Université du Québec en Abitibi-Témiscamingue

CONTRIBUTION DES PLANTATIONS À CROISSANCE RAPIDE AU STOCKAGE ET À LA STABILISATION DU CARBONE ORGANIQUE DU SOL EN LIEN AVEC LES TRAITS RACINAIRES

Thèse
présentée
comme exigence partielle
du doctorat sur mesure (sciences naturelles), écologie du sol et des racines

Par
Toky Jeriniaina Rabearison

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AVANT-PROPOS

Cette thèse est composée de cinq sections : une introduction générale, trois chapitres et une conclusion générale. L'introduction générale comprend le contexte, la revue de littérature, les problématiques, les objectifs et la méthodologie générale. Les Chapitres 1 à 3 forment le corps de la thèse, visant à répondre aux objectifs et à tester les hypothèses de recherche. Ils ont été rédigés en langue anglaise sous forme d'articles scientifiques destinés à être publiés dans des revues à comité de lecture. Le Chapitre 1 a été publié dans la revue Forest Ecology and Management en mars 2023. Le Chapitre 2 a été publié dans la revue Tree Physiology en septembre 2024 et le troisième sera soumis dans la revue Plant and Soil. Dans la conclusion générale, nous avons discuté et récapitulé les principaux résultats tout en suggérant de nouvelles perspectives pour la recherche.

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Rabearison, T. J., DesRochers, A., Poirier, V. Comment les traits fonctionnels des racines fines impactent-ils la croissance des arbres dans une plantation à croissance rapide ? 25e colloque de la Chaire AFD. Université du Québec en Abitibi-Témiscamingue (UQAT), Rouyn-Noranda, Québec (2023-11-28)

Rabearison, T. J., DesRochers, A., Poirier, V. Relation étroite entre les traits fonctionnels des racines fines et la productivité aérienne dans les plantations à croissance rapide. 16e colloque annuel du CEF. Université de Montréal, Montréal (2023-05-08)

Rabearison, T. J. Comment l'augmentation de la productivité du peuplier hybride impacte-t-elle la séquestration du C organique dans le sol ? Webinaire thématique 2RLQ, en ligne (2022-12-20)

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Rabearison, T. J., Poirier, V., Gillespie, A., Laganiere, J., DesRochers, A. Est-ce que l'augmentation de la productivité du peuplier hybride se traduit par une augmentation du carbone organique du sol ? Foire Gourmande. UQAT, Notre-Dame-Du-Nord, Québec (2022-08-13)

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1079	*Populus* x *jackii* (*Populus balsamifera* x *Populus deltoides*)
747210	*Populus balsamifera* x *Populus trichocarpa*
915005	*Populus balsamifera* x *Populus maximowiczii*
915319	*Populus maximowiczii* x *Populus balsamifera*
AIC	Akaike Information Criterion
BD	Bulk Density
C	Carbone
$CaCl_2$	Chlorure de calcium
CO_2	Dioxyde de carbone
COAM	Carbone organique associé aux minéraux
COP	Carbone organique particulaire
COS	Carbone organique du sol
CRSNG	Conseil de recherches en sciences naturelles et en génie du Canada
D	Diamètre
DBH	Diameter at breast height
DN2	*Populus deltoides* x *Populus nigra*
H	Hauteur
IPCC	Intergovernmental Panel on Climate Change
IUSS	International Union of Soil Sciences
Log	Logarithme
Loge	Logarithme naturel
MAOC	Mineral associated organic carbon
MFFP	Ministère des Forêts, de la Faune et des Parcs du Québec
N	Azote ou Nord
NLARS	New Liskeard Agricultural Research Station
NPK	Azote, phosphore et potassium
ns	Non Significatif
NSERC	Natural Sciences and Engineering Research Council of Canada

OC	Organic carbon
OM	Organic matter
ON	Ontario
P	Probabilité
P.	*Populus*
PCA	Principal component analyses
pH	Potentiel hydrogène
POC	Particulate organic carbon
PVC	Polyvinyl chloride
R^2	Coefficient de détermination
RCC	Root carbon concentration
RDM	Dry mass of whole fine roots
RDMC	Root dry matter content
RES	Root economics spectrum
RFM	Root fresh mass
RL	Total root length
RLD	Root length density
RMD	Root mass density
RNC	Root nitrogen concentration
RTD	Root tissue density
SEM	Standard errors of the mean
SER	Spectre économique racinaire
SOC	Soil organic carbon
SRL	Longueur spécifique des racines ou « specific root length »
UQAT	Université du Québec en Abitibi-Témiscamingue
V	Volume
VFR	0-0.2 mm diameter roots
W	West
WRB	World Reference Base for Soil Resources

RÉSUMÉ

Le sol joue un rôle clé dans l’atténuation des changements climatiques, étant le deuxième plus grand réservoir de carbone (C) de la biosphère après les océans. Dans ce contexte, les arbres à croissance rapide tels que les peupliers hybrides représentent des puits potentiels de C dans le sol puisqu’ils accumulent rapidement du C dans leur biomasse et pourraient transférer davantage de matière organique dans le sol. Ils contribuent également à répondre à la demande croissance mondiale en bois. Néanmoins, les effets du taux de croissance de ces arbres sur le stock de carbone organique du sol (COS) demeurent peu connus. De plus, nous ne savons pas exactement comment les traits chimiques (facilement décomposables ou récalcitrants) et architecturaux de leurs racines fines impactent le stockage et la stabilisation du COS. Pour clarifier ces interrogations, nous devrions également déterminer les effets de ces traits racinaires sur les taux de croissance des arbres, puisque les racines fines jouent un rôle central dans l'acquisition des nutriments du sol. En effet, chez les clones de peupliers hybrides, l’effet des traits racinaires tels que la longueur spécifique (SRL) et la densité en masse des racines sur le taux de croissance des arbres reste controversé, étant donné qu’ils sont phylogénétiquement proches.

Cette thèse a eu comme objectif de déterminer l’impact du taux de croissance des peupliers hybrides et des traits fonctionnels de leurs racines fines sur le stockage et la stabilisation du COS. Elle visait également à examiner les effets des traits racinaires sur le taux de croissance de ces arbres. Nous avons étudié une plantation de peupliers hybrides située à New Liskeard, ON, Canada et avons sélectionné cinq clones ayant des taux de croissance différents. Nous avons prélevé des carottes de sol à 0-20, 20-40 et 40-60 cm de profondeur dans le sol pour les analyses du sol (C et azote (N)) et des traits racinaires. Le COS a également été fractionné en carbone organique particulaire (> 53 µm, COP) et en carbone organique associé aux minéraux (< 53 µm, COAM) pour les analyses de la stabilisation du COS.

Nous n’avons pas trouvé de relation significative entre le stock de COS et le taux de croissance des arbres. Cependant, le clone avait des effets significatifs sur le stock de COS, avec les clones à productivité moyenne (1079 et 915005) stockant plus de COS entre 0 et 60 cm de profondeur que le clone le plus productif (DN2). Indépendamment du taux de croissance, nous soulignons l'importance de la sélection des clones/espèces pour maximiser le stockage du COS. La différence dans le stock de COS entre les clones était principalement observée dans la profondeur 20-40 cm suggérant le rôle significatif des racines. Nos analyses sur les traits racinaires ont révélé que les densités en longueur et en masse des racines étaient les meilleurs prédicteurs de l’augmentation du stock de COS et du COAM. Les racines fines facilement décomposables (c'est-à-dire riches en azote (N) et en composés solubles, avec des ratios lignine/N et C/N plus faibles) étaient également positivement corrélées avec le stock de COS et le COAM puisqu’elles pourraient être facilement consommées par les microorganismes du sol et favoriser l’adsorption des sous-produits microbiens sur les surfaces minérales. Ainsi, les traits racinaires qui augmentent le volume de sol exploré par les racines (densité en longueur élevée) et qui sont associés aux racines facilement décomposables jouent un rôle clé dans la stabilisation du COS chez les arbres à croissance rapide.

Par ailleurs, nous avons trouvé que le taux de croissance des arbres a été positivement corrélé avec le diamètre et la concentration en lignine des racines fines, mais négativement associé à la SRL et à la concentration en composés solubles. La théorie du spectre économique racinaire soutenant l'effet positif de la SRL sur la croissance des arbres n'a pas été alors vérifiée. Nous avons argumenté que les racines fines plus grosses et riches en lignine étaient plus avantageuses pour la croissance des arbres probablement grâce à la réduction des coûts de construction et maintien de racines et des pertes de C, ainsi qu'à l'augmentation de la colonisation mycorhizienne. La densité en masse de racines dans la profondeur 0-20 cm a également augmenté avec le taux de croissance des arbres, démontrant l'importance de l'exploration de l'horizon superficiel du sol par les racines pour le taux de croissance des arbres. Nous concluons ainsi que chez nos clones de peupliers hybrides, le taux de croissance des arbres a été soutenu par l'augmentation de la croissance en diamètre et en masse des racines fines pour développer la taille du système racinaire.

Mots-clés : carbone organique du sol, stabilisation de carbone, trait racinaire, racine fine, taux de croissance, arbre à croissance rapide, peuplier hybride, changements climatiques, horizon profond.

Keywords: soil organic carbon, carbon stabilization, root trait, fine root, tree growth rate, fast-growing tree, hybrid poplar, climate change, subsoil.

INTRODUCTION GÉNÉRALE

Mise en contexte. Notre planète est actuellement confrontée à un grand défi qui est de faire face aux conséquences néfastes des changements climatiques. Ces derniers sont principalement causés par l'augmentation continue des émissions de CO_2 atmosphérique, entrainant déjà des risques élevés d'événements extrêmes (sécheresses, incendies et inondation), l'augmentation des pertes d'espèces dans de nombreux écosystèmes et la réduction de la sécurité alimentaire (IPCC, 2023). Pour les écosystèmes forestiers en particulier, ces changements ont intensifié les feux et les invasions d'insectes, accentuant ainsi le risque de déclin et de mortalité de nombreuses zones forestières (Anderegg *et al.*, 2015 ; Balshi *et al.*, 2009 ; Hogg *et al.*, 2002). Dans ce contexte, le sol offre un grand potentiel d'atténuation de changements climatiques en stockant trois à quatre fois plus de carbone (C) que la végétation terrestre (Lehmann et Kleber, 2015 ; Schmidt *et al.*, 2011). L'initiative internationale "4 pour 1000", lancée lors de la 21^e Conférence des parties à la Convention-cadre des Nations Unies sur les changements climatiques en 2015, a également suggéré qu'une augmentation annuelle du stock de carbone organique du sol (COS) de quatre pour mille (4‰), dans les 30 premiers cm du sol, permettrait de compenser les émissions anthropiques annuelles de CO_2 dans l'atmosphère (Derrien *et al.*, 2016 ; Minasny *et al.*, 2017). Ce stockage du COS est principalement assuré par l'accumulation de litière, le renouvellement et l'exsudation racinaire des arbres (Derrien *et al.*, 2016 ; Sokol *et al.*, 2019).

Les plantations à croissance rapide telles que les peupliers hybrides (*Populus* spp.) sont souvent utilisées au Canada pour produire rapidement de la biomasse ligneuse sur des petites surfaces. Ces plantations stockent rapidement une quantité importante de C à la fois dans leurs parties aériennes et souterraines (Dewar et Cannell, 1992 ; Tuskan et Walsh, 2001 ; Weslien *et al.*, 2009). Il est également soutenu qu'elles pourraient accroitre le stock de COS par rapport aux arbres à croissance lente, grâce à l'accumulation rapide de litière et au renouvellement (*turnover*) rapide de leurs racines (Block *et al.*, 2006 ; Chomel *et al.*, 2014 ; Dewar et Cannell, 1992 ; Sartori *et al.*, 2007). La perspective de les utiliser comme puits supplémentaires de C dans le sol a donc suscité un intérêt croissant (Arevalo *et al.*, 2011 ; Chomel *et al.*, 2014). En général, le COS provenant de ces arbres à croissance rapide s'accumule davantage dans l'horizon superficiel du sol que dans les horizons plus profonds, en raison d'apports plus abondants de matière organique provenant de la litière sus-jacente et des racines (Howlett *et al.*, 2011 ; Moreno *et al.*, 2005). Toutefois, étant donné que les racines de ces arbres peuvent atteindre jusqu'à un mètre de profondeur (Dickmann *et al.*, 1996), ils pourraient également influencer significativement le stock du COS dans les horizons profonds.

Le stockage du COS est déterminé par l'équilibre entre les apports de C sous forme de matière organique et les pertes de C par respiration des microorganismes et des racines et par lixiviation (Epron *et al.*, 2006 ; Martí-Roura *et al.*, 2019 ; Schmidt *et al.*, 2011). La stabilisation du COS est un facteur clé dans ce processus puisqu'elle ralentit la minéralisation du COS et prolonge son temps de stockage. À cet effet, il existe trois mécanismes favorisant la stabilisation du COS : la récalcitrance, l'inaccessibilité spatiale aux décomposeurs en raison de son occlusion dans les agrégats du sol, et l'adsorption sur les surfaces minérales et métalliques du sol (Kleber *et al.*, 2011 ; von Lützow *et al.*, 2006 ; Poirier *et al.*, 2018b ; Sollins *et al.*, 1996). Plusieurs études ont observé que ce dernier est très probablement le mécanisme de stabilisation dominant dans les horizons profonds du sol (Kaiser *et al.*, 2002 ; Rumpel et Kögel-Knabner, 2011). Ces mécanismes de stabilisation du COS sont influencés à la fois par des facteurs abiotiques et biotiques, mais de nombreuses sources de données suggèrent que les racines contribuent davantage au COS que les composants aériens des plantes, en étant en contact étroit avec les sols (Ghafoor *et al.*, 2017 ; Rasse *et al.*, 2005).

Les racines fines, généralement définies comme étant des racines absorbantes d'un diamètre inférieur à 2 mm, peuvent impacter de façon significative le stockage du COS puisqu'environ 67 % de la production primaire nette annuelle leur est allouée dans les écosystèmes forestiers (Matamala *et al.*, 2003 ; Sun *et al.*, 2017 ; Weemstra *et al.*, 2016). Elles jouent également un rôle central dans l'acquisition des ressources du sol et ainsi dans la croissance des arbres (McCormack *et al.*, 2015). Pour mieux comprendre les effets des racines fines sur ces processus souterrains, les approches basées sur les traits fonctionnels ont été souvent utilisées dans la littérature (Bardgett *et al.*, 2014). Les traits fonctionnels des racines fines sont définis par Violle et al. (2007) comme toutes caractéristiques morphologique, physiologique ou phénologique du système racinaire, mesurables au niveau individuel. Selon l'hypothèse du spectre économique racinaire (Bardgett *et al.*, 2014 ; Reich, 2014 ; Roumet *et al.*, 2016), il existe deux stratégies de croissances des arbres liées à leurs traits racinaires. Les espèces à croissance rapide ont la stratégie d'acquisition de ressources qui serait associée à des racines fines plus petites et de durée de vie plus courte, contrairement aux espèces à croissance lente qui ont la stratégie de conservation de ressource (Comas *et al.*, 2002 ; Kramer-Walter *et al.*, 2016 ; McCormack *et al.*, 2012 ; Reich, 2014). Dans ce sens, les racines fines des arbres à croissance rapide présentaient souvent une longueur spécifique (SRL) et des concentrations en azote (N) plus élevées et des diamètres plus petits par rapport à celles des espèces à croissance lente (Comas *et al.*, 2002 ; Comas et Eissenstat, 2004 ; Roumet *et al.*, 2016 ; Wright et Westoby, 1999). Ces différences de traits racinaires pourraient expliquer les variations de stock et de stabilisation du COS entre les arbres moins productifs et ceux plus productifs.

Sylviculture intensive utilisant les peupliers hybrides. Les peupliers hybrides sont parmi les arbres à croissance la plus rapide de l'Amérique du Nord pour la production de biocarburants, d'énergie thermique et de pâte à papier (Sannigrahi *et al.*, 2010). Leur taux de croissance peut atteindre jusqu' à 28 m^3 ha^{-1} an^{-1} à l'âge de 13 ans dans des sites productifs (Truax *et al.*, 2014, 2018). Ils sont issus de croisements entre deux ou plusieurs espèces du genre *Populus* spp.*,* soumis à des cycles continus de sélections et de tests, dans le but d'améliorer leurs performances, notamment leur croissance et leur résistance aux maladies (Huda, 2014). Au Canada, les hybridations de peupliers sont majoritairement réalisées à partir de trois espèces indigènes : le peuplier baumier (*Populus balsamifera*), le peuplier deltoïde (*Populus deltoides*) et le peuplier de l'Ouest (*Populus trichocarpa*), et de deux espèces exotiques : le peuplier du Japon (*Populus maximowiczii),* le peuplier noir (*Populus* *nigra*) (Périnet *et al.*, 2010 ; Réseau Ligniculture Québec, 2011 ; Truax *et al.*, 2014). La descendance la plus performante issue du croisement est sélectionnée pour la génération suivante. Finalement, les arbres sélectionnés peuvent être multipliés par voie végétative (clonage) et commercialisés à n'importe quelle génération du processus de sélection (Huda, 2014). Dépendamment des parents impliqués dans le croisement et des arbres sélectionnés, le taux de croissance peut varier d'un clone à un autre. En outre, les avantages des peupliers hybrides ne se limitent pas seulement à l'approvisionnement rapide en bois, mais incluent également la réduction de la pression de récolte sur les forêts naturelles.

Différentes catégories de traits racinaires. Les traits racinaires peuvent être regroupés en cinq catégories : traits architecturaux, traits morphologiques, traits chimiques, traits physiologiques et traits symbiotiques (Poirier *et al.*, 2018b). La thèse s'est concentrée sur les trois premières catégories de traits puisque leur lien avec le taux de croissance des arbres et le stockage du COS est fréquemment observé dans la littérature (Poirier *et al.*, 2018b) et que leur analyse est faisable sur le plan méthodologique et matériel (Tableau 1). Pour les traits morphologiques, le diamètre moyen et la longueur spécifique des racines fines (SRL, voir tableau 1 pour la définition complète) sont reliés spécifiquement à la recherche de nutriments et au taux de croissance des arbres (Pérez-Harguindeguy *et al.*, 2013 ; Roumet *et al.*, 2008 ; Stokes *et al.*, 2009). Les racines fines ayant une SRL élevée seraient plus efficientes pour la croissance des arbres puisque plus de C sont alloués à l'élongation des racines fines que dans la biomasse, augmentant la capacité d'absorption (Eissenstat et Yanai, 1997). Les traits chimiques des racines fines, tels que les concentrations en C, en N, en composés solubles et en lignine sont associés au taux de décomposition. En effet, si les racines fines riches en N et en composés solubles sont facilement décomposables, celles riches en lignine et ayant un ratio C/N élevé ont des taux de décomposition plus faibles (Cambardella et Elliott, 1992 ; Poirier *et al.*, 2018b ; Wardle, 2004). Enfin, les traits architecturaux incluent, entre autres, les densités en masse et en longueur des racines fines, c'est-à-dire la masse et la longueur par unité de volume de sol (Tableau 1) et reflètent le volume du sol exploré par les racines fines

(Pérez-Harguindeguy *et al.*, 2013 ; Stokes *et al.*, 2009). Par conséquent, l'augmentation de ces traits architecturaux pourrait non seulement améliorer l'acquisition des nutriments dans le sol et la croissance des arbres, mais également le stockage du COS grâce à l'élargissement de la surface racinaire en contact avec le sol (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008).

Tableau 1
Description de traits racinaires étudiés

Trait racinaire	Unité	Définition
Traits morphologiques		
Longueur spécifique des racines (SRL)	$m\ g^{-1}$	Rapport entre la longueur et la masse sèche des racines fines.
Diamètre des racines fines	mm	Exprimé comme le diamètre moyen des racines fines.
Traits chimiques		
Concentration en C ou en N	$mg\ g^{-1}$	Concentration en C ou en N dans les tissus racinaires.
Concentration en hémicellulose	$mg\ g^{-1}$	L'hémicellulose se localise dans la lamelle moyenne et les parois primaires et secondaires des cellules végétales et se décompose plus rapidement que la lignine végétale.
Concentration en lignine	$mg\ g^{-1}$	La lignine est une molécule récalcitrante qui ne peut être décomposée que par des microorganismes spécifiques.
Concentration en composés solubles	$mg\ g^{-1}$	Les composés solubles sont des sucres simples, des acides aminés, des peptides, des composés phénoliques hydrosolubles, de la cire, du mucilage et des polysaccharides de stockage.
Traits architecturaux		
Densité en masse des racines	$g\ cm^{-3}$	Biomasse de racines fines par unité de volume de sol.
Densité en longueur des racines	$cm\ cm^{-3}$	Longueur de racines fines par unité de volume de sol

Source : (Poirier *et al.*, 2018b)

Stabilisation du carbone organique du sol et ses fractions fonctionnelles. Le fractionnement basé sur la taille des particules est une approche souvent utilisée dans la littérature pour étudier la stabilisation du COS (Giannetta *et al.*, 2019 ; Rovira *et al.*, 2010). Cette méthode a été adoptée dans cette thèse pour séparer les deux fractions fonctionnelles du COS : C organique particulaire (> 53 µm, COP) et C organique associé aux minéraux et retenu dans la fraction fine (< 53 µm, COAM). D'une part, le C organique particulaire dans la fraction grossière du sol est principalement composé de résidus végétaux (feuilles, bois ou racines) partiellement décomposés ou persistants et s'accumule principalement dans l'horizon superficiel du sol (Balesdent, 1996 ; Golchin *et al.*, 1998 ; Six *et al.*, 2002). D'autre part, le C organique retenu dans la fraction fine provient principalement du mécanisme d'adsorption de la biomasse et nécromasse microbienne sur les surfaces minérales et métalliques du sol (Giannetta *et al.*, 2019 ; Lehmann et Kleber, 2015). La production de ces sous-produits microbiens est facilitée par l'accumulation importante de composés organiques facilement décomposables qui nécessitent moins d'énergie pour être consommés par les microorganismes (Cotrufo *et al.*, 2013 ; Lehmann et Kleber, 2015 ; Schmidt *et al.*, 2011). Le COAM a récemment été reconnu comme étant plus stable à long terme que le COP (Cotrufo *et al.*, 2013 ; Poirier *et al.*, 2018b) ; et la stabilité globale du COS augmente avec la proportion du COAM (Rovira *et al.*, 2010). En effet, le renouvellement du COS est rapide dans les fractions grossières (Balesdent, 1996) et beaucoup plus lent pour les fractions fines (Basile-Doelsch *et al.*, 2007).

Problématique. Les plantations à croissance rapide utilisant le peuplier hybride ont un taux annuel élevé de production de biomasse aérienne (Truax *et al.*, 2012, 2014), favorisant probablement le stockage du COS par l'accumulation rapide de la litière. Par exemple, le stock de C du sol (78,5 Mg ha^{-1} dans les 20 premiers cm du sol) sous le peuplier hybride de 17,6 m de hauteur était supérieur de plus de 16 % à celui trouvé dans une plantation d'épinettes de Norvège (*Picea abies* L.) du même âge de 6,3 m de hauteur après 13 ans (Peichl *et al.*, 2006). Leurs racines pourraient également libérer du COS plus rapidement que celles des arbres à croissance lente, grâce au renouvellement répété des racines fines et l'accumulation et la décomposition à long terme des grosses racines (Block *et al.*, 2006 ; Dewar et Cannell, 1992). Cependant, les racines des espèces à croissance rapide peuvent également avoir des taux de respiration plus rapides et être décomposées plus rapidement que celles des espèces à croissance lente (Comas *et al.*, 2002 ; De Deyn *et al.*, 2008 ; Kane *et al.*, 2005), ce qui diminuerait le COS. Par conséquent, l'augmentation du taux de croissance aérienne des arbres ne garantit pas nécessairement l'accumulation de C dans le sol et la relation entre le taux de croissance aérienne des arbres et le stockage du COS reste peu évidente. L'étude de clones de peupliers hybrides ayant des taux de croissance différents pourrait offrir une excellente opportunité de déterminer cette relation. Considérant que la biomasse des racines fines varie significativement entre les clones de peuplier et entre les profondeurs du sol (Al Afas *et al.*, 2008), la relation entre le taux de croissance des arbres et le COS pourrait également varier selon la profondeur du sol.

