatment, which was assigned a foliar dry mass, as well as a nutrient concentration and a nutrient content of 100. The resulting vectors were interpreted in relation to the framework of Salifu and Timmer (2001) (Figure 4), which provides different options for nutritional interpretations (dilution, sufficiency, deficiency, luxury consumption, excess and depletion) depending on the direction of the vector. The length of the vector was important as it described the significance of the nutritional change induced by the treatment relative to the control.

To identify the variables explaining seedling growth and their effects, we performed a multiple linear regression analysis including all the variables measured in this study. We then ranked the resulting estimates by their p-values to assess their significance levels and to determine whether they positively or negatively influenced seedling growth. All statistical analyses were performed using R 4.2.1 software (R Core Team, 2021) with a significance level of $\alpha = 5\%$ for all analyses.



Vector direction	Change[1] in foliar: Mass	Concentration	Content	Interpretation
A	(+)	(-)	(+)	Dilution
B	(+)	0	(+)	Sufficiency
C	(+)	(+)	(+)	Deficiency
D	0	(+)	(+)	Luxury consumption
E	(-)	(++)	(+) or (-)	Excess
F	(-)	(-)	(-)	Excess
G	0 or (+)	(-)	(-)	Depletion

[1] (+) : Increased, (-) : Decreased, 0 : Unchanged

Figure 4 Framework for foliar nutritional interpretation of directional changes between treatments in unit needle mass, nutrient content, and nutrient concentration. Reproduced from Thiffault et al. (2006). [Soil Science Society of America Journal, Vol. 70, 694] with permission from [Evelyne Thiffault].

2.6 Results

2.6.1 Seedling growth

Overall survival of planted seedlings was 99.6% (± 2.3). Only manure increased annual shoot height growth of seedlings (Tableau 17, $p < 0.001$), by 37% in the single and combined soil amendment treatments (Figure 5).

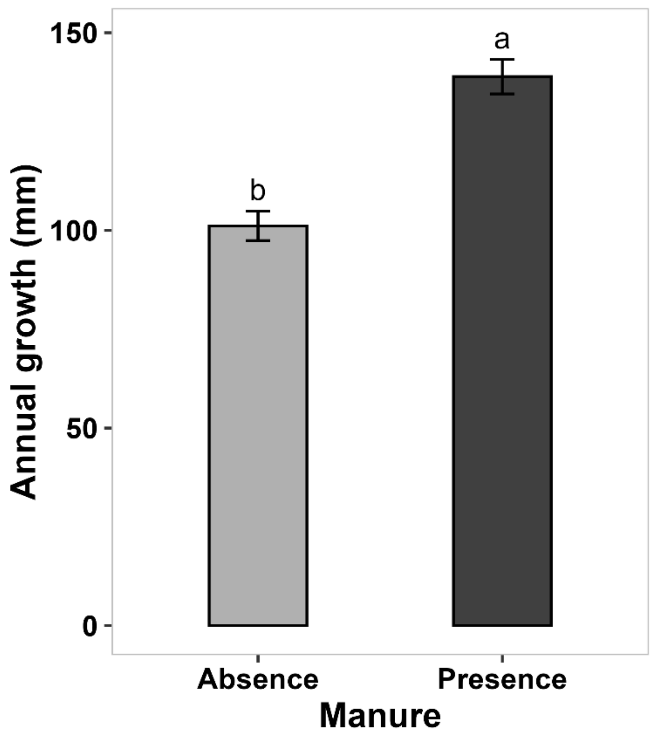


Figure 5 Mean (± standard error) of two years shoot height growth of white spruce seedlings according to the presence or absence of manure in treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

2.6.2 Foliar nutrients

Foliar macro-nutrients. Foliar N was influenced by manure (Tableau 17, $p < 0.001$) and wood ash additions (Tableau 17, $p < 0.05$), as they increased N concentrations by 17% and 7% respectively (Figures 6a, 6b). Foliar C/N was only influenced by manure addition (Tableau 17, $p < 0.001$); its presence reduced C/N ratios of seedlings by 17% relative to those not receiving manure (Figure 6c).

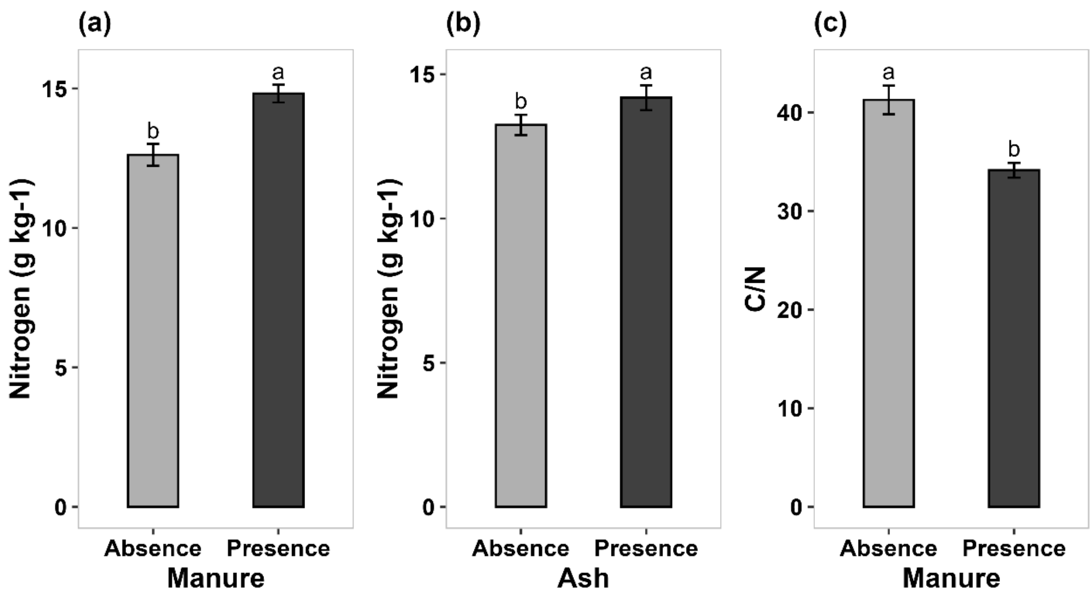


Figure 6 Mean (± standard error) foliar nitrogen concentrations according to the presence or absence of (a) manure and (b) wood ash in treatments, and (c) foliar C/N ratios of white spruce seedlings according to the presence or absence of manure in treatments, after two growing seasons. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed models.

Foliar Mg concentrations were similar among treatments (Tableau 17, $p > 0.05$), while foliar P differed according to manure and wood ash (Tableau 17, $p < 0.001$); P concentrations increased by 14% and 15% respectively (Figures 7a, 7b). Both foliar potassium (Tableau 17, $p < 0.001$) and calcium concentrations (Tableau 17, $p < 0.05$) increased with wood ash application; foliar K increased by 14% and foliar Ca by 29% relative to treatments without wood ash in the single and combined amendment treatments (Figures 7c, 7d).

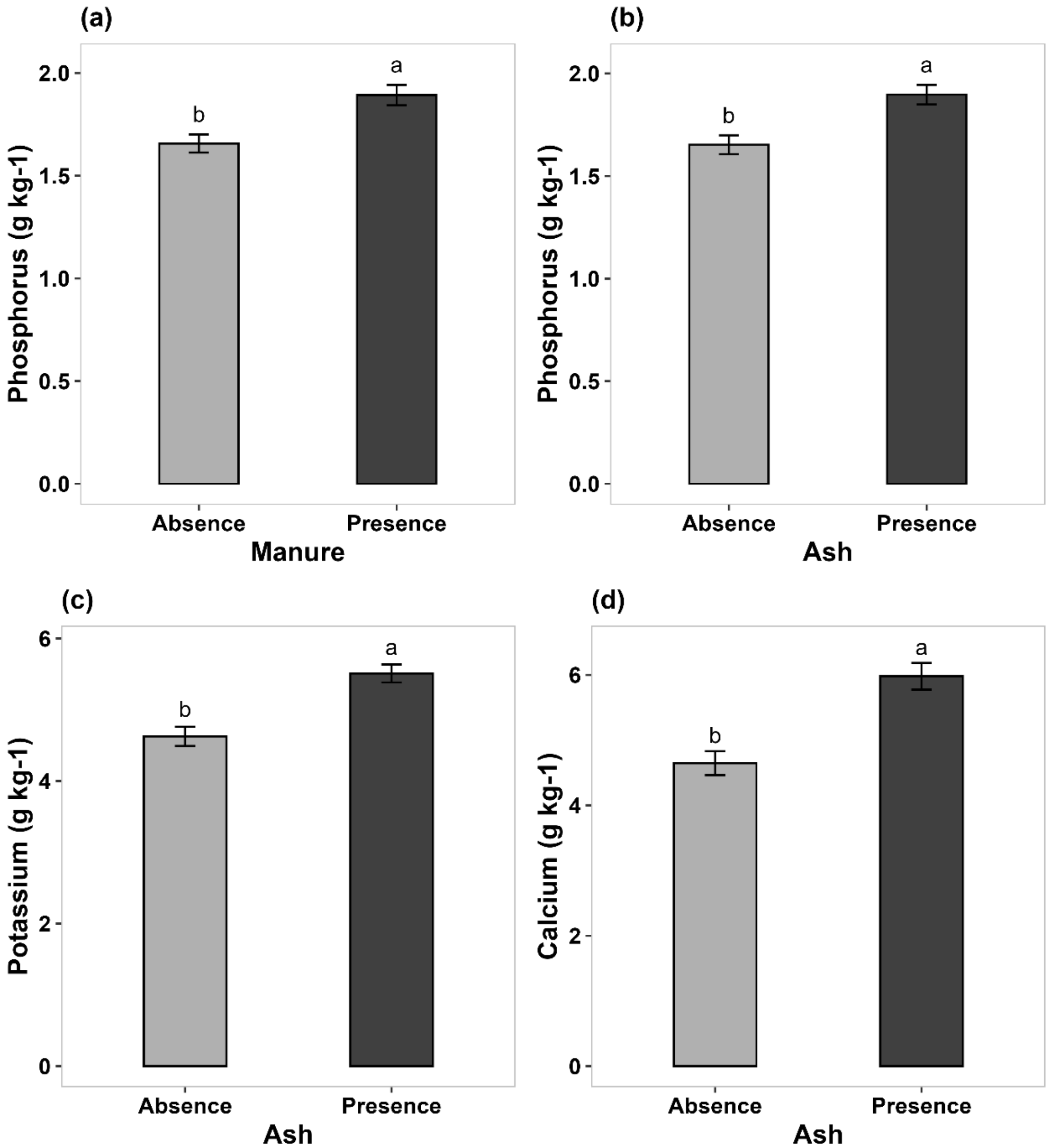


Figure 7 Mean (± standard error) foliar concentrations of phosphorus according to the presence or absence of (a) manure and (b) wood ash, and foliar concentrations of (c) potassium and (d) calcium according to the presence or absence of wood ash, after two growing seasons of white spruce seedlings. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed models.

Foliar micro-nutrients. Foliar Zn concentrations varied according to an interaction between biochar and wood ash (Tableau 17, $p < 0.05$), but pairwise comparisons showed no differences among treatments ($p > 0.05$). Foliar Cu concentrations differed according to wood ash (Tableau 17, $p < 0.05$), it increased by 26% compared to the absence of wood ash in treatments (Figure 8a). Foliar Al concentrations varied according to an interaction between biochar and wood ash (Tableau 17, $p < 0.05$), with biochar decreasing foliar Al by 56% in the absence of wood ash in treatments (Figure 8b). Foliar Bo concentrations changed according to a double interaction between biochar and wood ash, and wood ash and manure (Tableau 17, $p < 0.05$). Biochar increased foliar Bo by 41% in the absence of wood ash (Figure 8c), and wood ash increased foliar Bo by 73% in the absence of both biochar and manure (Figure 8d). Foliar Mn concentrations of spruce seedlings changed according to the simultaneous presence or absence of the three amendments (Tableau 17, $p < 0.05$). Presence of the three amendments decreased Mn concentrations except when biochar was present with wood ash and without manure, which increased foliar Mn by 49%, while the addition of biochar without wood ash and manure decreased foliar Mn by 27% (Tableau 4). The effect of the presence of manure, on the one hand, and that of wood ash, on the other, conditional on the presence or absence of two other amendments, decreased foliar Mn by an average of 42%. The strongest effect on Mn concentrations was found when wood ash was applied alone, as it decreased Mn by 46% (Tableau 4).

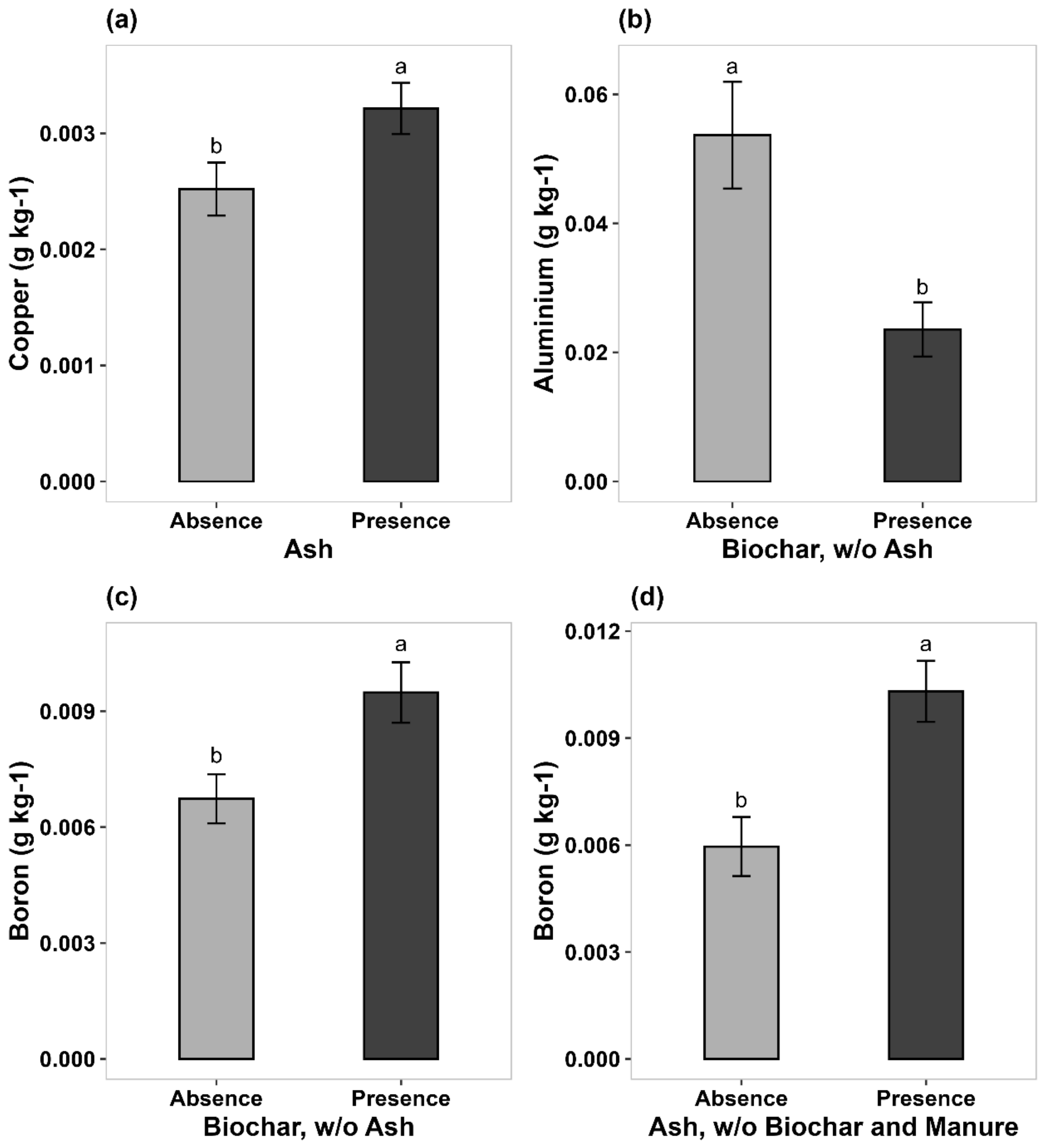


Figure 8 Mean (± standard error) foliar (a) copper concentrations with wood ash application, (b) aluminium concentrations with biochar and wood ash combination, and boron concentrations showing the double interaction between (c) biochar and wood ash, and (d) wood ash and manure, after two growing seasons of white spruce seedlings. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

Tableau 4 Results of pairwise comparisons of foliar manganese concentrations with or without biochar (B), wood ash (A) and manure (M) amendments. Zero and one stand for absence and presence of soil amendments respectively. See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

	Biochar	Wood ash	Manure
Manganese	B0 > B1 | A0 M0	A0 > A1 | B0 M0	M0 > M1 | B0 A0
	B0 < B1 | A1 M0	A0 > A1 | B1 M1	M0 > M1 | B1 A1

2.6.3 Vector analysis

Vector nomograms for wood ash (Figure 9) and manure (Figure 10) treatments showed that the length of the vector indicating the presence of the amendment (presence vector) was longer than that of the vector representing the absence of amendment (absence vector), suggesting a stronger effect of the amendment on seedling nutrition. All arrows showed deficiency effects (Figure 4, Shift C), suggesting that spruce seedlings were deficient in foliar nutrients, and the important amplitude of the presence vectors showed that spruce seedlings responded positively to the amendments. This was the case with wood ash for N, P, K and Ca (Figure 9), and with manure for N, P and K (Figure 10). The length of the vectors of foliar P indicated a greater deficiency of this element and a positive effect of manure and wood ash on P foliar nutrition compared to other foliar nutrients. Manure had a greater effect on foliar N nutrition than wood ash, whereas the effects of manure and wood ash on foliar K nutrition were comparable.

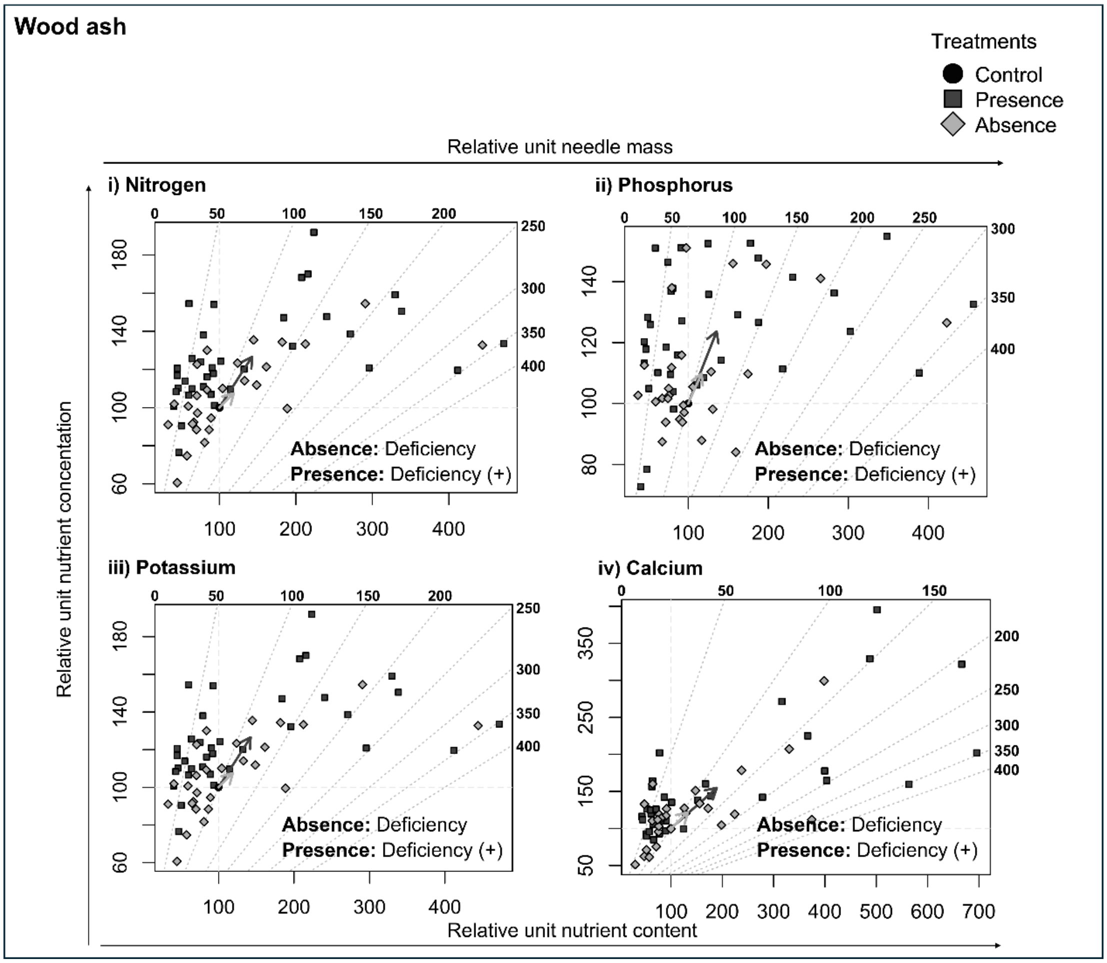


Figure 9 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) nitrogen, (ii) phosphorus, (iii) potassium and (iv) calcium of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of wood ash, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

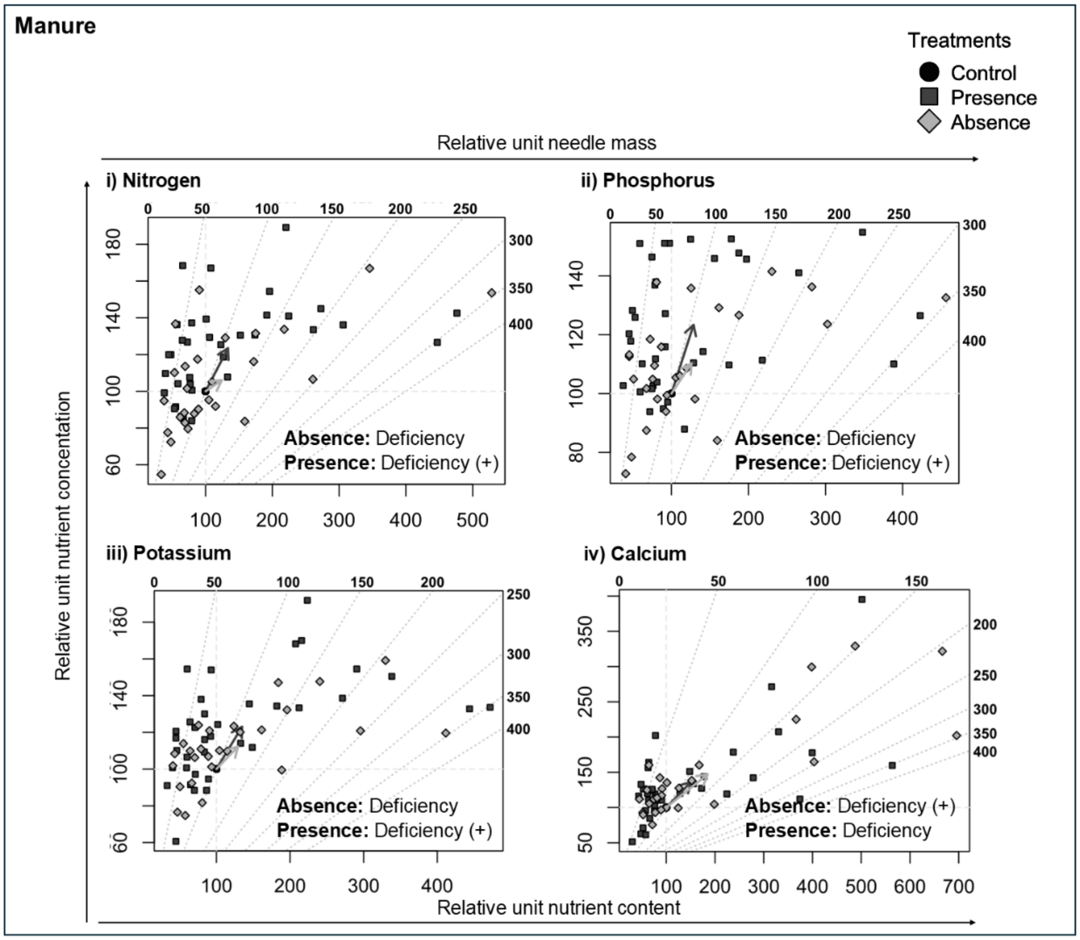


Figure 10 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) nitrogen, (ii) phosphorus, (iii) potassium and (iv) calcium of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of manure, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

2.6.4 Incident light and specific leaf area

Incident light significantly changed when manure was applied (Tableau 17, $p < 0.01$), as seedlings received 54% less light compared to the absence of manure amendment (Figure 11). Specific leaf area of spruce seedlings changed according to the simultaneous presence or absence of the three amendments (Tableau 17, $p < 0.05$). The presence of biochar, with manure and without wood ash, decreased SLA by 14%, whereas wood ash increased SLA by 30% in the presence of both biochar and manure. Manure, with wood ash and with or without biochar, increased SLA by 23% (Figure 12, Tableau 5).