Les arbres à croissance rapide se caractérisent souvent par des racines fines riches en N et composés solubles par rapport aux espèces à croissance lente, produisant des litières facilement décomposables (Comas et Eissenstat, 2004 ; Roumet *et al.*, 2016 ; Wright et Westoby, 1999). Ces traits racinaires seraient peu favorables au stockage du COS puisque les composés facilement décomposables pourraient rapidement retourner dans l'atmosphère sous forme de CO_2 (Bardgett, 2017 ; Sun *et al.*, 2021 ; Wardle, 2004). Ces composés facilement décomposables peuvent également entrainer une augmentation de l'activité microbienne et diminuer le stock

COS en accélérant la décomposition de la matière organique nouvellement ajoutée et celle déjà stable par l'effet de priming (Cheng *et al.*, 2014 ; Keiluweit *et al.*, 2015b). Dans ce sens, les racines fines riches en lignine seraient plus favorables au stockage du COS puisqu'elles produisent des composés organiques à faible taux de décomposition qui peuvent être stabilisés biochimiquement du fait de leur préservation sélective ou de leur récalcitrance (Golchin *et al.*, 1998 ; Six *et al.*, 2002 ; Wardle, 2004). Cependant, plusieurs études ont soutenu que les racines facilement décomposables nécessiteraient une faible énergie pour être consommées par les microorganismes (Cotrufo *et al.*, 2013 ; Poirier *et al.*, 2018b). La biomasse et la nécromasse microbiennes produites pourraient être facilement adsorbées sur les surfaces minérales et métalliques du sol, ce qui faciliterait l'accumulation de C organique associé aux minéraux (COAM) (Cotrufo *et al.*, 2013 ; Lehmann et Kleber, 2015 ; Schmidt *et al.*, 2011). Ainsi, les racines fines des arbres à croissance rapide ont tendance à accumuler préférentiellement du C dans le COAM qui est récemment reconnu comme étant plus stable à long terme que le POC (Cotrufo *et al.*, 2013 ; Poirier *et al.*, 2018b). Nous ne connaissons pas alors avec certitude quelle chimie des racines fines, facilement décomposables ou récalcitrantes, est la plus favorable au stockage et à la stabilisation du COS.

Par ailleurs, les arbres à croissance rapide ont généralement une densité en masse et en longueur des racines élevées pour améliorer le volume du sol exploré par les racines et l'accès aux nutriments du sol (Pérez-Harguindeguy *et al.*, 2013 ; Ravenek *et al.*, 2016 ; Stokes *et al.*, 2009). Ces traits architecturaux élargissent les surfaces des racines fines en contact avec le sol, ce qui contribuerait au stockage du SOC par le renouvellement des racines (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008). Des densités en masse et en longueur élevées de racines peuvent également contribuer à la stabilisation du COS par le mécanisme d'occlusion dans les microagrégats (Ontl *et al.*, 2015). Cependant, les effets de ces traits architecturaux sur la stabilisation du COS par le mécanisme impliquant les interactions avec les phases minérales du sol (COP et COAM) restent sous-explorés.

En ce qui concerne les traits morphologiques, les racines fines ayant une SRL plus élevée chez les arbres à croissance rapide ont souvent des taux de renouvellement rapides (Guo *et al.*, 2008 ; McCormack *et al.*, 2015), ce qui pourrait augmenter les apports de litière racinaire et le COS. Ces racines fines avec une SRL élevée pourraient également produire des matières organiques facilement décomposables, augmentant l'accumulation de COAM (Sun *et al.*, 2021 ; Xu *et al.*, 2021). Néanmoins, les effets des traits morphologiques des racines ne sont toujours pas clairs (Poirier *et al.*, 2018b), puisque la relation entre la SRL et la décomposition de la matière organique du sol peut également être négative (Hobbie *et al.*, 2010) ou non significative pour les espèces ligneuses (Aulen *et al.*, 2012 ; Roumet *et al.*, 2016). Ces incohérences pourraient s'expliquer par le fait que les traits racinaires exerçant un impact significatif sur la décomposition de la matière organique et le stockage du COS peuvent varier entre les espèces appartenant à des familles différentes (Roumet *et al.*, 2016). Ici, nous avons étudié différents clones de peupliers hybrides appartenant au même genre *Populus* spp, ce qui pourrait aider à mieux comprendre les effets des traits racinaires sur la stabilisation du COS.

Les arbres à croissance rapide devraient théoriquement avoir une SRL plus élevée et des diamètres de racines plus petits que les espèces à croissance lente (Comas *et al.*, 2002 ; Comas et Eissenstat, 2004 ; Wright et Westoby, 1999). En revanche, ces traits racinaires sont souvent associés à une courte durée de vie des racines et à des taux de respiration racinaire élevés, ce qui augmente les coûts de construction des racines fines et les pertes de C par la respiration et aurait un impact négatif sur le gain net global de C dans les arbres (Makita *et al.*, 2009 ; McCormack *et al.*, 2012 ; Pregitzer *et al.*, 1998 ; Weemstra *et al.*, 2020). De plus, la SRL et le diamètre des racines des espèces d'arbres n'étaient pas toujours corrélés avec les taux de croissance des arbres (Kramer-Walter *et al.*, 2016 ; Weemstra *et al.*, 2016, 2020). En effet, l'acquisition des nutriments dans le sol ne nécessite pas nécessairement ces traits racinaires définis *a priori* comme acquisitifs, mais aussi des traits architecturaux liés à la mobilité des nutriments dans le sol (Ravenek *et al.*, 2016). Par exemple, une augmentation de la densité en masse de racines a entrainé une expansion de la surface disponible des racines fines pour absorber efficacement les nutriments mobiles et moins mobiles dans le sol, améliorant le taux de croissance des arbres (Bauhus et Messier, 1999 ; Finér *et al.*, 2011 ; Hansson *et al.*, 2013). Par conséquent, il est d'abord nécessaire de clarifier cette relation entre taux de croissance et traits racinaires avant de bien expliquer les effets des traits racinaires sur la stabilisation du COS.

Ainsi, les questions suivantes ont été formulées : comment le taux de croissance des clones de peupliers hybrides affecte-t-il le stock de carbone du sol, notamment dans les horizons profonds ? Quels sont les traits racinaires qui sont en relation avec le taux de croissance aérienne des arbres ? Et enfin comment ces traits racinaires influencent-ils le stockage et la stabilisation du COS ?

Objectifs et hypothèses. L'objectif général de cette thèse était de déterminer l'impact du taux de croissance aérienne des arbres et des traits racinaires sur le stockage et la stabilisation du COS en utilisant des clones de peupliers hybrides ayant différents taux de croissance. Cette thèse visait également à examiner les effets des traits morphologiques, chimiques et architecturaux des racines fines sur le taux de croissance aérienne des arbres. Les trois principaux chapitres de thèse correspondent à nos trois objectifs spécifiques.

Le Chapitre 1 a cherché à évaluer si le stock de COS à différentes profondeurs du sol augmentait avec le taux de croissance aérienne des clones de peuplier hybrides. Nous avons supposé que les clones les plus productifs ayant des taux de croissance élevés stockeraient plus de COS que les clones les moins productifs. Nous nous attendions également à ce que les différences de COS entre ces clones soient plus importantes dans les horizons plus profonds que dans l'horizon superficiel. En effet, les clones les plus productifs pourraient atteindre des horizons plus profonds que les clones les moins productifs pour prélever les éléments nutritifs dans le sol et pourraient y libérer davantage de C (Dickmann *et al.*, 1996).

Le Chapitre 2 avait pour objectif d'examiner les relations explicites entre taux de croissance des arbres et traits morphologiques, chimiques et architecturaux des racines fines. En accord avec la théorie sur le spectre économique racinaire, nous avons émis l'hypothèse que la longueur spécifique, les concentrations en N et composés solubles de racines fines seraient positivement corrélées avec les taux de croissance des arbres, tandis que le diamètre moyen et la concentration en lignine des racines fines auraient l'effet inverse. Nous avons également prédit que les traits architecturaux (densité en masse et en longueur de racines) augmenteraient avec les taux de croissance des arbres puisqu'ils donnent aux arbres une forte intensité d'exploration du sol pour acquérir des nutriments.

Finalement, l'objectif du Chapitre 3 était de déterminer quels traits racinaires des clones sont liés au stockage et à la stabilisation du COS dans les horizons du sol. Nous avons supposé que les racines fines présentant des concentrations plus élevées en N et en composés solubles augmenteraient les stocks de SOC et de COAM. Elles libéreraient des composés facilement décomposables et faciliteraient l'accumulation de biomasse et de nécromasse microbiennes, qui vont interagir à leur tour avec la phase minérale du sol. Des densités en longueur et en masse élevées de racines fines augmentent le volume de sol exploré par les racines fines et contribueraient positivement au stockage du COS. Enfin, nous avons supposé que les racines fines ayant une longueur spécifique élevée et un diamètre plus petit produiraient des composés organiques facilement décomposables et augmenteraient le COAM.

Méthodologie générale. ***Zone d'étude.*** L'étude a été réalisée dans une plantation de peupliers hybrides située à la station de recherche agricole de New Liskeard, Université de Guelph, dans le nord-est de l'Ontario, Canada (47°31′15″ N, 79°39′52″ O, Figure 1). La région bénéficie d'un climat continental humide avec une température journalière moyenne de 2,6°C et une précipitation annuelle moyenne de 786 mm (576 mm de pluie et 222 cm de neige) d'après les données climatiques de 1981 à 2010 (station d'Earlton) (Environment Canada, 2023). Le site a un sol de texture loam argileux (Yan *et al.*, 2019) et de type gleysol humique (Canada Soil Survey Committee, 1987 ; IUSS Working Group WRB, 2015). La géologie superficielle régionale est caractérisée par des argiles et des sables lacustres provenant du lac postglaciaire Barlow (Rowe, 1972).

Le site expérimental a d’abord été labouré puis a fait l’objet d’un hersage croisé en octobre 2006, suivi d’un épandage d’herbicide au printemps 2007. Des boutures de peupliers hybrides ont été plantées au printemps 2007 à un espacement de 3,5 m x 3,5 m (816 tiges ha^{-1}) et fertilisés avec NPK 18-23-18 (110 g arbre^{-1}), à un taux de 89,76 kg ha^{-1}. Le dispositif était constitué de 3 blocs complets (3 répétitions), chacun comportant huit parcelles monoclonales de 100 arbres (10 x 10 arbres) distribuées aléatoirement à l’intérieur des blocs. Nous avons contrôlé la présence des adventices en effectuant un travail du sol entre les rangs à l’aide de disques, suivi d’applications d’herbicides entre les arbres (RoundupTM) pendant les deux premières années suivant l’établissement de la plantation. Durant les mesures des arbres et les échantillonnages du sol après 14 ans, nous avons observé une très faible présence de végétations adventices dans la plantation. Nous avons sélectionné cinq clones parmi les huit plantés, en fonction de leur taux de croissance aérienne, du moins productif au plus productif : 747210 (*P. balsamifera* × *P. trichocarpa*), 915005 (*P. balsamifera* × *P. maximowiczii*), 1079 (*Populus* × *jackii* (*P. balsamifera* × *P. deltoides*)), 915319 (*P. maximowiczii* × *P. balsamifera*) et DN2 (*P. deltoides* × *P. nigra*). Dans cette thèse, le taux de croissance des arbres est défini comme étant le volume total des troncs divisé par la superficie de la parcelle et l’âge de la plantation.

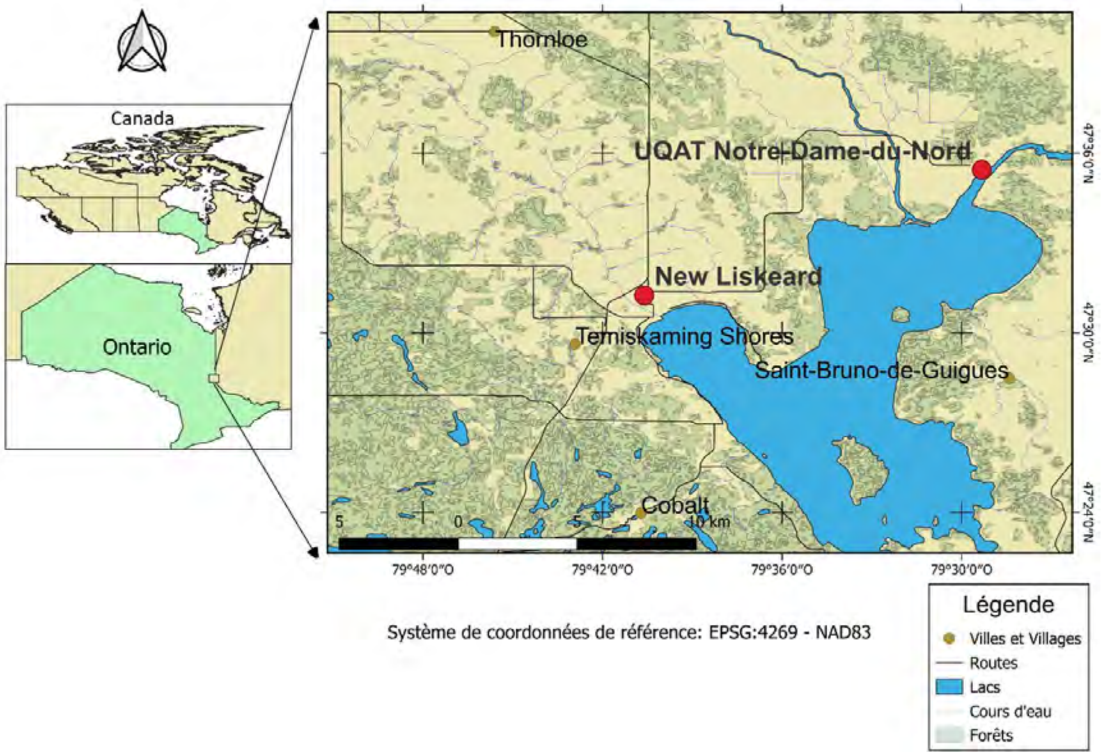

Figure 1
Localisation de la zone d'étude

Prélèvement de sols. L'échantillonnage du sol a été effectué systématiquement entre deux arbres dans chaque parcelle monoclonale (Figure 2b). Des carottes de sol ont été prélevées à deux distances (87,5 cm (quart) et 175,0 cm (centre)) d'un tronc d'arbre et à trois profondeurs de sol (0-20, 20-40 et 40-60 cm) à l'aide d'un cylindre en PVC de 10 cm de diamètre et de 20 cm de longueur (Figure 2c). Au total, 180 carottes de sol (2 arbres × 2 distances × 3 profondeurs × 5 clones × 3 blocs) ont été collectées dans des sacs en plastique, stockées dans une glacière et apportées au laboratoire pour les analyses ultérieures.

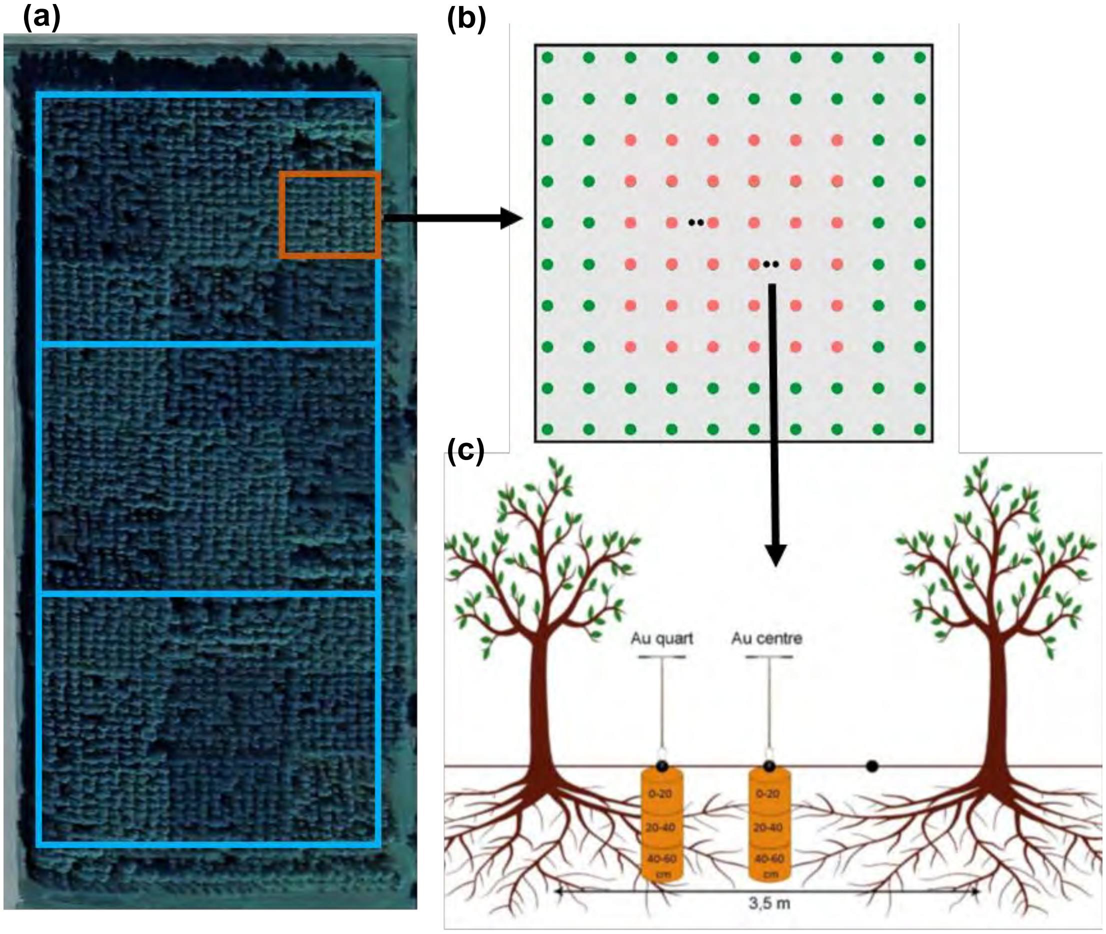

Figure 2
Méthode d’échantillonnage de sol. (a) Plantation de peuplier hybride avec les trois blocs (b) parcelle monoclonale avec les points d’échantillonnage systématique (en noir) et les arbres choisis pour les mesures dendrométriques (en rouge) et (c) distance et profondeur d’échantillonnage.

Source : Google Maps (2023) pour figure 2a

1. INCREASING TREE PRODUCTIVITY DOES NOT TRANSLATE INTO GREATER SOIL ORGANIC CARBON STORAGE

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Toky Jeriniaina Rabearison [a,*], Vincent Poirier [b], Adam Gillespie [c], Jérôme Laganière [d], Annie DesRochers [a]

[a] *Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 341 rue principale Nord, Amos, Québec J9T 2L8 , Canada*

[b] *Unité de recherche et de développement en agroalimentaire, Université du Québec en Abitibi-Témiscamingue, 79, Rue Côté, Notre-Dame-du-Nord, Québec J0Z 3B0, Canada*

[c] *School of Environmental Sciences, University of Guelph, 50 Stone Road East, Guelph, ON N1G 2W1, Canada*

[d] *Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Québec, Qc G1V 4C7, Canada*

*Corresponding author: TokyJeriniaina.Rabearison@uqat.ca

1.1 Résumé

Le stockage croissant du carbone (C) dans le sol fait partie des solutions prometteuses pour atténuer les changements climatiques. Les arbres à croissance rapide constituent un outil potentiel dans ce contexte puisqu'ils accumulent rapidement du C dans leur biomasse et pourraient transférer davantage de matière organique dans le sol. Toutefois, l'impact de la productivité aérienne des arbres à croissance rapide sur le stock du C organique du sol (COS) demeure méconnu. Cinq clones ayant des taux de croissance différents ont été sélectionnés dans une plantation de peuplier hybride située à New Liskeard, ON, Canada. Nous avons prélevé des carottes de sol à 87,5 et 175,0 cm du tronc ainsi qu'à 0-20, 20-40 et 40-60 cm de profondeur dans le sol pour en analyser les concentrations en C. Le clone le plus productif DN2 a stocké moins de COS (83 Mg C ha^{-1}) entre 0 et 60 cm de profondeur que les clones à productivité moyenne 1079 et 915005 (95 et 96 Mg C ha^{-1} respectivement), pendant que le clone le moins productif 747210 avait également un stock de COS plus faible comparé aux autres clones, mais pas de façon significative. Il n'y a pas eu de corrélation entre le stock de COS et la productivité aérienne des arbres et les stocks totaux de COS ont augmenté de 6% lorsque la distance de prélèvement était plus proche du tronc. La différence dans les stocks de COS entre les clones était principalement observée dans la profondeur 20-40 cm, suggérant le rôle significatif des racines dans le stockage du COS. Les ratios C/N du sol étaient significativement différents entre les clones, indiquant des différences dans les taux de décomposition de la matière organique. Il pourrait y avoir un compromis entre la productivité aérienne et le taux de décomposition pour augmenter le stockage du COS.

Mots-clés : carbone organique du sol, taux de croissance, horizon profond, racine, peuplier hybride, changements climatiques

1.2 Abstract

Increasing soil organic carbon (SOC) storage is one of the promising solutions to mitigate climate change. Fast-growing trees are a potential tool in this context as they rapidly accumulate C in their biomass and could transfer more organic matter (OM) into the soil. However, the relationship between aboveground productivity and SOC storage remains poorly understood. Five clones with different growth rates were selected from a 14-year-old hybrid poplar plantation located in New Liskeard, ON, Canada. We collected soil cores at 87.5 and 175.0 cm distance from the stem and at 0-20, 20-40 and 40-60 cm soil depth for soil C concentration analysis. The most productive clone DN2 (*Populus deltoides* x *P. nigra*) stored less SOC (83 Mg ha^{-1}) between 0 and 60 cm depth than the mid-productive clones 1079 *(Populus* x *jackii* (*P. balsamifera* x *P. deltoides*)) and 915005 (*P. balsamifera* x *P. maximowiczii*) (95 and 96 Mg ha^{-1} respectively), while the least productive clone 747210 (*P. balsamifera* x *P. trichocarpa*) also had a lower SOC stock (85 Mg ha^{-1}) compared to the other clones, but not significantly. There was no relationship between aboveground productivity and SOC stocks and total SOC stocks increased by 6 % when the sampling distance was closer to the tree stems. The difference in SOC stocks between clones was mostly observed at the 20-40 cm depth suggesting the significant effect of roots on SOC storage. Soil C/N ratios were significantly different between clones at 0-20 and 20-40 cm depths suggesting differences in OM decomposition rates between clones. There could be a trade-off between aboveground productivity and litter decomposition rate to increase SOC storage.

Keywords: soil organic carbon, growth rate, deep soil, root, hybrid poplar, climate change

1.3 Introduction

One of humanity's most significant challenge is coping with the consequences of global warming mainly caused by increasing global atmospheric CO_2 emissions (IPCC, 2021). Climate change has led to an increase in forest disturbances, such as wildfires and insect outbreaks, that have contributed to the decline and mortality of many forest ecosystems (Anderegg *et al.*, 2015 ; Balshi *et al.*, 2009 ; Cohen *et al.*, 2016 ; Hogg *et al.*, 2002 ; Parry *et al.*, 2003). To mitigate this, the international "4 per 1000" initiative aims to increase soil organic carbon (SOC) in the top 30 cm of soil annually by four per mil to offset annual anthropogenic CO_2 emissions (Derrien *et al.*, 2016 ; Minasny *et al.*, 2017). Soil C stocks represent approximately 60% of the ecosystem C stock in boreal forests, compared to 50% in temperate and 32% in tropical forests (Pan *et al.*, 2011). The elevated SOC in forest ecosystems could come from higher organic matter (OM) inputs derived from litter accumulation, root turnover and root exudation (Derrien *et al.*, 2016 ; Schmidt *et al.*, 2011 ; Sokol *et al.*, 2019). In this context, establishing fast-growing tree plantations to create additional soil C sinks has received increased interest in recent years (Chomel *et al.*, 2014 ; Meifang *et al.*, 2017 ; Qian *et al.*, 2022 ; Truax *et al.*, 2018).

Fast-growing plantations such as intensively managed hybrid poplar (*Populus* spp.) are being used around the world to rapidly produce wood biomass on smaller land areas compared to native forests. A significant amount of C is rapidly stored in above and belowground biomass of these trees (Dewar and Cannell, 1992 ; Tuskan and Walsh, 2001 ; Weslien *et al.*, 2009) and it is regularly argued that these plantations could be used to increase organic C in soils due to rapid litter accumulation and fast root turnover (Block *et al.*, 2006 ; Chomel *et al.*, 2014 ; Dewar and Cannell, 1992 ; Sartori *et al.*, 2007). As an example, Peichl et al. (2006) found that after 13 years, soil C stocks (78.5 Mg ha^{-1}) under 17.6 m – high hybrid poplar trees were more than 16% greater than those found in a spruce plantation of the same age with 6.3 m high trees. However, roots of fast-growing species can also have faster respiration rates and be decomposed more rapidly compared to those of slow-growing species (Comas *et al.*, 2002 ; De Deyn *et al.*, 2008 ; Kane *et al.*, 2005). Furthermore, variability in aboveground productivity has been widely documented for *Populus* genus

(Laureysens *et al.*, 2004, 2005 ; Truax *et al.*, 2012, 2014). Consequently, it is not clear how variation in aboveground productivity among fast-growing trees impacts SOC accumulation and storage.