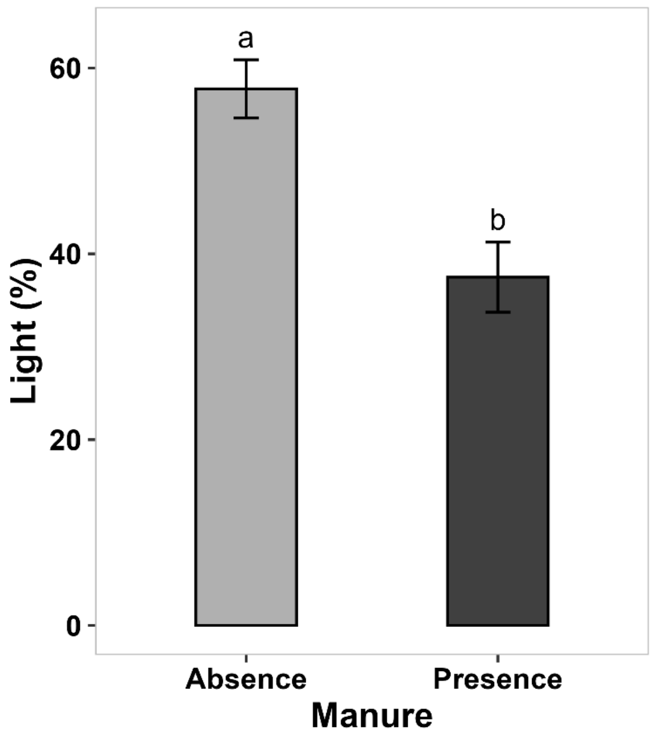


Figure 11 Mean (± standard error) incident light after two growing seasons according to the presence or absence of manure in treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

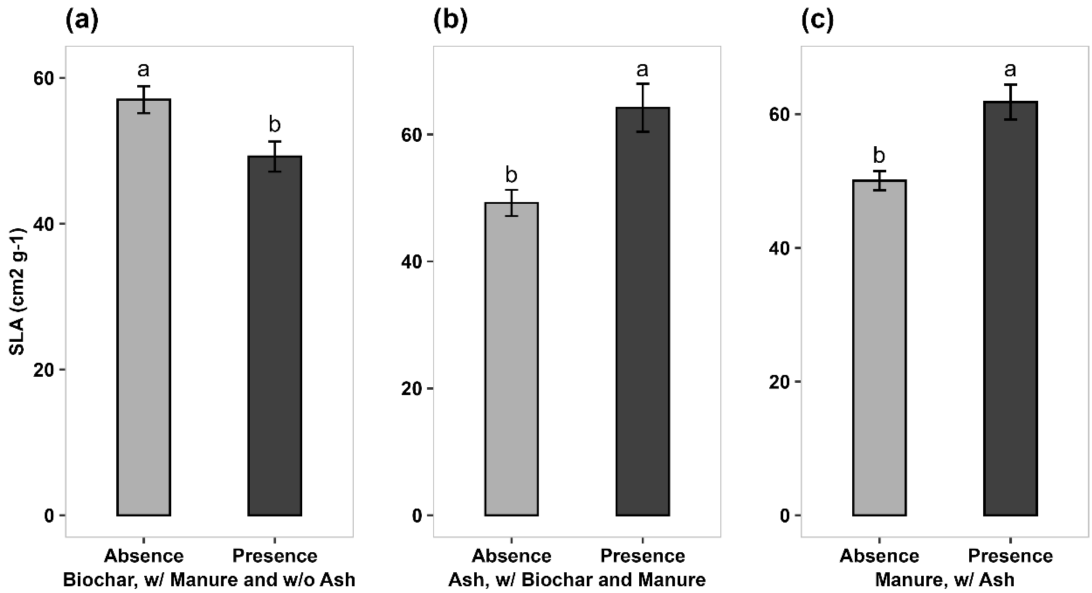


Figure 12 Mean (± standard error) specific leaf area (SLA) of seedlings after two growing seasons according to the triple significant interaction between the presence or absence of biochar, wood ash and manure in treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

2.6.5 Soil pH

A significant effect of the interaction between wood ash and soil depth was found for soil pH (Tableau 17, $p < 0.001$), as well as between biochar, manure, and soil depth (Tableau 17, $p < 0.05$). Pairwise comparisons showed that wood ash did not change soil pH at either soil depth ($p > 0.05$). Similarly, biochar with or without manure, and manure with or without biochar, did not alter soil pH at either soil depth. Soil pH increased from 4.52 to 4.79 between soil depths 15-30 cm to 0-15 cm, in the presence of biochar wood ash and absence of manure, and from 4.81 to 5.09 between soil depths 15-30 cm to 0-15 cm, with wood ash and manure in the absence of biochar (Tableau 5).

Tableau 5 Results of pairwise comparisons of specific leaf area (SLA) and soil pH with or without biochar (B), wood ash (A) and manure (M) amendments. Zero and one stand for absence and presence of soil amendments respectively. See supplementary material Tableau 17 for the results of ANOVA applied to the linear mixed model.

	Biochar	**Wood ash**	**Manure**	**Soil depth**
SLA	B0 > B1 | A0 M1	A0 < A1 | B1 M1	M0 < M1 | B0 A1	
			M0 < M1 | B1 A1	
pH	B0 <> B1 | M0, M1, 0-15 cm and 15-30 cm	A0 <> A1 | 0-15 cm and 15-30 cm	M0 <> M1 | B0, B1, 0-15 cm and 15-30 cm	pH 0-15 cm > pH 15-30 cm | B1A1M0
				pH 0-15 cm > pH 15-30 cm | B0A1 M1

2.6.6 Relationships among variables and their impact on seedling growth

The model testing all parameters measured in this study revealed that variables that best explained seedling growth were incident light, foliar calcium (Ca), zinc (Zn), soil pH at 15-30 cm soil depth, foliar magnesium (Mg), manganese (Mn) and copper (Cu) concentrations in decreasing order of significance. These variables were either positively or negatively related to seedling growth (Tableau 6). The adjusted R-squared indicated that the model explained approximately 47.98% of the variability in seedling growth. Among these variables, incident light and soil pH decreased growth, while foliar Zn and Cu increased growth. Adverse effects of foliar Ca, Mg and Mn on seedling growth were observed.

Tableau 6 The detailed parameter estimates for the multiple linear regression model describing the effects of soil pH, incident light, specific leaf area (SLA) and foliar nutrient concentrations on seedling growth. Values in bold indicate statistically significant differences ($p < 0.05$), and variables are classified according to their significance in the analysis.

	Estimate	Standard error	t-value	p-value
Intercept	119.38	3.29	36.24	**<2e-16**
Light	-16.31	-3.60	-4.53	**3.03e-05**
Ca	-19.35	6.42	-3.04	**0.0038**
pH 15-30 cm	-16.23	5.99	-2.71	**0.0089**
Zn	16.95	6.70	2.53	**0.014**
Mn	-9.44	4.18	-2.26	**0.028**
Cu	6.9	4.34	2.23	**0.030**
Mg	-7.89	3.74	-2.11	**0.039**
Al	-4.99	3.60	-1.39	0.17
N	6.52	5.56	1.17	0.24
pH 0-15 cm	6.00	6.77	0.89	0.38
B	2.67	3.58	0.75	0.46
K	2.92	6.15	0.48	0.64
P	-3.14	7.22	-0.43	0.66
SLA	-1.17	4.25	-0.28	0.78

2.7 Discussion

2.7.1 Factors influencing seedling growth and nutrient dynamics

In line with our hypothesis, manure significantly increased seedling growth by 37% (Figure 5). Results were similar whether manure was applied alone or with biochar, wood ash, or both. As N and P are usually the most limiting nutrients for tree growth in boreal forests (Maynard et al., 2014), manure mitigated N and P deficiencies (Tableaux 2, 3), resulting in increased seedling growth and foliar N and P concentrations (Figure 6a, 7a). Foliar N and P correlated positively with seedling growth (Figure 23; $r = 0.33$, $p < 0.01$). This was supported by vector analysis showing that spruce seedlings were deficient in N and P and responded positively to manure addition (Figure 10). Our vector analysis also indicated that seedlings were more deficient in P than N, but this must be interpreted with caution as needles were not collected on the first year after the application of amendments (Weetman, 1989) and N may have been diluted by seedling growth during the second growing season.

As hypothesized, manure increased SLA (Figure 12c), foliar N concentrations (Figure 6a), and reduced C/N ratios (Figure 6c), consistent with nutrient-rich environments (Lavorel et al., 2007; Zhang et al., 2020). While increased SLA generally indicates improved resource acquisition and growth (Garnier et al., 2016; Westoby, 1998; Wright et al., 2004), we found weak correlations between SLA and leaf nitrogen concentrations (Figure 23; $r = 0.25$, $p < 0.05$) and growth (Figure 23; $r = 0.07$, $p > 0.05$), suggesting other factors may contribute to observed differences. For example, Iida et al. (2014) reported water availability variations along the forest slope caused discrepancies between SLA and growth in subtropical seedlings, which is consistent with our experimental design located on a slope with different soil conditions.

Parameters explaining seedling growth indicated that light was the primary factor reducing seedling growth (Tableau 6), and seedlings growing with manure amendment received the least light (Figure 11). Although manure increased tree growth, it also increased the presence of understory vegetation and therefore reduced light at the base of seedlings where the measurement was taken. Foliar Ca concentrations and soil pH were also negatively related to seedling growth (Tableau 6), and a positive correlation was found between the two parameters (Figure 23, $r = 0.34$, $p < 0.01$). This was likely due to N deficiency in wood ash treatments, which increased foliar Ca and soil pH but did not promote growth due to the lack of sufficient nitrogen.

Foliar nutrients Zn, Mg, Mn and Cu concentrations were related to seedling growth, with Zn and Cu having a positive effect, and Mg and Mn having a negative effect (Tableau 6). Vectors diagrams showed that Zn and Cu were deficient (Figures 20, 21, 22), and amendments alleviated these deficiencies, improving growth as essential nutrients supported key physiological and metabolic processes (Påhlsson, 1989). Vectors of foliar Mg and Mn aligned with the excess and depletion arrows respectively suggesting that the amendments did not alleviate a nutrient deficiency for these elements (Figures 20, 21, 22).

Past experiments have suggested that wood ash application has a good potential in increasing seedling growth, especially in the case of organic matter-rich soils such as peatlands and upland forests (Augusto et al., 2008; Emilson et al., 2020; Huotari et al., 2015; Reid & Watmough, 2014; Saarsalmi et al., 2014). However, our study showed that wood ash failed to increase growth. This could be due to the lag time between ash fertilization and change in soil pH (Pitman, 2006), as trial duration time was the second most important factor influencing tree growth in a meta analysis (Reid & Watmough, 2014). Nevertheless, wood ash was efficient in increasing foliar nutrients such as N (Figure 6b), even though wood ash was N-poor (Tableaux 2, 3). Its effect could also be related to an increase in soil pH, as it increased by 0.2 units (from 4.68 without ash to 4.88 with ash), which may have led to greater microbial activity (Jokinen et al., 2006) enhancing N mineralization and thus N bioavailability (Brais et al., 2015). Wood ash also increased foliar Ca (Figure 7d), P (Figure 7b) and K concentrations (Figure 7c) in decreasing order. This is consistent with Ca being the most abundant nutrient in wood ash (Tableaux 2, 3) (Pärn, 2005), and with previous studies showing a significant increase in foliar Ca following wood ash application (Augusto et al., 2008). This latter meta-analysis also showed that wood ash increased foliar P and K nutrition in trees growing on mineral soils and highlighted the importance of adding N to produce a significant impact on growth despite increased foliar Ca, P and K, as both wood ash and mineral soils are N deficient (Augusto et al., 2008). Moreover, wood ash reduced foliar Mn concentrations (Tableau 4), which is toxic to plant growth at high levels and can reduce needle chlorophyll in white spruce seedlings (St.Clair & Lynch, 2005). We found a negative correlation between foliar Mn and seedling growth (Figure 23; $r = -0.28$, $p < 0.05$). Wood ash also increased foliar Bo (Figure 8d) and Cu (Figure 8a) concentrations consistent with Couch et al. (2021), where ash application increased foliar Bo in white spruce seedlings, and Augusto et al. (2008), where Cu was the only heavy metal to increase after wood ash application due to its high mobility.

Compared to manure, wood ash had no significant effect on seedling height growth. However, it increased SLA conditionally to the presence of biochar and manure (Figure 12b), and it increased foliar concentrations of N, P, K and Ca, essential nutrients for tree growth (Pallardy, 2008b). Our vector analysis indicated a positive response of seedlings to wood ash addition, which were deficient in the above-mentioned nutrients, and increased foliar dry mass. Despite this, wood ash did not result in increased height growth contrarily to manure. Nevertheless, seedling health, as revealed by increased SLA and major nutrient foliar concentrations may have been improved and this may impact tree growth in the future.

2.7.2 Effect of biochar on foliar nutrients

As hypothesized, biochar did not promote seedling growth most likely because seedlings were nitrogen deficient (Tableaux 2, 3). Other studies have found that the effect of biochar on growth could be neutral or even negative, because biochar can immobilise nitrogen due to high microbial activity, making it unavailable to plants (Gale et al., 2017; Gale & Thomas, 2019; Joseph et al., 2021). Some research suggests that using biochar in combination with an N source improves N retention and seedling growth more efficiently than biochar alone (Joseph et al., 2021; Robertson et al., 2012), likely due to the ability of biochar to adsorb nutrients released from the combined organic amendment on its surface area by functional groups (Shi et al., 2020) and improved N use efficiency (Song et al., 2020).

Biochar was also the only amendment which decreased SLA in the absence of wood ash and the presence of manure (Figure 12a), probably due to a lack of incident light and poor soil nutrition compared with other treatments. SLA correlated positively with foliar N, P, K and Cu concentrations (Figure 23, $p < 0.05$), all of which were not affected by biochar. However, in the absence of wood ash, it appears that biochar mitigated foliar Al toxicity in our acidic soils, resulting in reduced Al uptake by plants (Figure 8b) (Shetty et al., 2021). In acidic soils, Al can be toxic to plants and reduce their growth, especially seedlings which are more susceptible to toxicity than adult trees (Foy et al., 1978). Authors attributed Al toxicity alleviation by biochar to its liming capacity (Joseph et al., 2021). Biochar in the absence of wood ash increased soil pH by 0.11 units (from 4.62 to 4.73), reducing soil acidity by a factor of 2.2. Other mechanisms, such as the formation of complexes with biochar organic groups through reactions like esterification or surface adsorption and co-precipitating with silicate particles to create compounds like $KAlSi_3O_8$, may also contribute to reducing soil Al toxicity (Qian et al., 2013; Shetty et al., 2021).

2.7.3 Does combining amendments add value?

Contrary to our expectations, combining manure with biochar, wood ash, or both did not outperform single manure amendment in terms of growth benefit, as manure was the key to seedling growth. Soil fertilization improves growth only when growth-related physiological processes are optimized (Pallardy, 2008a). Environmental factors like water availability, light, and soil temperature significantly impact fertilization results (Linder & Rook, 1984). Growth is a complex process, involving multiple functions, including photosynthesis, respiration, absorption, and translocation (Pallardy, 2008a). White spruce is a slow-growing species that stores large nutrient reserves for long-term use (Bélanger et al., 2021), possibly explaining an apparent delayed growth with combined amendments. The increase in foliar nutrient concentrations bodes well for improved seedling growth in subsequent seasons. We expect that ongoing decomposition of the amendments will continue to benefit to the soil and soil pH, enhancing nutrient availability and promoting tree growth long term.

2.8 Conclusion

Our study showed that soil amendment application could benefit the short-term growth and foliar nutrition of planted white spruce seedlings in poorly regenerated forest sites. Manure resulted in the best spruce seedling growth outcomes and increased concentrations and contents of N and P deficient nutrients. At the scale of this study, co-application of manure with biochar, wood ash, or both did not change the results. Wood ash did not increase seedling growth, but it had a significant effect on several foliar nutrients, as it increased concentrations and contents of N, P, K and Ca deficient macronutrients that are essential for growth, while biochar decreased foliar Al concentrations which can suppress seedling growth.

Manure was an essential amendment since N and P were limiting to seedling growth. Therefore, we encourage the use of available nitrogen and phosphorus rich organic amendments in forestry as it could benefit tree productivity. Manure is commonly used in agriculture, but other by-products, such as paper sludge, are difficult to implement in agricultural systems and could have better potential in forestry while reducing landfill costs and environmental damage.

We conclude that soil amendment application could increase the productivity of plantations in the short term, but tree growth remains a complex process. Besides soil nutrient availability, other parameters could interfere with the seedling growth, such as water availability, light, and competition by understory vegetation. The main factors explaining seedling growth were foliar Zn and Cu concentrations, positively, and incident light, soil pH at 15-30 cm depth, and foliar Ca, Mg and Mn concentrations, negatively. We believe that soil dynamics are subject to temporal evolution, where short-term effects may diverge from long-term effects. Further studies are needed to determine the long-term effectiveness of soil amendments. Finally, although the failure of natural regeneration at our site may be multifactorial, we conclude that the addition of nitrogen and phosphorus rich amendments, even in the absence of herbicide use, benefited seedling growth.

2.9 Acknowledgments

The authors sincerely thank CRSNG Industrial Research Chair in Silviculture and Wood Production granted to Annie DesRochers (#IRCPJ547921- 18) for the scholarship and funding that made this research possible, as well as the Lake Duparquet Research and Teaching Forest for providing the location and facilities necessary for conducting the fieldwork. We also extend our gratitude to the laboratory staff from Notre-Dame-du-Nord Research Station, UQAT, and Laurentian Forestry Centre, Canadian Forest Service. Special thanks to Abigail Leavens and other field assistants for their valuable help in the laboratory and in the field.

3. SOIL AMENDMENTS ALTER UNDERSTORY VEGETATION COMPOSITION AND FUNCTIONAL DIVERSITY IN POORLY REGENERATED LOGGING SITES IN QUEBEC, CANADA

Ce chapitre a été soumis à la revue *Forest Ecology and Management* en février 2025.

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3.1 Résumé

Les amendements du sol sont de plus en plus utilisés dans les plantations de la forêt boréale pour améliorer la croissance des semis, mais leurs effets sur la végétation de sous-bois sont encore mal compris. Cette étude évalue l'impact des amendements [biochar (2,6 Mg ha^{-1}), cendre de bois (7 Mg ha^{-1}) et fumier (105 Mg ha^{-1})], appliqués seuls ou en combinaison, sur la végétation de sous-bois après deux saisons de croissance. Nous avons mesuré les indices de diversité et évalué la composition des communautés végétales de sous-bois. Les effets des amendements sur les traits fonctionnels des plantes ont été évalués au niveau des espèces. Nous avons également examiné la diversité fonctionnelle et calculé la moyenne pondérée par la communauté pour évaluer l'impact des amendements sur la composition fonctionnelle de la communauté végétale. Nos résultats soulignent que le fumier a significativement augmenté l'indice de diversité de Shannon de 1,87 à 2,13, a favorisé l'établissement de graminées et de légumineuses non indigènes avec une stratégie d'acquisition et une capacité de compétition. La diversité fonctionnelle était la plus élevée pour les traitements avec fumier (=19,90) et la plus faible pour les traitements sans fumier (=16,80). En revanche, le biochar et les cendres de bois n'ont pas modifié de manière significative la diversité végétale. Le biochar a maintenu une composition communautaire similaire à celle du contrôle, tandis que les cendres de bois, bien que se chevauchant avec le biochar, ont entraîné l'apparition d'espèces supplémentaires. Le biochar et les cendres de bois ont favorisé l'établissement de plantes herbacées rudérales et forestières et d'espèces ligneuses typiques des perturbations forestières, les cendres de bois augmentant de manière significative la concentration d'azote dans les feuilles de 9 % par rapport aux traitements sans cendres de bois. Ces résultats suggèrent que les amendements du sol modifient la diversité de la végétation de sous-bois et agissent comme des filtres fonctionnels sur les communautés végétales.

Mots-clés : Végétation de sous-bois, diversité, trait, moyenne pondérée de la communauté, diversité fonctionnelle.

3.2 Abstract

Soil amendments are increasingly used in boreal forest plantations to enhance seedling growth, but their effects on other compartments such as understory vegetation remain poorly understood. This study evaluates the impact of amendments [biochar (2.6 Mg ha-1), wood ash (7 Mg ha-1), and manure (105 Mg ha-1)], applied alone or in combination, on understory vegetation after two growing seasons. We measured diversity indices and evaluated understory vegetation community composition. The effects of amendments on plant functional traits were assessed at the species level. We also examined functional diversity and calculated the community-weighted mean to assess the impact of amendments on the functional composition of the plant community. Our results highlight that manure significantly increased Shannon index of diversity from 1.87 to 2.13, with more grasses and non-native legumes with an acquisitive strategy and competitive ability. Functional diversity was the highest for manure treatments (=19.90) and the lowest for treatments without manure (=16.80). In contrast, biochar and wood ash did not significantly alter plant diversity. Community composition was similar between the biochar and control treatments, while wood ash amendment, despite overlapping in plant composition with biochar, resulted in additional species. Biochar and wood ash treatments contained more ruderal and forest herbs and woody species typical of forest disturbances, with wood ash significantly increasing leaf nitrogen concentration by 9% compared to treatments without wood ash. Together, these findings suggest that soil amendments alter diversity of understory vegetation and act as functional filters on plant communities.

Keywords: Understory vegetation, diversity, traits, community-weighted mean, functional diversity

3.3 Introduction

Post-harvest plantation establishment is necessary when natural regeneration fails, as it enhances forest productivity to meet timber demand and contributes to carbon sequestration (Lal, 2005; Thiffault et al., 2024). Soil amendments, such as biochar, wood ash and manure can enhance the productivity of tree plantations (Lafleur et al., 2012; Reid & Watmough, 2014; Thomas & Gale, 2015). In Chapitre 2, we found that these amendments, particularly manure, increased foliar nitrogen (N) and phosphorus (P) concentrations of white spruce (*Picea glauca*) seedlings, as well as their height growth. However, we also observed reduction in light levels, raising concerns that amendments might have benefited understory vegetation. This could intensify competition for soil nutrients and light and inhibit seedling growth (Jobidon, 2000). Manure can contain weed propagules (Mendonça et al., 2021), which can introduce non-native species that may increase competition with target plants (Buss et al., 2018). A limited literature has been conducted on the effects of biochar, wood ash, and manure on forest understory vegetation diversity or functional diversity (Bieser & Thomas, 2019; Gundale et al., 2016). Soil amendments may be beneficial to growth and establishment of planted seedlings, but their effects on diversity and functioning of understory communities must be considered in the context of sustainable forest management practices.

Assessing changes in understory vegetation are often done by monitoring change in diversity indices, species richness, and areal cover of particularly the most abundant species (Garnier et al., 2004; Grime, 1998). A more recent approach uses the functional trait structure of communities as a tool to go beyond the descriptive taxonomic representation of patterns and explain the causal inferences through the functioning of ecosystems (Garnier et al., 2016). Functional traits provide insight into the ecological strategies of vascular plant species and are particularly useful for interpreting community-level responses to environmental gradients, including those induced by forest management (Lavorel et al., 2007). While the effects of soil amendments on functional traits have been explored in tree plantations (Neimane et al., 2021; Zhu et al., 2022), their impact on understory plant communities, especially from a functional perspective is less studied. Yet, the use of functional traits in this context offers a promising avenue to better understand whether practices that benefit tree growth, such as soil amendments, also support the recovery of diverse and functional understory vegetation to the same level before disturbance, For example, nutrient enrichment is often associated with increases in traits such as specific leaf area (SLA), leaf nitrogen concentration (LNC), and plant height at maturity, and decreases in leaf dry matter content (LDMC), reflecting a shift toward resource-acquisitive strategies (Garnier et al., 2016).

Biochar is a carbon-rich amendment that contains important concentrations of macro-elements, except nitrogen (Ippolito et al., 2015). Reported short-term effects of biochar on understory community composition are variable: in some cases, biochar had no impact on species total cover and community composition (Grau-Andrés et al., 2021), while in other cases, it decreased species richness (Gundale et al., 2016). These studies suggest that surface application of biochar does not significantly affect community vegetation unless it is incorporated into the soil, but then vegetation may be primarily influenced by soil disturbance rather than the biochar application (Gundale et al., 2016). Bieser and Thomas (2019) observed that biochar amendment increased cover of ruderal species such as *Rubus idaeus* and *Solidago canadensis*, and legumes including *Vicia cracca* that benefited from increased potassium availability in soil. Unlike biochar, wood ash is an inorganic amendment that is rich in macro-nutrients, but it also lacks nitrogen (Pitman, 2006). Previous studies have found either no impact (Ozolinčius et al., 2007) or minimal impact (Hart et al., 2019) of wood ash application on vascular plant cover, or species-specific changes in cover. For example, Arvidsson et al. (2002) found that wood ash amendment provided favorable conditions for some species to out-compete other species and increase their cover, for example in terms of light, water and nutrients (Jacobson & Gustafsson, 2001). In other cases, wood ash increased soil pH causing nitrogen immobilization, which disfavored cover of acidophilous dwarf shrubs (Jacobson & Gustafsson, 2001). We noted a lack of studies addressing how manure influences understory plant diversity and functional traits, an important gap that we address in the present study. Other nitrogen-rich organic fertilizers, such as the amino acid arginine, increased the abundance of the grass species *Avenella flexuosa* but had no effect on forbs and ericaceous shrubs (Hedwall et al., 2018).