Soil organic C concentration in the upper soil horizons, where organic matter inputs from leaf litter and roots are more abundant, is generally greater than in deeper soil layers (Howlett *et al.*, 2011 ; Moreno *et al.*, 2005). However, the deep soil can also contribute significantly to C storage due to their high storage capacity and their importance on long-term C stabilization via interactions with the soil mineral phase (Rumpel and Kögel-Knabner, 2011). As hybrid poplar roots can reach 1 m depth, they could release and accumulate C in deep soil layers relative to shallow-rooted species (Dickmann *et al.*, 1996). Considering that fine root biomass varies significantly among poplar clones and among soil layers (Al Afas *et al.*, 2008), the vertical distribution of SOC may differ for each clone. Furthermore, SOC distribution may also vary horizontally, as the influence of a tree on its surroundings is limited spatially. For example, SOC stock was greatest underneath the tree canopy and decreased with distance in an oak forest of central-western Spain due to the fact that tree canopy contributes to litter inputs (Howlett *et al.*, 2011). However, others also found that SOC stocks do not always differ with distance from trees (Oelbermann and Voroney, 2007 ; Peichl *et al.*, 2006).

The main objective of our study was to determine if SOC stocks at different soil depths increase with aboveground productivity using a hybrid poplar plantation containing several clones with different growth rates. We secondary tested the effect of distance from trees on SOC stocks. We expected that the most productive clones would store more C in the soil and that SOC would increase with decreasing sampling distance from the stems.

1.4 Materials and Methods

1.4.1 Site description

The study was performed in a hybrid poplar plantation established on agricultural land at the New Liskeard Agricultural Research Station in North-Eastern Ontario, Canada

(47°31′15″ N, 79°39′52″ W). Based on 29-year data (1981-2010, Earlton station), this region has a humid continental climate with an average daily temperature of 2.6°C and an average annual precipitation of 786 mm (576 mm rain and 222 cm snow) (Environment Canada, 2023). The soil is characterized by a clay loam texture (Yan *et al.*, 2019) and classified as a Humic Gleysol by Canada Soil Survey Committee (1987) or as Gleysols according to the IUSS Working Group WRB (2015). The regional surficial geology is characterized by clays and lacustrine sands derived from post-glacial Barlow Lake (Rowe, 1972).

The experimental field was ploughed in October 2006 and cross-cultivated with disks followed by herbicide applications in spring 2007 (RoundupTM). Hybrid poplar trees were planted in spring 2007 at a 3.5 m x 3.5 m spacing (816 stems ha^{-1}) and fertilized with NPK 18-23-18 (110 g tree^{-1}), at a rate of 89.76 kg ha^{-1}. Annual weed control was provided by cultivating between rows with disks followed by herbicide application between trees for the first two years after plantation establishment. The experimental design consisted of 3 replicate blocks each with 8 monoclonal plots of 100 trees (10 rows x 10 trees) randomly distributed within blocks.

We selected 5 clones within the 8 planted ones according to their productivity after 14 years, from the least productive to the most productive. The selected clones were: 1079 *(Populus* x *jackii* (*P. balsamifera* x *P. deltoides*)), 747210 (*P. balsamifera* x *P. trichocarpa*), 915005 (*P. balsamifera x P. maximowiczii*), 915319 (*P. maximowiczii x P. balsamifera*) and DN2 (*P. deltoides* x *P. nigra*).

1.4.2 Clone productivity

Field measurements were taken in July 2021 when the trees were 14 years old. We measured diameter at breast height (*DBH*) and tree height (*H*) in a 6 x 6 tree subplot for each monoclonal plot using a dendrometric tape and a Vertex 5 Hypsometer. We subsequently estimated stem volume (outside of the bark) of each tree from using the allometric equation established by Truax et al. (2014):

$$V = 0.1014 \times DBH^{2.5562} \qquad \textbf{Eq. 1}$$

where *V* is the stem volume outside of the bark (dm^3) and *DBH* is the diameter at breast height (cm). In this study, the average annual growth rate (m^3 ha^{-1} $year^{-1}$) was used to estimate the productivity of each hybrid poplar clone and was calculated by dividing total stem volume by subplot area and plantation age (Truax *et al.*, 2012, 2014).

1.4.3 Soil sampling and carbon analysis

Soil sampling was done in the same subplot (6 x 6 trees) selected for dendrometric measurements. For each subplot, soils were sampled between two trees in a systematic way. We collected the soil cores at two distances (87.5 cm (quarter) and 175.0 cm (center)) from a stem and at 3 soil depths (0-20, 20-40 and 40-60 cm) using a PVC cylinder (10 cm diameter and 20 cm length). A total of 180 soil cores (2 trees x 2 distances x 3 soil depths x 5 clones x 3 blocks) were collected in plastic bags, stored in a cooler and brought to the laboratory for further analysis.

We first removed and weighed pebbles and broke the soil into small pieces to facilitate air drying using 8 mm sieves. The pebble mass accounted for only 0.3% of the soil mass at most due to the clay loam texture of the soil. All air-dried soil samples were then ground to 2 mm before analysis. One soil subsample from each clone in each block and at each depth (n = 45) was selected to measure the average soil pH of the site. We measured the pH of 10 g of air-dried soil subsamples (< 2 mm) in 20 mL of 0.01 M $CaCl_2$ with a pH meter (Hach Sension+ MM374). The soil pH values reached 6.9 (±0.2), 7.4 (±0.2) and 7.6 (±0.1) for the 0-20, 20-40 and 40-60 cm depths respectively, suggesting the presence of inorganic C in our samples. Therefore, the C in our samples could not be considered as SOC solely. Accordingly, we followed the method of Kreyling et al. (2013) to distinguish organic and inorganic C from our soil samples. Subsamples (5 g) were heated for 4.5 h in a muffle furnace at 450 °C to combust OC. Heat-treated and non-heat-treated subsamples were analyzed for total C and nitrogen (N) concentrations by dry combustion (Vario MAX cube; Elementar, Langenselbold, Germany). Carbon in the non-heat-treated subsamples was considered as total C while C in the heat-treated subsamples was considered as inorganic C. Thus, we calculated the organic C concentration by subtracting the inorganic C concentration from the total C concentration.

Another 10 g subsample of each soil sample was oven-dried (105 °C, 72 h) to calculate its oven-dried mass. We then calculated the soil bulk density (*BD*, g. cm^{-3}) by using the Eq. 2 (Poeplau *et al.*, 2017), which is as follows:

$$BD = (mass_{sample} - mass_{pebbles})/(volume_{core} - \frac{mass_{pebbles}}{\rho_{pebbles}}) \qquad \textbf{Eq. 2}$$

Where $mass_{sample}$ and $mass_{pebbles}$ are the masses (g) of oven-dried samples and pebbles, respectively, $volume_{core}$ is the soil core volume (cm^3), and $\rho_{pebbles}$ which is equal to 2.6 g cm^{-3} is the approximate density of pebbles (Don *et al.*, 2007).

SOC stock (Mg ha^{-1}) for each depth was calculated by using the Eq. 3 (Poeplau *et al.*, 2017), which is as follows:

$$SOC\ stock = SOC\ concentration \times BD \times d \times (1 - \delta) \times 0.1 \qquad \textbf{Eq. 3}$$

where *SOC concentration* is the soil organic carbon concentration (g kg^{-1}), *BD* is the soil bulk density (g. cm^{-3}), d is the depth (cm) and δ is the pebble volume fraction (%/100). For the total soil profile, the *total SOC stock* is equal to the sum of the *SOC stock* for each soil depth. As we suggest the presence of inorganic C in our soil samples and we do not have the soil organic N values, we calculated the soil C/N ratios by dividing organic C by total N concentrations of the whole soil.

1.4.4 Statistical analysis

All statistical tests were performed using the statistical software R version 4.1.1 (R Development Core Team, 2013). Analysis of clone and distance effects were estimated using linear mixed models with the lme4 package and lmerTest package in R where block was considered as random effect (Bates *et al.*, 2015 ; Kuznetsova *et al.*, 2017). We calculated the estimates (SOC and total N concentrations, C/N ratio, bulk density, and SOC stock) for each clone by the average values in both distances (87.5 and 170 cm). We selected models with smallest AICc (Akaike Information

Criterion) with the aictab() function. To validate each model, we checked model assumptions (independence of residuals, equality of variance (homoscedasticity), and normality of residuals) by diagnostic graphs and Shapiro-Wilk tests. The model assumptions have been respected without data transformation. The predictor effect was significant when the probability level (*P*) was below the theoretical probability level $\alpha = 5\%$. The emmeans package in R was used as a *post-hoc* method to make pairwise comparisons when a significant effect was found for a variable (clone or distance) (Lenth *et al.*, 2018). Regression models were used to determine the relationship between clone growth rate and total SOC with the function lm () in R. The models were selected based on their relevance, i.e. adjusted coefficient of determination R^2 closer to 1 and lower p-value.

1.5 Results

1.5.1 Tree productivity and total SOC stocks (0-60 cm)

Mean tree characteristics (DBH, tree height and stem volume) for each clone were summarized in Tableau 2. Clone DN2 was the most productive, clone 747210 was the least productive and clones 915319, 1079 and 915005 had intermediate growth rates ($P < 0.001$, Figure 3). All hybrid poplar clones stored an average of 82.9 to 95.7 Mg ha^{-1} to a 60 cm depth. There were significant differences in total SOC stocks (0-60 cm) between clones ($P = 0.004$). The most productive clone (DN2) stored 13 % less SOC than the mid-productive clones 1079 and 915005 to a 60 cm depth (Figure 4). The least productive clone (747210) also stored less SOC, but the difference was not significant from that of the other clones. Consequently, there was no significant relationship between clone productivity and total SOC stocks ($P = 0.58$, Figure 5). Total SOC stocks increased by 6 % when the sampling distance was closer to the stem ($P = 0.03$, Figure 4).

Tableau 2
Mean tree characteristics (diameter at breast height, tree height and stem volume) for each clone.

Clone	DBH (cm)		Height (m)		Stem Volume (dm^3 tree^{-1})	
747210	17.40(±0.46)	d	16.31(±0.22)	d	174.67(±23.42)	d
915005	19.67(±0.26)	c	18.32(±0.17)	c	212.66(±6.76)	cd
1079	21.09(±0.27)	b	19.78(±0.20)	b	253.19(±7.59)	bc
915319	22.14(±0.24)	b	21.36(±0.19)	a	284.39(±7.70)	b
DN2	23.76 (±0.36)	a	21.35(±0.20)	a	346.55(±12.88)	a

Standard errors of the mean (SEM) are given in parentheses. Different letters indicate significant differences between clones ($P < 0.05$).

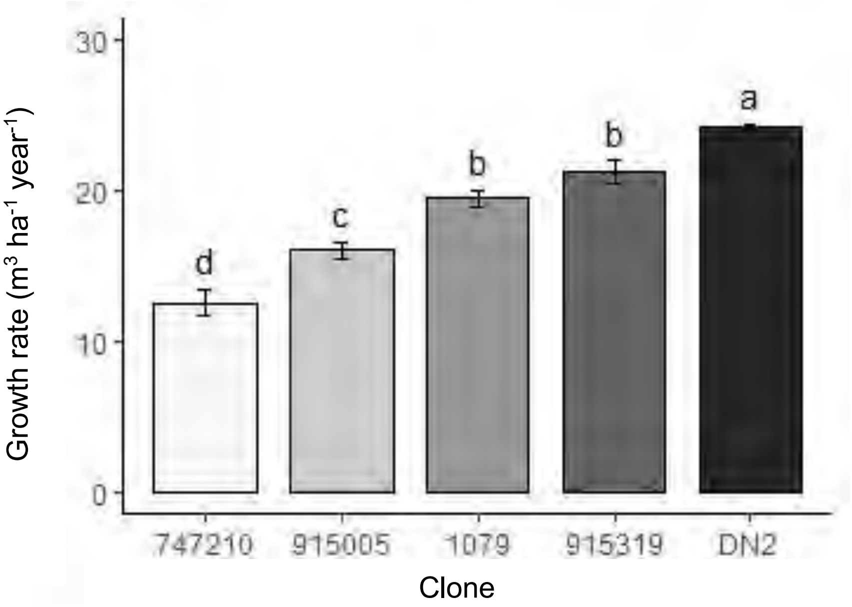

Figure 3
Mean (± SEM) clone growth rate after 14 years of planting. Different letters indicate a significant difference between clones ($P < 0.05$).

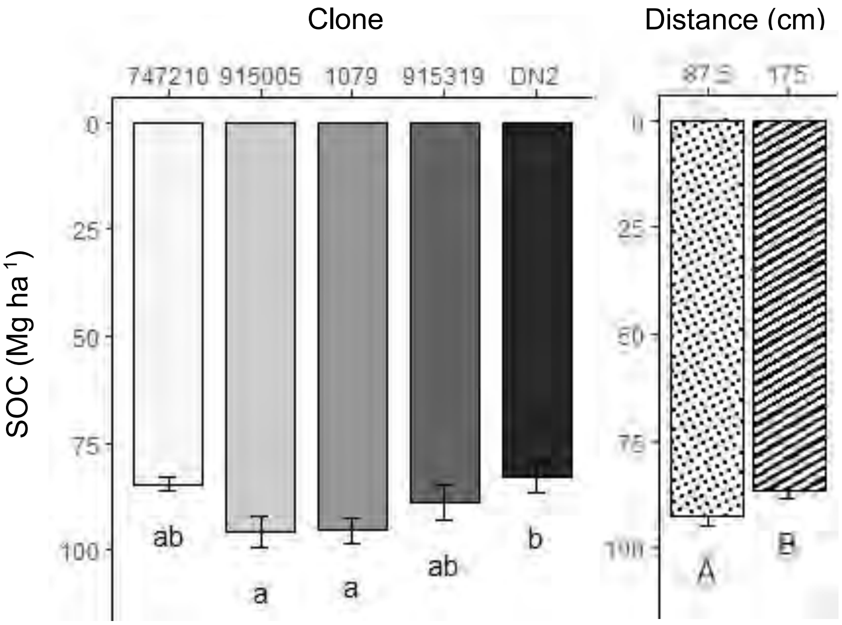

Figure 4
Mean (± SEM) of total SOC stock in the first 60 cm of depth for each clone and for each distance from the stem. Different lower-case letters indicate a significant difference between clones and different upper-case letters indicate a significant difference between distances (*P* < 0.05). Clones are arranged in ascending order of their growth rates.

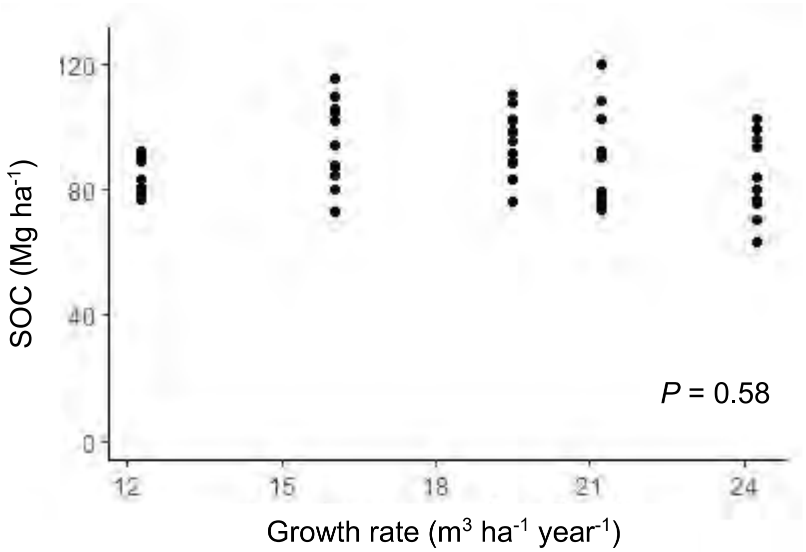

Figure 5
Relationship between growth rate and SOC stock in the first 60 cm of depth

1.5.2 SOC in each depth

SOC stocks were greater within the first 20 cm layers of the soil and decreased rapidly with increasing depth for all clones (Figure 6). However, SOC stocks at the 0-20 cm depth were not significantly different between clones at the significance level of α =0.05. The difference in SOC stocks between clones was only observed at the 20-40 cm depth (*P* = 0.01). The mid-productive clones 1079 and 915005 stored greater SOC i.e., 27.2 (± 2.8) and 27.1 (± 3.7) Mg ha^{-1}, respectively, at the 20-40 cm depth compared to the most productive clone (17.2 (±2.7) Mg ha^{-1}) (Figure 6). At the 40-60 cm layer, SOC stocks were significantly low and similar for all clones (*P* = 0.14). Relationships between aboveground productivity and SOC stocks at each depth were not significant (*P* > 0.05 for all depths).

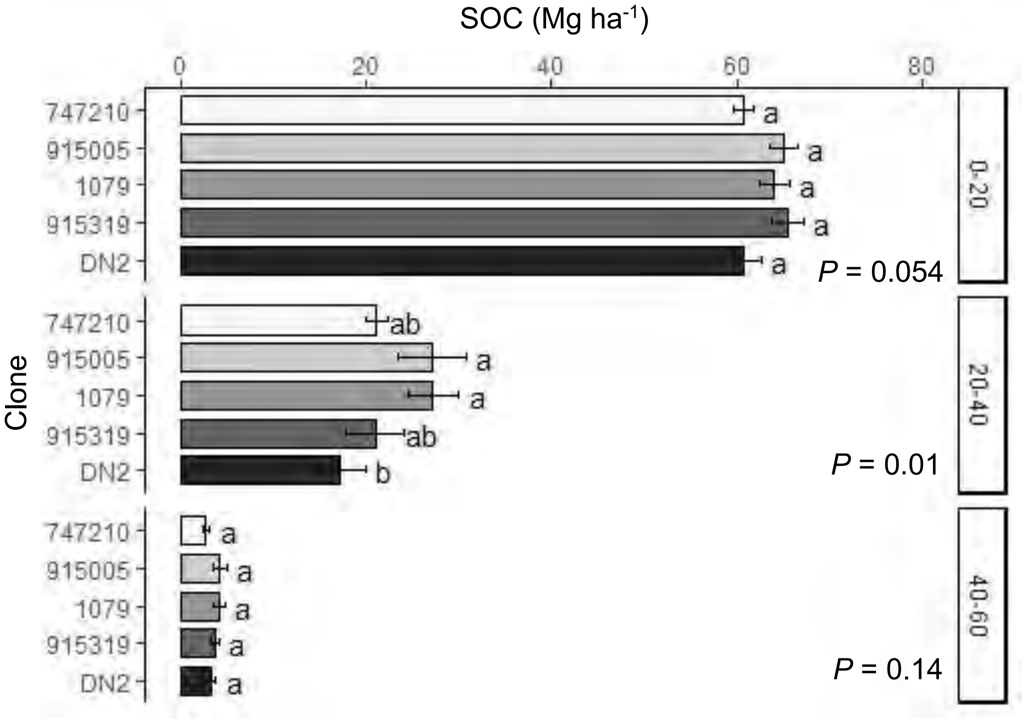

Figure 6
Mean (± SEM) of SOC stocks for each clone at each depth. Different letters indicate significant differences between clones at each depth (*P* < 0.05). Clones are arranged in ascending order of their growth rates.

1.5.3 Soil organic C concentration, C/N ratio and bulk density

There were significant differences in SOC concentrations (i.e., g kg^{-1}) between clones at depths of 0-20 ($P < 0.001$) and 20-40 cm ($P = 0.04$). SOC concentrations under clones DN2 and 747210 were lower than those under clones 1079 and 915005 at the 0-20 cm depth and SOC concentration under clone DN2 was lower than that under clone 1079 at the 20-40 cm depth (Tableau 3). Significant differences in total soil N concentration between clones were also observed at depths of 0-20 ($P < 0.001$) and 20-40 cm ($P < 0.05$) and the same trend as SOC concentration was observed (Tableau 3).

Soil C/N ratios were significantly different between clones at depths of 0-20 ($P < 0.001$) and 20-40 cm ($P = 0.04$). The least productive clone (747210) and clone 915319 had lower soil C/N ratios than clone 1079 in the topsoil (0-20 cm) while the most productive clone (DN2) had lower soil C/N ratio than clone 915005 at 20-40 cm depth (Tableau 3). In the 40-60 cm layer, the soil C/N ratios of all clones were similar (Tableau 3). In addition, there was no significant difference in soil bulk density between clones at all depths (0-20 cm ($P = 0.07$); 20-40 ($P = 0.49$) and 40-60 cm ($P = 0.92$)).

Tableau 3
Mean (± SEM) SOC concentration, C/N ratio and bulk density (BD) of the soil at each depth.

D (cm)	Clone	SOC concentration (g kg^{-1})	Total N concentration (g kg^{-1})	Soil C/N	BD (g cm^{-3})
0-20	747210	29.08(±0.54) b	2.57(±0.05) b	11.32(±0.07) b	1.05(±0.02) a
	915005	32.55(±0.58) a	2.80(±0.03) a	11.61(±0.13) ab	1.00(±0.01) a
	1079	32.60(±0.67) a	2.75(±0.06) a	11.88(±0.13) a	1.00(±0.01) a
	915319	30.99(±0.59) ab	2.73(±0.04) ab	11.36(±0.09) b	1.05(±0.02) a
	DN2	29.88(±0.82) b	2.57(±0.05) b	11.66(±0.15) ab	1.01(±0.02) a
20-40	747210	8.81(±0.66) ab	0.86(±0.06) ab	10.06(±0.09) ab	1.22(±0.04) a
	915005	11.49(±1.83) ab	1.05(±0.14) ab	10.76(±0.25) a	1.22(±0.03) a
	1079	12.29(±1.64) a	1.14(±0.13) a	10.43(±0.36) ab	1.17(±0.05) a
	915319	8.79(±1.29) ab	0.87(±0.10) ab	9.61(±0.44) ab	1.25(±0.03) a
	DN2	7.76(±1.42) b	0.78(±0.11) b	9.46(±0.51) b	1.22(±0.03) a
40-60	747210	1.05(±0.16) a	0.23(±0.01) a	4.54(±0.63) a	1.28(±0.02) a
	915005	1.69(±0.27) a	0.24(±0.01) a	6.37(±0.80) a	1.27(±0.02) a
	1079	1.61(±0.25) a	0.25(±0.01) a	6.41(±0.92) a	1.26(±0.03) a
	915319	1.46(±0.16) a	0.24(±0.01) a	6.03(±0.49) a	1.27(±0.02) a
	DN2	1.31(±0.18) a	0.22(±0.01) a	5.86(±0.74) a	1.28(±0.02) a

D: soil depth, SOC concentration: soil organic carbon concentration; Total N concentration: soil total nitrogen concentration; BD: soil bulk density. Different letters indicate significant differences between clones at each depth ($P < 0.05$). Clones are arranged in ascending order of their growth rates.

1.6 Discussion

1.6.1 Importance of productivity on SOC

SOC storage is determined in part by the balance between C inputs from above- and belowground biomass and root exudates against C losses through microbial decomposition, root respiration and leaching (Epron *et al.*, 2006 ; Martí-Roura *et al.*, 2019 ; Schmidt *et al.*, 2011). In our study, the most productive clone stored less SOC than the mid-productive clones to a depth of 60 cm. This result is inconsistent with our hypothesis and other studies that predicted increased soil carbon storage with increasing aboveground productivity (Peichl *et al.*, 2006 ; Weslien *et al.*, 2009). Higher productivity clones could supply more labile litter and root biomass. These greater labile C inputs (root exudation and litterfall) might have created favorable conditions for soil microbes for decomposition and enhanced the priming effect which is the stimulation of decomposition of recent as well as old or stable organic matter (Cheng *et al.*, 2014 ; Jansson and Hofmockel, 2020). The low soil C/N ratios at the 20-40 cm depth could also indicate the priming effect in this clone. For example, Dijkstra et al. (2006) demonstrated that the priming effect was positively related to plant productivity and in a study by Mack et al. (2004), SOC stock decreased with increased aboveground productivity (with increased nutrient availability through fertilization) in the Alaskan tundra due to accelerated decomposition. Other studies showed that increasing aboveground productivity of poplars did not enhance soil C stocks (Meifang *et al.*, 2017 ; Qian *et al.*, 2022). In addition, long-term litter manipulation experiments have shown that doubling litter inputs does not necessarily increase SOC stocks, potentially due to enhanced decomposition of new inputs and priming of old SOC (Lajtha *et al.*, 2018).

We also observed that the least productive clone likewise stored less organic C to a depth of 60 cm, but not significantly. The soil under this clone could receive less litter input as it produced less aboveground biomass. This clone also had lower soil C/N ratios in the topsoil (0-20 cm), indicating faster litter decomposition rates (Berg *et al.*, 1998 ; Taylor *et al.*, 1989 ; Yu *et al.*, 2019). However, further measurements are needed to confirm the litter decomposition rate of each clone as the soil C/N ratio is simply an indicator. For fast-growing trees, aboveground productivity could promote

SOC input, but there could be a trade-off between tree productivity and litter decomposition rate to increase SOC storage.