This study aimed to investigate the effects of single and combined soil amendments on (1) understory plant diversity and community composition, and (2) understory species and community-level traits and functional diversity, on a poorly regenerated amended site. We hypothesized that after two growing seasons, soil amendments would modify community composition and diversity indices of understory vegetation and shift functional traits because of changes in soil nutrients following treatments. More specifically, our first hypothesis was that manure treatments would modify the understory vegetation competing with planted seedlings by increasing diversity with more grasses as well as introducing non-native species (i.e. agricultural plants) compared to treatments without manure. Manure should also increase maximum height and acquisitive traits (i.e., increased SLA and LNC and decreased LDMC) because it is nitrogen rich. As a second hypothesis, we did not expect major changes in community composition or diversity indices following wood ash application because community composition changes tend to occur over the longer term with ash amendment (Moilanen et al., 2002). However, we expected an increase in LNC, as seen in Chapter 2, for white spruce seedlings grown under wood ash compared to treatments without it. Our third hypothesis was that biochar would slow decomposition and soil surface application would have effects similar to those of control treatments (soil disturbance), thus favoring ruderal species, with a tendency to decrease diversity indices, but with no difference from the controls in terms of functional traits.

3.4 Materials and methods

3.4.1 Site description

Situated within the balsam fir (*Abies balsamea*) - white birch (*Betula papyrifera*) domain of the mixedwood boreal forest in the Abitibi region, Quebec (Saucier et al., 2003), the experiment took place in the Lake Duparquet Research and Teaching Forest (FERLD) (48°30' N, 79°22' W). The climate is continental, with an average annual temperature of 1°C and total yearly precipitation of 989 mm, of which 30% occurs as snowfall (Environnement Canada, 2019). The experimental site is situated on a slope with an altitude ranging from 69 m to 320 m. The lower part of the slope featured a moderately well-drained clay-loam mineral soil, while the middle and upper sections had a rapidly drained loam mineral soil (Tableau 1). A completely randomized block design of three blocks (replicates) was configured to consider the gradient of soil texture across the slope. The study area, once dominated by a 93-year-old jack pine (*Pinus banksiana*) forest with aspen (*Populus tremuloides*), was clearcut in 2016. Natural regeneration was hindered by competition from ground vegetation and wet conditions at the bottom of the slope.

In November 2019, 3 m x 5 m plots across the slope at three positions: bottom, middle, and top, were scarified using an excavator equipped with a 1 m bucket (250 plots ha^{-1}). In June 2020, amendments were mechanically distributed on the soil surface within each plot, anticipating the subsequent planting of white spruce seedlings in July 2020, with each plot hosting an average of seven three-year-old seedlings, positioned two m apart (1500 seedlings ha^{-1}). Sourced from a provincial nursery, these seedlings were cultivated in 25-310 containers, featuring 25 cavities per container and 310 cm3 per cavity. The treatments included biochar (B) (2.6 Mg ha^{-1}), wood ash (A) (7 Mg ha^{-1}), manure (M) (105 Mg ha^{-1}), and control (no amendment) (Tableau 2). The soil amendments were applied both individually and in combinations of two and three amendments, totaling eight treatments (Tableau 3). The doses were cumulative; for example, the biochar-manure (BM) treatment consisted of 2.6 Mg ha^{-1} of B plus 105 Mg ha^{-1} of M. Biochar was derived from legacy bark woody compost and wood ash was produced from aspen, whereas manure originated from a local beef cattle farm.

3.4.2 Sampling

Data collection was done in three randomly chosen plots for each of the eight treatments in each of the three blocks, resulting in a total of 72 sampled plots. After two growing seasons, from mid-July to the end of August 2022, we conducted a survey of understory vegetation in the plots using a 1 m^2 quadrat for taxonomic and functional trait measurements. The quadrat was consistently positioned in a pre-defined location, specifically on the left side of the plot with a seedling inside it. Soil samples were collected at depths of 0-15 cm and 15-30 cm between early September and mid-October 2022.

3.4.3 Vegetation surveys

We identified all vascular plant species within the quadrats, including woody and herbaceous plants, which totalled 108 species (Tableau 20). We assessed the abundance of each species by visually estimating their percent cover from 0.1% to 100%.

3.4.4 Functional traits: leaf sampling and chemical analyses

Plant trait information was gathered through both empirical measurements and published data sourced from the Traits Of Plants In Canada (TOPIC) (Aubin et al., 2020) and Plant Trait (TRY) (Kattge et al., 2020) databases. We measured traits related to plant growth and leaf morphology, i.e., specific leaf area (SLA), leaf dry matter content (LDMC), and leaf nitrogen concentration (LNC) (Tableau 7) of the five most dominant vascular species in terms of cover (or less if insufficient) in each quadrat, resulting in 56 abundant species across all treatments and blocks, with an average cumulative cover of 80% across plots. For each species in each plot, we measured the height of 10 mature individuals if possible. We collected approximately 10 g of leaf samples for each species with scissors, selecting them from mature and healthy individuals across the plot. The leaves were placed in a plastic bag with distilled water to maintain their water saturation and refrigerated (max 48 h). Subsequently, the petiole was removed and excess water was removed with cotton tissue. Leaf area of the 10 randomly selected leaves was measured using a scanner (300-600 dpi) and Winfolia software (WinFOLIA Pro 2022, Régent Instruments Inc., Québec, QC, Canada). Leaf mass was weighed before and after drying (60°C, 72 h) to determine the dry mass. Dried leaves were ground to 2 mm (Retsch ZM 200 Ultra Centrifugal Mill, Haan, Germany), ensuring thorough cleaning of the grinder between each blend to prevent cross-contamination. Total N concentration was assessed through dry combustion (Vario MAX cube, Elementar, Langenselbold, Germany). We completed our database with 10 other traits taken from the TOPIC and TRY databases (Tableau 7). Traits were related to plant morphology, regeneration strategy, dispersion, and resource utilization, and were selected to investigate the ability of plants to persist, disperse, colonize and compete within a community (Reich, 2014).

Tableau 7 Summary of functional traits selected for this study.

Trait	Description (code or unit)	Function
Plant morphology		
Raunkiaer Life Form[1]	Chamaephyte: herbaceous, perennating buds between 1 mm and 25 cm from ground (Ra.ch)	Persistence
	Geophyte: herbaceous, perennating buds in the ground (Ra.g)	
	Hemicryptophyte: herbaceous, perennating buds on the surface of the ground (Ra.h)	
	Helophyte: herbaceous, perennating buds submerged in mud (Ra.hel)	
	Micro & nano phanerophyte: woody perennial, buds between 25 mm and 8 m from ground (Ra.mc)	
	Mega & meso phanerophyte: woody perennial, buds located ≥ 8 m from ground (Ra.mg)	
	Therophyte: does not overwinter, annual plant (Ra.t)	
Life cycle[1]	Annual (1), Bi-annual (2) or Perennial (3)	Persistence
Growth[1]	Slow (0), Moderate (0.5), or Fast (1)	Competition
Lateral extension[1]	Absence of vegetative propagation (0)	Colonization
	Compact: occurs by sprouting from root/stem (phanerophyte) or by bulbs/bulbettes, corm/caudex, tubers (non-phanerophyte) (0.1)	
	Moderate: occurs by layering, root suckers or rhizomes (phanerophyte), or by bulbils or layering (non-phanerophyte) (0.5)	
	Extensive: occurs by root suckers or rhizomes (phanerophyte), by rhizomes, stolons or plant fragments (non-phanerophyte) (1)	
Maximum height[2]	Shortest distance between the upper boundary of the main photosynthetic tissues and the ground level (cm)	Competition

Tableau 7 (suite)

Specific leaf area[2]	Ratio of the one-sided area of a leaf to the oven-dried leaf mass (SLA, cm2 g-1)	Persistence
Leaf dry matter content[2]	The oven-dry weight of a leaf divided by its water-saturated fresh weight (LDMC, mg g-1)	Persistence
Regeneration and dispersion		
Seed dispersal vector[1]	Dispersal by insect (D.an), bird (D.bi), water (D.e), explosive discharge (D.ex), animal other than bird (D.ez), by wind (D.w), animal (D.zz) or unassisted (D.g),	Dispersal
Seed persistance[1]	Short viability: ≤ 1 year (0), Semi-permanent: > 1-5 years (0.5), Permanent: > 5 years (1)	Persistence
Flowering phenology1	The presence of flowers in spring (0) or in summer or early fall (1)	Competition
Mode of reproduction[1]	Seeds only/non-clonal (0), Mainly by seeds but vegetation propagation possible (1), Frequent vegetative propagation (2)	Colonization
Resource utilization		
Water preference[1]	Habitat xeric or xeric-mesic (0), Habitat mesic (1), No preference (2), Habitat humid or humid-mesic (3)	Competition
Light requirement[1]	Shade tolerant, <2h of direct sunlight (1), Shade mid-tolerant, 2-5 h of direct sunlight (3), Shade intolerant, needs >6h of direct sunlight at mid-summer (6)	Competition
Leaf nitrogen concentration[2]	Concentration of nitrogen in the foliage (LNC, mg g-1)	Competition

[1]Trait value taken from TOPIC (Traits Of Plants in Canada) and TRY databases; [2]Trait value measured in the field and laboratory.

3.4.5 Soil sampling and chemical analysis

Soil was sampled 30 to 50 cm away from each of the three preselected seedlings in each plot at depths of 0-15 cm and 15-30 cm using an auger. The samples were then air-dried and ground to 2 mm using a Humboldt hammer mill (Dayton Electric Mfg. Co., Lake Forest, IL 60045, USA). Composite samples were created by mixing equal weights of dried and ground soil from the three pseudo-replicate samples. Soil pH was measured in a 0.01 M $CaCl_2$ solution (Hendershot et al., 2008b). Total carbon and nitrogen were determined by dry combustion using a Vario MAX cube elemental analyzer (Elementar, Langenselbold, Germany). There was no inorganic carbon in the soil samples and thus total carbon was considered equivalent to soil organic carbon. Available P and exchangeable K were obtained through the use of a Mehlich III extraction solution (Ziadi & Sen Tran, 2008) followed by inductively coupled plasma (ICP) and an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA).

3.4.6 Light measurements

To assess the level of light intercepted by understory vegetation, measurements were made in late July 2023 using a plant canopy analyzer, LAI-2000 (LI-COR Inc., Lincoln, Nebr.), positioned 30 cm above the base of a randomly chosen seedling in each plot. Additionally, light readings were taken in an open field adjacent to each plot for reference purposes. The incident light was obtained as a ratio of the light at 30 cm from the base of the seedling relative to the reference light. Low light levels indicated the presence of dense understory vegetation that blocked light from reaching the base of seedlings, whereas high light levels indicated lower vegetation cover that allowed light to reach the base of seedlings.

3.5 Statistical approach

Two main approaches, i.e. taxonomic and functional, were considered to assess the response of understory vegetation to the application of soil amendments. Regarding the taxonomic approach, we calculated three diversity indices. First, we calculated species richness, which is the number of species encountered in each quadrat per plot. Second, Shannon diversity and InvSimpson indices were calculated using the vegan package, version 2.6-8 (Oksanen et al., 2020). A generalized linear mixed model was fitted for species richness using Poisson distribution family for counting data, and a linear mixed model was computed for Shannon and InvSimpson indices separately. To assess the effect of soil amendments, either used individually or in combination, on the diversity indices, we computed a presence or absence factor for each amendment and fitted the interaction between the three binary factors as a fixed effect in the models, while block was fitted as a random effect. The DHARMa package was used to check whether the fitted models respected the assumptions of homoscedasticity and normal distribution (Hartig, 2018).

We also sought to understand how amendments affect understory vegetation community composition. To achieve this, we carried out three analyses on Bray-Curtis distance matrix of abundance data (proportion of individuals). First, we conducted multilevel pairwise comparisons with 9999 random permutations, between single and combined amendments to assess their differences from the control, as well as one-to-one comparisons between amendments, using pairwise adonis2 function from the vegan package (Martinez Arbizu, 2020). Second, we performed a permutational multivariate analysis of variance (PERMANOVA) with 9999 random permutations to assess the effect of the presence or absence of biochar, wood ash and manure. Then, we conducted a Principal coordinate analysis (PCoA) using the same Bray-Curtis distance matrix of species abundance with the PCoA function from the vegan package (Laliberté et al., 2014). We used the Cailliez correction to address negative eigenvalues (Gower & Legendre, 1986). Environmental conditions (light, mean soil pH, C/N ratio, phosphorus (P) and potassium (K) concentrations at 0-15 cm and 15-30 cm depths) were included as predictors in the PCoA. We tested for differences between the two soil depths for these variables and found no significant differences; therefore, we used the average values across both depths in the analysis. We used the Envfit function from the vegan package with 999 permutations to fit species vectors to the ordination, displaying only significant species ($p < 0.05$) in the figure.

For the functional approach, we measured traits for the most abundant species and computed a linear mixed model for each trait to assess how soil amendment treatments affected functional traits at the species level. The fixed effects in the models consisted of the interaction between the presence or absence of each of the three soil amendments, while the random effects were the block and the plot. To address the effects of soil amendments on the community functional composition, we measured the community-weighted mean (Garnier et al., 2004), which focuses on environmental selection of traits, according to the following equation:

$$CWM = \sum_{i=1}^{n} p_i \times trait_i$$ **Eq. 1**

Where n is the total number of species in the community, pi represents the relative abundance of species i, and traiti expresses the value of the trait of species i. We performed multilevel pairwise comparisons using 9999 permutations to assess differences between each amendment (single and combined) and the control, as well as one-to-one comparisons between amendments, using pairwise adonis2 function from the vegan package (Martinez Arbizu, 2020). Then a permutational multivariate analysis of variance (PERMANOVA) with 9999 random permutations was computed to assess the effect of soil amendment treatments on functional community composition, using Gower distance on the resulting CWM matrix. To visualize the community functional composition, we performed a principal component analysis (PCA) on CWM matrix.

Functional diversity was measured using Rao's quadratic entropy index, which expresses the dissimilarity expected between a randomly selected pair of individuals (Rao, 1982; Ricotta & Moretti, 2011). A linear mixed model was fitted to assess the impact of the presence or absence of soil amendments on Rao index, with block as a random effect. In all fitted models, when assumptions of homoscedasticity and normal distribution were not met, a log or square root transformation was applied to response variables. Maximum height, SLA, LNC, and the Rao index were log-transformed, while LDMC was square root transformed. Statistical analyses were conducted in R version 4.2.1 (R Core Team, 2021), using a significance threshold of $\alpha = 0.05$.

3.6 Results

3.6.1 Impact of amendments on diversity indices

Manure was the only amendment that significantly increased the Shannon index (Tableau 19, $p < 0.01$) from 1.87 to 2.13 compared to treatments without manure (Figure 13a). There was a trend for biochar to impact Shannon and InvSimpson indices (Tableau 19, $p < 0.1$). The presence of biochar tended to increase Shannon index from 1.91 to 2.09 (Figure 13a) and InvSimpson index from 5.46 to 6.43 (Figure 13c) compared to its absence, but the effects were not significant. Manure also showed a trend to increase InvSimpson index, from 4.88 to 7.01 (Tableau 19, $p = 0.1$) (Figure 13c).

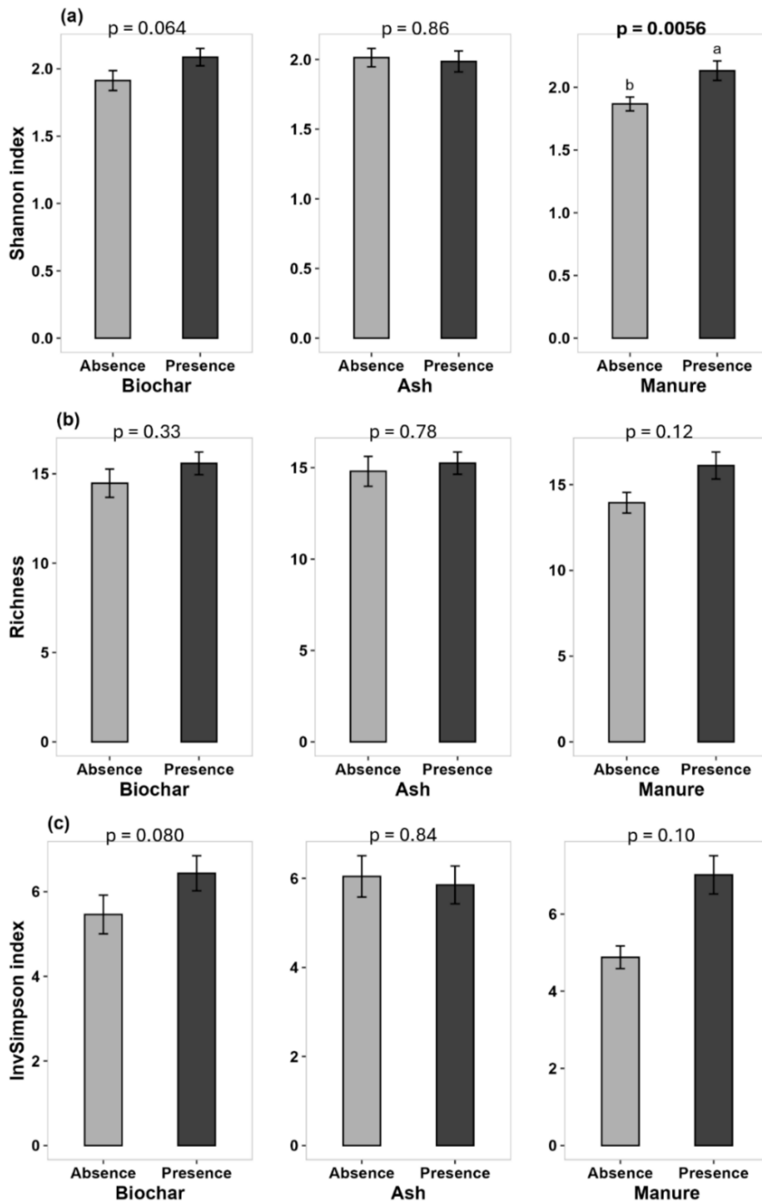

Figure 13 Mean (± standard error) (a) Shannon index, (b) species richness, and (c) InvSimpson index according to the presence or absence of biochar, wood ash and manure, after two growing seasons following amendment treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableaux 18 and 19 for the results of ANOVA applied to the generalized and linear mixed models.

3.6.2 Understory vegetation community composition

Pairwise adonis2 comparisons revealed that most single and combined amendments had significant effects on community composition and differed from the control, except for biochar and the biochar–wood ash combination (Tableau 8). Combining biochar with other amendments generally did not alter community composition, as seen in comparisons such as A vs. BA, M vs. BM, and AM vs. BAM, similar communities were observed (Tableau 8). In contrast, wood ash and manure altered the composition of the understory community (PERMANOVA; $p < 0.05$, Tableau 9). Principal component analysis isolated the treatments without wood ash and manure (biochar and control) in the top left of the plot from the rest of the treatments along the first and second axes (10.4% and 7.2% of variance explained respectively; Figure 14a). However, the wood ash ellipse overlapped to a large extent with treatments without wood ash and manure. The application of manure altered community composition, since treatments with manure had a community composition that differed from treatments with wood ash, but were not different from the combined addition of wood ash and manure along the second axis (Figure 14a). Treatments on the right of the plot were characterized by low light levels reaching the planted seedlings and high soil C/N ratios and P concentrations. Soil pH was intermediate among all amendments and showed no strong association with any treatment (but was higher in the presence of wood ash and manure than other amendments; Figure 14a).

Manure treatments were associated with legumes such as *Vicia cracca* (VICCRA) and *Trifolium pratense* (TRIPRA), herbaceous species such as *Fallopia cilinodis* (FALCIL) and *Impatiens capensis* (IMPCAP), and grass *Phleum pratense* (PHLPRA), whereas treatments with wood ash were characterized by shrubs such as *Corylus cornuta* (CORCOR), and *Diervilla lonicera* (DIELON), herbaceous species such as *Cornus canadensis* (CORCAN), *Eurybia macrophylla* (EURMAC), *Maianthemum canadense* (MAICAN), *Apocynum androsaemifolium* (APOAND) and *Diodia teres* (DIOTER), as well as the fern *Pteridium aquilinum* (PTEAQU) (Figure 14b).

Treatments without wood ash and manure (biochar and control) were associated with the presence of multiple species including herbs like *Fragaria virginiana* (FRAVIR), *Pilosella spp*. (PILSP), *Scirpus spp.* (SCISP), *Symphyotrichum puniceum* (SYMPUN), *Juncus spp.* (JUNSP) and *Carex spp.* (CARSP), shrubs like *Rubus pubescens* (RUBPUB), and grasses like *Calamagrostis canadensis* (CALCAN), which were characterized by high light levels and high soil K concentrations (Figures 14a, 14b).

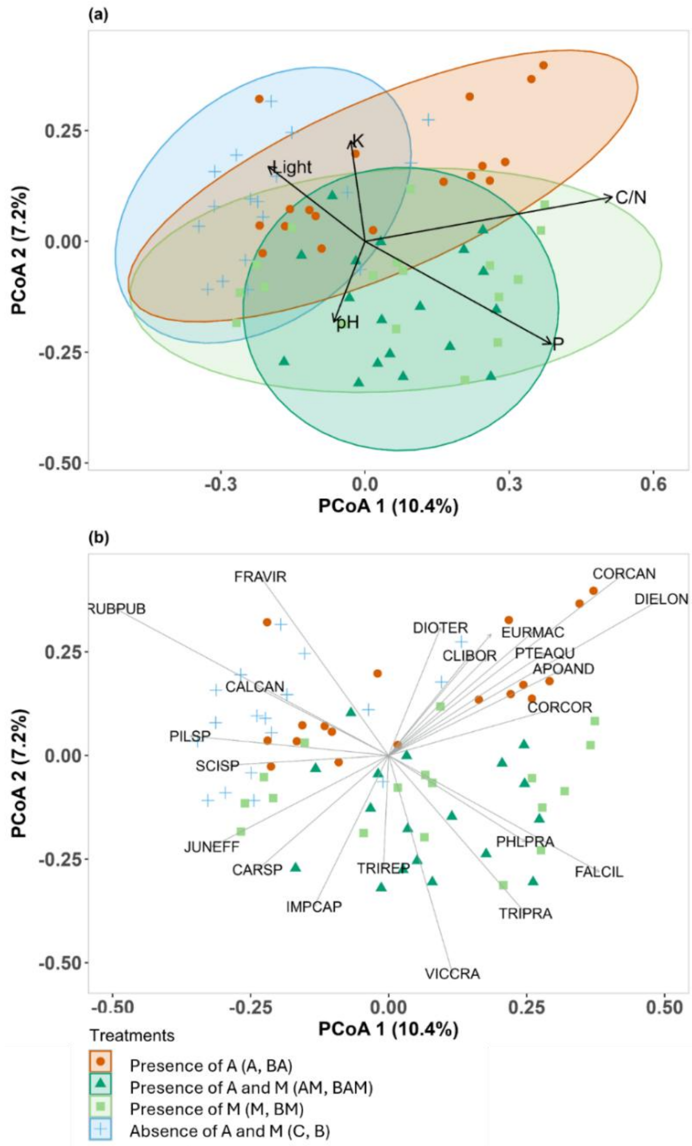

Figure 14 Principal coordinate analysis (PCoA) based on the Bray-Curtis distance of understory plant community composition. Treatments consist of the presence of wood ash (A), manure (M), both wood ash and manure, as well as their absence in treatments. The symbols correspond to the centroids per treatments. The ellipses represent 95% confidence intervals of the mean positioned according to treatments. Explanatory variables are depicted as black arrow vectors and consist of light, as well as the mean values of soil pH, C/N ratio, phosphorus (P) and potassium (K) concentrations averaged across the 0-15 cm and 15-30 cm depths. The percentages of variance explained by each axis are included. See Tableau 20 for species code details.

Tableau 8 Pairwise adonis2 comparisons of understory vegetation community data among treatments (p-values). Treatments consist of biochar (B), wood ash (A), manure (M), biochar-manure, (BM), biochar-wood ash (BA), wood ash-manure (AM), biochar-wood ash-manure (BAM), and control (CTL). Values in bold indicate statistically significant differences (p < 0.05).

	CTL	B	A	M	BA	BM	AM	BAM
CTL								
B	0.41							
A	**0.015**	**0.018**						
M	**0.0027**	**0.0017**	**0.017**					
BA	0.061	**0.028**	0.32	**0.001**				
BM	**0.0012**	**0.0018**	**0.0052**	0.17	**0.007**			
AM	**< 0.001**	**< 0.001**	**0.0018**	0.72	**0.0016**	0.072		
BAM	**< 0.001**	**< 0.001**	**0.0099**	0.32	**0.0022**	0.26	0.52	

Tableau 9 Permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distance transformed community data. Treatments consist of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

	Df	Sum of squares	Mean of squares	R2	F statistics	p-value
B	1	0.38	0.38	0.019	1.54	0.052
A	1	0.62	0.62	0.032	2.54	**0.0007**
M	1	1.60	1.60	0.082	6.54	**0.0001**
B : A	1	0.20	0.20	0.010	0.82	0.62
B : M	1	0.26	0.26	0.013	1.05	0.33
A : M	1	0.44	0.44	0.023	1.81	**0.015**
B : A : M	1	0.25	0.25	0.013	1.00	0.38
Residuals	64	15.68	0.24	0.81		
Total	71	19.43		1.00		

3.6.3 Functional traits of the most abundant species

Manure addition affected all four functional traits measured on the most abundant understory species (Tableau 19, $p < 0.05$). Maximum height, specific leaf area and leaf nitrogen concentration were 34% (from 33.20 to 44.70 cm), 17% (from 214 to 251 cm^2 g^{-1}) and 30% (from 16.00 to 20.80 g kg^{-1}) higher, respectively, in the manure treatments compared to treatments without manure (Figures 15a, 15b, 15c), whereas leaf dry matter content decreased by 9% in treatments with manure (Figure 15d; from 281 to 258 mg g^{-1}). Leaf nitrogen concentration also increased by 9% with wood ash amendment (Tableau 19, $p < 0.05$) compared to treatments without wood ash (Figure 15d; from 17.60 to 19.20 g kg^{-1}).

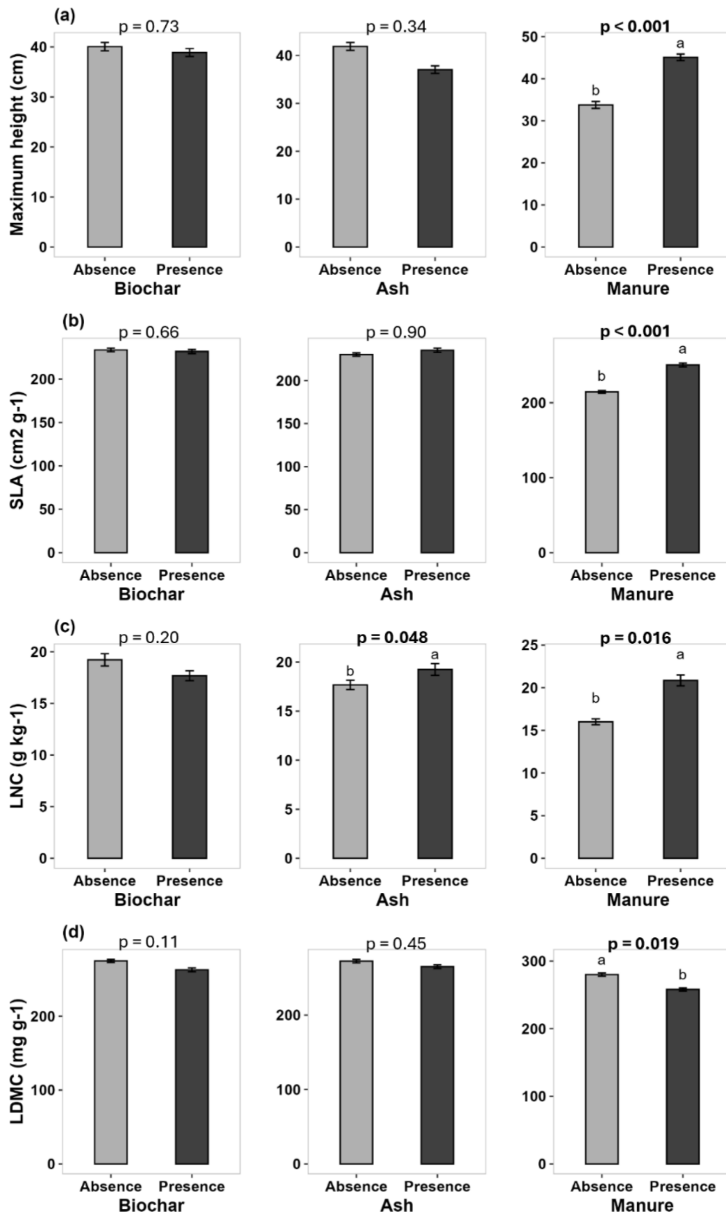

Figure 15 Mean (± standard error) (a) maximum height, (b) specific leaf area (SLA), (d) leaf dry matter content (LDMC) according to the presence or absence of manure, and leaf nitrogen concentration (LNC) according to the presence or absence of (c) manure and (d) wood ash, after two growing seasons following amendment treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 19 for the results of ANOVA applied to the linear mixed models.

3.6.4 Community functional composition and diversity

Pairwise adonis2 comparisons revealed that the functional composition of the community in manure-treated plots differed from the control, whereas single and combined biochar and wood ash treatments showed no significant differences from the control (Tableau 10). The functional composition of the community varied significantly according to wood ash and manure treatments (PERMANOVA; $p < 0.05$, Tableau 11). As seen in the principal component analysis of the community-weighted mean, it separated the functional composition of the community according to the first axis (25.86% of variance explained; Figure 16a), and revealed that the addition of manure combined with wood ash altered the functional composition of the community; treatments combining wood ash and manure shifted to the left side of the plot, contrasting with treatments without wood ash nor manure on the right, while manure alone treatment was intermediate between the two former treatments. Wood ash alone overlapped with all treatments (Figure 16a). Additionally, manure was the treatment with the highest Rao's index of functional diversity (=19.90) compared to treatments without manure (=16.80) (Tableau 19, $p < 0.05$; Figure 17).

Vegetation present in the wood ash and manure treatments shared multiple functional traits typical of competitive and persistent species with acquisitive traits, such as shade intolerance, high specific leaf area (SLA) and leaf nitrogen concentration (LNC), low leaf dry matter content (LDMC), as well as summer or early fall flowering. They were also associated with species exhibiting the highest values of maximum height, and dispersal by explosive discharge hemicryptophytes (Figure 16b). On the opposite side of the plot, treatments without manure favored the establishment of a functional community with vegetative reproduction, extensive lateral extension, fast-growing with permanent seeds and high leaf dry matter content (LDMC). Species were mainly micro and nano phanerophytes with a seed dispersal by birds (Figure 16b).

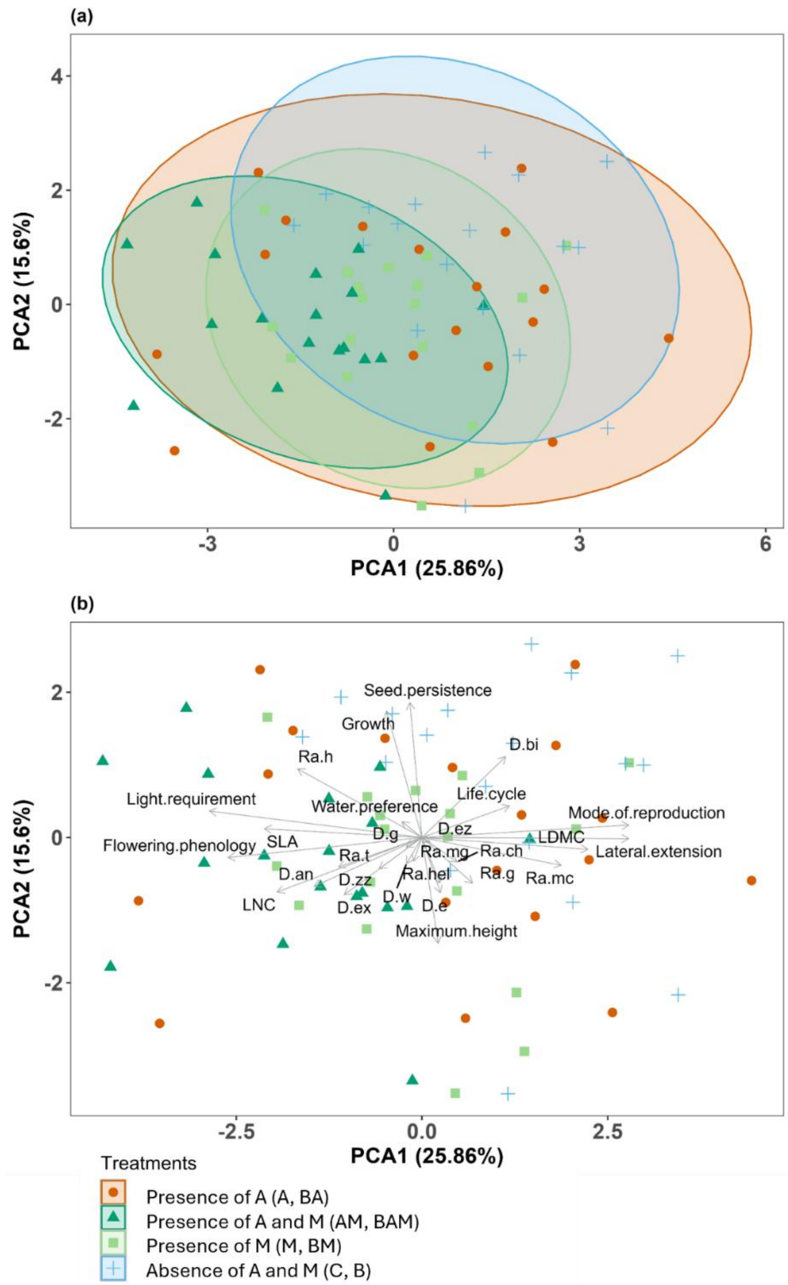

Figure 16 Principal component analysis (PCA) of community-weighted mean (CWM) of functional traits. Treatments consist of the presence of wood ash (A), manure (M), both wood ash and manure, as well as their absence in treatments. The symbols correspond to the centroids per treatments. Community-weighted means are depicted as light gray arrow vectors, and the percentages of variance explained by each axis are included. See Tableau 7 for trait code details.

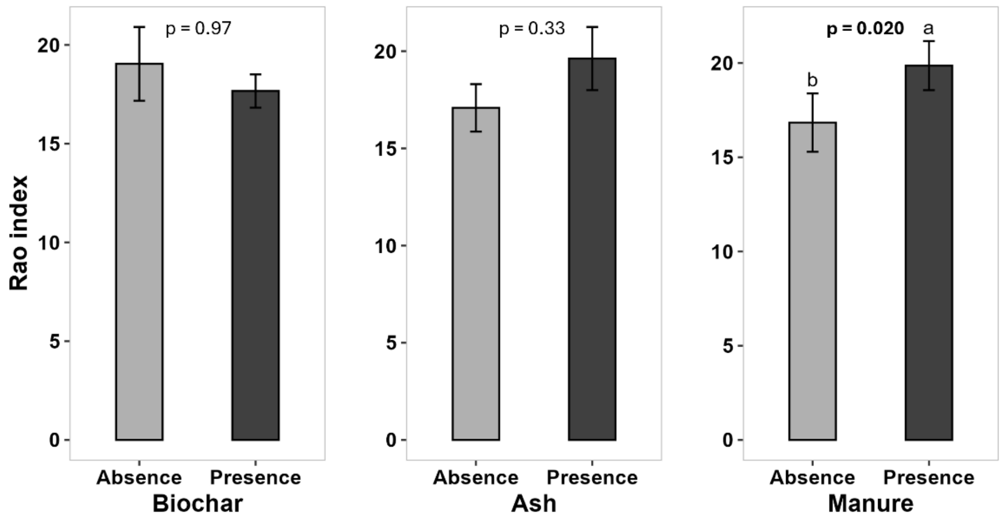

Figure 17 Mean (± standard error) Rao index according to the presence or absence of biochar, wood ash and manure after two growing seasons following amendment treatments. Different letters indicate significant differences between treatments ($p < 0.05$). See supplementary material Tableau 19 for the results of ANOVA applied to the linear mixed models.

Tableau 10 Pairwise adonis2 comparisons of community-weighted mean (CWM) of functional traits data among treatments (p-values). Treatments consist of biochar (B), wood ash (A), manure (M), biochar-manure, (BM), biochar-wood ash (BA), wood ash-manure (AM), biochar-wood ash-manure (BAM), and control (CTL). Values in bold indicate statistically significant differences (p < 0.05).

	CTL	B	A	M	BA	BM	AM	BAM
CTL								
B	0.5903							
A	0.5589	0.8963						
M	**0.0233**	0.1354	0.1686					
BA	0.2891	0.8483	0.9236	0.3346				
BM	**0.0213**	0.2314	0.2329	0.6215	0.5473			
AM	**0.0057**	**0.0416**	**0.09**	0.2717	0.1111	0.3129		
BAM	**0.0409**	0.1914	0.2275	0.9749	0.3004	0.8573	0.4938	

Tableau 11 Permutational multivariate analysis of variance (PERMANOVA) based on Gower distance transformed community-weighted mean (CWM) of functional traits data. Treatments consist of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

	Df	Sum of squares	Mean of squares	R2	F statistics	p-value
B	1	0.033	0.033	0.019	1.54	0.13
A	1	0.063	0.063	0.037	2.95	**0.0042**
M	1	0.15	0.15	0.087	6.90	**0.0001**
B : A	1	0.019	0.019	0.011	0.88	0.54
B : M	1	0.0090	0.0090	0.0053	0.42	0.92
A : M	1	0.045	0.045	0.026	2.10	**0.030**
B : A : M	1	0.012	0.012	0.0072	0.57	0.82
Residuals	64	1.36	0.021	0.81		
Total	71	1.69		1.00		

3.7 Discussion

3.7.1 How does the diversity of the understory vegetation community respond to soil amendments?

Consistent with our first hypothesis, manure increased the diversity of the understory vegetation, as reflected by the highest Shannon index values (Figure 13a). Manure altered species composition compared to the control (Tableau 8), as well as to wood ash and treatments without wood ash and manure (Figure 14a). These changes were driven by the establishment of nitrogen-fixing species like Vicia cracca and agricultural plants such as Trifolium pratense (Figure 14b). Manure can contain weed propagules and seed banks from agricultural plants (Mendonça et al., 2021), thus introducing invasive non-native species to fertilized forest sites; these species can be important competitors for soil nutrients, water and light (Buss et al., 2018). Manure also favored grasses such as Phleum pratense, which can invade intensively harvested sites (De Grandpré et al., 2014; Harvey et al., 1995), as well as herbs such as Impatiens capensis with the acquisitive strategy (rapid growth and acquisition of resources) (Aubin et al., 2020) (Figure 14b). Manure treatments also promoted the re-establishment of forest species such as the herbaceous forest species *Fallopia cilinodis* (Figure 14b), which is shade-intolerant and proliferates rapidly in scarified sites (Hupperts et al., 2020). The levels of light reaching the planted seedlings were reduced under manure treatments because of understory vegetation height (Figure 14a), suggesting increased competition for planted seedlings (Jobidon, 2000; Shropshire et al., 2001), although these treatments concomitantly resulted in increased white spruce seedling height growth and survival (Chapitre 2) . In the short term, the positive fertilizing effect of manure on tree seedling growth outweighed competing vegetation, but it remains uncertain whether this positive effect will persist in the long term.

Consistent with our second hypothesis, wood ash did not alter diversity indices. However, it changed community composition (Tableau 9) and differed from the control (Tableau 8). While wood ash partially overlapped with treatments without wood ash and manure (Figure 14a), suggesting these treatments shared similarities in terms of community composition, it promoted the re-establishment of a combination of forest herbs and shrubs, such as *Cornus canadensis* which can quickly spread vegetatively under abundant light (Hart & Chen, 2006), along with *Corylus cornuta* and *Diervilla lonicera* (Figure 14b), shrubs that are typically found after intensive harvesting (Haeussler & Bergeron, 2004), as well as in the shrub layers that are characteristic of boreal forests in Quebec (Chapman et al., 2020). The herbs *Cornus canadensis, Diervilla lonicera* and *Apocynum androsaemifolium* are known to establish after fire (Haeussler & Bergeron, 2004; Hart & Chen, 2006; Schoennagel & Waller, 1999), suggesting that wood ash can somewhat emulate natural disturbance by fire. *Pteridium aquilinum*, a soil pioneer fern that is shade intolerant, nutrient demanding and typical of forest disturbance (Bock & Van Rees, 2002; Haeussler & Bergeron, 2004; Hart & Chen, 2006), reached a mean maximum height of 65 cm under wood ash treatments, with some individuals growing as tall as 111 cm, which can cause substantial light competition for seedlings and hinder their growth (Gaudio et al., 2011).

Contrary to our expectations and previous findings by Gundale et al. (2016), biochar did not reduce understory species richness. While diversity indices such as Shannon and Inverse Simpson showed a slight increasing trend (Figures 13a, 13c), biochar treatments did not change community composition compared to the control (Tableau 8), consistent with our third hypothesis and Grau-Andrés et al. (2021). Control and biochar were favorable to the establishment of ruderal species (Figure 14b), reflecting natural succession on a clearcut forest site. Ruderal species were also observed by Bieser and Thomas (2019) after biochar application. However, unlike their study, we did not observe any legumes under biochar treatments. Bieser and Thomas (2019) reported increased legume abundance linked to higher K concentrations that favored root nodulation. In our study, biochar-treated soils had relatively high K concentrations (Figure 14a), but this did not result in legume establishment. Instead, species present were mainly invasive and shade-intolerant herbs, such as *Carex spp, Scirpus spp.* and *Fragaria virginiana*, that are known to regenerate after forest harvest disturbance (De Grandpré et al., 2014; Harvey et al., 1995), as well as *Pilosella spp.,* which reproduces rapidly from underground roots, rhizomes or runners (De Clerck-Floate et al., 2024). Biochar and control also favored the presence of forest species like the shrub *Rubus pubescens* that was probably pre-established and released after soil disturbance (De Grandpré et al., 2014), as well as grasses like *Calamagrostis canadensis*, which regenerates rapidly from underground rhizomes (Hart & Chen, 2006), and can overgrow planted white spruce seedlings in clearcut boreal forest sites (Hogg & Lieffers, 1991; Lieffers et al., 1993). The important presence of these species may account for the absence of a significant effect of biochar treatments on the height growth of planted white spruce seedlings (Chapitre 2). However, the level of light reaching tree seedlings increased following biochar treatment compared to treatments that included ash and manure (Figure 14a), indicating that understory vegetation in biochar-treated plots did not strongly compete with planted seedlings for light; therefore, these species may be limiting other belowground resources.

Overall, we found that manure promoted a more diverse and compositionally distinct understory, likely accelerating early successional dynamics and introducing competitive species, including some non-native plants. In contrast, many species observed under control, biochar, and wood ash were typical of forest disturbance or pre-established species prior to harvest, with biochar having a similar community composition as control, and wood ash sharing few species with control and biochar, but introducing other shrubs, herbs and ferns. These results led to the hypothesis that community assembly under these treatments, especially biochar, was likely driven by the environmental filter of soil disturbance and site history, rather than other environmental changes resulting from the application of amendments, as was argued by Gundale et al. (2016) that vegetation may be primarily influenced by soil disturbance rather than the biochar application.

3.7.2 Understory vegetation community functional response

Limited studies have examined functional traits of understory vegetation following soil amendments, especially in boreal forests. Our results show that soil amendment treatments shifted functional traits at the species level and led to different community functional composition and functional diversity. These effects varied by amendment type, indicating different filtering mechanisms operating through nutrient availability (Garnier et al., 2016). Consistent with our second hypothesis, wood ash increased LNC of the most abundant species (Figure 15c), coherent with its ability to increase soil organic matter mineralization and thus increasing available nitrogen for plant uptake (Johansen et al., 2021; Saarsalmi et al., 2010). Similar increases in LNC were observed for needles of spruce seedlings grown under the same conditions (Chapitre 2). However, at the community-weighted mean level, wood ash did not produce a clear modification of functional traits, unless it was combined with manure (Figures 16a, 16b).

Manure, in contrast, induced a marked shift toward an acquisitive strategy with high SLA and LNC traits, and decreased LDMC at both species and community levels (Figures 15, 16). These traits are indicators of rapid resource acquisition, fast-growing strategies and short life spans (Reich, 2014; Wright et al., 2004). Increased maximum height under manure treatments also suggests increased competitive ability (Falster & Westoby, 2003). The addition of manure to wood ash resulted in higher SLA and LNC and lower LDMC and introduced shade-intolerant species, consistent with plants having an acquisitive strategy (Figure 16b). This is in line with previous studies that found that plants responded to increased fertility by increasing acquisitive traits (Garnier et al., 2016). The prevalence of acquisitive species in manure treatments may have significant implications for ecosystem function. These species are characterised by high nutrient uptake rates, rapid tissue turnover and increased microbial activity, including elevated production of root-associated extracellular enzyme. These factors enhance the decomposition of organic matter and the release of nutrients, thereby accelerating nutrient cycling and improving short-term nutrient availability (Han et al., 2023; Wendling et al., 2016). This shift in functional composition towards acquisitive traits likely reinforces fast resource turnover and productivity, which are particularly important during the early stages of succession. At this stage, these traits allow plants to quickly capture available resources such as light, water, and nutrients when they are temporarily abundant following disturbance.

Functional diversity offered additional insights beyond the CWM regarding trait dispersion; the increased Rao index for manure treatments (Figure 17) indicated divergence of traits among species, resulting in species compositions that were less similar to each other (Grime, 2006; Ricotta & Moretti, 2011). A possible explanation to this pattern is the introduction of non-native species by manure, which brought new species with contrasting traits to the forest site and created a regenerating plant community with divergent traits after disturbance and amendment (Grime, 2006).

In contrast, biochar and control were associated with persistent seeds, spring flowering, and shade-tolerant species, suggesting slower growing strategies with less nutrient rich soils (Figures 16a, 16b). The presence of species with persistent seeds is likely due to plot scarification, which exposed the seed bank and facilitated germination (Haeussler et al., 2002). The occurrence of these traits is possibly related to the presence of woody perennial forest species. However, these results are not intuitive and easy to elucidate. It appears that traits under biochar treatments were not a direct effect of the amendment application, but a consequence of site disturbance, or related to site history, because they didn’t differ from the control treatment.

Together, these findings suggest that soil amendments act as functional filters on plant communities. Wood ash and biochar had more subtle effects, with wood ash modifying some nutrient-related traits and biochar resembling the control. Manure, in particular, drives strong changes in trait composition and diversity, likely due to increased fertility and potential seed input. These differences highlight how soil amendments can influence not only taxonomic diversity but also the functional composition of regenerating forest communities, with implications for succession, competition, and ecosystem functioning. These trait shifts. toward acquisitive, fast-growing strategies under manure treatments, can support a broader range of ecosystem functions, such as nutrient cycling and soil structure. However, the introduction of non-native species means that the resulting understory communities differ from pre-disturbance forest vegetation. While these species may not reflect historical baselines, we do not think they are detrimental to the system. Our previous work showed that they do not hinder tree growth (Chapitre 2), and over time, as canopy trees develop, they are expected to outcompete and shade out many of these shorter understory species. From a restoration perspective, this transitional assemblage may still contribute positively to early successional dynamics and long-term forest development.

3.8 Conclusion

Our findings revealed that the short-term application of soil amendment treatments in a forest plantation after a clear-cut had a significant impact on understory vegetation communities and their functional traits. From a taxonomic perspective, manure treatments increased diversity and favored the establishment of grasses and legumes with introduced non-native species, through both nutrient enrichment and seed input. In contrast, wood ash and biochar favored the establishment of perennial woody shrubs and herbs, without a significant impact on diversity indices. Understory plants generally consisted of forest and ruderal species, typical of post-forest harvesting and soil disturbance, suggesting that forest management practices had a greater influence on vegetation communities than soil amendment application in the case of biochar and wood ash. The mid- to long-term effects of soil amendments on the regenerating vegetation community at this logging site deserve further investigation, especially that of manure. Soil amendments will continue decomposing and altering soil nutrient availability, which will have a continued impact on understory vegetation composition.

From a functional standpoint, manure acts as a strong environmental filter, favoring plants with acquisitive strategies and competitive ability at both the species and community levels and had the highest functional diversity. In contrast, functional patterns associated with biochar and wood ash were less easy to interpret, possibly because the short timescale of this study, the limited number of sampled traits, or the possibility that these amendments had minimal effect on the measured functional composition.

We conclude that the observed species composition and functional community are shaped by multiple factors, with biotic and abiotic filters leading to the resulting community structure. This study highlights the importance of combining taxonomic and functional approaches as complementary methodologies to obtain a global view of the response of understory vegetation to the application of soil amendments in forest ecosystems. Long-term studies may be required to assess if these changes persist or if patterns and differences among treatments will become more pronounced.

3.9 Acknowledgements

The authors extend their sincere gratitude to the CRSNG Industrial Research Chair in Silviculture and Wood Production granted to Annie DesRochers (#IRCPJ547921- 18) for the scholarship and funding that made this research possible. We also thank the Lake Duparquet Research and Teaching Forest for carrying out the application of the soil amendments, and for providing the location and facilities necessary for conducting the field and laboratory work. Our appreciation goes to the laboratory staff at Notre-Dame-du-Nord Research Station, UQAT, and Laurentian Forestry Centre, Canadian Forest Service. Special thanks are due to field assistants for their invaluable help both in the laboratory and in the field.

4. INTERACTIONS BETWEEN SOIL AMENDMENTS SHAPE NUTRIENT AVAILABILITY IN BOREAL FORESTS

Ce chapitre est a été soumis à la revue *New Forests* en avril 2025.