1.6.2 Potential contribution of roots to C storage in the deep soil

After 14 years of planting, we found that the differences in SOC stocks between clones were mostly observed at the deeper 20-40 cm depth. As Rumpel and Kögel-Knabner (2011) emphasized the importance of plant roots as significant sources of OM in deep soil, differences in root traits may have led to the difference observed in SOC stock between clones. Several studies reported a significant variation in fine root biomass and production among different poplar clones due to the parental genetic difference (Al Afas *et al.*, 2008 ; Dickmann *et al.*, 1996 ; Lukac *et al.*, 2003). This fine root production variation may have contributed to the variation of SOC stocks between clones. As hypothesized, we also found that SOC stocks increased with the decrease in distance between sampling point and the stem. The soil located directly below the tree canopy likely receives more OM because of higher litterfall, and additionally, due to abundant roots present near the main stem (Howlett *et al.*, 2011). Changes in soil microclimatic conditions under trees could also affect SOC stocks as decreasing soil temperature could reduce OM decomposition and promote SOC storage (Ding *et al.*, 2014 ; Zhang *et al.*, 2016).

The most productive clone (DN2) could have produced roots that accelerated the decomposition rate and reduced SOC stocks. It could have more fine roots than the other clones since a clone issued from the same crossbreed (*P. deltoides* x *P. nigra*) had the highest fine root biomass and the longest fine roots in a study that compared root characteristics between five poplar clones (Al Afas *et al.*, 2008). The increase in fine root production could be related to a higher nutrient demand since clones from this crossbreed had higher leaf N concentrations and lower C/N ratios (branch and stem) than other clones (Pearson *et al.*, 2010). Fine roots have greater root respiration rates than coarse roots (DesRochers *et al.*, 2002 ; Roumet *et al.*, 2016). On the other hand, Finzi et al. (2015) also found that fine roots produce more exudates than coarser roots, which would enhance the priming effect and further reduce C stocks in the soil (Dijkstra *et al.*, 2006).

For the mid-productive clones that stored more SOC, their roots could be more resistant to the decomposition compared to those of the other clones since their soil C/N ratio was higher in the 20-40 cm soil layer (Tableau 3). Lower root decomposition rates could be related to higher root C and lignin concentrations and lower root N, hemicellulose and water-soluble compound concentrations (Aulen *et al.*, 2012 ; Ma *et al.*, 2016 ; Roumet *et al.*, 2016 ; Wang *et al.*, 2010 ; Zhang and Wang, 2015). However, these root traits were not measured in our study and would need to be experimentally determined. The roots of mid-productive clones could have higher recalcitrant compound concentration that requires specific degradation enzymes for decomposition (de Boer *et al.*, 2005 ; Zak *et al.*, 2006). Wardle (2004) reported that recalcitrant organic compounds contributed more to short-term SOC storage than high quality litter because of their resistance to enzymatic attack.

1.6.3 Potential of fast-growing plantations to sequester C in the soil

SOC sequestration is influenced by several factors including the abundance of plant-derived inputs, their decomposition rate, and their stabilization through interaction with soil minerals (Mueller *et al.*, 2015). All soil C/N ratios ranged from 6 to 12 in our study, suggesting that OM decomposition rates had reached a very advanced stage (Bui and Henderson, 2013 ; Fazhu *et al.*, 2015). Fast-growing plantations generally provide high-quality OM rich in labile and low molecular weight compounds that require a low amount of energy for their decomposition (Agren and Bosatta, 1987). Consequently, in a “litter-centered” approach, fast-growing plantations contribute less to SOC stabilization and storage in the short term (Parton *et al.*, 1987 ; Poirier *et al.*, 2018b ; Wardle, 2004). However, recent studies have confirmed that labile and high quality organic compounds are more efficiently consumed by microorganisms and that the microbial biomass and necromass produced are easily stabilized by soil mineral phases (Cotrufo *et al.*, 2013 ; Lehmann and Kleber, 2015 ; Schmidt *et al.*, 2011). Poirier et al. (2018a) also found that they promoted the formation of water-stable macroaggregates in the rhizosphere. Fast-growing trees would thus be more conductive to long-term storage of SOC than slow-growing ones.

Converting cultivated or abandoned agricultural land to short-rotation woody plantations has been widely reported to reverse the process of C loss and increase SOC storage (Arevalo *et al.*, 2011 ; Garten, 2002 ; Grigal and Berguson, 1998). For example, SOC stocks of hybrid poplar plantations increased by 13 Mg ha^{-1} at the 0-50 cm depth after 11 years compared to that of agricultural land and the rate of increase in the SOC was 2 Mg ha^{-1} year^{-1} (Arevalo *et al.*, 2011). However, afforested lands can also store less soil carbon than abandoned land left to natural succession (Thibault *et al.*, 2022). Fast-growing plantations acted as a soil C source during the initial years of establishment due to low input from tree biomass and litter and due to soil preparation and weed control that could accelerate OM decomposition (Arevalo *et al.*, 2011 ; Grigal and Berguson, 1998). Hybrid poplar plantations reached pre-plantation levels of soil C only after 7 years in central Alberta, Canada (Arevalo *et al.*, 2011) or 15 years in Minnesota, USA (Grigal and Berguson, 1998). Fast-growing trees could thus require at least 10 to 15 years to be considered as soil C sinks.

Our results showed that our hybrid poplar plantation established on agricultural land in North-Eastern Ontario, Canada, stored up to 95.73 Mg ha^{-1} to a depth of 60 cm after 14 years. SOC stock in the top 60 cm was lower in our study than in a 9-year-old hybrid poplar plantation (Arevalo *et al.*, 2011). Since both studies have the same previous land use patterns, soil type (Gleysol versus Luvisol), climatic conditions or clone could be the cause of the difference in SOC stocks. However, SOC concentration in the top 20 cm (31g kg^{-1} on average), in our study, was higher compared to the finding by Oelbermann and Voroney (2007) in a 13-year-old agroforestry system using hybrid poplar (DN-177: *P. deltoides* x *P. nigra*) in southern Canada (17 g kg^{-1}). Soil type and land use patterns could explain this difference (intensively managed plantations on Gleysol *versus* agroforestry system on Luvisol). According to Laganière et al. (2010), clay-rich soils have the potential to accumulate more SOC than soils with a lower clay content. Another reason could be the difference in tree density. Indeed, the tree density was higher in our study (816 trees ha^{-1}) compared to the agroforestry system from Oelbermann and Voroney (2007) (133 trees ha^{-1}), which would have increased OM input from litterfall and root turnover. Truax et al. (2018) also found that higher density plantations of poplars led to greater soil carbon stocks after 14 years. In summary, many other factors, such as previous land use patterns, soil type, climatic conditions species or clone and tree density should be taken into consideration for increasing SOC storage using fast-growing plantations.

1.7 Conclusion

For our fast-growing plantation using hybrid poplars, there was no significant relationship between tree productivity and SOC stocks. Differences in SOC stocks were mostly observed between clones. Mid-productive clones stored more SOC than the most productive clone, possibly because they had lower decomposition rate of litter inputs and native organic matter. Here, we report a potential trade-off between aboveground productivity and organic matter decomposition rate to increase SOC storage within fast growing plantations. Our results also suggest that tree roots could play a significant role in SOC storage, especially in the deeper soil horizons. Further studies are needed to experimentally determine if significant differences in specific root traits exist among hybrid poplar clones to specify the roles of tree roots in SOC storage. By increasing global timber supplies, fast-growing trees could reduce pressures on natural forests that are important C sinks. Therefore, they could have a significant positive impact on the global C cycle.

1.8 Acknowledgements

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2. HOW IS TREE GROWTH RATE LINKED TO ROOT FUNCTIONAL TRAITS IN PHYLOGENETICALLY RELATED POPLAR HYBRIDS?

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Toky Jeriniaina Rabearison [1], Vincent Poirier [2], Jérôme Laganière [3], Annie DesRochers [1]

[1] *Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 341 rue principale Nord, Amos, Québec J9T 2L8, Canada*

[2] *Unité de recherche et de développement en agroalimentaire, Université du Québec en Abitibi-Témiscamingue, 79, Rue Côté, Notre-Dame-du-Nord, Québec J0Z 3B0, Canada*

[3] *Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Québec, Qc G1V 4C7, Canada*

Author for correspondence: Toky Jeriniaina Rabearison

Email: TokyJeriniaina.Rabearison@uqat.ca

2.1 Résumé

Les racines fines jouent un rôle crucial dans l'acquisition des nutriments et de l'eau, contribuant ainsi à la croissance des arbres. Les racines fines ayant une longueur spécifique (SRL) élevée et un diamètre plus petit sont souvent considérées comme facilitant la croissance rapide des arbres. Cependant, les incohérences dans la littérature ne fournissent pas de base claire sur l'effet des traits fonctionnels des racines, tels que la SRL ou la densité en masse des racines, sur le taux de croissance des arbres chez les arbres phylogénétiquement proches. Notre objectif était d'examiner la relation entre le taux de croissance des arbres et les traits fonctionnels des racines, en utilisant des clones présentant différents taux de croissance dans une plantation de peupliers hybrides située à New Liskeard, ON, Canada. Des échantillons de racines fines (diamètre < 2 mm) ont été prélevés à l'aide de carottes de sol dans les profondeurs 0-20, 20-40 et 40-60 cm, et analysés pour avoir leurs traits morphologiques, chimiques et architecturaux. Une SRL élevée et des racines fines plus petites étaient associées aux clones les moins productifs, ce qui n'est pas cohérent avec la théorie sur le spectre économique racinaire (SER). Cependant, le clone le plus productif avait un diamètre de racines fines plus gros et des concentrations en lignine de racines plus élevées, réduisant probablement les coûts de construction et d'entretien des racines ainsi que les pertes de C. Par conséquent, dans les profondeurs 0-20 et 20-40 cm, le taux de croissance des arbres a montré des corrélations positives avec le diamètre des racines et les concentrations en lignine de racines, mais des corrélations négatives avec la SRL et la concentration en composés solubles. L'augmentation de la densité en masse de racines dans la profondeur 0-20 cm a favorisé le taux de croissance des arbres, montrant l'importance de l'exploration de l'horizon superficiel du sol par les racines pour la croissance des arbres. Nous concluons que la variation des traits racinaires ne suit pas toujours la théorie sur le SER et soutenons que le taux de croissance rapide des arbres peut également être dû à la croissance en diamètre et en masse des racines fines chez les arbres phylogénétiquement proches.

Mots-clés : arbre à croissance rapide, racine fine, peuplier hybride, spectre économique racinaire, horizon profond, productivité des arbres.

2.2 Abstract

Fine roots play a crucial role in soil nutrient and water acquisition, significantly contributing to tree growth. Fine roots with a high specific root length (SRL) and small diameter are often considered to help trees grow fast. However, inconsistencies in the literature do not provide a clear basis on the effect of root functional traits, such as SRL or root mass density (RMD), on tree growth rate in phylogenetically related trees. Our aim was to examine relationships between tree growth rate and root functional traits, using clones displaying different growth rates in a hybrid poplar plantation located in New Liskeard, ON, Canada. Fine roots (diameter < 2 mm) samples were collected using soil cores at depths of 0-20, 20-40 and 40-60 cm, and analyzed for morphological, chemical and architectural traits. High SRL and thin fine roots were associated with the least productive clones, which is not consistent with the root economics spectrum (RES) theory. However, the most productive clone had larger fine root diameter and higher root lignin concentrations, probably reducing root construction and maintenance costs and C losses. Therefore, at the 0-20 and 20-40 cm depths, tree growth rates showed positive correlations with root diameter and root lignin concentrations, but negative correlations with SRL and root soluble compounds concentration. Increasing RMD at the 0-20 cm depth promoted tree growth rates, showing the importance of soil exploration in the topsoil for tree growth. We conclude that fine root variation does not always follow the RES hypothesis and argue that the rapid growth rate of trees may also be driven by fine root growth in diameter and mass in phylogenetically related trees.

Keywords: fast-growing tree, fine root, hybrid poplar, root economics spectrum, subsoil, tree productivity

2.3 Introduction

Fast-growing plantations could help meet the world's growing demand for harvested wood products by rapidly producing high woody biomass on small land areas. For instance, hybrid poplars (*Populus* spp.) can grow three times higher than spruce trees of similar age in the boreal and temperate climate of Canada (Chomel *et al.*, 2014 ; Peichl *et al.*, 2006). Even among hybrid poplar clones, a great variability in growth rates can be observed as they can originate from different parentage (Laureysens *et al.*, 2004 ; Truax *et al.*, 2014). One of the key factors behind these differences is fine root development, because they play a central role in soil resource acquisition (McCormack *et al.*, 2015). Fine roots are usually defined as the most distal, ephemeral and absorptive roots less than 2 mm in diameter (D) (Guo *et al.*, 2008 ; Ostonen *et al.*, 2017). To better understand the influence of fine roots ($D < 2$ mm) on tree growth rates, a functional trait-based approach is often applied in the literature (Bardgett *et al.*, 2014 ; Cadotte *et al.*, 2009 ; Roscher *et al.*, 2012). Understanding how growth strategies are linked to functional root traits could help improve management and selection of clones/varieties to establish fast-growing plantations.

According to the root economics spectrum (RES) hypothesis, morphological and chemical traits of fine roots show interspecific variation depending on the plant's growth strategy (Bardgett *et al.*, 2014 ; McCormack *et al.*, 2012 ; Reich, 2014 ; Roumet *et al.*, 2016). While the "acquisitive" strategy is said to enhance rapid tree growth with faster foraging, thinner and shorter lifespan roots, the "conservative" strategy is related to slower foraging, thicker and longer lifespan roots (Comas *et al.*, 2002 ; Kramer-Walter *et al.*, 2016 ; McCormack *et al.*, 2012 ; Reich, 2014). Previous studies report that fast-growing trees exhibit higher specific root length (SRL), root nitrogen (N) concentrations and smaller root diameters than slow-growing species (Comas *et al.*, 2002 ; Comas and Eissenstat, 2004 ; Roumet *et al.*, 2016 ; Wright and Westoby, 1999). Fine roots with high SRL would be more efficient for tree growth as more C is allocated into fine root elongation than in biomass, increasing absorption capacity (Eissenstat and Yanai, 1997). However, high SRL and thin fine roots are often associated with short root lifespan and high root respiration rates, which increases C costs of fine root maintenance and C losses through respiration, negatively impacting overall net C gain of trees (Makita *et al.*, 2009 ; McCormack *et al.*, 2012 ; Pregitzer *et al.*, 1998 ; Weemstra *et al.*, 2020). Consequently, the positive relationship between increased SRL and tree growth remains unclear.

Several studies showed that SRL, root diameter and root N concentrations of tree species did not always correlate with tree growth rates (Kramer-Walter *et al.*, 2016 ; Weemstra *et al.*, 2016, 2020) as nutrient acquisition in soils does not necessarily require root traits *a priori* defined as acquisitive but also other root traits linked to soil nutrient mobility (Ravenek *et al.*, 2016). Among architectural traits of fine roots, root mass density (RMD) or root length density (RLD), i.e., fine-root mass or length per unit soil volume, determines the soil exploration intensity of roots (Pérez-Harguindeguy *et al.*, 2013 ; Stokes *et al.*, 2009). Increasing RMD leads to an increase in root surface area available to efficiently absorb mobile and less mobile nutrients, and thus to improve tree growth rates (Bauhus and Messier, 1999 ; Finér *et al.*, 2011 ; Hansson *et al.*, 2013). However, there is still a lack of studies confirming the effects of these root traits on the rapid growth of some trees such as hybrid poplars. According to Weemstra et al. (2020), tree species can use two distinct strategies to increase root surface area and soil nutrient uptake: allocate more C into root growth to increase RMD of fine roots or develop longer fine roots (higher SRL). It remains unclear whether acquisition and architectural traits of fine roots vary in a coordinated way or play a separate role in reaching faster growth rates in plantations.

Variation in fine root traits may not necessarily follow the RES hypothesis but be explained solely by the fact that studied tree species belonged to different orders or groups, for example conifers versus broadleaves (Lwila *et al.*, 2021 ; Tobner *et al.*, 2013 ; Valverde-Barrantes *et al.*, 2015). In temperate tree species, Valverde-Barrantes et al. (2015) argued that the substantial differences in root traits between species groups can cause profound divergences in resource acquisition strategies among them. In order to minimize the potential effect of high-level phylogenetic differences on the relationship between aboveground growth rates and fine-root traits, our study focused exclusively on species belonging to the same genus but with different growth rates. We studied hybrid poplar clones from different parentages considered as different species but belonging to the same genus *Populus*, thereby minimizing phylogenetic differences.

In this research, we aimed to compare fine root traits between hybrid poplars clones having different growth rates, to examine the relationships between aboveground growth rate and morphological, chemical and architectural traits of fine roots in phylogenetically related trees. We used the arbitrary but commonly applied definition of fine roots as those having less than 2 mm in diameter. As previous studies found that tree fine roots (D < 2 mm) can include several branching orders that differ in morphology and function (McCormack *et al.*, 2015 ; Pregitzer *et al.*, 1998, 2002), we further divided our fine roots into 3 diameter classes: < 0.2, 0.2-1 and 1-2 mm. In line with the RES theory, we hypothesized that SRL, root N and soluble compounds concentrations would be positively correlated to tree growth rates, whereas root diameter would have the opposite effect. Great root length and mass densities give trees a high intensity of soil exploration to acquire nutrients; hence, we predicted that they would increase tree growth rates.

2.4 Materials and Methods

2.4.1 Study site

The study was conducted in an experimental plantation of hybrid poplars at the New Liskeard Agricultural Research Station in North-Eastern Ontario, Canada (47°31′15″ N, 79°39′52″ W). The area is characterized by a humid continental climate with an average daily temperature of 2.6°C and an average annual precipitation of 786 mm (576 mm rain and 222 cm snow) based on 29-year data (1981-2010, Earlton station) (Environment Canada, 2023). The soil in this region has a clay loam texture and is classified as a Humic Gleysol (Canada Soil Survey Committee, 1987 ; Rabearison *et al.*, 2023 ; Yan *et al.*, 2019).

The site was ploughed and cross-cultivated with agricultural disks in October 2006, followed by pre-emergent herbicide applications in spring 2007. One-year-old hybrid poplar rooted cuttings were planted in spring 2007 with the spacing of a 3.5 m x 3.5 m

(816 stems ha^{-1}). All trees were spot fertilized solely at planting with NPK 18-23-18 (110 g $tree^{-1}$), at a rate of 89.76 kg ha^{-1} for optimal initial growth, without additional fertilization over the years. The experimental design consisted of three replicate blocks, each containing eight monoclonal plots of 100 trees (10 rows × 10 trees) randomly distributed within blocks. We controlled the presence of weeds by cultivating between rows with disks followed by herbicide applications between trees (RoundupTM) for the first two years after plantation establishment.

2.4.2 Clone selection and growth rate

After 14 growing seasons, we selected five clones from the eight planted ones based on their growth rates and their parentage, ranging from the least to the most productive: 747210 (*P. balsamifera* × *P. trichocarpa*), 915005 (*P. balsamifera* × *P. maximowiczii*), 1079 *(Populus* × *jackii* (*P. balsamifera* × *P. deltoides*)), 915319 (*P. maximowiczii* × *P. balsamifera*) and DN2 (*P. deltoides* × *P. nigra*). For each monoclonal plot, we measured diameter at breast height (DBH) of trees to estimate the growth rate of each clone. Average tree characteristics (diameter at breast height, tree height and stem volume) for each clone can be found in Rabearison et al. (2023). Tree growth rate (Tableau 4) was calculated as total stem volume divided by plot area and plantation age (Truax *et al.*, 2012, 2014).

Tableau 4
Growth rates and labels of studied hybrid poplar clones

Clone	Mean growth rate (m^3 ha^{-1} $year^{-1}$)		label
747210	12.58 (±0.92)	d	Least productive
915005	16.04 (±0.61)	c	Second least productive
1079	19.49 (±0.57)	b	Mid-productive
915319	21.23 (±0.78)	b	Second most productive
DN2	24.25 (±0.20)	a	Most productive

Data are from Rabearison et al. (2023). Standard errors of the mean (±SEM) are given in parentheses. Different letters indicate significant differences between clones ($P < 0.05$).

2.4.3 Root sampling

Sampling was systematically done between two trees in each monoclonal plot in July 2021. Soil cores were collected at two distances (87.5 cm and 175.0 cm) from a stem and at three soil depths (0-20, 20-40 and 40-60 cm) using a PVC cylinder measuring 10 cm in diameter and 20 cm in length. We had 6 replicates (2 trees per block × 3 blocks) for each clone, distance and depth. After being stored in plastic bags and a cooler, a total of 180 samples (6 replicates × 2 distances × 3 soil depths × 5 clones) were brought to the laboratory for further analysis. We soaked the soil cores in water containing sodium hexametaphosphate (50 g L^{-1}) overnight to disperse soil particles adhering to the roots due to the clay loam texture of the soil (Smucker *et al.*, 1982 ; Yan *et al.*, 2019). Roots were washed and rinsed to completely remove soil particles using a hydropneumatic elutriation system (Root washer, Gillison's Variety Fabrication Inc., Benzonia, MI, USA) according to Smucker et al. (1982). The roots were visually sorted to select only living and fine roots (D < 2 mm) of hybrid poplars for further analysis. While living fine roots were more rigid and flexible, dead roots were fragile, darker in color and broke easily. We were unable to collect enough roots from a soil core at the 40-60 cm depth to carry out all root analyses, so we had to mix root samples from two trees of the same clone, the same distance and the same block at this depth. A total of 150 root samples were available for analysis, including 60, 60, and 30 samples from depths of 0-20 cm, 20-40 cm and 40-60 cm respectively.

2.4.4 Root trait analysis

All washed fine roots were spread into a 20 × 25 cm transparent tray filled with deionized water to minimize overlap between roots and scanned as grayscale images at 400 dpi resolution with a transmitted light source (Epson Perfection V800; Epson, Ontario, Canada). We subsequently used WinRhizo Pro 2019 software (Regent Instruments, Quebec, Canada) to determine average root diameter (D, mm), total root length (RL), root length of three diameter classes (< 0.2 mm, 0.2-1 mm and 1-2 mm) and root volume. We calculated the percentage in length of each root size class by multiplying the length of each class by 100 and dividing by RL. It should be noted that we were unable to determine the mass for each root size class as it was not possible to separate and weigh the different root size classes manually. Thus, we measured

SRL values for whole fine roots (D < 2 mm), but not for each root size class. All scanned and weighed roots were then oven dried for 48 hours at 60°C to determine dry mass of whole fine roots (RDM). Specific root length (SRL, m g^{-1}) was calculated as the ratio of total root length to RDM. Root dry matter content (RDMC, mg g^{-1}) was obtained as RDM divided by root fresh mass (RFM). Root tissue density (RTD, g cm^{-3}) was calculated as RDM divided by root volume. We calculated root mass density (RMD, g cm^{-3}) as the ratio of the total root dry mass (RDM) to the soil volume where the roots were extracted. Root length density (RLD, cm cm^{-3}) was obtained by multiplying RMD by SRL.

Dried root samples were finely ground using a 2 mm sieve and an ultra-centrifugal mill (ZM200, Retsch GmbH., Haan, Germany). We analyzed root carbon (RCC) and nitrogen (RNC) concentrations by dry combustion (Vario MAX cube; Elementar, Langenselbold, Germany). Water-soluble compounds, hemicelluloses and lignin concentrations (mg g^{-1}) of fine roots were obtained by the method of Van Soest et al. (1991) using a fiber analyzer (Fibersac 24; Ankom, Macedon, NJ, USA).

2.4.5 Statistical analysis

All statistical tests were done using R software version 4.2.2 (R Development Core Team, 2013). We first used principal component analyses (PCA) to obtain an overview of the multidimensional variation of fine-root traits and to select all root traits with best significant contributions by using *prcomp* function and factoextra package. As variations in root traits were notably less pronounced at the 20-40 and 40-60 cm depths than at the 0-20 cm depth (Figures 7 and S1), statistical analyses were carried out separately at each depth. Selected root traits were compared between clones (6 replicates) at each depth by using linear mixed models where block was considered as random effect (lme4 and lmerTest packages, Bates et al., 2014 ; Kuznetsova et al., 2017). The predictor effect was significant when the probability level (*P*) was below the theoretical probability level $\alpha = 5\%$. Model assumptions (independence of residuals, equality of variance (homoscedasticity), and normality of residuals) were tested by diagnostic graphs and Shapiro-Wilk tests and the assumptions of selected models were met without data transformation. The emmeans package in R was used as a *post-hoc* method to make pairwise comparisons when there were significant differences in root traits between clones (Lenth *et al.*, 2018).

Relationships between tree growth rates and root traits were determined using linear mixed models. We selected models with smaller AICc (Akaike Information Criterion) by *aictab* function and AICcmodavg package and only the best root trait models were presented. Logarithmic transformations were performed for variable RMD at the 0-20 cm depth to meet model assumptions. We also performed linear mixed models with two root traits as predictors to define the best model, using *lmer* and *aictab* functions, while avoiding collinear predictors (i.e. RMD and RLD). Two coefficients of determination can be used in linear mixed models: the marginal R^2 and the conditional R^2 which are, respectively, the variance explained by the fixed effect (trait) and the variance explained by the fixed effect (trait) and random effect (block); we used only the marginal R^2 (shown as R^2 in this study) as it only considers the root trait effect (*r.squaredGLMM* function, MuMin package, Barton, 2009 ; Nakagawa and Schielzeth, 2013). The effects of distance from trees were not significant for all root traits hence were dropped, but data from both distances were retained to determine clone effects and the relationship between tree growth rate and root traits.