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4.1 Résumé

Les sols des forêts boréales mixtes peuvent subir une perte de productivité après l'exploitation forestière, en particulier lorsque les conditions du sol sont altérées. De plus, une régénération insuffisante de la végétation peut entraîner une perte de nutriments, dont la disponibilité augmente souvent après une perturbation. Cette étude examine les effets des amendements de sol sur les propriétés chimiques d'une plantation forestière établie sur un site mal régénéré naturellement après l'exploitation. Le biochar (2,6 Mg ha^{-1}), les cendres de bois (7 Mg ha^{-1}) et le fumier (105 Mg ha^{-1}) ont été appliqués seuls ou en combinaison, et leurs effets sur les propriétés chimiques du sol minéral ont été évalués après deux saisons de croissance. En utilisant un plan en blocs aléatoires complets, nous avons mesuré le pH du sol, le carbone total, les concentrations en macro- et micronutriments, et la CEC à deux profondeurs (0-15 cm et 15-30 cm). Le biochar n'a pas modifié le carbone et l’azote totaux, mais il a diminué l'aluminium et la CEC (- 18 %) et augmenté le manganèse (+ 53 %). L'application conjointe de biochar et de fumier a augmenté le magnésium échangeable (+ 106 %). Les cendres de bois ont augmenté le pH du sol (+ 7 %), le rapport C/N (+ 12 %) et le phosphore (+ 30 %). Elles ont également augmenté l'aluminium (+ 26 %) et diminué l'azote total lorsqu'elles étaient combinées au fumier (- 33 %). Les cendres de bois sans fumier ont augmenté la CEC (+ 14 %), mais combinées au biochar et au fumier, elles ont diminué la CEC (- 26 %). Enfin, le fumier a réduit le carbone (- 18 %) et l’azote totaux (- 27 %) et plusieurs macro- et micronutriments (K_{exch}, Ca_{exch}, Mg_{exch}, Mn, Al, Na), avec des effets plus marqués lorsqu'il était combiné avec des cendres ou en l'absence de biochar. Cependant, le fumier a augmenté la disponibilité en azote, comme le suggère un rapport minéral/total N plus élevé (+ 53 %). Cette étude met en évidence le potentiel des combinaisons d'amendements pour améliorer la fertilité des sols dans les écosystèmes forestiers boréaux mal régénérés, et met en lumière les interactions complexes entre les amendements et leur influence sur la composition chimique des sols à différentes profondeurs.

Mots-clés : Sol, Biochar, Cendres de bois, Fumier, Interaction des amendements

4.2 Abstract

The soils of mixed boreal forests can suffer a loss of productivity after logging, particularly when soil conditions are altered. In addition, insufficient vegetation recovery can lead to a loss in nutrients, the availability of which often increases after disturbance. This study investigated the effects of soil amendments on chemical properties of a forest plantation established on a poorly regenerated site by natural regeneration following harvesting. Biochar (2.6 Mg ha^{-1}), wood ash (7 Mg ha^{-1}), and manure (105 Mg ha^{-1}) were applied alone or in combination, and their effects on mineral soil chemistry were assessed after two growing seasons. Using a randomized complete block design, we measured soil pH, total carbon, macro- and micronutrient concentrations, and CEC at two depths (0-15 cm and 15-30 cm). Biochar did not change total carbon and nitrogen, but it decreased aluminium and CEC (-18%), and increased manganese (+53%). Co-application of biochar and manure increased exchangeable magnesium (+106%). Wood ash increased soil pH (+7%), C/N ratio (+12%) and phosphorus (+30%). It also increased aluminium (+26%) and decreased total nitrogen when combined with manure (-33%). Wood ash without manure increased CEC (+14%), but combined with biochar and manure, it decreased CEC (-26%). Finally, manure decreased total carbon (-18%), nitrogen (-27%), and several macro- and micronutrients (K_{exch}, Ca_{exch}, Mg_{exch}, Mn, Al, Na), with stronger effects when combined with ash or in the absence of biochar. However, manure increased nitrogen availability as suggested by a higher mineral/total N ratio (+53%). This study highlights the potential of soil amendment combinations to improve soil fertility in poorly regenerated boreal forest ecosystems, and sheds light on the complex interactions between soil amendments and their influence on soil chemical composition at different depths.

Keywords: Soil, Biochar, Wood ash, Manure, Amendments interaction

4.3 Introduction

Clearcutting in boreal forests generally leads to a short-term increase in soil nutrient availability known as the assart effect (Kimmins, 2004; Kreutzweiser et al., 2008). When the vegetation cover is not rapidly reinstalled, this can lead to nutrient losses (Kiser & Fox, 2012). This is important because some nutrients, particularly nitrogen (N) and phosphorus (P), are largely deficient in boreal forests (Maynard et al., 2014). In this context, soil amendments may provide a sustainable solution for soil fertilization of poorly regenerated forest sites (Larney & Angers, 2012). Biochar and wood ash are amendments of interest for supplying nutrients to managed soils in Canadian boreal forests (Bieser & Thomas, 2019), while manure has rarely been applied in this context (Han et al., 2016). There is a lack of knowledge about the chemical properties of amended forest soils, especially when two or three amendments are used in combination.

Biochar is produced by pyrolysis using a variety of organic matter feedstocks and results in a carbon (C) rich soil amendment with important concentrations of macronutrients, except for N (Ippolito et al., 2015). Biochar could promote long-term soil C sequestration (Lehmann et al., 2006). Although relatively few studies have focused on biochar applications in forest ecosystems (Page-Dumroese et al., 2016), some have reported increases in soil pH, cation exchange capacity (CEC), and exchangeable cation concentrations (Ca_{exch}, Mg_{exch} et K_{exch}), along with higher total C and N concentrations and increased C/N ratios (Biederman & Harpole, 2013; Robertson et al., 2012; Thomas & Gale, 2015). Biochar's high porosity and large surface area adsorbs nutrients and reduces nutrient leaching (Major et al., 2009). It enhances cation retention, improving soil nutrient availability and fertility through increased CEC (Lehmann, 2007; Van Zwieten et al., 2010).

Wood ash is a N-poor inorganic soil amendment that is high in calcium, potassium, magnesium and phosphorus (Pitman, 2006). Wood ash has been used as a soil amendment in Scandinavia for decades (Pitman, 2006) and its application in Canadian forests is steadily increasing (Hannam et al., 2018). It has a strong liming (Augusto et al., 2008) and fertilizing capacity to substitute soil nutrient deficiencies (Vance, 1996).

Studies have mostly examined the effect of wood ash on forest floor (Augusto et al., 2008; Bélanger et al., 2021; Bognounou et al., 2023; Brais et al., 2015; Johansen et al., 2021; Ozolincius et al., 2006), and showed that it increased soil pH, available phosphorus, exchangeable cation concentrations (Ca_{exch}, Mg_{exch} and K_{exch}) and N mineralization. However, attention has been drawn to heavy metal contamination, the bioavailability of which is reduced by elevated soil pH (Augusto et al., 2008; Dimitriou et al., 2006).

Manure is a N-rich organic amendment that is sourced and widely used in agriculture. Its rare use in forestry benefited soils with C sequestration (Lafleur et al., 2012), increased soil pH, total N, available P, exchangeable K, Ca, Mg concentrations (Han et al., 2016). However, adverse effects of manure amendment have been reported due to a priming effect that increased mineralisation of native organic matter, resulting in reduced soil organic carbon. Changes in microbial activity following the addition of fresh organic matter, can cause an imbalance between C supply and C decomposition rates (Fontaine et al., 2004).

Implementing by-products as amendments for soil fertilization can help improve soil quality through organic matter input and nutrient supply (Larney & Angers, 2012). While individual soil amendments are known to generally improve specific soil properties, the combined use of soil amendments to leverage their complementary properties remains underexplored. This study investigates how application of single and combined amendments (i.e. biochar, wood ash, and manure), influence short-term soil chemical properties of a poorly regenerated forest sites to determine the potential of these treatments to improve soil quality and forest ecosystems productivity. We hypothesized that the application of soil amendments would increase soil pH, with wood ash having the most important effect because of its liming properties. Biochar was expected to increase soil total C, while manure should substantially elevate soil total N compared to other amendments. We also anticipated that wood ash would enhance macronutrient concentrations (P, K_{exch}, Ca_{exch} and Mg_{exch}) availability and consequently increase CEC, again due to its liming effect. Additionally, we expected wood ash to reduce Al concentrations because of its ability to increase soil pH and reduce metals bioavailability. Expected effects of soil amendments on soil chemical properties are presented in Tableau 12.

Tableau 12 Expected effects of increase (+) or decrease (-) in soil properties following the presence of biochar (B), wood ash (A) and manure (M) compared to their absence in treatments.

	Total C	Total N	C/N	N_{min}/ N_{tot}	Available P	Base cations	CEC	Al	pH
Biochar	(+)	?				(+)	(+)		(+)
Ash				?	(+)	(+)	(+)	(–)	(+)
Manure	(+)	(+)		?	(+)	(+)	(+)		(+)

4.4 Materials and methods

4.4.1 Study site

The research was conducted in the Lake Duparquet Research and Teaching Forest (FERLD), located in the Abitibi region of northwestern Quebec (48°30' N, 79°22' W). This area has a continental climate, with an average annual temperature of 1°C and annual precipitation of 989 mm, 30% of which falls as snow (Environnement Canada, 2019). The study site is within a mixedwood boreal forest characterized by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) (Saucier et al., 2003). The site was situated on a south-facing slope (8 to 15% gentle slope) previously occupied by a 93-year-old jack pine (*Pinus banksiana*) - aspen (*Populus tremuloides*) mixed forest that was clear-cut in 2016, leaving logging residues on-site. Natural regeneration failure was noticed by 2019, likely due to harsh competing understory vegetation and moderate drainage at the bottom of the slope, which initiated this study.

The experiment was set up as a randomized complete block design with three blocks, aligned along a longitudinal gradient of soil texture and drainage. The bottom slope featured moderately well-drained clay-loam soil, while the middle and top slopes had rapidly draining loam soil (Tableau 1). Soils were all classified as melanic brunisols with coarse-textured deposits of glaciolacustrine tills (Soil Classification Working

Group, 1998). In November 2019, soil scarification was performed on 3 x 5 m plots using an excavator with a 1 m² bucket (250 plots ha^{-1}). Amendments were spread on the soil surface in June 2020, and white spruce seedlings were planted in July 2020 to address the lack of natural regeneration. Each plot hosted an average of seven three-year-old seedlings planted 2 m apart (1500 seedlings ha^{-1}). The seedlings were sourced from a provincial nursery and grown in 25-310 containers (25 cavities per container, 310 cm³ per cavity). Treatments included biochar (B) (2.6 Mg ha^{-1}), wood ash (A) (7 Mg ha^{-1}), manure (M) (105 Mg ha^{-1}), and a control (no amendment) (Tableau 2). These treatments were applied both individually and in combinations (Tableau 3). The doses were cumulative; for example, the biochar-wood ash-manure (BAM) treatment included 2.6 Mg ha^{-1} of B, 7 Mg ha^{-1} of A and 105 Mg ha^{-1} of M. The properties of the amendments used in this study are already documented in Chapitre 2.

4.4.2 Field measurements

Seedlings were sampled in September 2022 for growth and foliar nutrients, while soils were sampled in the first two weeks of October 2022, marking the end of the second growing season of seedlings. We measured annual growth of all the planted seedlings in the same plots sampled for soils. Annual growth was estimated by measuring length of the annual shoot of seedlings. Current year needles were sampled from three randomly selected seedlings per plot and were subsequently analysed for foliar nutrient concentrations. Mineral soil was sampled within three randomly selected plots (n = 3) for each treatment and block (replicate). Soil samples were collected 30 to 50 cm away from three preselected seedlings in each plot at two depths: 0-15 cm and 15-30 cm, using an auger.

4.4.3 Laboratory analyses

Needles from the three randomly selected seedlings were combined to form a composite sample, and oven-dried for 72h at 60°C. We weighed 100 randomly picked needles to determine foliar dry mass. Needles were ground to 2 mm using a Retsch ZM 200 Ultra Centrifugal Mill (Haan, Germany) prior to chemical analysis. Total C and N were obtained through dry combustion in a Vario MAX cube elemental analyzer

(Elementar, Langenselbold, Germany). Macro- and micronutrient concentrations, including P, K, Ca, Mg, Mn, Al, Fe were determined using inductively coupled plasma optical emission spectrometry (ICP-OES; Optima 7300 DV, PerkinElmer, Waltham, MA, USA) following ashing at 500°C for 2 hours and extraction in 1 M HCl, according to Kalra (1997). To measure the absolute amount of foliar nutrients, nutrient content of needles was calculated based on the dry mass of 100 needles and their nutrient concentration (content = concentration × foliar dry mass).

Soil samples were air-dried and ground to 2 mm using a Humboldt hammer mill (Dayton Electric Mfg. Co., Lake Forest, IL, USA). We mixed equal quantities of the three soil samples to form composite samples. Soil pH was measured in a 0.01 M $CaCl_2$ solution (Hendershot et al., 2008b) and soil texture was determined using the hydrometer method (Kroetsch & Wang, 2008). Available P and exchangeable P, K, Ca, Mg, Mn, Al, Fe, and Na were extracted using a Mehlich III solution (Ziadi & Sen Tran, 2008) and analyzed with inductively coupled plasma (ICP) and an optical emission spectrometry (Optima 7300 DV, PerkinElmer, Waltham, MA, USA). The effective cation exchange capacity (CEC) was calculated by summing the exchangeable cations (K, Ca, Mg, Mn, Al, Fe, Na) (Hendershot et al., 2008a). Mineral nitrogen (ammonium, $N\text{-}NH_4^+$, and nitrate, $N\text{-}NO_3^-$) was analyzed using flow injection analysis (FIA) on a Lachat QuikChem® 8500 Series 2 following Maynard et al. (2008). The gravimetric water content of air-dried soil was determined by oven-drying at 105°C for 24 hours and a correction was made to report concentrations measured on air-dried soil on a per 105°C dry soil basis.

Soil amendments were air-dried and ground to 2 mm using a Humboldt hammer mill (Dayton Electric Mfg. Co., Lake Forest, IL, USA). Both soil samples and amendments were analyzed for total carbon (C) and nitrogen (N) content using dry combustion in a Vario MAX cube elemental analyzer (Elementar, Langenselbold, Germany). Total P, K, Ca, Mg, Mn, Cu, Zn, Al, Fe, Mo, and B were measured by inductively coupled plasma (ICP) using optical emission spectrometry (Optima 7300 DV, PerkinElmer, Waltham, MA, USA) after ashing at 500°C for 2 hours and recovering in 1 M HCl following the method described by Kalra (1997).

4.5 Statistical approach

The software R 4.2.1 was used to conduct all statistical analyses (R Core Team, 2021). Linear mixed models were fitted separately for each soil parameter using the lme4 package (Bates et al., 2015). Soil amendments were treated as fixed effect, and a presence (1) or absence (0) factor was assigned to each soil amendment, as we fitted the interaction of the three factors to determine how the presence or absence of biochar, wood ash, and manure, both individually and in combination, affected the parameters studied. Blocks were fitted as random effect. Models were run separately for soil parameters in soil depths at 0-15 cm and 15-30 cm. Pairwise post hoc comparisons were performed using Tukey's Honestly Significant Difference (Tukey HSD) test using the emmeans package to evaluate differences between factor levels (Lenth et al., 2018). The DHARMa package was used to check whether the fitted models respected the assumptions of homoscedasticity and normal distribution (Hartig, 2018). To satisfy these assumptions, some soil variables (C, N, P, K, Ca, Mg, Mn and Na) were log-transformed. For all analyses, a significance level of $\alpha = 5\%$ was set. Redundancy analysis with the vegan package (Oksanen et al., 2020) was used to assess how soil amendments and soil nutrient concentrations correlated with seedling growth and foliar nutrient contents. For that, we fitted a matrix with response variables including seedling growth and foliar nutrient contents, and a second matrix with predictors which consisted of amendments and soil nutrient concentrations.

4.6 Results

4.6.1 Soil nutrients

Soil carbon and nitrogen. Biochar did not change total soil C or N at either soil depth (Tableau 13). At the 0-15 cm soil depth, wood ash significantly increased C/N ratios by 12%, while manure significantly decreased soil total C by 18% (Tableau 13). Manure and wood ash presence in treatments significantly decreased total N at the 15-30 cm soil depth, with a decrease of 27% and 33% by manure and wood ash respectively, compared to their absence in treatments. Manure also increased the ratio of mineral N to total N at the 0-15 cm soil depth by 53% (Tableau 13).

Tableau 13 Results of pairwise comparisons of soil total carbon, total nitrogen, soil C/N ratio, and mineral nitrogen to total nitrogen ratio, with or without biochar (B), wood ash (A) and manure (M) amendments at depths of 0-15 cm and 15-30 cm. Zero and one stand for absence and presence of soil amendments respectively. A vertical line indicates that the significant effect is conditional to the treatment that follows the line. See supplementary material Tableau 21 for the results of ANOVA applied to the linear mixed models.

		C (g kg^{-1})	**N (g kg^{-1})**	**C/N**	**N_{min}/N_{tot}**
0 – 15 cm	**Biochar**	<>	<>	<>	<>
	Wood ash	<>	<>	A0 < A1 22.6 to 25.4 (±1.4) +12% (p=0.029)	<>
	Manure	M0 > M1 24.9 to 20.4 (±2.3) -18% (p=0.023)	<>	<>	M0 < M1 3.4 to 5.2 (±0.96) +53% (p=0.011)
15 – 30 cm	**Biochar**	<>	<>	<>	<>
	Wood ash	<>	A0 > A1 | M1 0.92 to 0.62 (±0.01) -33 % (p=0.015)	<>	<>
	Manure	<>	M0 > M1 | A1 0.85 to 0.62 (±0.01) -27% (p=0.0098)	<>	<>

Note: <> indicates no statistical differences.

Soil macronutrients. Macronutrient concentrations varied according to soil amendments; biochar significantly increased Mg_{exch} in the presence of manure at 0-15 cm soil depths, by 106%. Wood ash significantly increased P at both soil depths, by 27% at 0-15 cm and 33% at 15-30 cm. Manure decreased K_{exch}, Ca_{exch} and Mg_{exch} concentrations at both soil depths. For K_{exch} and Mg_{exch}, the effects were more pronounced in the absence of biochar, with decreases ranging 58-68%. Under manure treatment, the decreases ranged from 31% to 37%. Manure also decreased Ca_{exch} by 39% at 15-30 cm soil depth (Tableau 14).

Tableau 14 Results of pairwise comparisons of soil macronutrients with or without biochar (B), wood ash (A) and manure (M) amendments at depths of 0-15 cm and 15-30 cm. Zero and one stand for absence and presence of soil amendments respectively. A vertical line indicates that the significant effect is conditional to the treatment that follows the line. See supplementary material Tableau 21 for the results of ANOVA applied to the linear mixed models.

<table>
<tr><th></th><th></th><th>P_{avail}
(mg kg^{-1})</th><th>K_{exch}</th><th>Ca_{exch}
(cmolc kg^{-1})</th><th>Mg_{exch}</th></tr>
<tr><td rowspan="3">**0 – 15 cm**</td><td>**Biochar**</td><td><></td><td><></td><td><></td><td>B0 < B1 | M1
0.63 to 1.3 (±0.2)
+106%
(p=0.011)</td></tr>
<tr><td>**Wood ash**</td><td>A0 < A1
7.1 to 9.0 (±2.6)
+27%
(p=0.025)</td><td><></td><td><></td><td><></td></tr>
<tr><td>**Manure**</td><td><></td><td>M0 > M1
0.29 to 0.20 (±0.03)
-31%
(p=0.013)</td><td><></td><td>M0 > M1 | B0
1.5 to 0.63 (±0.2)
-58%
(p=0.0054)</td></tr>
</table>

Tableau 14 (suite)

<table>
<tr><td rowspan="3">**15 – 30 cm**</td><td>**Biochar**</td><td><></td><td><></td><td><></td><td><></td></tr>
<tr><td>**Wood ash**</td><td>A0 < A1
6.6 to 8.8 (±2.6)
+33%
(p=0.0039)</td><td><></td><td><></td><td><></td></tr>
<tr><td>**Manure**</td><td><></td><td>M0 > M1 | B0
0.41 to 0.13 (±0.05)
-68%
(p=0.0001)</td><td>M0 > M1
5.4 to 3.3 (±0.9)
-39%
(p=0.018)</td><td>M0 > M1
1.9 to 1.2 (±0.3)
-37%
(p=0.039)</td></tr>
</table>

Note: <> indicates no statistical differences.

Soil micronutrients, effective cation exchange capacity and pH. Soil amendments had different effects on micronutrient concentrations. Biochar increased Mn concentrations by 53% and decreased Al concentrations by 18% at both soil depths. Fe concentrations increased by 14% under biochar treatment at 15-30 cm soil depth. Biochar also reduced effective cation exchange capacity (CEC) at both soil depths (-10% at 0-15 cm soil depth), and the effect was conditioned by the presence of wood ash and the absence of manure at 15-30 cm soil depth (-26%) (Tableau 15). Wood ash, in the absence of manure, increased Al concentrations by 24% and 28% at 0-15 cm and 15-30 cm soil depths, respectively. Effects on CEC varied according to the presence or absence of other amendments; wood ash increased CEC when applied without manure by 14%, but the addition of biochar and manure reversed this tendency and resulted in a significant decrease in CEC by 26% (Tableau 15). Manure reduced all three micronutrient concentrations, i.e. Mn, Al and Na, at both soil depths. Manure reduced Al concentrations by 17% and 19% in the presence of wood ash, and Na concentrations by 56% in the absence of biochar at 15-30 cm soil depth. Manure also reduced CEC in the presence of wood ash at both soil depths and in the absence of biochar at 15-30 cm depth, with reductions of 18% to 29% (Tableau 15). Wood ash was the only amendment that significantly changed soil pH, with a 7% increase from 4.66 to 4.97 at 0-15 cm soil depth. No significant effect on soil pH at both soil depths was noticed under biochar and manure treatments, except a slight increase from 4.79 to 4.84 for manure treatments at 0-15 cm soil depth (Tableau 15).

Tableau 15 Results of pairwise comparisons of soil micronutrients, effective cation exchange capacity and pH with or without biochar (B), wood ash (A) and manure (M) amendments at depths of 0-15 cm and 15-30 cm. Zero and one stand for absence and presence of soil amendments respectively. A vertical line indicates that the significant effect is conditional to the treatment that follows the line. See supplementary material Tableau 21 for the results of ANOVA applied to the linear mixed models.

		Mn	**Al** **(cmolc kg^{-1})**	**Fe**	**Na**	**CEC**	**pH**
0 – 15 cm	**Biochar**	B0 < B1 0.058 to 0.089 (±0.01) +53% (p=0.031)	B0 > B1 17.7 to 14.6 (±0.9) -17% (p=0.0015)	<>	<>	B0 > B1 24.1 to 21.8 (±0.6) -10% (p=0.0086)	<> 4.82 to 4.81 -0.2%
	Wood ash	<>	A0 < A1 | M0 14.5 to 18.0 (±1.1) + 24% (p=0.011)	<>	<>	A0 < A1 | M0 22.4 to 25.6 (±0.9) +14% (p=0.0094)	A0 < A1 4.66 to 4.97 (±0.08) +7% (p=0.0017)
	Manure	M0 > M1 0.098 to 0.050 (±0.01) -49% (p=0.0027)	M0 > M1 | A1 18.0 to 15.0 (±1.1) -17% (p=0.030)	<>	<>	M0 > M1 | A1 25.6 to 21.1 (±0.9) -18% (p=0.0004)	<> 4.79 to 4.84 +1%

Tableau 15 (suite)

15 – 30 cm	**Biochar**	B0 < B1 0.051 to 0.078 (±0.01) +53% (p=0.043)	B0 > B1 18.4 to 15.1 (±1.0) -18% (p=0.002)	B0 < B1 1.4 to 1.6 (±0.09) +14% (p=0.018)	<>	B0 > B1 | A1M0 31.1 (±1.7) to 23.0 (±1.6) -26% (p=0.0011)	<> 4.76 to 4.73 -0.6%
	Wood ash	**<>**	**A0 < A1 | M0** **14.9 to 19.1 (±1.2)** **+28%** **(p=0.0047)**	**<>**	**<>**	**A0 > A1 | B1M1** **25.9 to 19.3 (±1.6)** **-26%** **(p=0.0059)**	**<>** **4.69 to 4.79** **+2%**
	Manure	M0 > M1 0.080 à 0.050 (±0.01) -38% (p=0.037)	M0 > M1 | A1 19.1 à 15.4 (±1.2) -19% (p=0.012)	<>	M0 > M1 | B0 0.14 à 0.062 (±0.02) -56% (p=0.002)	M0 > M1 | B0A1 31.1 (±1.7) à 22.0 (±1.6) -29% (p=0.0003)	<> 4.74 to 4.75 +0.2%

Note: <> indicates no statistical differences.

Tableau 16 Expected and observed effects of increase (+) or decrease (-) in soil properties following the presence of biochar (B), wood ash (A) and manure (M) compared to their absence in treatments.