2.5 Results

2.5.1 Variations in root traits between hybrid poplar clones

Root traits among hybrid poplar clones showed multidimensional variations at the 0-20 cm depth according to PCA (Figure 7). The first PCA axis accounted for 27.8% of overall variation and was related to SRL, D, RCC and RNC, while the second PCA axis explained 23.1% of overall variation and mainly reflected differences in RMD, RLD, root lignin concentration and RDMC. Net differences in fine root traits between the most productive clone (DN2) and the least productive one (747210) were observed along these two PCA axis (Figure 7).

The most productive clones (DN2 and 915319) produced thicker fine roots than the least productive clone (747210) at the 0-20 and 20-40 cm depths ($P < 0.001$ for both soil depths, Figure 8a). At the 40-60 cm depth, average fine root diameter of the most productive clone (DN2) exceeded that of the mid-productive clone (1079) ($P < 0.05$, Figure 8a). In contrast, the most productive clones (DN2 and 915319) had lower SRL than mid-productive clone (1079) and the least productive clone (747210) at the 0-20 depth ($P < 0.001$, Figure 8b). The mid-productive clone (1079) had the highest SRL at the 20-40 cm depth ($P < 0.001$) and had higher SRL compared to clone DN2 at the 40-60 cm depth ($P < 0.05$) (Figure 8b). Furthermore, the second most productive clone (915319) had higher root dry matter content (RDMC), i.e., dry mass divided by fresh mass of fine roots, than the most productive clone (DN2) and clone 1079 at the 0-20 and 20-40 cm depths ($P < 0.001$ for both soil depths, Figure 8c). RDMC values were not significantly different between clones at the 40-60 cm depth (Figure 8c).

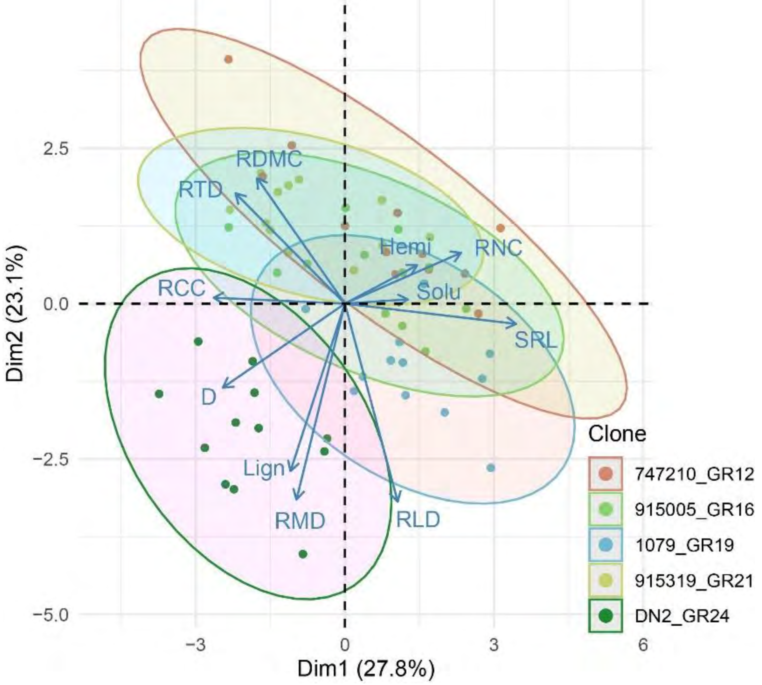

Figure 7
PCA of fine-root traits at 0-20 cm depth. Each colored region represents a labeled clone with its parentage coding and growth rate (GR, m^3, ha^{-1}, $year^{-1}$) and has a confidence interval of 95%. D: average root diameter, Hemi: root [hemicellulose], Lign: root [lignin], RCC: root [carbon], RDMC: root dry matter content, RLD: root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density, Solu: root [soluble compounds] and SRL: specific root length

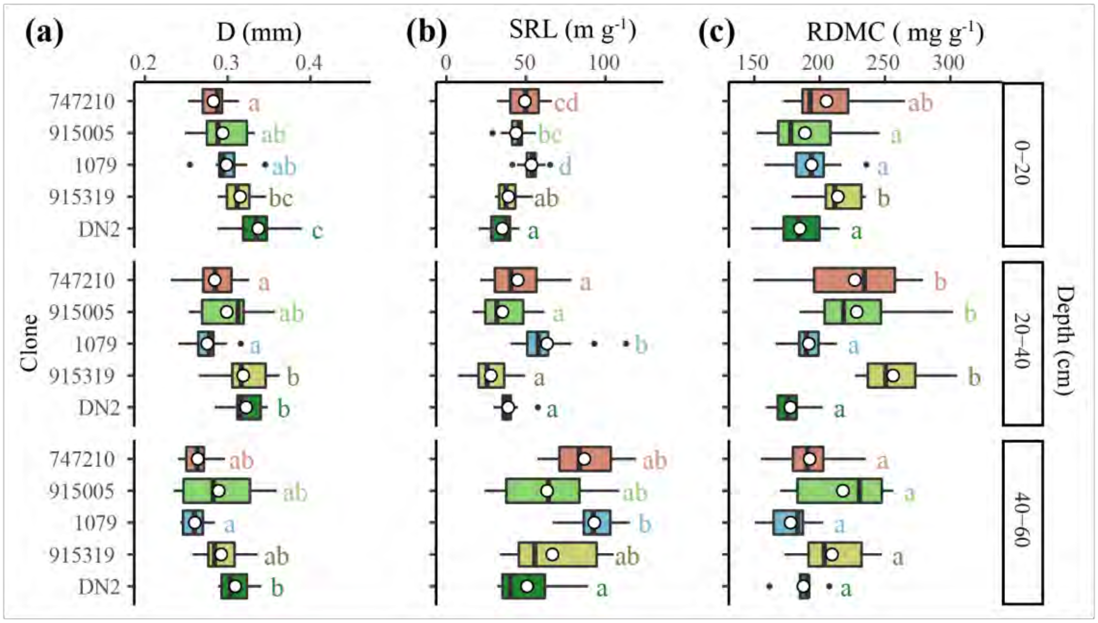

Figure 8
Differences in (a) average root diameter (D), (b) specific root length (SRL) and (c) root dry mass content (RMDC) between clones at each depth. Boxplots include the median (black vertical lines) and the mean (white circles) of each root trait for each clone at each depth. Different letters indicate significant differences between clones at each depth (*P* < 0.05). Clones are arranged in ascending order of their growth rates, from top to bottom.

In terms of chemical trait differences, fine roots of most productive clones (DN2 and 915319) had higher C concentrations than those of the mid-productive clones (1079 and 915005) at the 0-20 cm depth ($P < 0.001$, Figure 9a). Root C concentrations were also greater for the most productive clone DN2 than for clone 915005 at the 20-40 cm depth ($P < 0.05$, Figure 9a). However, the most productive clone (DN2) had the lowest root N concentrations at the 0-20 cm depth ($P < 0.001$) and lower root N concentrations than the mid-productive clone (1079) at the 20-40 cm depth ($P < 0.01$) (Figure 9b). The highest lignin concentrations were observed in fine roots of the most productive clone (DN2) at the 0-20 cm depth, as well as in those of this clone and clone 1079 at the 20-40 cm depth ($P < 0.001$ for both soil depths, Figure 9c). At the 40-60 cm depth, there were no significant differences between clones for root C, N and lignin concentrations (Figure 9abc).

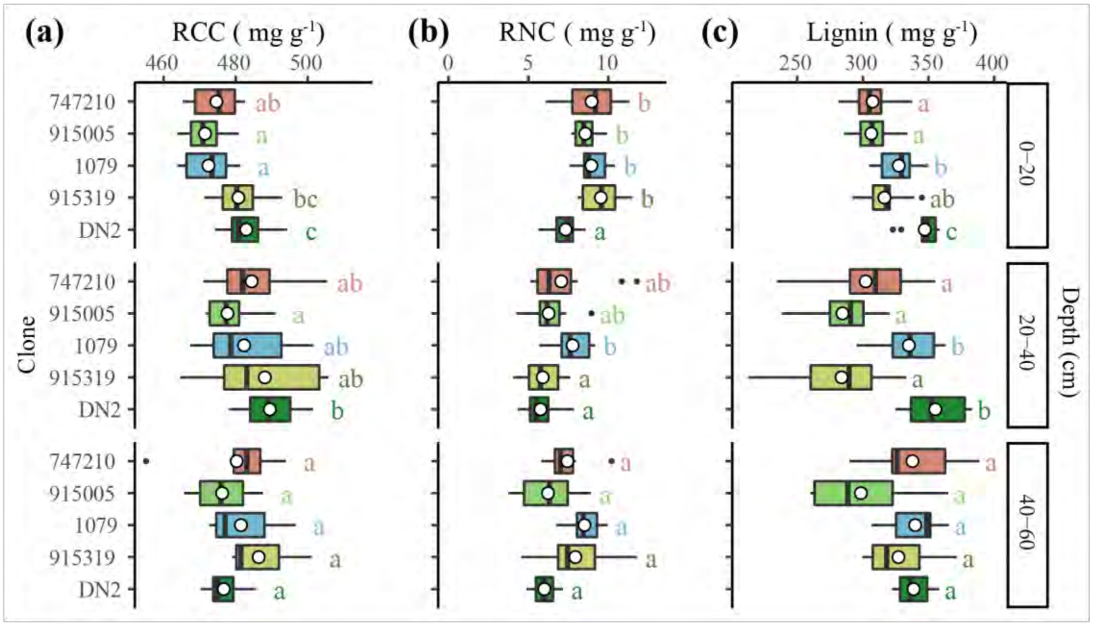

Figure 9
Differences in (a) root carbon concentration (RCC), (b) root nitrogen concentration (RNC) and (c) root lignin concentration between clones at each depth. Boxplots include the median (black vertical lines) and the mean (white circles) of each root trait for each clone at each depth. Different letters indicate significant differences between clones at each depth (*P* < 0.05). Clones are arranged in ascending order of their growth rates, from top to bottom.

The most productive clone (DN2) had the greatest RMD among all the clones at the 0-20 cm depth ($P < 0.001$, Figure 10a). However, the second most productive clone (915319) had lower RMD compared to all clones except for the least productive clone (747210) at this depth (Figure 10a). RMD of the mid-productive clone (915005) was greater than those of the least productive clone (747210) and clone 915319 at the 20-40 cm depth ($P < 0.01$, Figure 10a). Furthermore, the most productive clone (DN2) had greater RMD than clones 1079 and 915319 at 40-60 cm depth ($P < 0.01$, Figure 10a). For RLD, the most productive (DN2) and the mid-productive (1079) clones distributed more root length at the 0-20 and 20-40 cm depth compared to clone 915319 and the least productive clone (747210) ($P < 0.001$ for both soil depths, Figure 10b). The most productive clones (DN2) also had greater RLD than clone 915319 at the 40-60 cm depth ($P < 0.01$, Figure 10b).

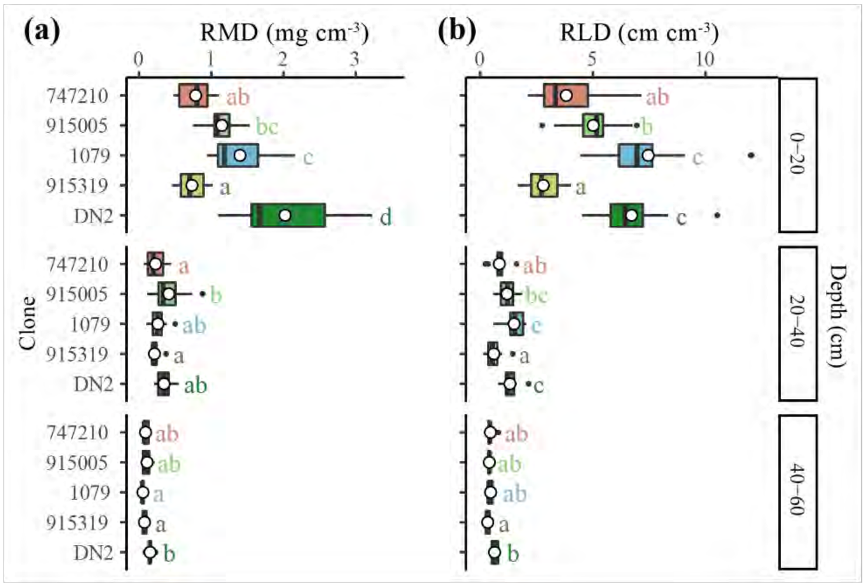

Figure 10
Differences in (a) root mass density (RMD) and (b) root length density (RLD) between clones at each depth. Boxplots include the median (black vertical lines) and the mean (white circles) of each root trait for each clone at each depth. Different letters indicate significant differences between clones at each depth (*P* < 0.05). Clones are arranged in ascending order of their growth rates, from top to bottom.

2.5.2 Relationship between tree growth rates and root traits

The increase in tree growth rate was mainly linked to a reduced percentage in length of 0-0.2 mm roots relative to the total length of fine roots (VFR, $P < 0.001$), associated with an increase in root lignin concentration ($P < 0.001$) in the topsoil (0-20 cm) (Growth rate = 28.47 – 0.55 × (VFR) + 0.08 × (Lignin); $R^2 = 0.63$). The percentage in length of 0-0.2 mm roots was also negatively correlated with tree growth rate at the 20-40 and 40-60 cm depths (Figure 11a). However, the percentage in length of 0.2-1 mm roots at the 0-20 cm depth strongly increased with aboveground growth rates ($P < 0.001$ and $R^2 = 0.50$) and this correlation was also observed at the other soil depths (Figure 11b). Tree growth rates increased with the percentage of 1-2 mm roots at the 0-20 cm depth, although no correlation was found at the 20-40 and 40-60 cm depths (Figure 11c). In addition, mean diameter of fine roots was positively correlated with tree growth rate at all soil depths, with a stronger relationship for the topsoil layer ($P < 0.001$ and $R^2 = 0.46$, Figure 12a). In contrast, an increase in SRL at 0-20 and 40-60 cm depths was related to lower tree growth rate (Figure 12b). Root lignin concentration was also positively correlated with tree growth rate at the 20-40 cm depth (Figure 13a). Conversely, tree growth rates were negatively associated with an increase in root soluble compounds concentration at all soil depths (Figure 13b). For architectural traits, RMD was positively associated with tree growth rates at the 0-20 cm depth ($P < 0.001$, $R^2 = 0.23$, Figure 14) but did not correlate with tree growth rate at the other soil depths ($R^2 = 0.00$ns and $R^2 = 0.08$ns for 20-40 cm and 40-60 cm depths respectively). RLD exhibited a weak positive correlation with tree growth rates at the 0-20 cm depth ($P < 0.05$, $R^2 = 0.08$), but had no correlations at the other depths ($R^2 = 0.04$ns and $R^2 = 0.08$ns for 20-40 cm and 40-60 cm depths respectively).

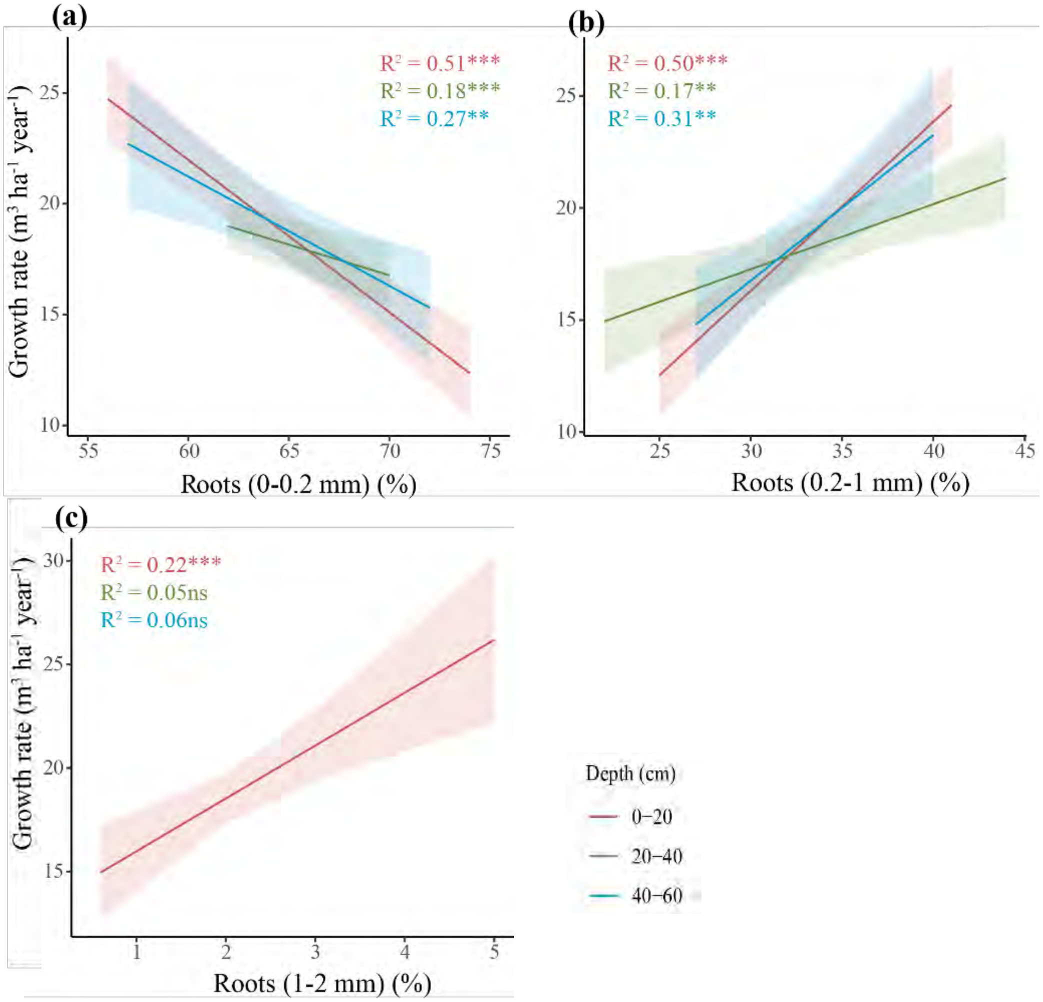

Figure 11
Correlation between tree growth rate and percentages in length of different root size classes. *, *P* < 0.001; **, *P* < 0.01; *, *P* < 0.05; ns, not significant. Shaded areas represent the 95% confidence intervals (n=60 for the 0-20 and 20-40 cm depths and n=30 for the 40-60 cm depth, where n values correspond to data pairs of both tree growth rate and root traits).**

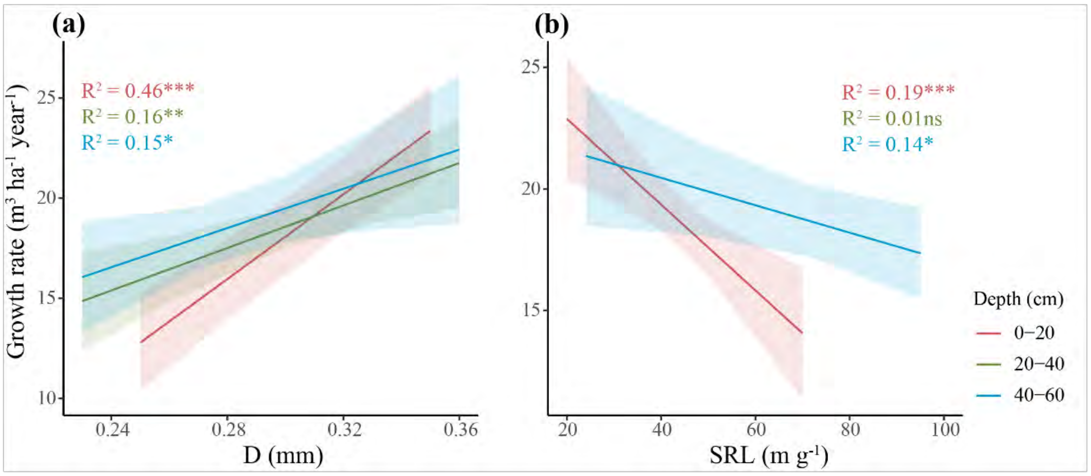

Figure 12

Correlation between tree growth rates and (a) average root diameter (D) or (b) specific root length (SRL). *, *P* < 0.001; **, *P* < 0.01; *, *P* < 0.05; ns, not significant. Shaded areas represent the 95% confidence intervals (n=60 for the 0-20 and 20-40 cm depths and n=30 for the 40-60 cm depth, where n values correspond to data pairs of both tree growth rate and root traits).**

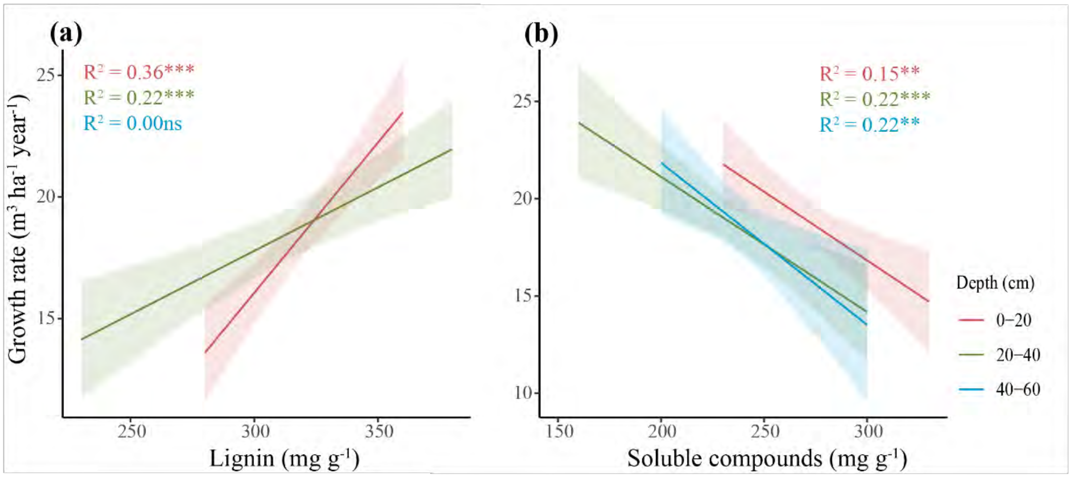

Figure 13

Correlation between tree growth rates and (a) root lignin or (b) root soluble compounds concentrations. *, *P* < 0.001; **, *P* < 0.01; *, *P* < 0.05; ns, not significant. Shaded areas represent the 95% confidence intervals (n=60 for the 0-20 and 20-40 cm depths and n=30 for the 40-60 cm depth, where n values correspond to data pairs of both tree growth rate and root traits).**

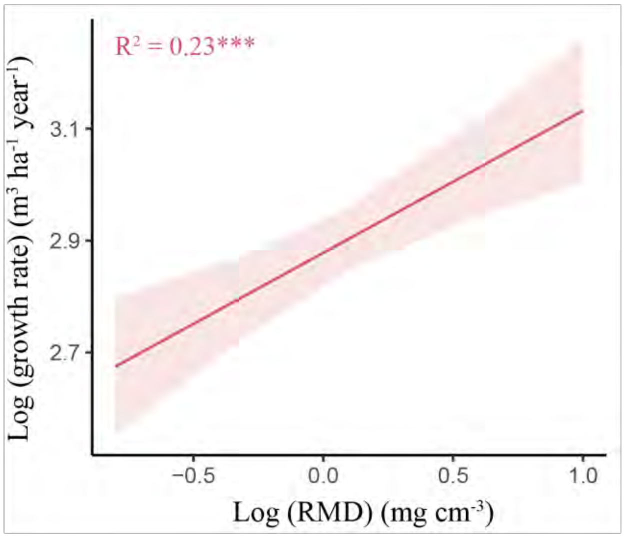

Figure 14
Correlation between tree growth rates and root mass density (RMD) at the 0-20 cm depth. *, *P* < 0.001. Shaded areas represent the 95% confidence intervals (n=60, where n values correspond to data pairs of both tree growth rate and RMD).**

2.6 Discussion

2.6.1 Why didn't the root economics spectrum (RES) work in our fast-growing plantation?

Contrary to our expectations, SRL was not positively related to tree growth rate in our plantation and our results pointed in fact toward the opposite relationship. Consequently, our results, along with many other tree studies (e.g Kramer-Walter *et al.*, 2016 ; Valverde-Barrantes *et al.*, 2015 ; Weemstra *et al.*, 2020), did not align with the RES theory. The latter states the importance of higher SRL for nutrient foraging (Eissenstat and Yanai, 1997). Several authors argued that high SRL is more associated with soil constraints (low fertility and water stress) than with rapid tree growth (Kramer-Walter *et al.*, 2016 ; Laliberté *et al.*, 2015 ; Olmo *et al.*, 2014). Since SRL did not have a positive relationship with tree growth rate, it is likely that our trees had sufficient soil nutrients and water, which could explain why the RES theory did not work in our fast-growing trees. Increasing SRL and decreasing fine root diameter also generally leads to shorter fine-root lifespan, increasing root C construction costs and probably having negative impacts on tree growth (McCormack *et al.*, 2012 ; Weemstra *et al.*, 2016). Conversely, thicker fine roots observed in the two most productive clones

(DN2 and 915319) was associated with increased tree growth, perhaps due to their longer lifespans and reduced construction costs.