	Total C	Total N	C/N	Nmin/ Ntot	Availa ble P	Base cations	CEC	Al	pH
B (expected)	(+)	?				(+)	(+)		(+)
B (observed)	<>	<>	<>	<>	<>	(+)	(–)	(–)	<>
A (expected)				?	(+)	(+)	(+)	(–)	(+)
A (observed)	<>	(–)	(+)	<>	(+)	(–) / <>	(+) / (–)	(+)	(+)
M (expected)	(+)	(+)		?	(+)	(+)	(+)		(+)
M (observed)	(–)	(–)	<>	(–)	<>	(–)	(–)	(–)	<>

4.6.2 Soil and seedling nutrient relationships

Manure was positively related with foliar nutrient contents of white spruce seedlings (dashed arrows) but was opposed to soil nutrient concentrations (solid arrows) at both soil depths (Figures 18a, 18b). These relationships suggest that manure enhanced seedling foliar nutrient contents, while the observed decrease in soil nutrient concentrations resulted from seedlings nutrient uptake. Additionally, the shorter arrow lengths for soil nutrients at the 15-30 cm depth compared to the 0-15 cm depth indicate that these effects were more pronounced in the upper soil layer. The positive relationship of wood ash with soil variables, especially P_{avail}, K_{exch}, Ca_{exch}, C/N ratio and soil pH at the 0-15 cm depth and P_{avail} and N_{min}/N_{tot} ratio at the 15-30 cm depth, suggests that the presence of this amendment in the treatments improved soil conditions. This tendency did not translate into improved foliar nutrients after wood ash application as suggested by the negative relationship between this treatment and foliar nutrients. Moreover, biochar was positively related with soil variables, but its effect on soil and seedlings was limited compared to wood ash and manure showed by the negligible length of the vector.

(a)

(b)

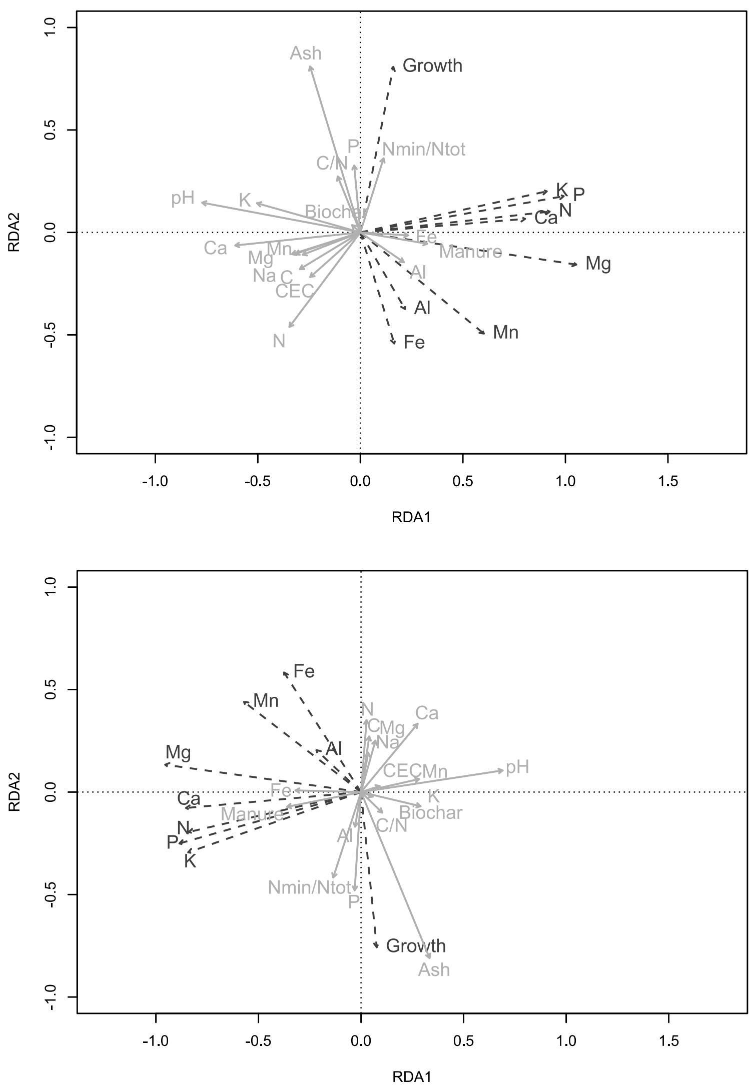

Figure 18 Redundancy analysis (RDA) biplot illustrating the relationships between seedling nutrient contents and soil nutrient concentrations at depths of (a) 0-15 cm and (b) 15-30 cm. Seedling growth and foliar nutrient contents (C, N, P, K, Ca, Mg, Mn, Al and Fe) are represented by black dashed arrow vectors, and explanatory variables are represented by gray solid arrow vectors and include amendment treatments (i.e., the presence of biochar, wood ash and manure), soil pH, C/N and Nmin/Ntot ratios, soil nutrients (C, N, Pavail, Kexch, Caexch, Mgexch, Mn, Na, Al and Fe) and CEC.

4.7 Discussion

4.7.1 How do biochar and wood ash affect carbon and nitrogen dynamics?

Contrary to our hypothesis of increased soil carbon following biochar application (Tableau 16), biochar had no effect on soil total carbon (Tableau 13), contradicting previous findings of increased total carbon following biochar application (Page-Dumroese et al., 2016). Our results suggest that there was either a balance between carbon input from biochar and carbon mineralization, no change in total carbon due to the low application rate of biochar, or that the study duration was too short to observe decomposition and carbon release into the soil, especially considering that biochar was applied on the soil surface. Similarly, there was no effect of biochar on total nitrogen, an observation that is also supported by other studies (Sackett et al., 2015; Zhao et al., 2019), or on mineral N (Palviainen et al., 2018). These findings may be explained by the high C/N ratio of biochar (Tableau 2), which could lead to N limitation and mineral N retention by the N-limited microflora (Prommer et al., 2014).

Wood ash was the only soil amendment to significantly impact soil C/N, as these ratios increased by 12% (Tableau 13). Furthermore, the combination of wood ash and manure decreased total N (Tableau 13), which is consistent with the direction of change in C/N ratios with wood ash, as well as with the increased N_{min}/N_{tot} ratio by manure, although these effects occurred at different soil depths. Previous studies have shown increased N mineralisation rates following wood ash application (Brais et al., 2015), which could explain the observed reduction in total N. This reduction is likely due to plant uptake of mineralized N (Pitman et al., 2024), particularly in the presence of manure, a N rich amendment. This result is supported by the negative correlation between soil nutrients and seedling foliar nutrients (Figure 18), indicating nutrient uptake from the soil by seedlings.

4.7.2 How does wood ash affect soil nutrients?

Wood ash increased soil pH (Tableau 15) as we had predicted (Tableau 16). Augusto et al. (2008) highlighted the liming effect of wood ash on acidic forest soils due to its important carbonate contents. In addition to soil pH, wood ash increased soil P concentration at both soil depths, which was also found in other studies (An & Park, 2021; Johansen et al., 2021; Park et al., 2005; Pugliese et al., 2014). We had predicted that soil Al would decrease following wood ash application (Tableau 12), but it rather increased, in the absence of manure; Pitman et al. (2024) had also found an increase in Al in the early years of wood ash application despite the increase in soil pH caused by wood ash application and argued that the high Al mobility in soils only starts to decrease with soil pH above 4.5. In our case, pH was 4.8, and the negative correlation found between Al and pH ($r = -0.31$, $p < 0.001$) (data not shown) indicates a reduction in Al concentrations as soil pH increases. Accordingly, Brady and Weil (1996) found decreased Al levels after wood ash application, as the reduction in acidity lowered the solubility of this element.

4.7.3 Effects of biochar on soil nutrients

Synergetic interaction of biochar and manure. Complementary effects of biochar and manure combination were observed in terms of increased soil Mg_{exch} by biochar only in the presence of manure (Tableau 14). Studies have shown that the application of biochar to forest soils can increase the availability of Mg_{exch} through reducing soil acidity, which increases magnesium exchangeability, particularly in acidic soils (Liu et al., 2023; Sackett et al., 2015). The combination of biochar and manure resulted in a slight but non-significant increase in soil pH from 4.78 to 4.81, indicating that the observed increase in Mg_{exch} was unlikely due to reduced soil acidity in our case. However, manure served as a source of Mg (Tableaux 2, 3), suggesting that biochar played a role in retaining these nutrients. This is consistent with Liang et al. (2024) that reported similar findings.

Is biochar effective in alleviating soil metals? The use of biochar is currently attracting attention for mitigating soil toxicity (Joseph et al., 2021). In this study, biochar effectively reduced soil Al concentrations at both soil depths (Tableau 15), and we observed similar results in spruce foliar nutrients (Chapitre 2). Other studies have also highlighted the ability of biochar to mitigate Al toxicity in acidic soils, through its liming effects (Van Zwieten et al., 2015), but this was not the case in this study as soil pH was unaffected by biochar amendment (Tableau 15). Biochar could also directly reduce soil Al toxicity by the formation of complexes between soil Al^{3+} cations with biochar, including mechanisms such as surface adsorption, ion-exchange between Al^{3+} and K^{+}, Ca^{2+} and Mg^{2+}, which results in Al fixation on biochar surfaces, or by co-precipitating with silicate particles to form compounds such as $KAlSi_3O_8$ (Qian et al., 2013; Shetty et al., 2021). Biochar application however increased soil Mn concentrations at both soil depths (Tableau 15), similarly to Butnan et al. (2015). They attributed these increases to dissolved organic molecules produced by the biochar that chelated soil Mn. However, Mn uptake by plants was species dependent and also depended on the chelated form of Mn (Butnan et al., 2015). In our case, increased Mn in soils did translate into increased foliar Mn as these two arrow were in opposite directions (Figure 18).

4.7.4 Unexpected adverse effects of manure on soil nutrients

Contrary to our expectations of increased soil nutrients following manure application (Tableau 16), manure decreased C and most of macro- and micronutrients (N, K_{exch}, Ca_{exch}, Mg_{exch}, Mn and Al), as well as CEC (Tableaux 13, 14, 15). These effects were sometimes conditioned by the presence of wood ash, the absence of biochar, or with both conditions combined. The decrease of total C and N suggests high C and N losses and an imbalance between C and N inputs from manure and losses, which may be multifactorial, as discussed below. Similar results were observed in previous studies where manure application induced a priming effect, an accelerated mineralisation of native soil organic matter due to increased organic matter activity, resulting in reduced soil organic carbon and nitrogen immobilization (Fontaine et al., 2004; Kuzyakov et al., 2000). In Chapitre 2, manure treatments significantly increased seedling growth and leaf N contents of understory vegetation compared to treatments without manure, suggesting that manure amendment greatly increased N uptake by plants and could have depleted soils. Accordingly, manure correlated positively with foliar nutrient contents and negatively with soil nutrient concentrations (Figure 18). In addition, the reduction in soil N was enhanced by the presence of wood ash, and the combination of the two amendments increased soil pH from 4.64 to 4.95, suggesting that manure enhanced organic matter mineralization due to a higher soil pH. The lower C/N ratio of manure (Tableau 2) may also have increased N mineralization (Prommer et al., 2014), as observed by Liu et al. (2020), especially for manures with low C/N ratios (<12). Manure used in our study had a C/N ratio of 18, which may still be considered low given the typically low nitrogen content of boreal forest soils. Furthermore, manure was the only amendment that significantly affected N_{min}/N_{tot} ratios by 53% (Tableau 13), suggesting an increase in mineral N availability following manure treatments This aligns with previous findings showing that manure application increases soil nitrogen availability, by enhancing organic matter mineralization, microbial biomass, and nutrient cycling (Leytem et al., 2024; Liu et al., 2020; Saka et al., 2017). Finally, aluminium concentrations significantly decreased in response to manure addition in the presence of wood ash, indicating decreased exchangeable Al by manure when combined with wood ash (Tableau 15). Tang et al. (2007) showed that reduced acidity by animal manure was effective in reducing Al concentrations in acidic soil, which could explain our results since manure combined with wood ash increased soil pH by 0.3 units (not significant) and a negative correlation was found between soil pH and Al ($r = -0.31$, $p < 0.001$) (data not shown).

4.7.5 Antagonistic interaction between biochar and wood ash

Wood ash elevated CEC in the absence of manure, as reported in previous studies demonstrating its efficiency to increase CEC in acidic boreal forest soils (Arvidsson & Lundkvist, 2003; Ingerslev et al., 2014; Kahl et al., 1996; Saarsalmi et al., 2001). Wood ash thus enhanced soil nutrient retention, but when applied in combination with both biochar and manure, wood ash decreased CEC, indicating an adverse interaction between amendments. Antagonist effects of biochar combination with other organic amendments were reported before, where amendments alone had better outcomes compared to when they were combined with biochar (Bonanomi et al., 2017). Biochar can interact with other amendments in terms of nutrient availability by inducing microbial immobilization of nutrients, though this effect has predominantly been observed for nitrogen (Joseph et al., 2021). Furthermore, the immobilization of nutrients is more likely to happen when the C/N ratio of the amendment in higher than 30 to 35 (Hodge et al., 2000), which was the case of both our biochar and wood ash. The negative effect of biochar on CEC is likely to be stronger in soils with high Ca^{2+} concentrations (Hailegnaw et al., 2019), such as when ash is also added.

4.8 Conclusion

Regeneration failure is a common issue for clear-cut sites within the boreal forest, and soil amendments offer a sustainable approach to soil fertilization. Our results highlight significant changes in soil chemical properties depending on the combination of amendments. At the scale of this study, biochar application did not alter soil C and N, likely due to its slow decomposition and N immobilisation potential. However, it reduced Al concentrations while increasing Mn concentrations. Wood ash increased soil C/N ratios, and extractable P and reduced soil acidity. However, it elevated Al concentrations and, when combined with manure, it reduced total N. Manure application increased N availability, but led to a significant decrease of soil total C and N, along with other macro- and micronutrients (K_{exch}, Ca_{exch}, Mg_{exch}, Mn, Al, Na) and CEC, with stronger effects when combined with ash or in the absence of biochar, potentially due to a priming effect and/or enhanced nutrient uptake by seedlings.

Our results revealed that biochar and manure had complementary effects, with biochar increasing Mg_{exch} when applied with manure. In contrast, amendments also exhibited antagonistic interactions, where wood ash without manure increased base cations availability and CEC, but in the presence of biochar and manure, it decreased these values, suggesting that biochar application led to nutrient immobilization. Overall, these findings emphasize the importance of considering amendment interactions in soil amendment strategies. While some combinations, such as biochar and manure, appear to have synergistic benefits, others, particularly biochar and wood ash, may require further investigation to understand their potential effects.

4.9 Acknowledgements

The authors extend their sincere gratitude to the CRSNG Industrial Research Chair in Silviculture and Wood Production granted to Annie DesRochers (#IRCPJ547921- 18) for the scholarship and funding that made this research possible. We also thank the Lake Duparquet Research and Teaching Forest for carrying out the application of the soil amendments, and for providing the location and facilities necessary for conducting the field and laboratory work. Our appreciation goes to the laboratory staff at Notre-Dame-du-Nord Research Station, UQAT, and Laurentian Forestry Centre, Canadian

Forest Service. Special thanks are due to field assistants for their invaluable help both in the laboratory and in the field.

5. CONCLUSION GÉNÉRALE

Nombreux sont les facteurs qui peuvent compromettre le processus de régénération naturelle à la suite des coupes totales en forêt boréale mixte, notamment une compétition importante de la végétation de sous-bois. Dans un contexte où l'utilisation des herbicides est prohibée, nous avons proposé l'application des amendements de sol (biochar, cendres de bois et fumier) comme un outil de restauration forestière complémentaire au reboisement et au travail mécanique du sol. D'une part, nous avons considéré l'action des amendements sur une triple composante de l'écosystème forestier. À savoir les semis par leur croissance et leur nutriments foliaires, le sol par ses propriétés chimiques, et la végétation de sous-bois par une approche taxonomique et fonctionnelle. Cette démarche nous a permis d'avoir une vue d'ensemble sur les mécaniques qui régissent l'écosystème forestier. D'autre part, nous avons appliqué les amendements choisis individuellement et en combinaison, afin de profiter de leurs différentes propriétés physico-chimiques, et de déceler les potentiels effets synergiques et antagonistes, et c'est ce qui a fait l'objet de cette thèse.

Nos résultats ont permis de démontrer que les amendements de sol sont un outil de restauration forestière efficace dans un contexte d'échec de régénération naturelle en raison d'une forte compétition de la végétation de sous-bois (Chapitre 2). L'application du fumier, par sa richesse en azote et en phosphore, a permis d'augmenter la croissance annuelle des semis après deux saisons de croissance, ainsi que leur concentration foliaire en azote et en phosphore. Les cendres de bois et le biochar n'ont pas été efficaces pour augmenter la croissance des semis, mais leur application a permis d'améliorer la nutrition foliaire des arbres. Les cendres de bois ont permis d'augmenter la concentration en N, P, K et Ca des semis qui est essentielle à la croissance, tandis que le biochar a permis de réduire la concentration en Al foliaire, qui peut être toxique pour la croissance des semis et freiner leur croissance. L'analyse vectorielle a permis de montrer que les semis étaient déficients en macronutriments essentiels à leur croissance, tels que N, P, K et Ca, et que l'apport des amendements, notamment le fumier et les cendres de bois, a permis de combler cette carence et d'enrichir les semis tout en améliorant significativement leur croissance dans le cas du fumier. À l'échelle de cette étude, l'application combinée des amendements n'a pas significativement amélioré la croissance des semis par rapport à l'application individuelle du fumier. Toutefois, nos résultats suggèrent un potentiel d'amélioration avec les cendres de bois, compte tenu de leurs effets favorables sur les nutriments foliaires. De plus, la combinaison des amendements pourrait s'avérer bénéfique à plus long terme, en raison de la réduction de l'acidité du sol et de la décomposition progressive des amendements, favorisant ainsi un apport continu en éléments nutritifs.

L'effet des amendements sur la végétation de sous-bois demeure peu étudié dans le contexte de la restauration forestière, alors même que cette strate joue un rôle clé dans l'écosystème. Une meilleure compréhension de ces interactions est essentielle pour anticiper les impacts des amendements, notamment afin d'éviter une augmentation de la compétition de la végétation de sous-bois ou l'introduction d'espèces non indigènes via des amendements issus de résidus non forestiers, comme le fumier, qui pourraient nuire à la croissance des espèces ciblées dans le plan de l'aménagement forestier. Cette thèse a permis d'étudier l'effet des amendements sur la végétation de sous-bois à travers une approche taxonomique et fonctionnelle (Chapitre 3). Elle a ainsi mis en évidence les changements affectant les indices de diversité et la composition de la communauté végétale, ainsi que les traits fonctionnels, aussi bien au niveau de l'espèce qu'à celui de la communauté, grâce au calcul des traits agrégés et de la diversité fonctionnelle. Bien que l'apport du fumier ait favorisé la croissance des semis, il a également entraîné une augmentation de la diversité de la végétation de sous-bois, notamment par l'apparition d'espèces non indigènes comme le trèfle rouge, ainsi que de légumineuses et de graminées adoptant des stratégies de croissance rapide et de forte compétition. Cet effet, non recherché dans le cadre de l'amendement des sols, mérite un suivi particulier, car une modification de la composition du sous-bois pourrait engendrer un changement d'état de l'écosystème. Toutefois, ce changement de communauté végétale n'a pas eu d'effet négatif sur la croissance des semis dans le cadre de cette étude. De plus, il est plausible que cette compétition diminue avec le temps, à mesure que les arbres prennent de l'ampleur, puisque la végétation de sous-bois possède une hauteur maximale limitée, contrairement aux semis d'arbres qui continueront à croître. Ce chapitre a permis de démontrer l'importance de combiner les deux approches, taxonomiques et fonctionnelles, pour une meilleure compréhension de l'effet des amendements sur la végétation de sous-bois.

L'étude de l'effet des amendements sur les propriétés chimiques des sols en forêt boréale est grandissante, mais peu d'études ont considéré l'effet du fumier d'une part, ou de la combination de plusieurs amendements d'autre part. Cette thèse a permis d'explorer les effets de l'interaction des amendements, et de déceler les effets synergiques des effets antagonistes (Chapitre 4). Nos résultats ont montré une absence d'effet du biochar sur le carbone et l'azote totaux du sol, mais le biochar a permis de diminuer la concentration de l'aluminium et d'augmenter celle du manganèse. Toutefois, un effet synergique a été relevé entre le biochar et le fumier, puisque cette combinaison a permis d'augmenter le magnésium échangeable. Les cendres de bois ont été efficaces pour réduire l'acidité du sol, tout en augmentant le ratio C/N et le phosphore disponible. Toutefois, les cendres de bois ont augmenté la concentration en aluminium du sol et ont réduit l'azote total en combinaison avec le fumier. Les cendres de bois ont aussi permis d'augmenter la CEC, tandis que leur apport avec le biochar et le fumier a inversé les effets et a diminué la CEC. L'apport du fumier a réduit le carbone et l'azote totaux, ainsi que plusieurs macro-, micronutriments et métaux (K_{exch}, Ca_{exch}, Mg_{exch}, Mn, Al, Na), avec des effets plus importants en l'absence du biochar et en présence des cendres de bois. Ces effets négatifs sont fort probablement le résultat d'un effet d'amorçage induit (« priming effect ») par l'apport d'une dose importante de fumier, mais aussi de l'absorption des nutriments par les plantes, comme l'ont montré les relations négatives entre les nutriments dans le sol et ceux dans les feuilles. Toutefois, le fumier a permis d'augmenter la disponibilité de l'azote dans le sol.

On peut conclure que la dose de fumier appliquée a eu un effet non souhaité sur le sol, en provoquant des pertes importantes en nutriments. Bien que la combinaison du fumier avec le biochar ait été testée, ses effets bénéfiques potentiels n'ont pas pu être mis en évidence, probablement en raison de la dose élevée de fumier, qui a masqué l'effet des autres amendements. Ainsi, pour optimiser l'efficacité du fumier et limiter les pertes, notre recommandation serait d'appliquer le fumier à des doses plus faibles, en combinaison avec le biochar. Ce dernier pourrait favoriser la rétention de l'azote dans le sol, en réduire les pertes et en prolonger la disponibilité pour les plantes.

Limites et perspectives. Cette étude présente certaines limites qu'il conviendrait d'explorer dans de futurs travaux. L'une des principales contraintes concerne la dose de fumier appliquée. Bien qu'elle ait été déterminée sur la base de la littérature (Benke et al., 2010), une application trop importante en une seule fois a induit un important effet d'amorçage non souhaité. Ce phénomène a entraîné une perte de nutriments supérieure aux apports réels, réduisant ainsi le bénéfice pour les sols et augmentant le risque de contamination de la nappe phréatique. Il serait pertinent de réduire la dose de fumier appliquée, afin de mieux l'adapter aux capacités de rétention et d'assimilation du sol et des semis d'épinette blanche. Une approche plus progressive, répartissant les apports sur plusieurs mois ou années, permettrait également d'optimiser leur assimilation par la végétation et de limiter les pertes. Cela dit, bien que ces ajustements soient souhaitables du point de vue environnemental, leur mise en œuvre reste à évaluer en fonction des contraintes logistiques et économiques. Au final, un apport unique à dose plus élevée, tel que celui testé dans cette étude, demeure peut-être la modalité la plus réaliste sur le plan opérationnel.

Une autre limite de cette étude réside dans sa courte durée, qui a restreint l'ampleur des effets observables, notamment pour le biochar. Son processus de décomposition, relativement lent, n'a pas permis d'en mesurer pleinement les impacts à l'échelle temporelle considérée. Des effets plus prononcés pourraient être attendus à plus long terme, au fur et à mesure de sa dégradation et de son intégration progressive dans le sol.

Enfin, les traits fonctionnels étudiés se limitaient aux feuilles, en raison de leur accessibilité, de la facilité de mesure et des coûts réduits. Cependant, une analyse des traits racinaires aurait permis de mieux caractériser les différences entre traitements et d'affiner notre compréhension des mécanismes d'adaptation des espèces de sous-bois. L'intégration de traits liés à l'acquisition des nutriments, tels que le taux de croissance, la longueur spécifique des racines (SRL), l'architecture du système racinaire, ou encore la capacité d'absorption de l'azote organique, constituerait une perspective intéressante pour de futures recherches. Par ailleurs, l'absence de mesures des propriétés biologiques du sol, incluant notamment la colonisation mycorhizienne, constitue une autre importante, car elles sont essentielles pour comprendre le rôle des micro-organismes dans la transformation, la nutrition, la disponibilité des nutriments, et la croissance des semis d'épinettes blanches.

Implications. À travers les résultats de cette thèse, nous sommes en mesure d'émettre des recommandations pratiques dans le contexte de l'aménagement forestier. Premièrement, l'application des amendements contribue à soutenir l'économie circulaire, en valorisant des résidus agricoles et forestiers qui seraient autrement éliminés par incinération ou, par enfouissement, des pratiques coûteuses et génératrices de gaz à effet de serre. Le recyclage de ces résidus par épandage représente ainsi une option de gestion plus durable et moins impactante sur le plan environnemental. Toutefois, pour maximiser les bénéfices environnementaux de cette pratique, il est essentiel de tenir compte de la provenance des amendements, afin de limiter les distances de transport et les émissions associées. Ensuite, l'application localisée du fumier sur des microsites de plantation se révèle être une stratégie efficace, réduisant les coûts tout en limitant son absorption par la végétation de sous-bois en dehors des microsites.

Le fumier n'est pas l'unique source de matière organique azotée envisageable. Des travaux supplémentaires devraient également s'intéresser à d'autres matières organiques riches en azote. En effet, la valorisation du fumier en milieu forestier semble moins porteuse, étant donné qu'il constitue une ressource précieuse et largement utilisée en agriculture. Les boues d'épuration, aux propriétés similaires, constituent une ressource sous-exploitée. Contrairement au fumier, qui est bien valorisé en milieu agricole, les boues d'épuration sont encore largement destinées à l’enfouissement ou à l’incinération. Explorer leur potentiel en tant qu’amendement pour les sols forestiers pourrait ainsi représenter une voie prometteuse pour conjuguer restauration écologique et valorisation des résidus organiques. Toutefois, plusieurs enjeux doivent être pris en compte, notamment l’acceptabilité sociale, le risque de contamination des bassins versants selon les types de sols et la topographie, ainsi que les contraintes logistiques et environnementales. En effet, la présence possible de pathogènes et de substances toxiques impose une planification rigoureuse des opérations, notamment pour respecter les délais réglementaires entre épandage et enfouissement, et pour garantir la santé et la sécurité des reboiseurs intervenant après l’épandage.

Cette thèse a apporté une contribution significative à l’avancement des connaissances sur l’utilisation des amendements organiques dans le cadre de la restauration forestière, en mettant en lumière non seulement leurs effets sur les propriétés physico-chimiques des sols, mais également sur la réponse nutritionnelle des semis. Cependant, notre étude a révélé que la relation entre les nutriments présents dans le sol et ceux dans les plantes n’est pas toujours linéaire. Bien qu’une corrélation positive entre l’enrichissement du sol et la croissance des plantes soit fréquemment attendue, nos résultats montrent que cette relation est bien plus complexe et varie en fonction des types d’amendements appliqués. Ces observations soulignent l’importance de ne pas simplifier cette dynamique et d’approfondir l’étude des facteurs influençant la réponse des plantes en contexte de restauration.

Cette étude a mis en évidence que l’apport des amendements de sol tels que le fumier, les cendres de bois et le biochar pouvait contribuer de façon significative à l’amélioration de la productivité forestière, notamment grâce à une croissance annuelle des semis plus importante. Toutefois, leur intégration à grande échelle soulève des questions économiques importantes, liées autant au coût des matières qu’à leur transport et à leur application en milieu forestier. Si le fumier, appliqué à forte dose, a démontré un effet positif sur la productivité, les quantités nécessaires sont telles que sa rentabilité à l’échelle opérationnelle demeure limitée, malgré son faible coût de production. Ceci suggère que des travaux supplémentaires devraient viser à identifier des doses optimales plus faibles, permettant de maximiser son effet tout en réduisant les coûts. Les cendres de bois, accessibles et peu coûteuses, représentent une alternative intéressante, bien que leurs effets soient généralement plus modérés. Le biochar, plus onéreux à l'achat, est quant à lui appliqué à des doses plus faibles et offre un bon équilibre entre efficacité et coût d'application. Pour soutenir une prise de décision éclairée en matière de restauration forestière, des études complémentaires devraient porter sur l'évaluation des coûts réels d'acquisition, de logistique et d'épandage de ces amendements par rapport aux gains économiques associés à l'amélioration de la productivité forestière.

ANNEXE A – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 2

Tableau 17 Results of ANOVA applied to the linear mixed models. Treatments consist of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

ANOVA	Sum of squares	Mean square	Degree of freedom	DenDF	F value	p value
annual growth ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	271	271	1	1.97	0.08	0.81
A	493	493	1	2.03	0.14	0.74
M	67229	67229	1	58.85	19.37	**4.598e-0.5**
B : A	3784	3784	1	58.59	1.09	0.30
B : M	393	393	1	58.79	0.11	0.74
A : M	12489	12489	1	58.75	3.60	0.06
B : A : M	937	937	1	58.71	0.27	0.60
N ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.79	0.79	1	2	0.20	0.70
A	15.97	15.97	1	60	4.04	**0.049**
M	86.88	86.88	1	60	21.99	**1.626e-0.5**
B : A	2.94	2.94	1	60	0.74	0.39
B : M	12.44	12.44	1	60	3.15	0.08
A : M	0.13	0.13	1	60	0.03	0.85
B : A : M	6.86	6.86	1	60	1.74	0.19
C/N ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	4.54	4.54	1	2	0.10	0.78
A	99.94	99.94	1	60	2.23	0.14
M	915	915	1	60	20.44	**2.952e-05**
B : A	6.87	6.87	1	60	0.15	0.70
B : M	74.48	74.48	1	60	1.66	0.20
A : M	1.02	1.02	1	60	0.02	0.88
B : A : M	41.37	41.37	1	60	0.92	0.34

Tableau 17 (suite)

P ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.01	0.01	1	2	0.19	0.71
A	1.08	1.08	1	60	17.71	**8.74e-0.5**
M	1	1	1	60	16.45	**0.0001**
B : A	0.02	0.02	1	60	0.26	0.61
B : M	0.008	0.008	1	60	0.13	0.72
A : M	0.0003	0.0003	1	60	0.004	0.95
B : A : M	0.0002	0.0002	1	60	0.003	0.96
K ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.24	0.24	1	60	0.48	0.49
A	14.02	14.02	1	60	27.85	**1.903e-06**
M	5.11	5.11	1	2	10.14	0.09
B : A	0.54	0.54	1	60	1.07	0.30
B : M	0.81	0.81	1	60	1.60	0.21
A : M	0.42	0.42	1	60	0.84	0.36
B : A : M	0.17	0.17	1	60	0.34	0.56
Ca ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.33	0.33	1	60	0.26	0.61
A	18.91	18.91	1	4	14.73	**0.02**
M	0.02	0.02	1	60	0.02	0.90
B : A	3.71	3.71	1	60	2.89	0.09
B : M	0.08	0.08	1	60	0.06	0.80
A : M	1	1	1	60	0.78	0.38
B : A : M	4.13	4.13	1	60	3.22	0.08
Mg ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.04	0.04	1	58	2.31	0.13
A	0.002	0.002	1	2	0.13	0.75
M	0.02	0.02	1	2	1.19	0.39
B : A	0.006	0.006	1	58	0.39	0.53
B : M	0.0009	0.0009	1	58	0.06	0.81

Tableau 17 (suite)

A : M	0.00003	0.00003	1	58	0.002	0.96
B : A : M	0.002	0.002	1	58	0.10	0.75
Mn ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.003	0.003	1	60	0.42	0.52
A	0.09	0.09	1	4	13.27	**0.02**
M	0.08	0.08	1	60	12.45	**0.0008**
B : A	0.03	0.03	1	60	4.02	**0.049**
B : M	0.003	0.003	1	60	0.46	0.50
A : M	0.003	0.003	1	60	0.40	0.53
B : A : M	0.04	0.04	1	60	6.93	0.01
Cu ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	8.2700e-08	8.2700e-08	1	2.51	0.05	0.83
A	8.6806e-06	8.6806e-06	1	57.73	5.61	**0.02**
M	1.7821e-06	1.7821e-06	1	3.73	1.15	0.35
B : A	2.6450e-06	2.6450e-06	1	57.73	1.71	0.20
B : M	6.7200e-08	6.7200e-08	1	57.73	0.04	0.83
A : M	5.0000e-07	5.0000e-07	1	57.73	0.32	0.57
B : A : M	2.2756e-06	2.2756e-06	1	57.73	1.47	0.23
Zn ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.000008	0.000008	1	57.98	0.03	0.87
A	0.0008	0.0008	1	3.32	2.62	0.19
M	0.0003	0.0003	1	2.24	0.92	0.43
B : A	0.001	0.001	1	57.98	4.32	**0.04**
B : M	0.0005	0.0005	1	57.98	1.78	0.19
A : M	0.0006	0.0006	1	57.98	1.90	0.17
B : A : M	0.0005	0.0005	1	57.98	1.85	0.18
Al ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.003	0.003	1	3.12	6.31	0.08
A	0.0008	0.0008	1	57.57	1.49	0.23
M	0.00004	0.00004	1	3.26	0.07	0.80

Tableau 17 (suite)

B : A	0.002	0.002	1	57.57	4.04	0.049
B : M	0.00008	0.00008	1	57.57	0.16	0.69
A : M	0.00036	0.00036	1	57.57	0.67	0.42
B : A : M	0.0002	0.0002	1	57.57	0.35	0.55
Bo ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	2.12e-05	2.12e-05	1	2	2.74	0.24
A	1.81e-05	1.81e-05	1	58	2.26	0.14
M	6.39e-07	6.39e-07	1	2	0.08	0.80
B : A	3.68e-05	3.68e-05	1	58	4.60	**0.04**
B : M	5.72e-06	5.72e-06	1	58	0.71	0.40
A : M	4.03e-05	4.03e-05	1	58	5.04	**0.03**
B : A : M	3.25e-06	3.25e-06	1	58	0.41	0.53
light ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	49.45	49.45	1	64	0.38	0.54
A	73.97	73.97	1	64	0.56	0.45
M	1131	1131	1	64	8.63	**0.005**
B : A	15.23	15.23	1	64	0.12	0.73
B : M	19.88	19.88	1	64	0.15	0.70
A : M	117	117	1	64	0.89	0.35
B : A : M	10.51	10.51	1	64	0.08	0.78
SLA ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	31.98	31.98	1	57.53	0.70	0.41
A	175	175	1	2.86	3.83	0.15
M	234	234	1	3.68	5.10	0.09
B : A	155	155	1	57.53	3.39	0.07
B : M	145	145	1	57.53	3.17	0.08
A : M	318	318	1	57.53	6.94	**0.01**
B : A : M	204	204	1	57.53	4.44	**0.04**

Tableau 17 (suite)

pH ~ B*A* M*horizon + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | block : horizon) + (1 | plot)						
B	0.002	0.002	1	60	0.06	0.80
A	0.04	0.04	1	3.90	1.28	0.32
M	0.004	0.004	1	60	0.14	0.71
horizon	0.09	0.09	1	2.01	3.15	0.22
B : A	0.08	0.08	1	60	2.67	0.11
B : M	0.01	0.01	1	60	0.40	0.53
A : M	0.05	0.05	1	60	1.88	0.17
B: horizon	0.002	0.002	1	62	0.06	0.80
A : horizon	0.39	0.39	1	62	13.70	**0.0005**
M : horizon	0.01	0.01	1	62	0.42	0.52
B : A : M	0.04	0.04	1	60	1.59	0.21
B : A : horizon	0.008	0.008	1	62	0.27	0.60
B : M : horizon	0.20	0.20	1	62	7.02	**0.01**
A : M : horizon	0.005	0.005	1	62	0.18	0.67
B : A : M : horizon	0.03	0.03	1	62	1.07	0.30

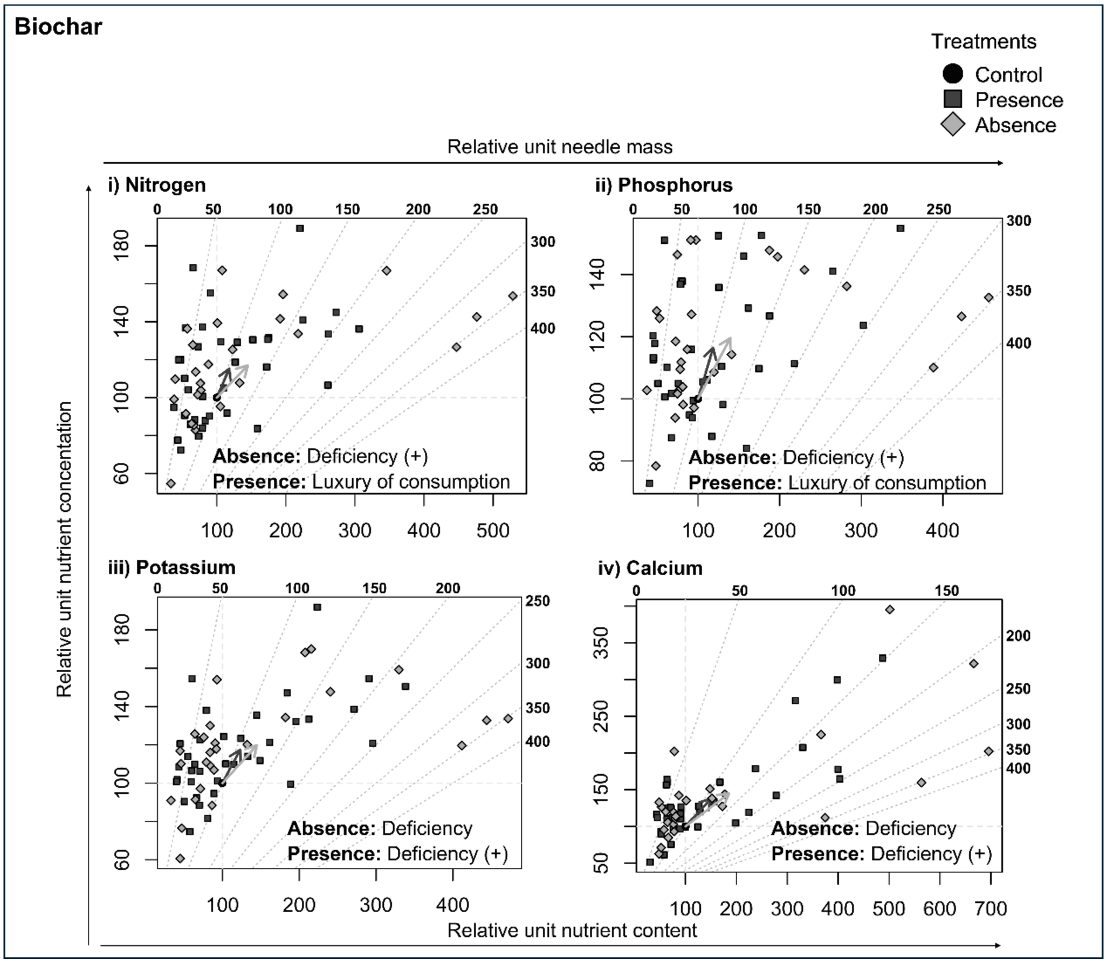

Figure 19 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) nitrogen, (i) phosphorus, (iii) potassium and (iv) calcium of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of biochar, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

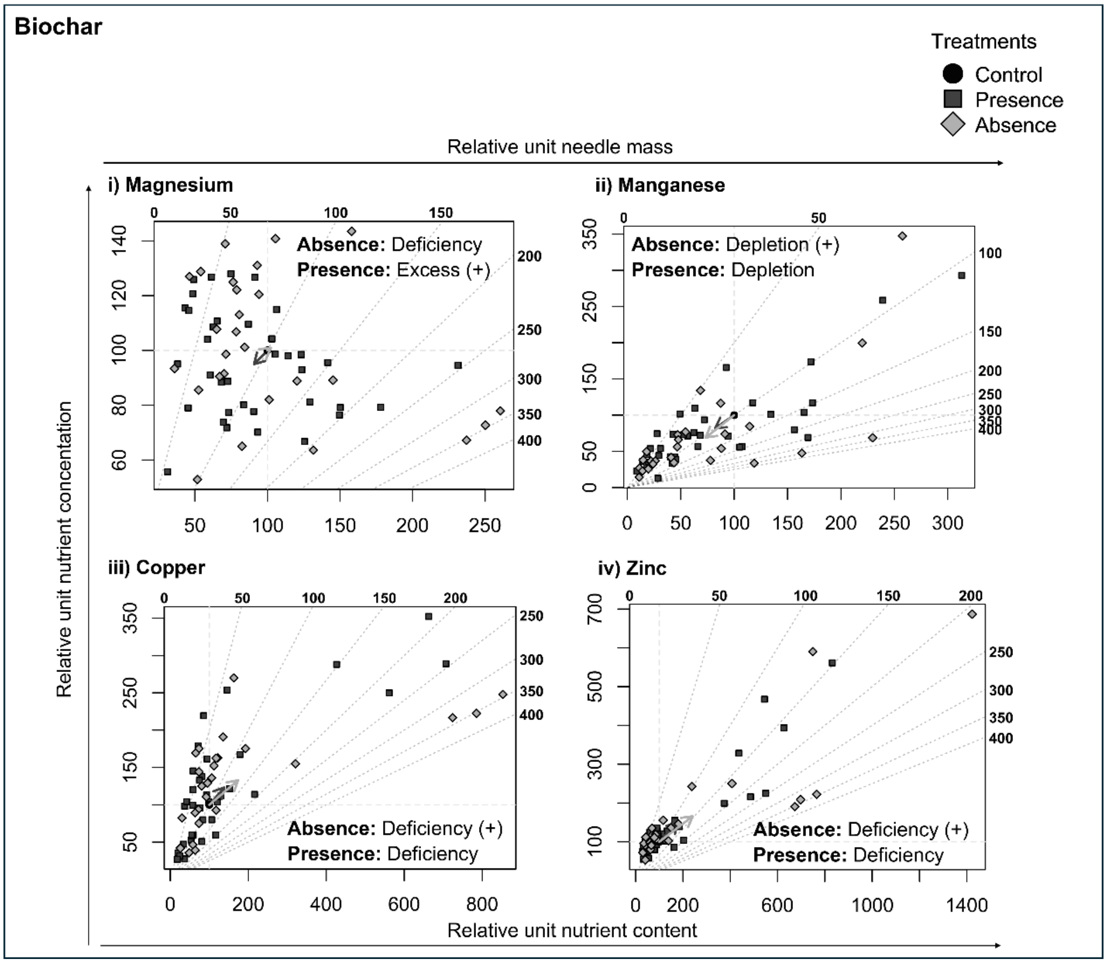

Figure 20 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) magnesium, (ii) manganese, (iii) copper, and (iv) zinc of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of biochar, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

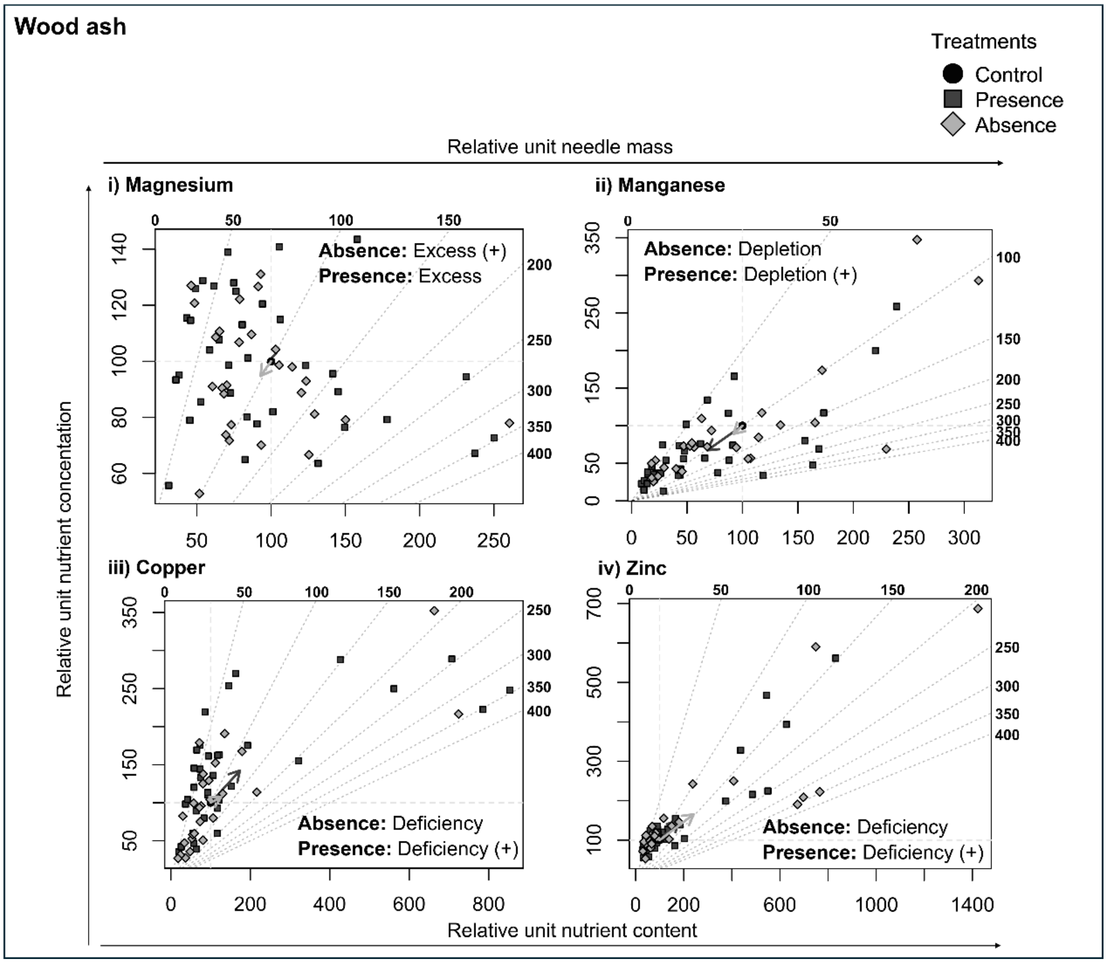

Figure 21 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) magnesium, (ii) manganese, (iii) copper, and (iv) zinc of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of wood ash, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

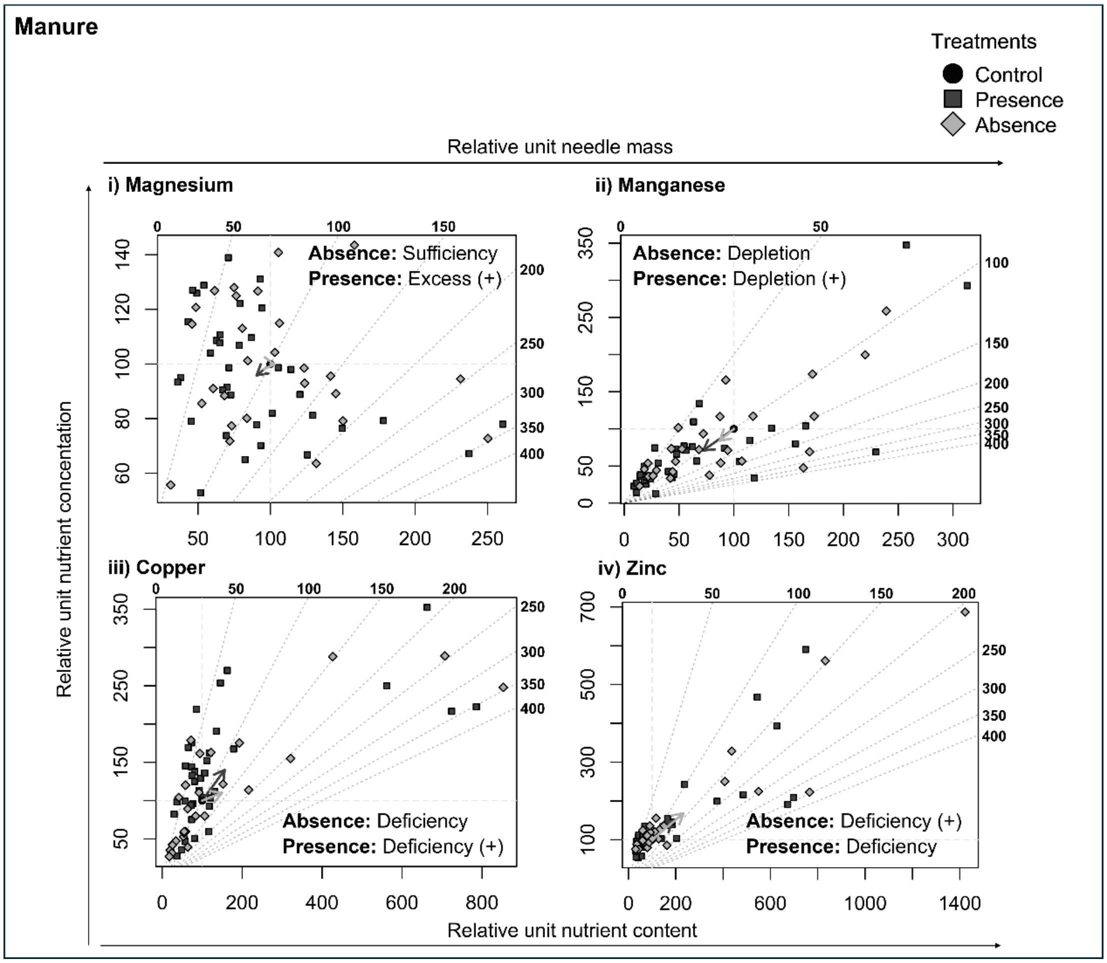

Figure 22 Vector nomograms illustrating the relative changes in foliar dry mass, nutrient concentration, and nutrient content of (i) magnesium, (ii) manganese, (iii) copper, and (iv) zinc of white spruce seedlings after two growing seasons. Treatments consist of the presence or absence of manure, with the control set as the reference treatment. The (+) sign indicates the longest arrow.