The thicker, more C-rich and lignified fine roots observed in the most productive clones could also be the result of greater C assimilation during photosynthesis, enabling the construction of more transport roots and thus the exploitation of a greater soil volume. According to the surplus C hypothesis, C fixed by photosynthesis would have exceeded the C requirements of trees in these most productive clones, leading to the transfer of surplus C to roots (Prescott *et al.*, 2020). On the contrary, a higher concentration of root soluble compounds and thinner fine roots in the less productive clones could indicate a reduced C allocation to fine roots. There would be little or no surplus C from photosynthesis in these clones, indicating that soil nutrients probably were not limiting for tree growth (Pausch and Kuzyakov, 2018 ; Prescott *et al.*, 2020). Otherwise, trees would have surplus fixed C if soil nutrients were limiting for tree growth, but photosynthesis continued normally (Kannenberg and Phillips, 2017 ; Prescott *et al.*, 2020). In this sense, the higher root N concentrations suggest that soil N was not limiting for tree growth.

Our least productive clones (747210 and 915005) not only had thinner fine roots in the upper soil layer, but also higher root N compared with the most productive clone (DN2), suggesting higher root respiration rates, as thin fine roots rich in N usually have greater metabolic activity (Eissenstat, 1992 ; Makita *et al.*, 2009 ; Pregitzer *et al.*, 1998) and increased respiration rates (DesRochers *et al.*, 2002 ; Makita *et al.*, 2009). The increase in root respiration rates could increase C losses through root maintenance (Eissenstat, 1992 ; McCormack *et al.*, 2012). This could explain why clones with thinner and N-rich fine roots had slower growth rates, contrarily to our first hypothesis. Of all our fine root size categories, the fact that only the proportion in length of the very fine roots (D < 0.2 mm) showed a negative correlation with tree growth rate indicates that it could be these very fine roots that had the highest respiration rates, negatively impacting tree growth (Eissenstat, 1992 ; McCormack *et al.*, 2012 ; Pregitzer *et al.*, 1998). We also found negative relationships between tree growth rates and soluble compounds concentrations, also pointing in the direction of increased root respiration costs, as respiration rates often increase with the concentration of root soluble compounds (Atkin *et al.*, 2000 ; Lambers *et al.*, 2002).

The positive relationships between tree growth rate and fine root diameter, as well as the proportions in length of larger fine roots (0.2-1 mm and 1-2 mm), could reflect greater axial transport capacity of thicker fine roots through increasing stele diameter (cylinder of vascular tissues in the root center), crucial for allocating more nutrients to aboveground components of trees (Fitter, 1987 ; Jia *et al.*, 2013 ; Kong *et al.*, 2014). The positive effects of the 1-2 mm root class on tree growth rate nevertheless disappeared in deeper soil layers, possibly due to their lower nutrient uptake capacity and the low nutrients content of the subsoil (Jobbágy and Jackson, 2000 ; Rumpel and Kögel-Knabner, 2011). Thicker fine roots can penetrate soils more easily than thinner fine roots (Hodge *et al.*, 2009 ; Materechera *et al.*, 1992), thus facilitating the absorption of both mobile and less mobile nutrients. Furthermore, species or soil type in our experimental site could also be additional factors contributing to the inconsistency of our results with RES theory, as they can impact significantly root morphology (Materechera *et al.*, 1992 ; Tobner *et al.*, 2013). One limitation of this study is that we were unable to obtain the mass of each root size class (Root trait analysis section), and therefore unable to determine the tree growth rate-SRL relationship for each root size class.

2.6.2 Increased soil exploration by fine roots can promote tree growth rate

Root mass density (RMD) and RLD were highest in our most productive clone (DN2) and positively correlated with tree growth rate at the 0-20 cm depth, confirming our second hypothesis. The increase in these root architectural traits, in agreement with Bauhus and Messier (1999), underlines the relevance of soil exploration by fine roots to increase tree growth. Many studies in boreal and temperate forests showed that high RMD led to high aboveground growth rates, suggesting an increase in nutrients absorbed by fine roots through extended root surface area in contact with soils (Hansson *et al.*, 2013 ; Tschaplinski and Blake, 1989 ; Weemstra *et al.*, 2020). Additionally, great RLD could facilitate the access to less mobile nutrients in soils such as phosphorus (Bauhus and Messier, 1999 ; Ravenek *et al.*, 2016). Similarly, in a mature forest with larger trees, trees adjusted their fine roots by increasing the size of the root system (greater RMD and RLD) rather than by increasing acquisitive fine roots (higher SRL), to match the growing demand for belowground resources (Li *et al.*, 2019). Furthermore, the positive correlation between these traits (RMD and RLD) and tree growth rate could also indicate that fine root growth in terms of mass and length would require a significant transfer of C fixed by photosynthesis from aboveground biomass.

We noted that a positive relationship between root architectural traits and tree growth rate was only observed at the 0-20 cm depth, suggesting the importance of acquiring nutrients in the topsoil, where nutrients are usually more abundant. There was no relationship between tree growth rates and RMD and RLD in the subsoil (20-40 and 40-60 cm), likely because of the low nutrient concentration in these soil layers (Jobbágy and Jackson, 2000 ; Rumpel and Kögel-Knabner, 2011). However, the most productive clone (DN2) seemed to explore slightly more of the subsoil, with greater RMD and RLD compared to clone 915319, maybe acquiring non-negligible amounts of nutrients.

The genetic differences between clone parentage could be an important factor in the variations in RMD and RLD as the only clones which exhibited higher values of these traits (DN2 and 1079) were issued from a *P. deltoides* cross. The clones issued from *P. nigra* also had greater RMD and total root length than the clones derived from *P. tricocarpa* (Al Afas *et al.*, 2008), which corresponds to our observation of high RMD and RLD in clone DN2, issued from a cross between *P. deltoides* and *P. nigra*. The intensity of soil exploration, i.e., the mass or length of fine roots per unit volume of soil, appears to be species-specific and would represent an effective tree growth strategy in our fast-growing plantation.

Clone 915319 had lower RLD and RMD but higher root N concentration and root dry mass content (RDMC) compared with clone DN2 at the 0-20 cm depth, showing clear differences in their root traits even though both clones were the most productive and had similar fine root mean diameters. Therefore, they appear to have different growth strategies, where fine roots of clone 915319 contained less water but more N than those of the most productive clone (DN2) at the 0-20 cm depth. Higher N concentrations in fine roots of clone 915319 suggest that their fine root cells could contain greater amounts of proteins linked to higher root cellular activity including nutrient assimilation and transport (Jia *et al.*, 2013 ; Pregitzer *et al.*, 1998 ; Ryan *et al.*, 1996). Thus, the growth strategy of the most productive clone (DN2) could be to maximize the volume of soil explored (great RMD and RLD), while that of the second most productive clone (915319) to have fewer but more absorptive fine roots to acquire nutrients efficiently. However, further analyses of root anatomy and aboveground traits (net photosynthesis, phenology, specific leaf area) are needed to better explain the differing growth strategies. This study revealed other effective tree growth strategies that are more related to soil exploration by fine roots and may help understand why RES theory has not worked in other studies of fast-growing plantations. Our findings on the links between root traits and tree growth rate could help improve species selection and management of fast-growing trees.

2.7 Conclusion

Our study of a fast-growing plantation using various hybrid poplar clones revealed a different angle on the impact of fine root functional traits on tree growth rate. Surprisingly, the root economics spectrum theory did not align with our findings, as traits associated with resource acquisition (high SRL, thin fine roots) did not result in high tree growth rates. However, mean diameter of fine roots was positively related to tree growth rate, probably due to the extended lifespan and reduced respiration rates of these fine roots, decreasing root construction and maintenance costs, respectively. The thicker, more lignified fine roots observed in the most productive clones could also be the result of greater C assimilation during photosynthesis, with surplus C being transferred to roots. The strategy of enhancing soil exploration intensity linked with greater root mass density also proved effective in promoting tree growth within our plantation, where rapid tree growth was accompanied by substantial fine root growth in terms of diameter and mass to increase the root system size and nutrient acquisition. Extending this study to encompass lifespan and respiration rates of fine roots could provide further insights into relationships between tree growth rates and root traits.

2.8 Acknowledgements

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3. HOW DO FINE ROOT TRAITS OF FAST-GROWING TREES STABILIZE SOIL ORGANIC CARBON?

Ce chapitre sera soumis à la revue Plant and Soil

Toky Jeriniaina Rabearison [a,*], Vincent Poirier [b], Jérôme Laganière [c], Annie DesRochers [a]

[a] *Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 341 rue principale Nord, Amos, Québec J9T 2L8 , Canada*

[b] *Unité de recherche et de développement en agroalimentaire, Université Du Québec en Abitibi-Témiscamingue, 79, Rue Côté, Notre-Dame-du-Nord, Québec J0Z 3B0, Canada*

[c] *Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Québec, Qc G1V 4C7, Canada*

*Corresponding author: TokyJeriniaina.Rabearison@uqat.ca

3.1 Résumé

Le sol représente un réservoir de carbone organique (COS) plus important que la végétation terrestre, offrant un grand potentiel de réduction des conséquences négatives généralisées des changements climatiques. Dans les forêts et les plantations d'arbres, les racines fines ont un effet significatif sur la stabilisation du COS par leurs traits fonctionnels. Cependant, nous ne savons pas exactement quels traits chimiques (facilement décomposables ou récalcitrantes) et quels traits architecturaux de racines fines sont les plus propices à la stabilisation du COS. Nous avons eu pour objectif d'évaluer les effets des traits fonctionnels des racines sur le stockage et la stabilisation du COS. Nous avons étudié cinq clones de peupliers hybrides ayant différents traits racinaires situés à New Liskeard, ON, Canada et avons collecté des échantillons de sol et de racines fines (< 2 mm de diamètre) en utilisant des carottes de sol dans les profondeurs 0-20, 20-40 et 40-60 cm. Le COS a été fractionné en carbone organique particulaire (> 53 µm, COP) et en carbone organique associé aux minéraux (< 53 µm, COAM). Nous avons découvert que la densité en longueur des racines était le meilleur prédicteur de l'augmentation du stock de COS et du COAM parmi tous les traits racinaires. Les racines fines facilement décomposables (c'est-à-dire riches en azote (N) et en composés solubles, avec des ratios lignine/N et C/N plus faibles) étaient également positivement corrélées aux stocks de COS et aux COAM puisqu'elles pourraient être facilement consommées par les microorganismes du sol et favoriseraient l'adsorption des sous-produits microbiens sur les surfaces minérales. Ainsi, les traits racinaires qui augmentent le volume de sol exploré par les racines (densité en longueur élevée) et qui sont associés à des composés organiques facilement décomposables jouent un rôle clé dans la stabilisation du COS.

Mots-clés : carbone organique du sol, stabilisation du carbone, racines fines, trait racinaire, peuplier hybride, changements climatiques

3.2 Abstract

Soil represents a larger reservoir of soil organic carbon (SOC) than terrestrial vegetation, offering a great potential for reducing the widespread adverse consequences of climate change. In forests and tree plantations, fine roots significantly impact SOC stabilization through their functional traits. However, it is not obvious which fine root chemistry (easily decomposable or recalcitrant), and architecture is the most conducive to SOC stabilization. We aimed to assess the effects of root functional traits on SOC storage and stabilization. We studied five hybrid poplar clones with different root traits located in New Liskeard, ON, Canada and collected soil samples and fine roots (< 2 mm diameter) using soil cores at depths of 0-20, 20-40 and 40-60 cm. Soil organic carbon was separated into particulate organic carbon (> 53 μm, POC) and mineral-associated organic carbon (< 53 μm, MAOC) fractions. We found that root length density (RLD) was the best predictor of increased SOC stocks and MAOC among all root traits. Easily decomposed fine roots (i.e., rich in nitrogen (N) and soluble compounds and lower lignin/N and C/N ratios) were also positively correlated to SOC stocks and MAOC, as they could be readily consumed by soil microorganisms and enhance adsorption of microbial by-products onto mineral surfaces. Thus, root traits that increase the soil volume explored by fine roots (high RLD) and are associated with easily decomposed organic compounds play a key role in SOC stabilization.

Keywords: soil organic carbon, carbon stabilization, fine root, root trait, hybrid poplar, climate change

3.3 Introduction

Soils store three to four times more organic carbon (C) than terrestrial vegetation, acting as a major sink for atmospheric CO_2 (Lehmann and Kleber, 2015 ; Schmidt *et al.*, 2011). Increasing soil organic carbon (SOC) storage thus offers a great potential for reducing the widespread adverse consequences of climate change such as the high risk of extreme events (droughts and wildfire), increasing species losses in many ecosystems and reduced food security (IPCC, 2023). High SOC stocks additionally serve to improve soil fertility and structure, and hence crop or forest productivity (Lal *et al.*, 2015). In forests and tree plantations, litter, root turnover and exudates are the main source of inputs of SOC (Epron *et al.*, 2006 ; Martí-Roura *et al.*, 2019 ; Schmidt *et al.*, 2011). Numerous lines of evidence indicate that roots contribute to SOC to a greater extent than aboveground components, especially by being in close contact with soils (Ghafoor *et al.*, 2017 ; Rasse *et al.*, 2005). Fine roots, typically defined as absorptive roots with a diameter less than 2 mm, are especially linked to plant C allocation strategies, with 33 to 67 % of annual net primary production being allocated to fine roots in forest ecosystems (Matamala *et al.*, 2003 ; Sun *et al.*, 2017 ; Weemstra *et al.*, 2016). Thus, fine roots can significantly modulate SOC storage (Bardgett *et al.*, 2014).

Trait-based approaches have been proposed to improve our understanding of the fine root impacts on SOC storage and stabilization (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008). For instance, lignin-rich fine roots generally produce organic compounds with a low decomposition rate that could increase SOC stocks (Cambardella and Elliott, 1992 ; Poirier *et al.*, 2018b ; Wardle, 2004). These compounds are mainly from partially decomposed or persistent root fragments, form particulate organic C (POC) and could be more abundant in topsoils (Six *et al.*, 2002). They can be biochemically stabilized because of their selective preservation or recalcitrance (Balesdent, 1996 ; Golchin *et al.*, 1998 ; Six *et al.*, 2002). However, their long-term stabilization is uncertain as recalcitrant compounds like lignin appear to have slow degradation rates only at the early stage of decomposition, but their later degradation would occur at the same or higher rate as the overall litter decomposition (Gleixner *et al.*, 1999 ; Marschner *et al.*, 2008 ; Sollins *et al.*, 2006). Decomposition of recalcitrant compounds also requires high energy (more enzymatic reactions), increasing C losses during microbial respiration (Bahri *et al.*, 2008 ; Lehmann and Kleber, 2015 ; Marschner *et al.*, 2008).

Fine roots rich in N and soluble compounds, on the other hand, generally produce easily decomposed organic materials and are often considered not conducive to SOC storage since the C produced can quickly return to the atmosphere as CO_2 (Bardgett, 2017 ; Sun *et al.*, 2021 ; Wardle, 2004). High quality (i.e. easily decomposed) C such as root exudates can lead to an increase in microbial activity and a decrease in SOC stocks by accelerating the decomposition of new and old organic matter (OM) through a priming effect (Cheng *et al.*, 2014 ; Keiluweit *et al.*, 2015a). However, several studies argued that easily decomposed organic compounds would require low energy to be consumed by microorganisms, facilitating the accumulation of mineral-associated organic C (MAOC) through adsorption of the microbial biomass and necromass produced onto mineral and metal surfaces (Cotrufo *et al.*, 2013 ; Lehmann and Kleber, 2015 ; Schmidt *et al.*, 2011). This SOC stabilization mechanism is probably more dominant in deeper soil layers, where the mineral phase of soils is more present (Kaiser *et al.*, 2002 ; Rumpel and Kögel-Knabner, 2011). MAOC was recently recognized as being more stable in the long-term than POC (Cotrufo *et al.*, 2013 ; Poirier *et al.*, 2018b). For instance, fast-growing trees tend to produce labile and easily decomposed fine roots and preferentially accumulate C in MAOC, while slow-growing trees tend to release recalcitrant compounds (De Deyn *et al.*, 2008 ; Poirier *et al.*, 2018b ; Wardle, 2004). Thus, the study of hybrid poplar clones with different root traits could offer a great opportunity to test which fine root chemistry, easily decomposable or recalcitrant, are most conducive to SOC stabilization.

Fast-growing trees generally have high root mass density (RMD) and root length density (RLD), i.e., great fine root mass and length per unit soil volume, which improves soil exploration intensity and access to soil nutrients (Pérez-Harguindeguy *et al.*, 2013 ; Ravenek *et al.*, 2016 ; Stokes *et al.*, 2009). These root architectural traits expand the surface of fine roots in contact with the soil, which contributes to SOC storage through root turnover (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008). High RMD and RLD can also contribute to SOC stabilization through the occlusion mechanism in microaggregates (Ontl *et al.*, 2015). However, the direct relationship between RMD and RLD and the stabilization mechanism involving interactions with soil mineral phases (POC and MAOC) remains underexplored.

For morphological traits, fine roots with smaller diameters and higher SRL are likely to have fast turnover rates (Guo *et al.*, 2008 ; McCormack *et al.*, 2015), that might increase root litter inputs and SOC. Fine roots with high SRL could also produce easily decomposed and high-quality organic materials, leading to an accumulation of MAOC (Sun *et al.*, 2021 ; Xu *et al.*, 2021). Nevertheless, as argued by Poirier et al. (2018b), the impacts of morphological root traits are still unclear as the relationship between SRL and OM decomposition can also be negative (Hobbie *et al.*, 2010) or non-significant for trees or woody dicots (Aulen *et al.*, 2012 ; Roumet *et al.*, 2016). These inconsistencies could be explained by the fact that root traits exerting a significant impact on OM decomposition and SOC storage can vary between species belonging to different families (Roumet *et al.*, 2016). Here, we studied different hybrid poplar clones belonging to the same genus, which could help better understand the effects of root traits on SOC stabilization.

We aimed to assess the effects of chemical, architectural and morphological traits of fine roots on SOC storage and stabilization. Particulate size fractionation, a convenient approach for studying SOC stabilization, was used in this study to separate SOC into particulate organic C (> 53 µm, POC) and mineral-associated organic C (< 53 µm, MAOC) fractions (Samson *et al.*, 2020 ; Xu *et al.*, 2021). We first assumed that fine roots with higher N and soluble compounds concentrations would increase SOC stocks and MAOC as they would release easily decomposed organic compounds and facilitate the accumulation of microbial biomass and necromass. High root length and mass densities increase the soil volume explored by fine roots and would also contribute positively to SOC stocks. Finally, we also hypothesized that fine roots with great SRL and smaller diameter would produce easily decomposed root litter and consequently increase MAOC.

3.4 Materials and Methods

3.4.1 Site description

The experimental site is located at the New Liskeard Agricultural Research Station in North-Eastern Ontario, Canada (47°31′15″ N, 79°39′52″ W). The site consisted of a hybrid poplar plantation and was characterized by a Gleysol with clay loam texture (IUSS Working Group WRB, 2015 ; Rabearison *et al.*, 2023 ; Yan *et al.*, 2019). Climatic data from 1981 to 2010 classify the region as having a humid continental climate with an average daily temperature of 2.6°C and an average annual precipitation of 786 mm (576 mm rain and 222 cm snow) (Environment Canada, 2023). The regional surficial geology is marked by clays and lacustrine sands derived from post-glacial Barlow Lake (Rowe, 1972).

The plantation site preparation and experimental design were the same as in Rabearison et al. (2023). Briefly, one-year-old hybrid poplar rooted cuttings were planted in spring 2007 with a spacing of a 3.5 m × 3.5 m (816 stems ha^{-1}) and fertilized with NPK 18-23-18 (110 g $tree^{-1}$), at a rate of 89.76 kg ha^{-1}. The experimental design featured three replicate blocks, each containing eight monoclonal plots of 100 trees (10 rows × 10 trees) randomly distributed within blocks. From the eight originally planted clones, we selected five clones from diverse parentages with different root traits: 747210 (*P. balsamifera* × *P. trichocarpa*), 915005 (*P. balsamifera* × *P. maximowiczii*), 1079 *(Populus* × *jackii* (*P. balsamifera* × *P. deltoides*)), 915319 (*P. maximowiczii* × *P. balsamifera*) and DN2 (*P. deltoides* × *P. nigra*).

3.4.2 Soil sampling and preparation

Sampling was carried out when the plantation was 14 years old (2021). Soil sampling was conducted between two trees in a systematic way in each monoclonal plot. We collected soil cores at two distances (87.5 cm (quarter) and 175.0 cm (center)) from a stem and at three soil depths (0-20, 20-40 and 40-60 cm) using a PVC cylinder measuring 10 cm in diameter and 20 cm in length. We had 6 replicates (2 trees per block × 3 blocks) for each clone, distance and depth. This process resulted in a total of 180 soil cores (6 replicates × 2 distances × 3 soil depths × 5 clones), which were collected in plastic bags, stored in a cooler and brought to the laboratory for further analysis.

We initially broke each soil core into smaller pieces and carefully mixed them to ensure sample homogeneity. The pebbles were extracted, weighed and found to account for no more than 0.3 % of the soil mass in each sample. We then wet-weighed each soil sample and separated approximately 300 g of subsamples for soil analysis. The remaining portion of each soil sample, constituting around 85 % of the total mass, were also wet-weighed and stored in the refrigerator for root analysis. These wet masses were needed to calculate the adjusted soil volume required to determine SOC stocks and root architectural traits.

3.4.3 Soil analysis

Samples designated for soil analysis were air-dried and ground to 2 mm before analysis. To verify the presence of inorganic C in our samples, we took 10 g of 45 air-dried soil subsamples (one tree × one distance (center) × 3 soil depths × 5 clones × 3 blocks) to measure the average soil pH of the site. The pH of air-dried soils was measured in 20 mL of 0.01 M $CaCl_2$ with a pH meter (Hach Sension+ MM374). Mean soil pH for the 0-20, 20-40, and 40-60 cm depths were 6.9 (± 0.2), 7.4 (± 0.2), and 7.6 (± 0.1), respectively, indicating the likely presence of inorganic C in our samples. Accordingly, we distinguished organic C from inorganic C in our bulk soil samples in accordance Kreyling et al. (2013). Subsamples (5 g) underwent a 4.5-hour heating process in a muffle furnace at 450 °C to combust OC. Both heat-treated and non-heat-treated subsamples were then analyzed by dry combustion to obtain C and nitrogen (N) concentrations (Vario MAX cube; Elementar, Langenselbold, Germany). We considered the C in the non-heat-treated subsamples as total C and the C in the heat-treated subsamples as inorganic C. Organic C concentration was thus determined as the difference between total C concentration and inorganic C concentration.

Soil moisture content at 105 °C (72 h) was measured on another 10 g subsample to calculate the oven-dried mass of soil samples. Soil *bulk density* (g. cm^{-3}) was calculated using the Eq. 4 (Poeplau *et al.*, 2017), which is as follows:

$$Bulk\ density = (M_{sample} - M_{pebbles})/(V_{core} - \frac{M_{pebbles}}{\rho_{pebbles}}) \qquad \textbf{Eq. 4}$$

Where M_{sample} and $M_{pebbles}$ are the masses (g) of oven-dried samples and pebbles, respectively, V_{core} is the soil core volume (cm^3), and $\rho_{pebbles}$ which is equal to 2.6 g cm^{-3} is the approximate density of pebbles (Don *et al.*, 2007). Finally, we calculated *SOC stock* (Mg ha^{-1}) for each depth by using the Eq. 5 (Poeplau *et al.*, 2017), which is as follows:

$$SOC\ stock = SOC\ concentration \times bulk\ density \times d \times (1 - \delta) \times 0.1 \qquad \textbf{Eq. 5}$$

Where *SOC concentration* is the soil organic carbon concentration (g kg^{-1}), *d* is the depth (cm) and *δ* is the pebble volume fraction (%/100).