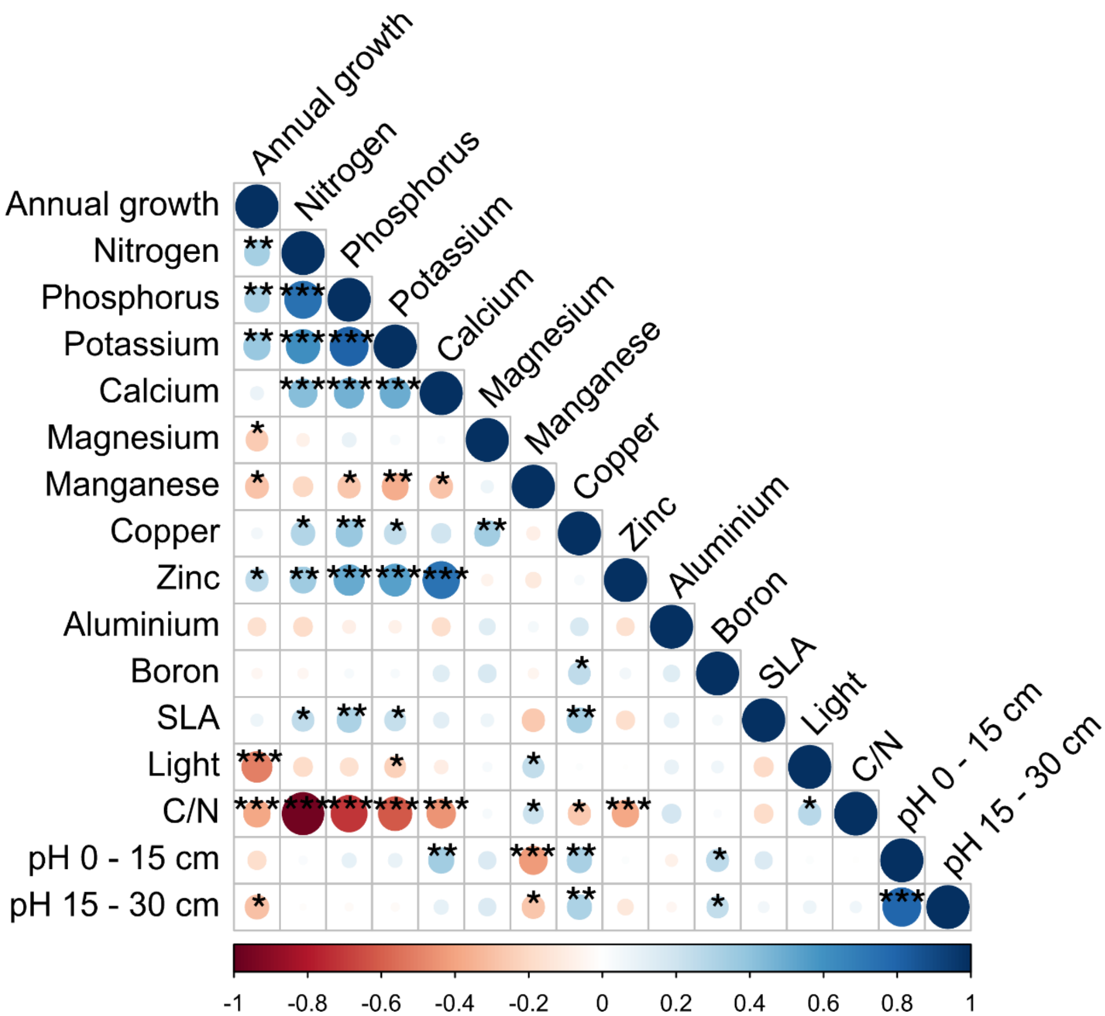

Figure 23 Correlation matrix between soil pH, intercepted light, seedling growth, specific leaf area (SLA) and foliar nutrients. Colors indicate the correlation strength, with blue representing positive correlations and red representing negative correlations. The asterisks represent significant levels, *p < 0.05, **p < 0.01, *** p < 0.001.

ANNEXE B – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 3

Tableau 18 Results of ANOVA applied to the generalized linear mixed models. Treatments consisted of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

ANOVA	Degree of freedom	Sum of squares	Mean square
richness ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)			
Intercept	642	1	< 2 e-16
B	0.96	1	0.33
A	0.077	1	0.78
M	2.45	1	0.12
B : A	3.39	1	0.065
B : M	0.33	1	0.56
A : M	0.71	1	0.40
B : A : M	0.096	1	0.76

Tableau 19 Results of ANOVA applied to linear mixed models. Treatments consisted of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

ANOVA	Sum of squares	Mean square	Numerator degrees of freedom	Denominator degrees of freedom	F value	p-value
Shannon index ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.55	0.55	1	60	3.56	**0.064**
A	0.0057	0.0057	1	2	0.037	0.86
M	1.26	1.26	1	60	8.20	**0.0056**
B : A	0.035	0.035	1	60	0.23	0.64
B : M	0.00015	0.00015	1	60	0.0010	0.97
A : M	0.067	0.067	1	60	0.44	0.51
B : A : M	0.00036	0.00036	1	60	0.0023	0.96

Tableau 19 (suite)

InvSimpson index ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	17.04	17.04	1	58	3.17	0.080
A	0.26	0.26	1	2	0.049	0.84
M	45.77	45.77	1	2	8.52	0.10
B : A	1.11	1.11	1	58	0.21	0.65
B : M	0.061	0.061	1	58	0.011	0.92
A : M	1.60	1.60	1	58	0.30	0.59
B : A : M	1.93	1.93	1	58	0.36	0.55
log (maximum height) ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	0.11	0.11	1	1.99	0.16	0.73
A	0.93	0.93	1	2	1.33	0.37
M	19.50	19.50	1	49.59	27.99	2.75 e-06
B : A	5.20	5.20	1	57.40	7.46	0.0083
B : M	0.0021	0.0021	1	57.40	0.0030	0.96
A : M	0.70	0.70	1	57.40	1.01	0.32
B : A : M	0.12	0.12	1	57.40	0.18	0.67
log (SLA) ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	0.030	0.030	1	3.71	0.23	0.66
A	0.0025	0.0025	1	3.21	0.019	0.90
M	3.01	3.01	1	57.74	22.67	1.33 e-05
B : A	0.057	0.057	1	57.74	0.43	0.51
B : M	0.14	0.14	1	57.74	1.02	0.32
A : M	0.00056	0.00056	1	57.74	0.0042	0.95
B : A : M	0.031	0.031	1	57.74	0.23	0.63

Tableau 19 (suite)

sqrt (LDMC) ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	19.30	19.30	1	60.21	2.66	0.11
A	4.96	4.96	1	4	0.68	0.45
M	42.14	42.14	1	60.21	5.80	0.019
B : A	0.72	0.72	1	60.21	0.099	0.75
B : M	0.59	0.59	1	60.21	0.081	0.78
A : M	6.15	6.15	1	60.21	0.85	0.36
B : A : M	0.15	0.15	1	60.21	0.021	0.89
log (LNC) ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M) + (1 | plot)						
B	0.26	0.26	1	3.05	2.65	0.20
A	0.41	0.41	1	57.54	4.09	0.048
M	1.66	1.66	1	3.89	16.72	0.016
B : A	0.13	0.13	1	57.54	1.30	0.26
B : M	0.085	0.085	1	57.49	0.85	0.36
A : M	0.014	0.014	1	57.51	0.14	0.71
B : A : M	0.050	0.050	1	57.51	0.50	0.48
log (Rao index) ~ B*A* M + (1 | block) + (1 | block : B) + (1 | block : A) + (1 | block : M)						
B	0.00020	0.00020	1	60	0.0017	0.97
A	0.14	0.14	1	4	1.23	0.33
M	0.68	0.68	1	60	5.74	0.020
B : A	0.25	0.25	1	60	2.09	0.15
B : M	0.077	0.077	1	60	0.66	0.42
A : M	0.078	0.078	1	60	0.67	0.42
B : A : M	0.074	0.074	1	60	0.63	0.43

Tableau 20 Species names list in all sampled quadrats.

ID	Species	Six-letter code
1	*Abies balsamea*	ABIBAL
2	*Acer spicatum*	ACESPI
3	*Achillea millefolium*	ACHMIL
4	*Agrostis gigantea*	AGRGIG
5	*Agrostis hyemalis*	AGRHYE
6	*Agrostis spp.*	AGRSP
7	*Alnus crispa*	ALNVIR
8	*Alnus incana*	ALNINC
9	*Anaphalis margaritacea*	ANAMAR
10	*Apocynum androsaemifolium*	APOAND
11	*Aralia nudicaulis*	ARANUD
12	*Athyrium angustum*	ATHANG
13	*Athyrium filix femina*	ATHFILFEM
14	*Betula papyrifera*	BETPAP
15	*Bromus ciliatus*	BROCIL
16	*Calamagrostis canadensis*	CALCAN
17	*Carex spp.*	CARSP
18	*Chamaenerion angustifolium*	CHAANG
19	*Clintonia borealis*	CLIBOR
20	*Coptis trifolia*	COPTRI
21	*Cornus alternifolia*	CORALT
22	*Cornus canadensis*	CORCAN
23	*Cornus rugosa*	CORRUG
24	*Cornus sericea*	CORSIR
25	*Corylus cornuta*	CORCOR
26	*Diervilla lonicera*	DIELON
27	*Diodia teres*	DIOTER
28	*Dryopteris carthusiana*	DRYCAR

Tableau 20 (suite)

29	*Dryopteris spp.*	DRYSP
30	*Elymus repens*	ELYREP
31	*Epilobium ciliatum*	EPICIL
32	*Epilobium spp.*	EPISP
33	*Equisetum arvense*	EQUARV
34	*Equisetum sylvaticum*	EQUSYL
35	*Erigeron canadensis*	ERICAN
36	*Eurybia macrophylla*	EURMAC
37	*Euthamia graminifolia*	EUTGRA
38	*Eutrochium maculatum*	EUTMAC
39	*Fallopia cilinodis*	FALCIL
40	*Fragaria virginiana*	FRAVIR
41	*Galeopsis bifida*	GALBIF
42	*Galium spp.*	GALSP
43	*Galium triflorum*	GALTRI
44	*Geranium dissectum*	GERDIS
45	*Geranium pusillum*	GERPUS
46	*Geum aleppicum*	GEUALL
47	*Geum macrophyllum*	GEUMAC
48	*Glyceria striata*	GLYSTR
49	*Impatiens capensis*	IMPCAP
50	*Juncus brevicaudatus*	JUNBRE
51	*Juncus effusus*	JUNEFF
52	*Juncus spp.*	JUNSP
53	*Juncus tenuis*	JUNTEN
54	*Lactuca biennis*	LACBIE
55	*Leucanthemum vulgare*	LEUVUL
56	*Linnaea borealis*	LINBOR
57	*Lonicera canadensis*	LONCAN

Tableau 20 (suite)

58	*Lonicera hirsuta*	LONHIR
59	*Lotus corniculatus*	LOTCOR
60	*Lysimachia borealis*	LYSBOR
61	*Maianthemum canadense*	MAICAN
62	*Mertensia paniculata*	MERPAN
63	*Oenothera biennis*	OENBIE
64	*Phalaris arundinacea*	PHAARU
65	*Phleum pratense*	PHLPRA
66	*Picea spp.*	PICSP
67	*Pilosella spp.*	PILSP
68	*Pinus banksiana*	PINBAN
69	*Plantago major*	PLAMAJ
70	*Poa palustris*	POAPAL
70	*Populus tremuloides*	POPTRE
72	*Potentilla norvegica*	POTNOR
73	*Prunus pensylvanica*	PRUPEN
74	*Pteridium aquilinum*	PTEAQU
75	*Ranunculus acris*	RANACR
76	*Ranunculus spp.*	RANSP
77	*Ribes cynosbati*	RIBCYN
78	*Ribes triste*	RIBTRI
79	*Rubus idaeus*	RUBIDA
80	*Rubus pubescens*	RUBPUB
81	*Rumex britannica*	RUMBRI
82	*Salix bebbiana*	SALBEB
83	*Salix discolor*	SALDIS
84	*Salix spp.*	SALSP
85	*Scirpus spp.*	SCISP
86	*Solidago rugosa*	SOLRUG
87	*Solidago spp.*	SOLSP

Tableau 20 (suite)

88	*Sonchus arvensis*	SONARV
89	*Sonchus spp.*	SONSP
90	*Sorbus americana*	SORAME
91	*Streptopus lanceolatus*	STRLAN
92	*Symphyotrichum spp.*	SYMSP
93	*Symphyotrichum lanceolatum*	SYMLAN
94	*Symphyotrichum puniceum*	SYMPUN
95	*Taraxacum officinale*	TAROFF
96	*Thalictrum pubescens*	THAPUB
97	*Trifolium aureum*	TRIAUR
98	*Trifolium hybridum*	TRIHYB
99	*Trifolium pratense*	TRIPRA
100	*Trifolium repens*	TRIREP
101	*Typha latifolia*	TYPLAT
102	*Vaccinium angustifolium*	VACANG
103	*Vaccinium myrtilloides*	VACMYR
104	*Veronica serpyllifolia*	VERSER
105	*Viburnum edule*	VIBEDU
106	*Viburnum nudum*	VIBNUD
107	*Vicia cracca*	VICCRA
108	*Viola spp.*	VIOSP

ANNEXE C – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 4

Tableau 21 Results of ANOVA applied to the linear mixed models. Treatments consisted of the presence or absence of biochar (B), wood ash (A) and manure (M). Values in bold indicate statistically significant differences (p < 0.05).

	ANOVA	Sum of squares	Mean square	Numerator degrees of freedom	Denominator degrees of freedom	F value	p-value
				pH ~ B*A* M + (1 | block)			
0 – 15 cm	**B**	0.0032	0.0032	1	62	0.020	0.89
	A	1.69	1.69	1	62	10.70	**0.0017**
	M	0.042	0.042	1	62	0.27	0.61
	B : A	0.25	0.25	1	62	1.60	0.21
	B : M	0.0093	0.0093	1	62	0.059	0.81
	A : M	0.27	0.27	1	62	1.74	0.19
	B : A : M	0.097	0.097	1	62	0.61	0.44
				pH ~ B*A* M + (1 | block)			
15 – 30 cm	**B**	0.014	0.014	1	62	0.097	0.76
	A	0.17	0.17	1	62	1.25	0.27
	M	0.0026	0.0026	1	62	0.018	0.89
	B : A	0.39	0.39	1	62	2.79	0.010
	B : M	0.28	0.28	1	62	2.03	0.16
	A : M	0.18	0.18	1	62	1.28	0.26
	B : A : M	0.31	0.31	1	62	2.22	0.14
				Log(C) ~ B*A* M + (1 | block)			
0 – 15 cm	**B**	0.067	0.067	1	62	0.20	0.65
	A	0.0065	0.0065	1	62	0.020	0.89
	M	1.76	1.76	1	62	5.41	**0.023**
	B : A	0.019	0.019	1	62	0.059	0.81

Tableau 21 (suite)

	B : A	0.019	0.019	1	62	0.059	0.81
	B : M	0.11	0.11	1	62	0.34	0.56
	A : M	0.45	0.45	1	62	1.37	0.25
	B : A : M	0.0035	0.0035	1	62	0.011	0.92
				Log(C) ~ B*A* M + (1 | block)			
15 – 30 cm	**B**	0.24	0.24	1	62	0.75	0.39
	A	0.033	0.033	1	62	0.10	0.75
	M	0.056	0.056	1	62	0.17	0.68
	B : A	0.026	0.026	1	62	0.080	0.78
	B : M	0.069	0.069	1	62	0.21	0.64
	A : M	1.75	1.75	1	62	5.45	**0.023**
	B : A : M	0.16	0.16	1	62	0.51	0.48
				Log(N) ~ B*A* M + (1 | block)			
0 – 15 cm	**B**	0.089	0.089	1	62	0.39	0.53
	A	0.44	0.44	1	62	1.92	0.17
	M	0.83	0.83	1	62	3.68	0.059
	B : A	0.11	0.11	1	62	0.48	0.49
	B : M	0.040	0.040	1	62	0.18	0.68
	A : M	0.50	0.50	1	62	2.20	0.14
	B : A : M	0.23	0.23	1	62	1.04	0.31
				Log(N) ~ B*A* M + (1 | block)			
15 – 30 cm	**B**	0.011	0.011	1	62	0.077	0.78
	A	0.14	0.14	1	62	1.018	0.32
	M	0.21	0.21	1	62	1.56	0.22
	B : A	0.058	0.058	1	62	0.43	0.52
	B : M	0.29	0.29	1	62	2.11	0.15
	A : M	0.87	0.87	1	62	6.36	**0.014**
	B : A : M	0.22	0.22	1	62	1.62	0.21

Tableau 21 (suite)

			C/N ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	82.49	82.49	1	62	2.98	0.089
	A	139	19	1	62	5.02	**0.029**
	M	35.16	35.16	1	62	1.27	0.26
	B : A	0.16	0.16	1	62	0.0057	0.94
	B : M	67.86	67.86	1	62	2.45	0.12
	A : M	15.74	15.74	1	62	0.57	0.45
	B : A : M	40.53	40.53	1	62	1.46	0.23
			C/N ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	27.04	27.04	1	62	1.85	0.18
	A	31.38	31.38	1	62	2.15	0.15
	M	6.74	6.74	1	62	0.46	0.50
	B : A	0.22	0.22	1	62	0.015	0.90
	B : M	10.74	10.74	1	62	0.73	0.39
	A : M	36.58	36.58	1	62	2.50	0.12
	B : A : M	1.76	1.76	1	62	0.12	0.73
			Log(P) ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	0.24	0.24	1	62	0.55	0.46
	A	2.36	2.36	1	62	5.31	**0.025**
	M	0.21	0.21	1	62	0.47	0.49
	B : A	0.93	0.93	1	62	2.087	0.15
	B : M	0.038	0.038	1	62	0.056	0.77
	A : M	0.026	0.026	1	62	0.058	0.81
	B : A : M	0.23	0.23	1	62	0.53	0.47
			Log(P) ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	0.0002	0.0002	1	62	0.0004	0.98
	A	3.47	3.47	1	62	8.98	**0.0039**
	M	0.91	0.91	1	62	2.37	0.13

Tableau 21 (suite)

	B : A	1.27	1.27	1	62	3.28	0.075
	B : M	0.17	0.17	1	62	0.43	0.51
	A : M	0.0005	0.0005	1	62	0.0013	0.97
	B : A : M	0.57	0.57	1	62	1.48	0.23
Log(K) ~ B*A* M + (1 | block)							
0 – 15 cm	**B**	0.23	0.23	1	62	0.54	0.47
	A	1.56	1.56	1	62	3.68	0.060
	M	2.74	2.74	1	62	6.46	**0.013**
	B : A	0.93	0.93	1	62	2.19	0.14
	B : M	1.51	1.51	1	62	3.56	0.064
	A : M	0.28	0.28	1	62	0.66	0.42
	B : A : M	0.00004	0.00004	1	62	0.0001	0.99
Log(K) ~ B*A* M + (1 | block)							
15 – 30 cm	**B**	0.0079	0.0079	1	62	0.015	0.90
	A	0.0029	0.0029	1	62	0.0056	0.94
	M	6.10	6.10	1	62	11.84	**0.0010**
	B : A	2.00	2.00	1	62	3.89	0.053
	B : M	3.35	3.35	1	62	6.50	**0.013**
	A : M	0.57	0.57	1	62	1.10	0.30
	B : A : M	0.043	0.043	1	62	0.084	0.77
Log(Ca) ~ B*A* M + (1 | block)							
0 – 15 cm	**B**	1.59	1.59	1	62	3.094	0.083
	A	0.0088	0.0088	1	62	0.017	0.90
	M	1.96	1.96	1	62	3.81	0.055
	B : A	1.02	1.02	1	62	1.98	0.16
	B : M	0.43	0.43	1	62	0.84	0.36
	A : M	0.77	0.77	1	62	1.50	0.22
	B : A : M	0.031	0.031	1	62	0.061	0.80

Tableau 21 (suite)

			Log(Ca) ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	0.72	0.72	1	62	0.95	0.33
	A	1.92	1.92	1	62	2.53	0.12
	M	4.49	4.49	1	62	5.90	**0.018**
	B : A	2.57	2.57	1	62	3.38	0.071
	B : M	2.06	2.06	1	62	2.71	0.10
	A : M	1.06	1.06	1	62	1.39	0.24
	B : A : M	0.11	0.11	1	62	0.15	0.70
			Log(Mg) ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	1.60	1.60	1	62	2.71	0.10
	A	0.23	0.23	1	62	0.38	0.54
	M	2.35	2.35	1	62	3.99	0.050
	B : A	0.67	0.67	1	62	1.14	0.29
	B : M	2.55	2.55	1	62	4.33	**0.042**
	A : M	0.63	0.63	1	62	1.07	0.30
	B : A : M	0.24	0.24	1	62	0.40	0.53
			Log(Mg) ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	1.34	1.34	1	62	1.31	0.26
	A	2.59	2.59	1	62	2.53	0.12
	M	4.54	4.54	1	62	4.43	**0.039**
	B : A	0.97	0.97	1	62	0.95	0.33
	B : M	3.15	3.15	1	62	3.08	0.084
	A : M	1.32	1.32	1	62	1.28	0.26
	B : A : M	0.057	0.057	1	62	0.056	0.81
			Sqrt(Mn) ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	0.065	0.065	1	62	4.87	**0.031**
	A	0.0046	0.0046	1	62	0.35	0.56
	M	0.13	0.13	1	62	9.78	**0.0027**
	B : A	0.012	0.012	1	62	0.94	0.34

Tableau 21 (suite)

	B : M	0.000017	0.000017	1	62	0.0013	0.97
	A : M	0.026	0.026	1	62	1.98	0.16
	B : A : M	0.0069	0.0069	1	62	0.51	0.48
			Sqrt(Mn) ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	0.059	0.059	1	62	4.26	**0.043**
	A	0.0057	0.0057	1	62	0.41	0.52
	M	0.063	0.063	1	62	4.56	**0.037**
	B : A	0.017	0.017	1	62	1.26	0.27
	B : M	0.0033	0.0033	1	62	0.24	0.63
	A : M	0.018	0.018	1	62	1.28	0.26
	B : A : M	0.00013	0.00013	1	62	0.0098	0.92
			Al ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	179	179	1	62	11.08	**0.0015**
	A	10.94	10.94	1	62	0.68	0.41
	M	1.37	1.37	1	62	0.085	0.77
	B : A	2.14	2.14	1	62	0.13	0.72
	B : M	0.79	0.79	1	62	0.049	0.83
	A : M	132	132	1	62	8.17	**0.0058**
	B : A : M	4.13	4.13	1	62	0.25	0.61
			Al ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	187	187	1	62	10.41	**0.0020**
	A	21.48	21.48	1	62	1.20	0.28
	M	6.68	6.68	1	62	0.37	0.54
	B : A	2.87	2.87	1	62	0.16	0.69
	B : M	0.42	0.42	1	62	0.023	0.88
	A : M	171	171	1	62	9.53	**0.0030**
	B : A : M	2.48	2.48	1	62	0.14	0.71

Tableau 21 (suite)

			Fe ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	0.57	0.57	1	62	2.65	0.11
	A	0.25	0.25	1	62	1.16	0.28
	M	0.00001	0.00001	1	62	0.0001	0.99
	B : A	0.00007	0.00007	1	62	0.0003	0.98
	B : M	0.041	0.041	1	62	0.19	0.66
	A : M	0.13	0.13	1	62	0.61	0.44
	B : A : M	0.04	0.04	1	62	0.20	0.65
			Fe ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	1.47	1.47	1	62	5.95	**0.018**
	A	0.85	0.85	1	62	3.43	0.069
	M	0.0035	0.0035	1	62	0.014	0.91
	B : A	0.0011	0.0011	1	62	0.0044	0.95
	B : M	0.56	0.56	1	62	2.27	0.14
	A : M	0.24	0.24	1	62	0.95	0.33
	B : A : M	0.16	0.16	1	62	0.64	0.43
			Log(Na) ~ B*A* M + (1 | block)				
0 – 15 cm	**B**	0.11	0.11	1	62	0.53	0.47
	A	0.027	0.027	1	62	0.13	0.71
	M	0.56	0.56	1	62	2.82	0.098
	B : A	0.0019	0.0019	1	62	0.0095	0.92
	B : M	0.62	0.62	1	62	3.12	0.082
	A : M	0.025	0.025	1	62	0.12	0.73
	B : A : M	0.0015	0.0015	1	62	0.0078	0.93
			Log(Na) ~ B*A* M + (1 | block)				
15 – 30 cm	**B**	0.044	0.044	1	62	0.11	0.74
	A	0.43	0.43	1	62	1.04	0.31
	M	2.64	2.64	1	62	6.47	**0.013**

Tableau 21 (suite)

	B : A	0.34	0.34	1	62	0.83	0.37
	B : M	1.68	1.68	1	62	4.11	**0.047**
	A : M	0.014	0.014	1	62	0.035	0.85
	B : A : M	0.022	0.022	1	62	0.053	0.82
				CEC ~ B*A* M + (1 | block)			
0 – 15 cm	**B**	99.05	99.05	1	62	7.35	**0.0086**
	A	12.19	12.19	1	62	0.90	0.34
	M	78.40	78.40	1	62	5.82	0.019
	B : A	22.03	22.03	1	62	1.64	0.20
	B : M	27.39	27.39	1	62	2.03	0.16
	A : M	109	109	1	62	8.07	**0.0060**
	B : A : M	22.08	22.08	1	62	1.64	0.20
				CEC ~ B*A* M + (1 | block)			
15 – 30 cm	**B**	126	126	1	62	5.23	**0.025**
	A	27.68	27.68	1	62	1.15	0.29
	M	217	217	1	62	9.05	**0.0038**
	B : A	135	135	1	62	5.60	**0.021**
	B : M	107	107	1	62	4.44	**0.039**
	A : M	147	147	1	62	6.12	**0.016**
	B : A : M	1.53	1.53	1	62	0.064	0.80

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