3.4.4 Soil fractionation

Particle-size fractionation involved another 10 g air-dried soil subsample, initially ground to 2 mm. Each 10 g subsample was placed into a 250 mL plastic bottle and agitated in distilled water with 10 glass beads (6 mm diameter) overnight under continuous and regular movement to completely disperse soils (Balesdent *et al.*, 1991 ; Poirier *et al.*, 2013). The soil samples were physically fractionated by wet sieving with distilled water and 53 µm sieve. The remaining soil fractions on the 53 µm sieve and those that passed through were collected in two separate beakers, corresponding to the particulate fraction (≥ 53 µm) and the fine fraction (< 53 µm) respectively. These fractions were oven-dried at 60°C for 48 hours and weighed. Soil samples were mainly composed of the fine fraction at around 96 % of total mass, whereas the particulate fraction was 4 %. The concentration of mineral-associated organic C ($MAOC_{concentration,}$ g kg^{-1} fraction), which represents organic C in the fine fraction, was determined using the same method as for SOC concentration in the bulk soil.

To take into account the distribution of the fine fraction in the bulk soil, we used the amount of *MAOC* (g kg^{-1} soil) in the entire study (d'Annunzio *et al.*, 2008), which were calculated as follows:

$$MAOC_{amount} = \frac{(MAOC_{concentration} \times M_{fine\,fraction})}{M_{soil}} \qquad \textbf{Eq. 6}$$

where *MAOC* $_{concentration}$ is the concentration of mineral-associated organic C (g kg^{-1} fraction) and M_{sol} and $M_{fine\ fraction}$ are the dry mass of the bulk soil used for fractionation and the fine fraction, respectively, using soil moisture content at 105 °C.

The amount of OC in the particulate fraction (POC, g kg^{-1} soil) was estimated by subtracting MAOC (g kg^{-1} soil) from SOC in the bulk soil (Cambardella and Elliott, 1992 ; Xu *et al.*, 2021). This approach of determining POC has been found to be more precise than direct analysis of OC retained by the sieve (Cambardella and Elliott, 1992) and has been adopted in many studies (Martins *et al.*, 2012 ; Samson *et al.*, 2020 ; Xu *et al.*, 2021).

3.4.5 Root analysis

Soil subsamples stored for root analysis were first soaked in water containing sodium hexametaphosphate (50 g L^{-1}) overnight to disperse soil particles adhering to the roots due to the clay loam texture of the soil (Yan *et al.*, 2019). We then washed and rinsed roots to completely remove soil particles using a root washer (Gillison's Variety Fabrication Inc., Benzonia, MI, USA) according to Smucker et al. (1982). The visual sorting process focused on retaining live and fine roots (2 mm diameter) of hybrid poplars for subsequent analysis. Live fine roots were distinguished by their flexibility and lighter color, while dead roots were characterized as fragile, darker color, and susceptibility to breaking. At the 40-60 cm depth, we were unable to collect enough roots from a soil core to conduct all root analyses, so we had to mix root samples from two trees of the same clone, the same distance and the same block at this depth. In total, 150 root samples were obtained, comprising of 60, 60, and 30 samples from the 0-20, 20-40 cm, and 40-60 cm depths, respectively.

Each washed root sample was evenly spread into a transparent tray measuring 20 × 25 cm and filled with deionized water to minimize overlap between roots. Average root diameter (D, mm), total root length (RL) and root volume were determined using a scanner at 400 dpi resolution (Epson Perfection V800; Epson, Ontario, Canada) and WinRhizo Pro 2019 software (Regent Instruments, Quebec, Canada). After the scanning process, root samples were then weighed and oven dried for 48 hours at 60°C to determine root dry mass (RDM). Specific root length (SRL, m g^{-1}) was calculated by dividing the total root length by RDM. Root tissue density (RTD, g cm^{-3}) was calculated as the ratio of RDM to root volume. Root mass density (RMD, g cm^{-3}) was obtained as the total root dry mass (RDM) divided by the soil volume where the roots were extracted. Root length density (RLD, cm cm^{-3}) was calculated by dividing the total root length by the soil volume.

Finally, we ground the dry root samples (60°C) to 2 mm with an ultra-centrifugal mill (ZM200, Retsch GmbH., Haan, Germany). Root carbon (RCC) and nitrogen (RNC) concentrations were analyzed by dry combustion (Vario MAX cube; Elementar, Langenselbold, Germany). Water-soluble compounds, hemicellulose, cellulose and lignin concentrations (mg g^{-1}) of fine roots were determined by the method of Van Soest et al. (1991) using a fiber analyzer (Fibersac 24; Ankom, Macedon, NJ, USA).

3.4.6 Statistical analysis

All statistical tests and figures were performed using R software version 4.2.2 (R Development Core Team, 2013). Linear mixed models were used to assess the relationship between each root trait and SOC stock, MAOC or POC, where block was considered as random effect, using *lmer* function (lme4 and lmerTest packages, Bates et al., 2014; Kuznetsova et al., 2017). We first used data from both distances (87.5 cm (quarter) and 175.0 cm (center)) from a stem and all soil depths in the linear mixed models. The total number of observations was n = 150 for SOC and MAOC, while n = 113 for POC as we were unable to estimate the POC value for 37 soil samples mainly located at the 40-60 cm depth due to the very low percentages of particulate fraction (less than 4 %) and SOC concentrations at this depth. In linear mixed models, the marginal R^2 and the conditional R^2 respectively represent the variance explained by the fixed effects (trait) and the variance explained by the fixed (trait) and random effects (block); we used only the marginal R^2 (shown as R^2 in this study) as it only takes into account root trait effects (*r.squaredGLMM* function, MuMin package, Barton, 2009 ; Nakagawa and Schielzeth, 2013). Root traits were selected based on significant *P*-value ($P < 0.05$), R^2 closer to 1 (and arbitrarily greater than 0.20) and lowest AICc (Akaike Information Criterion) using *aictab* function and AICcmodavg package (Tables S1, S2 and S3). Subsequently, linear mixed models with two root traits as predictors were also performed to define the best models, using *lmer* and *aictab* functions, while avoiding collinear predictor variables (i.e. RMD and RLD, and fine root Lignin/N and C/N ratio). We also tested linear mixed models using data at each soil depth to determine specific effects of root traits at each soil depth. Model assumptions (independence of residuals, equality of variance (homoscedasticity), and normality of residuals) were determined by diagnostic graphs and Shapiro-Wilk tests and logarithmic transformations were applied to RMD and RLD variables to meet assumptions.

3.5 Results

3.5.1 Soil organic carbon stock and root traits

Increasing root length density (RLD) ($P < 0.001$) and decreasing root lignin/N ratio ($P < 0.001$) had the largest positive impact on SOC stocks when data from both distances and all soil depths were included in the analysis ($R^2 = 0.81$, Figure 15 and Tableau 5). SOC stock also increased strongly with root mass density (RMD) ($R^2 = 0.73$, $P < 0.001$, Figure 16a). For chemical traits, root soluble compounds ($R^2 = 0.27$) and N ($R^2 = 0.24$) concentrations had positive relationships with SOC stocks ($P < 0.001$ for both traits, Figure 17ab). However, fine root C/N ratio was negatively correlated with SOC stock ($R^2 = 0.25$, $P < 0.001$, Figure 16b). Root lignin concentrations were not related to SOC stocks (Tableau S4). Specific root length (SRL) had a significant correlation with SOC stock, but with $R^2 = 0.08$ when data from both distances and all soil depths were included in the analysis (Tableau S4).

At the 0-20 cm depth, root tissue density (RTD) was negatively correlated to SOC stock for soil samples located 87.5 cm from a stem ($R^2 = 0.24$, $P < 0.01$, Tableau 5).

In addition, RLD was positively linked to SOC stock for soil samples located at the 20-40 cm depth and 175 cm from a stem ($R^2 = 0.24$, $P < 0.01$, Tableau 5).

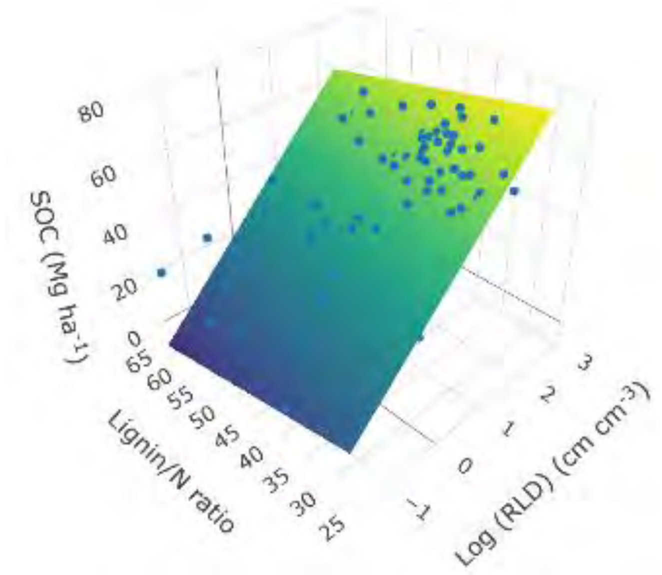

Figure 15
Relationship between soil organic carbon (SOC) and root length density (RLD) and root lignin/N ratio. Data include soil samples from both distances (87.5 cm and 175.0 cm) from a stem and all soil depths (n=150). See Tableau 5 for model details (equation, P and R^2).

Tableau 5
Best models describing relationships between root traits and soil organic carbon (SOC).

Soil depth	Distance from a stem	n	Model	*P*	R^2
All depths	Both distances	150	SOC = 46.52 + 19.05 × Log_e (RLD) – 0.43 × (Lignin/N)	RLD: < 0.001; Lignin/N: < 0.001	0.81
0-20	87.5 cm (Quarter)	30	SOC = 80.20 – 51.22× (RTD)	< 0.01	0.24
20-40	175.0 cm (center)	30	SOC = 11.12 + 8.62 × (RLD)	< 0.01	0.24

SOC: soil organic C, RLD: root length density, Lignin/N: root lignin/nitrogen ratio, RTD: root tissue density

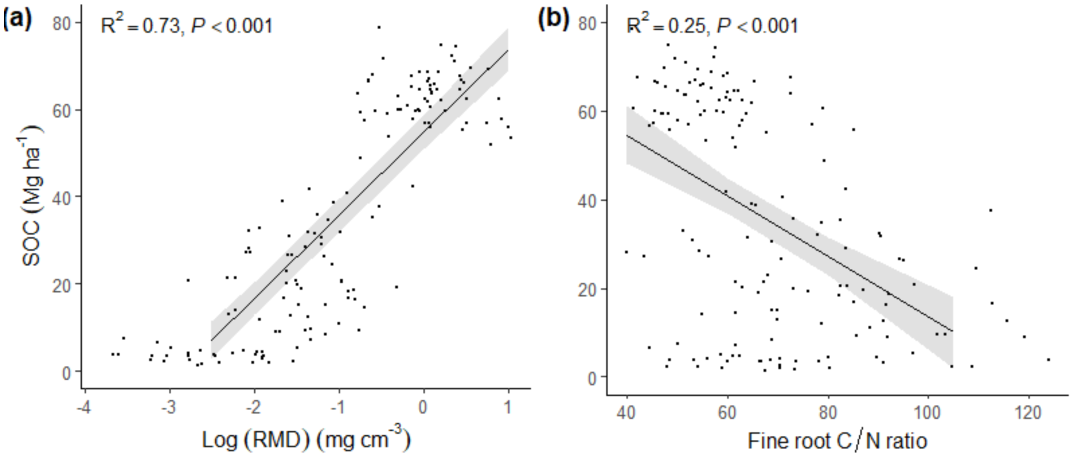

Figure 16
Relationships between soil organic carbon (SOC) and root mass density (RMD) (a) or fine root C/N ratio (b). Data include soil samples from both distances (87.5 cm and 175.0 cm) from a stem and all soil depths (n=150). Shaded areas represent the 95% confidence intervals. Note that log-transformed data are presented here for RMD.

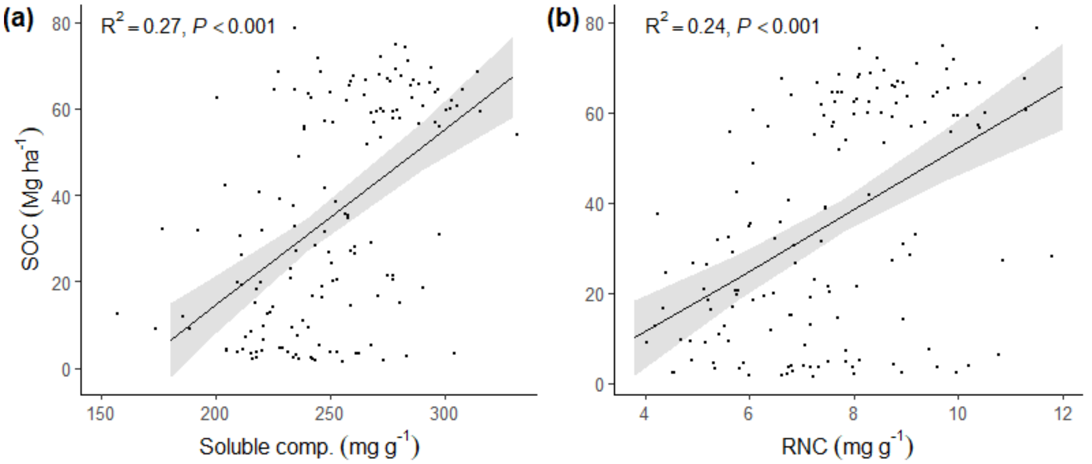

Figure 17
Relationships between soil organic carbon (SOC) and root soluble compounds (Soluble comp.) (a) and nitrogen concentrations (RNC) (b). Data include soil samples from both distances (87.5 cm and 175.0 cm) from a stem and all soil depths (n=150). Shaded areas represent the 95% confidence intervals.

3.5.2 Organic carbon amount in each soil fraction

A higher amount of mineral-associated organic C (MAOC) was linked to increasing RLD ($P < 0.001$) and decreasing root lignin/N ($P < 0.001$) when soil samples from both distances and all soil depths were considered ($R^2 = 0.82$, Figure 18a and Tableau 6). MAOC also had strong and positive associations with RMD ($R^2 = 0.72$, $P < 0.001$, Figure 19a). In addition, root soluble compounds ($R^2 = 0.29$) and N ($R^2 = 0.25$) concentrations were positively correlated with MAOC for chemical root traits ($P < 0.001$ for both traits, Figure 20ab). However, fine root C/N ratio had negative relationships with MAOC ($R^2 = 0.26$, $P < 0.001$, Figure 19b). At the 20-40 cm depth, positive correlations between MAOC and RLD were observed for soil samples collected 175.0 cm from a stem ($R^2 = 0.28$, $P < 0.01$, Tableau 6).

Particulate organic C (POC) increased with increasing RLD ($P < 0.001$) and decreasing root lignin/N ($P < 0.05$), but the correlation ($R^2 = 0.69$) was less strong than that of MAOC (Figure 18b and Tableau 6). POC was also positively correlated with RMD ($R^2 = 0.62$, $P < 0.001$), with root soluble compounds ($R^2 = 0.26$, $P < 0.001$) and N ($R^2 = 0.19$, $P < 0.001$) concentrations (Figures 19a and 20ab). In contrast, POC was negatively correlated with fine root C/N ratio ($R^2 = 0.22$, $P < 0.001$, Figure 19b). There was no relationship between root lignin concentration and POC when data from both distances and all soil depths were included (Tableau S6). At the 0-20 cm depth, POC had positive relationship with RLD for soil samples collected 175.0 cm from a stem ($R^2 = 0.27$, $P < 0.01$, Tableau 6).

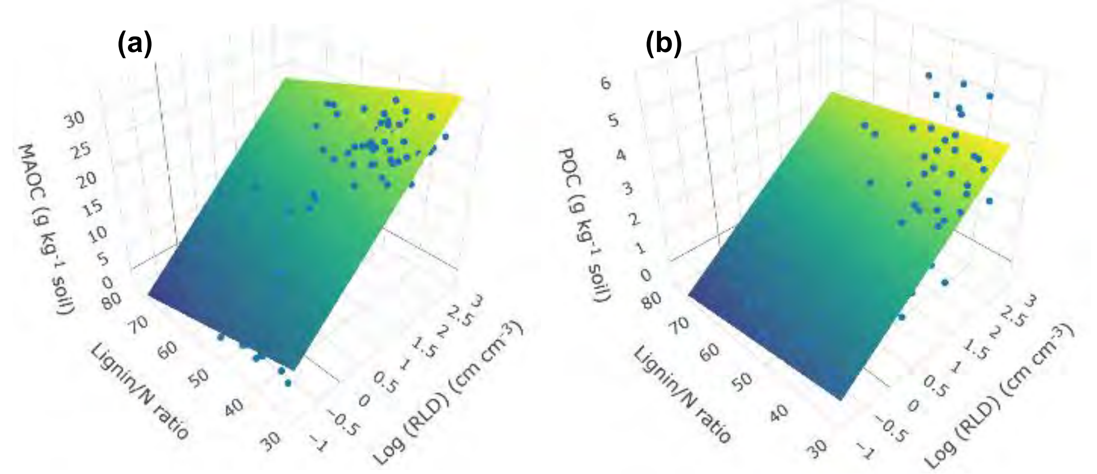

Figure 18
Relationships between mineral-associated organic C (MAOC) (a) or particulate organic C (POC) (b) and root length density (RLD) and root lignin/N ratio. Data included samples from both distances from a stem and all soil depths (n=150 for MAOC and n = 113 for POC). See Tableau 6 for model details (equation, *P* and R^2).

Tableau 6
Best models describing relationships between root traits and organic carbon in each soil fractions.

Soil depth	**Distance from a stem**	**n**	**Model**	***P***	**R^2**
All depths	Both distances	150	MAOC = 20.76 + 8.41 × Log$_e$ (RLD) – 0.21 × (Lignin/N)	RLD: < 0.001; Lignin/N: < 0.001	0.82
20-40	175.0 cm (center)	30	MAOC = 3.74 + 4.20× (RLD)	< 0.01	0.28
All depth	Both distances	113	POC= 1.90 + 1.32× Log$_e$ (RLD) – 0.02 × (Lignin/N)	RLD: < 0.001; Lignin/N: < 0.05	0.69
0-20	175.0 cm (center)	30	POC= 2.01 + 0.25 × (RLD)	< 0.01	0.27

MAOC: mineral-associated organic C, POC: particulate organic C, RLD: root length density, Lignin/N: root lignin/nitrogen ratio

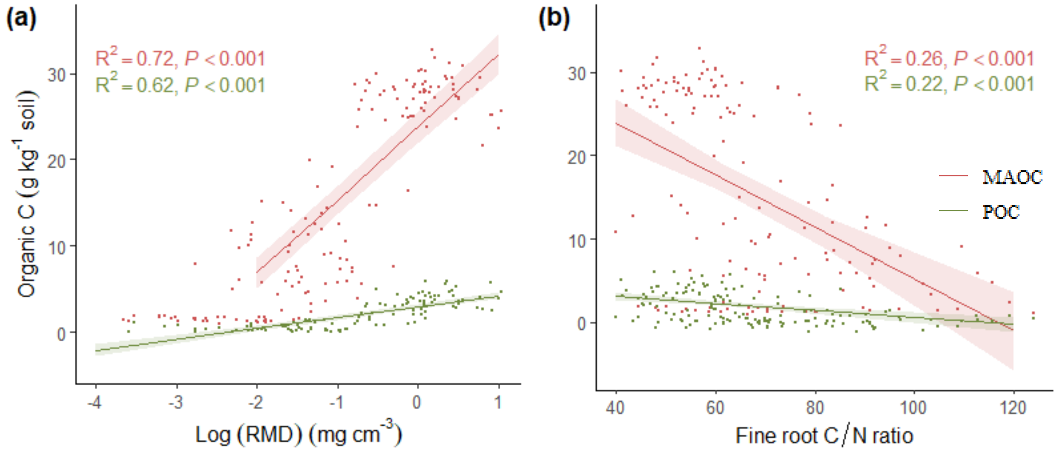

Figure 19
Relationships between mineral-associated organic C (MAOC) or particulate organic C (POC) and root mass density (RMD) (a) or fine root C/N ratio (b). Data included samples from both distances from a stem and all soil depths (n=150 for MAOC and n = 113 for POC). Shaded areas represent the 95% confidence intervals. Note that log-transformed data are presented here for RMD.

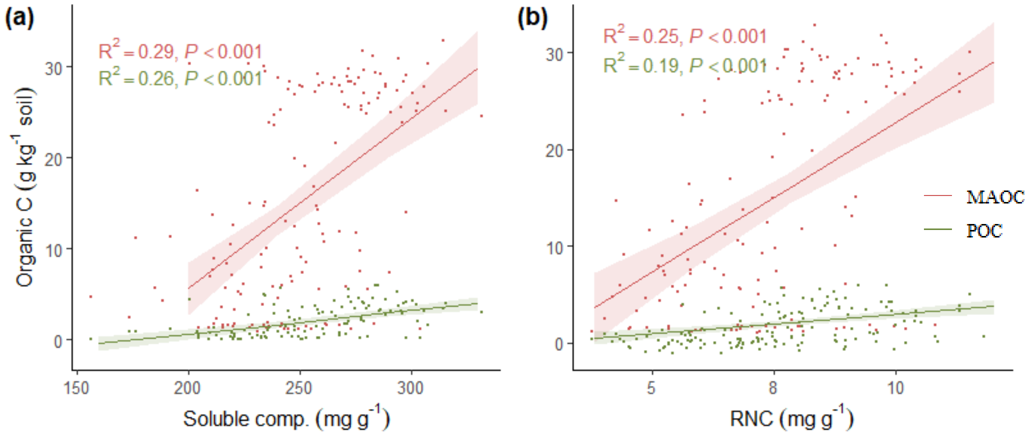

Figure 20
Relationships between mineral-associated organic C (MAOC) or particulate organic C (POC) and root soluble compounds (Soluble comp.) (a) or nitrogen concentrations (RNC) (b). Data included samples from both distances from a stem and all soil depths (n=150 for MAOC and n=113 for POC). Shaded areas represent the 95% confidence intervals.

3.6 Discussion

3.6.1 Root architectural traits as the best predictors of SOC storage and stabilization

Root length density (RLD) was the best predictor of SOC storage of all root traits in our study. In line with our second hypothesis, we demonstrated robust and positive relationships between root architectural traits (RLD and RMD) and SOC stocks, as they indicate a high soil volume explored by fine roots, i.e. an increased root surface area in contact with soils (Pérez-Harguindeguy *et al.*, 2013). This increase probably enhances the quantity of root exudates and turnover released into soils (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008), which could explain the observed rise in SOC stocks. Looking specifically at each depth, RLD effect was mainly observed at the 20-40 cm depth, suggesting the importance of fine roots with high RLD as substantial sources of OM in deeper soil layers (Rumpel and Kögesl-Knabner, 2011). Furthermore, high RMD could also reflect high root production, leading to increased C inputs to soils, and explaining the increase in SOC (Liu *et al.*, 2022).

RLD had the greatest positive correlations with both mineral-associated organic C (MAOC) and particulate organic C (POC), followed by RMD, but the correlations were stronger for MAOC than for POC. Fine roots with higher RLD and RMD included both smaller N-rich and larger lignin-rich fine roots. In this sense, high RLD and RMD could be associated not only with increased labile organic materials (root exudates), ensuring the formation of MAOC (Cotrufo *et al.*, 2013 ; Liang *et al.*, 2017 ; Xu *et al.*, 2021), but also with release of variously decomposed root fragments, contributing more to POC (Bardgett *et al.*, 2014 ; De Deyn *et al.*, 2008 ; Golchin *et al.*, 1998). However, as 96 % of our soil consisted of fine fractions, C from fine roots were mainly released into the soil fine fraction, which can explain the strong relationship for MAOC compared to that for POC.

3.6.2 How easily decomposable versus recalcitrant fine roots impact SOC storage and stabilization?

Supporting our hypothesis, we found positive correlations between root N and soluble compounds concentrations and SOC stock, as well as mineral-associated organic C (MAOC). These results aligned with Beidler et al. (2023) and suggested that fine roots with these traits released a large amount of OM into the bulk soil and soil fine fraction. First, fine roots rich in N and soluble compounds are more easily decomposable and can be efficiently consumed by soil microbes, i.e., less C lost through microbial respiration (Cotrufo *et al.*, 2013 ; Roller and Schmidt, 2015 ; Shao *et al.*, 2019). C produced through this microbial anabolism is likely to become less preferable compounds for microorganisms to consume (Liang *et al.*, 2017), which can explain the increase in SOC stock. Secondly, microbial biomass and necromasss produced could also readily be adsorbed onto mineral and metal surfaces, leading to the formation of stable organo-mineral complexes or MAOC (Cotrufo *et al.*, 2013 ; Lavallee *et al.*, 2020 ; Xu *et al.*, 2021). In addition, N-rich fine roots probably release a large amount of root exudates (labile compounds) in tree species (Sun *et al.*, 2017, 2021), also explaining the increase in SOC stocks and MAOC in our study. N-rich organic compounds are also characterized by a strong affinity with clay particles and can play a key role in binding to mineral surfaces in our site (Knicker, 2011). Thus, as we found no effect of root lignin concentrations on SOC stocks and MAOC, only easily decomposable fine roots positively impacted SOC stabilization in our plantation.

The negative relationships between lignin/N and C/N ratios of fine roots and SOC stock and MAOC also suggest that easily decomposed compounds enhance SOC and MAOC accumulation, as lower values of these two ratios indicate faster degradation rates of fine roots (Berg *et al.*, 1998 ; McCormack *et al.*, 2012 ; Yu *et al.*, 2019). However, lignin/N ratio had a stronger relationship with SOC and MAOC than C/N ratio, suggesting that lignin/N ratio is a better predictor of root decomposability than C/N ratio (Roumet *et al.*, 2016). Lignin, known for its resistance to enzymatic attack, limits OM decomposition rates, while high N is an essential for the microorganism metabolism and facilitates decomposition (Berg and McClaugherty, 2008 ; Roumet *et al.*, 2016).

We found that particulate organic C (POC) also increased with root N and soluble compounds concentrations, although the relationship was weaker than that of MAOC. Consequently, fine roots rich in N and soluble compounds also accumulated organic matter in POC, such as the remains of fine roots fragments that are still partially decomposed. The microbial necromass produced after decomposition of fine roots rich in N and soluble compounds could also be incorporated into POC if not adsorbed in soil minerals or occluded in aggregates (Li *et al.*, 2023). However, this hypothesis needs to be verified by further measurements of microbial necromass. In addition, our results did not align with some studies that found that increased POC was associated with lignin-rich fine roots (Golchin *et al.*, 1998 ; Six *et al.*, 2002) probably due to the low proportion of particulate fraction in our soils, not facilitating C accumulation in this fraction.

Our expectations linking morphological traits and SOC were not confirmed by our results as we found either very weak correlations or no relationship between specific root length (SRL) or fine root diameter and MAOC (Tableau S5). This could be explained by the fact that root morphological traits do not consistently relate to OM decomposition (Aulen *et al.*, 2012 ; Roumet *et al.*, 2016), whereas the latter seems to be a crucial mechanism for MAOC accumulation in our fast-growing plantation. Nevertheless, we found negative correlations between root tissue density (RTD) and SOC stock at the 0-20 cm depth, indicating that fine roots with great RTD released less organic C in the upper soil layers. Increasing RTD suggests an extension in fine root lifespan and a reduction in root decomposition rates (Eissenstat and Yanai, 1997 ; Roumet *et al.*, 2006 ; Ryser, 1996), reducing root turnover and C transferred into the bulk soil. According to Sun et al. (2021), fine roots of trees with high RTD were also associated with a low amount of root exudates, explaining the reduced SOC stock.

3.7 Conclusion

Our research on a hybrid poplar plantation with multiple clones reveals the important effect of root functional traits on SOC storage and stabilization. Despite perceptions suggesting that easily decomposed fine roots reduced SOC stock, we found the opposite to be true. Soil organic C stocks increased with higher root N and soluble compounds concentrations, as well as lower root lignin/N and C/N ratios. Mineral-associated organic C also increased with these easily decomposed fine roots, indicating an increase in SOC stabilization. Easily decomposable compounds are efficiently consumed by soil microbes, facilitating the interaction of microbial by-products (biomass and necromass) with soil mineral phase and the MAOC accumulation. In addition, our results highlight the importance of associating these fine root traits with root architectural traits to ensure substantial soil C inputs. Greater RLD and RMD increase the soil volume explored by fine roots, probably increasing the transfer of organic material into soils. These increases in RLD and RMD also enhanced MAOC, which is long-term stable. Fine roots with great RLD also proved to be important sources of OM in deeper soil layers.

3.8 Acknowledgements

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CONCLUSION GÉNÉRALE

Cette thèse a contribué à mettre en lumière les mécanismes par lesquels les arbres à croissance rapide peuvent contribuer au stockage et à la stabilisation du carbone organique du sol (COS) et par conséquent à l'atténuation des changements climatiques. Nous avons examiné les impacts de la composante aérienne des arbres par le taux de croissance sur ce stockage de COS et ceux de la composante souterraine, avec un accent particulier sur les racines fines. Cette thèse a également permis de mieux comprendre les effets des traits racinaires sur la croissance des arbres, dans le but d'améliorer la gestion et la sélection d'espèces pour établir des plantations à croissance rapide.

Stockage du COS et taux de croissance des arbres. L'étude de clones de peupliers hybrides ayant différents taux de croissance nous a permis de déterminer la relation entre le stock de COS et le taux de croissance des arbres (Chapitre 1). Contrairement à notre hypothèse, nos résultats ont révélé qu'il n'y avait pas de relation significative entre le stock de COS dans les 60 premiers cm du sol et le taux de croissance des arbres. Néanmoins, l'identité du clone a eu des effets significatifs sur ce stockage, avec les clones à productivité moyenne (1079 et 915005) stockant plus de COS que le clone le plus productif (DN2). L'augmentation des apports de litière provenant de la biomasse aérienne ne conduit donc pas nécessairement à un stock plus élevé de COS. Le faible stock de COS chez le clone le plus productif pourrait être dû à une décomposition rapide de la litière aérienne ou par un 'priming effect' de la matière organique du sol (Lajtha *et al.*, 2018). Par conséquent, outre le taux de croissance des arbres, la qualité de la matière organique, représentée par son taux de décomposition, est également un facteur à considérer pour déterminer le stockage du COS.

Il convient de noter que le clone le moins productif (747210) stockait également moins de COS dans la profondeur de 0 à 60 cm. Ce clone transférerait alors moins de litière provenant de sa partie aérienne, ce qui a diminué le stock de COS. Par conséquent, il semble que le taux de croissance des arbres reste quand même un facteur déterminant pour le stockage du COS. Nous soulignons l'importance de la sélection des clones/espèces qui ont des taux de croissance aérienne assez élevés et des pertes de C plus faibles lors de la décomposition de la matière organique. De nombreux autres facteurs, tels que les modes d'utilisation antérieurs des terres, le type de sol, les conditions climatiques, la densité de plantation et la présence des végétations adventices, doivent être également pris en considération lorsque nous utilisons des plantations à croissance rapide.

Stockage du COS et traits architecturaux des racines fines. Les résultats du Chapitre 1 ont suggéré un rôle significatif des racines dans le stockage du COS puisque les différences de stocks de COS entre les clones ont été principalement observées dans la profondeur 20-40 cm. Les densités en masse et en longueur des racines fines étaient les meilleurs prédicteurs du stock de COS, avec des corrélations positives robustes (Chapitre 3). Ces traits architecturaux indiquent une augmentation du volume du sol exploré par les racines et de la surface racinaire en contact avec le sol, ce qui accroitrait probablement la quantité d'exsudats et le renouvellement (*turnover*) racinaire. Ainsi, les racines fines capables d'explorer un plus grand volume du sol sont des sources importantes de matière organique, notamment dans les horizons plus profonds du sol.

Les clones DN2 et 1079 sont les peupliers hybrides qui ont eu des densités en masse et en longueur élevées parmi tous les clones (Chapitre 2). Pour le cas du clone DN2, les densités en masse et en longueur élevées n'étaient pas suffisantes pour stocker davantage de COS. En revanche, ces traits ont augmenté le stock de COS pour le clone 1079 puisqu'ils étaient associés à des racines riches en N et composés solubles. Nous avons ainsi souligné l'importance de choisir des arbres ayant en même temps des densités en masse et en longueur élevées de racines et des racines facilement décomposables (voir section suivante) pour assurer un stockage élevé du COS (Chapitre 3).

Stockage du COS et chimie des racines (facilement décomposables versus récalcitrantes). Nous avons présumé dans le Chapitre 1 que le stock élevé de COS chez les clones à productivité moyenne (1079 et 915005) serait dû à des racines plus riches en composés récalcitrants (C et lignine) et plus difficiles à décomposer que celles du clone le plus productif (DN2) (Wardle, 2004). En revanche, les résultats de notre Chapitre 2 ont révélé le contraire puisque les racines fines de ces clones à productivité moyenne présentaient des concentrations plus élevées en N, mais plus faibles en C et en lignine par rapport à celles du clone DN2. Par conséquent, le stockage élevé de COS dans les clones à productivité moyenne a été favorisé par des racines facilement décomposables, mais pas par des racines récalcitrantes ou difficilement décomposables.

Notre Chapitre 3 a confirmé la corrélation positive entre les concentrations en N et en composés solubles dans les racines fines et le stock de COS. Les racines fines riches en N et en composés solubles peuvent être consommées efficacement par les microorganismes du sol, réduisant le C perdu pendant la respiration microbienne. Par ailleurs, la corrélation négative entre les ratios lignine/N et C/N des racines fines et le stock de COS suggérait également l'effet positif des racines facilement décomposables sur le stock de COS. Seule la densité tissulaire des racines présentait une corrélation suffisamment évidente avec le stock de COS parmi tous les traits morphologiques de racines fines. Nous avons trouvé des corrélations négatives entre la densité tissulaire des racines et le stock de COS, indiquant que les racines fines ayant une densité tissulaire élevée libéraient moins de C dans le sol. L'augmentation de la densité tissulaire des racines suggère une prolongation de la durée de vie des racines fines et une réduction du taux de décomposition des racines (Eissenstat et Yanai, 1997 ; Roumet *et al.*, 2006 ; Ryser, 1996), réduisant ainsi le renouvellement des racines et le transfert du C dans le sol.

Stabilisation du COS et traits racinaires. Le fractionnement par taille du sol nous a permis de mieux étudier la relation entre traits racinaires et stabilisation du COS. Les traits architecturaux de racines ont eu des effets positifs considérables sur le C organique associé aux minéraux (COAM) et le C organique particulaire (COP). Les racines fines ayant des densités en masse et en longueur élevées comprenaient à la fois des racines plus petites et plus riches en N et des racines plus épaisses et plus riches en lignine, assurant le transfert de C organique dans ces deux fractions du sol. Les traits architecturaux des racines fines des arbres à croissance rapide jouent donc un rôle important les mécanismes de stabilisation du COS. Nous avons également trouvé que les racines fines facilement décomposables (riches en N et en composés solubles et ayant de faibles ratios C/N et lignine/N) ont également augmenté le COAM. Cependant, nous n’avons trouvé aucun effet de la lignine des racines fines sur le COAM ou sur COP. Ainsi, entre les racines facilement décomposables et récalcitrantes, seules les racines facilement décomposables favorisaient la stabilisation du COS dans notre plantation.

Traits racinaires et taux de croissance des arbres. Nous avons examiné les effets des traits racinaires sur le taux de croissance des arbres en utilisant des espèces phylogénétiquement proches, c’est-à-dire des clones de peupliers hybrides (Chapitre 2). Pour mieux étudier ces effets des traits racinaires, les racines fines ont été séparées en trois classes de diamètre. Contrairement à la théorie du spectre économique racinaire, nous avons trouvé que les racines fines présentant une SRL et des concentrations en N et en composés solubles élevées étaient associées à un faible taux de croissance des arbres, tandis que les racines fines plus grosses étaient liées à un taux de croissance élevé des arbres. D’une part, nous avons argumenté que les racines fines plus grosses étaient plus avantageuses pour la croissance des arbres, probablement grâce à la réduction des coûts de construction et du taux de respiration des racines fines et de leur pénétration plus facile dans le sol comparées aux racines fines plus petites. Par conséquent, la croissance des arbres et l’acquisition de nutriments dans le sol ne nécessitent pas toujours des traits racinaires *a priori* « acquisitifs », mais peuvent également être favorisées par des racines fines plus grosses. D’autre part, le taux de croissance pourrait également avoir influencé les traits racinaires. En effet, le taux de croissance aérienne plus élevé des arbres pourrait résulter d’une plus grande assimilation de C lors de la photosynthèse et à un surplus de C transféré aux racines, expliquant une proportion de racines fines plus épaisses et lignifiées plus grande chez les clones les plus productifs. La relation de causalité entre les traits racinaires et le taux de croissance des arbres pourrait donc être bidirectionnelle dans cette étude.

La densité en masse des racines dans la profondeur 0-20 cm était positivement associée au taux de croissance aérienne des arbres. L’augmentation de la densité en masse des racines élargit la surface racinaire en contact du sol, facilitant l’accès aux nutriments mobiles et moins mobiles du sol. La stratégie consistant à augmenter l’intensité l’exploration du sol, liée à une densité plus élevée en masse des racines s’est avérée efficace pour assurer la croissance des arbres dans notre plantation.

Les seuls clones (DN2 et 1079) ayant des densités en masse et en longueur élevées des racines fines dans notre étude sont issus du croisement avec *P. deltoides*. Selon Al Afas et al. (2008), les clones issus du croisement avec *P. nigra* présentaient également une densité en masse plus élevée de racines, ce qui est similaire à notre résultat pour le clone DN2 issu du croisement entre *P. deltoides* et *P. nigra*. Par conséquent, les traits racinaires dépendraient également de la génétique des clones de peupliers hybrides. De plus, même si les clones 915219 et DN2 étaient tous les deux les plus productifs, le clone 915319 a eu des densités en masse et en longueur de racines fines plus faibles, mais une concentration plus élevée en N comparé au clone DN2. Ainsi, plusieurs traits racinaires seraient spécifiques à chaque espèce et cette spécificité pourrait engendrer des stratégies de croissance très contrastées entre les espèces.

Implications. Chez nos clones de peuplier hybride, les clones 915005 et 1079, qui ont stocké plus de C organique dans le sol, seraient donc plus recommandés si la gestion des plantations avait pour but de contribuer à l’atténuation des changements climatiques. Au niveau des traits racinaires, il serait important de sélectionner des espèces d'arbres dont les racines sont capables d'explorer un plus grand volume de sol et sont facilement décomposables pour augmenter la stabilisation à long terme du COS. Comparées aux plantations de résineux, les plantations à croissance rapide utilisant des feuillus ont généralement des racines plus faciles à décomposer, les rendant potentiellement plus favorables à la stabilisation à long terme du COS. Par conséquent, la considération des plantations à croissance rapide dans le cadre de l'initiative internationale "4 pour 1000" nécessite plus d'approfondissement. Dans ce sens, il est également important de considérer d'autres variables comme la structure et la texture du sol, l'utilisation antérieure des terres et l'espèce.

Par ailleurs, les arbres ou clones ayant une stratégie d'exploration du sol (densité en masse élevée de racines) et des racines fines plus épaisses (clones DN2 et 915319) seraient plus pertinents si l'objectif d'aménagement était la production de bois. Ces clones plus productifs ont alloué davantage de C tant dans les parties aériennes et souterraines que les clones moins de productifs. Nous recommandons également des sols bien structurés et peu compacts qui facilitent l'exploration du sol par les racines fines et l'acquisition de nutriments.

Limites et perspectives. Dans notre étude, les effets du taux de croissance aérienne des arbres et des traits racinaires sur le stock de COS ont été examinés en utilisant des clones de peuplier hybride présentant différents taux de croissance, mais qui sont tous des arbres à croissance rapide. Pour élargir le champ de recherche, il serait pertinent d'augmenter le nombre de clones/espèces de peupliers ou d'inclure des espèces à croissance lente afin d'obtenir une gamme plus large de taux de croissance. Il est essentiel de noter que les feuillus ont généralement des traits aériens (feuilles, canopée) et racinaires très différents de ceux des conifères. Par conséquent, les futures études pourront utiliser exclusivement plusieurs espèces de conifères, ce qui aiderait à faire des comparaisons entre ces deux groupes (conifères et feuillus).

Les racines fines ont joué un rôle crucial dans le stockage du COS dans notre étude. Quant aux grosses racines, nous n'avons pas eu les moyens techniques et méthodologiques pour collecter leur biomasse dans notre plantation. Une évaluation des impacts de la biomasse racinaire totale sur le stockage du COS pourrait également être pertinente, puisque les racines plus grosses peuvent transférer davantage de matière organique dans le sol possiblement par la mortalité racinaire (Truax *et al.*, 2018). De plus, nous serions en mesure de déterminer si l'augmentation de la croissance aérienne des arbres impliquerait également une croissance racinaire significative. Par ailleurs, il serait également important d'évaluer les impacts de la litière de feuilles sur le stockage de COS afin de séparer les effets de la litière des feuilles de ceux des racines.

Plusieurs traits racinaires qui ont des impacts positifs sur le COS dans notre étude sont associés à un renouvellement rapide de racines et des exsudats racinaires plus importants. Ces deux variables racinaires n'ont pas été analysées dans notre étude, bien qu'elles soient directement liées au stockage du COS. Par conséquent, la considération de ces variables racinaires serait également une piste à explorer dans les futures études pour mieux comprendre la relation entre traits racinaires et stockage et stabilisation du COS.

Les résultats de notre Chapitre 2 suggèrent des relations potentielles entre le taux de croissance de l'arbre et la durée de vie et le taux de respiration des racines fines. Ces deux dernières variables racinaires n'ont pas été déterminées dans cette thèse. La recherche future pourrait donc inclure ces deux traits pour approfondir la compréhension des effets des traits fonctionnels de racines fines sur la croissance des arbres. En outre, une des limites de notre Chapitre 2 a été que nous n'avons pas pu obtenir la masse de chaque classe de taille de racines fines puisqu'il n'a pas été possible de séparer et de peser manuellement les différentes classes de taille de racines fines. Par conséquent, nous n'avons pas pu déterminer la relation entre le taux de croissance des arbres et la SRL pour chaque classe de taille de racines fines. Une des solutions consisterait à recatégoriser les racines fines en deux classes (0-1 mm et 1-2 mm), facilitant la séparation de ces deux nouvelles classes. La perspective d'intégrer les traits de la composante aérienne (photosynthèse nette, phénologie, surface foliaire) serait également très pertinente pour avoir un aperçu global des facteurs favorisant le taux de croissance des arbres.

Par ailleurs, comme l’interaction des sous-produits microbiens avec la phase minérale du sol serait un mécanisme important de stabilisation du COS chez les plantations à croissance rapide, il serait alors intéressant d’étudier l’impact du microbiome du sol sur le stockage et la stabilisation du COS en lien avec les traits racinaires. Dans ce sens, les futures études pourront spécifier le rôle des fonctions microbiennes (les champignons mycorhiziens et saprotrophes et les bactéries copiotrophes et oligotrophes) sur le stockage et la stabilisation du COS.

ANNEXE A – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 2

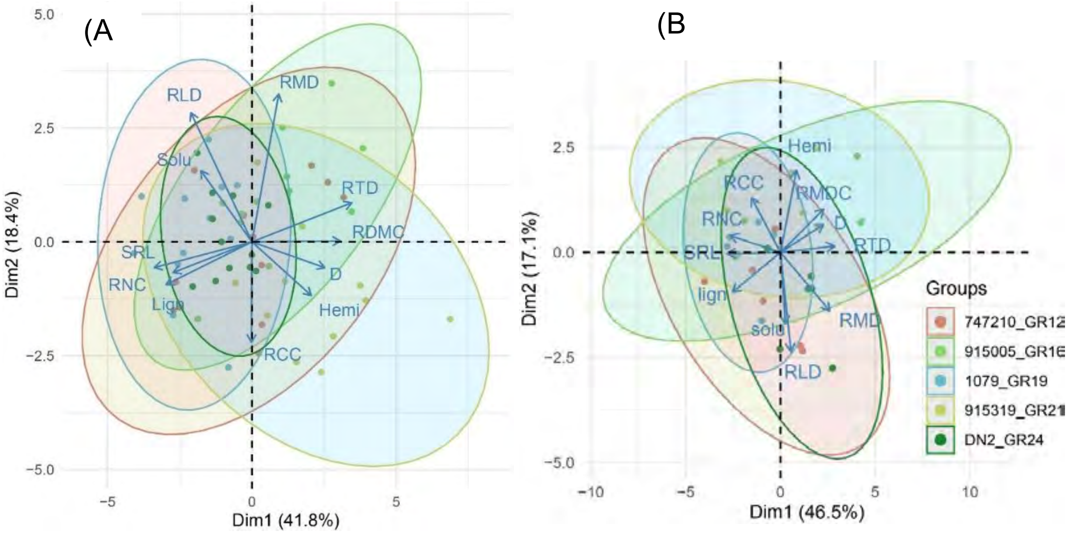

Figure S1
PCA of fine-root traits at 20-40 (A) and 40-60 cm (B) depths. Each color represents one clone that is labeled with its parentage coding and growth rate (GR). D: average root diameter, Hemi: root [hemicellulose], Lign: root [lignin], RCC: root [carbon], RDMC: root dry matter content, RLD: root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density, Solu: root [soluble compounds] and SRL: specific root length.

Tableau S1
Model selection on relationships between root traits and tree growth rates at the 0-20 cm depth according to AIC.

Root trait	**Estimate**	***P***	**R^2**	**AICc**	**ΔAICc**
D	105.77	**<0.001**	0.46	320.77	0
Lignin	0.12	**<0.001**	0.36	326.08	5.31
RMD	3.74	**<0.001**	0.25	335.08	14.31
RCC	0.27	**<0.001**	0.21	338.16	17.39
SRL	-0.18	**<0.001**	0.19	340.07	19.3
Soluble compounds	-0.07	**<0.01**	0.15	342.48	21.71
RNC	-0.99	**0.02**	0.09	346.68	25.91
RLD	0.53	**0.03**	0.08	347.48	26.71
Hemicellulose	-0.06	0.32	0.02	351.37	30.6
RDMC	-0.01	0.5	0.00	351.9	31.13
Cellulose	-0.01	0.56	0.00	352.01	31.24
RTD	4.39	0.71	0.00	352.14	31.44

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RDMC: root dry matter content, RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

Tableau S2
Model selection on relationships between root traits and tree growth rates at the 20-40 cm depth according to AIC.

Root trait	Estimate	*P*	R^2	AICc	ΔAICc
Lignin	0.05	**<0.001**	0.22	327.46	0
Soluble compounds	-0.07	**<0.001**	0.22	327.77	0.32
D	53.08	**<0.01**	0.16	331.68	4.22
RMDC	-0.04	**<0.01**	0.11	334.86	7.41
Hemicellulose	-0.10	**0.02**	0.10	335.8	8.34
RNC	-0.74	**0.04**	0.07	337.23	9.78
RCC	0.10	**0.04**	0.06	337.57	10.11
RTD	-7.72	0.07	0.06	338.23	10.78
RLD	1.74	0.13	0.04	339.35	11.9
RMD	2.30	0.53	0.00	341.23	13.77
SRL	-0.02	0.55	0.01	341.26	13.81
Cellulose	0.00	0.9	0.00	341.61	14.16

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RDMC: root dry matter content, RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

Tableau S3
Model selection on relationships between root traits and tree growth rates at the 40-60 cm depth according to AIC.

Root trait	Estimate	*P*	R^2	AICc	ΔAICc
Soluble compounds	-0.08	**<0.01**	0.22	174.06	0
D	49.02	**0.03**	0.15	176.62	2.55
SRL	-0.06	**0.03**	0.15	176.75	2.68
RLD	6.83	0.13	0.08	179.13	5.06
RMD	21.07	0.14	0.08	179.14	5.08
Cellulose	0.03	0.23	0.05	179.92	5.86
RNC	-0.36	0.39	0.03	180.65	6.59
Hemicellulose	0.05	0.49	0.02	180.94	6.87
RTD	5.37	0.52	0.01	181	6.93
Lignin	0.00	0.68	0.00	181.24	7.17
RDMC	0.00	0.92	0.00	181.4	7.33
RCC	0.00	0.96	0.00	181.41	7.34

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RDMC: root dry matter content, RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

ANNEXE B – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 3

Tableau S4
Model selection on relationships between each root trait and soil organic carbon stock (SOC) according to aictab and lmer functions. Data included soil samples from all distances from a stem and all soil depths (n=150).

Root trait	Estimate	*P*	R^2	AICc	ΔAICc
Log_e (RLD)	20.83	< **0.001**	0.78	1231.12	0.00
Log_e (RMD)	19.07	**< 0.001**	0.73	1261.70	30.58
Soluble compounds	0.41	**< 0.001**	0.27	1334.19	103.07
Lignin/N	-1.21	**< 0.001**	0.27	1334.40	103.28
Fine root C/N	-0.68	**< 0.001**	0.25	1338.60	107.48
RNC	6.81	**< 0.001**	0.24	1340.16	109.04
Cellulose	-0.19	**< 0.001**	0.10	1365.18	134.06
RCC	-0.69	**< 0.001**	0.08	1368.18	137.06
SRL	-0.31	**< 0.001**	0.08	1369.10	137.98
Hemicellulose	-0.55	**< 0.01**	0.07	1369.52	138.40
D	65.23	ns	0.00	1378.83	147.71
RTD	-14.76	ns	0.00	1379.53	148.41
Lignin	-0.02	ns	0.00	1380.00	148.89

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

Tableau S5

Model selection on relationships between each root trait and mineral-associated organic C (MAOC) according to aictab and lmer functions. Data included soil samples from all distances from a stem and all soil depths (n=150).

Root trait	Estimate	*P*	R^2	AICc	ΔAICc
$\mathrm{Log_e}$ (RLD)	9.26	< **0.001**	0.79	913.98	0.00
$\mathrm{Log_e}$ (RMD)	8.43	**< 0.001**	0.72	950.43	36.45
Soluble compounds	0.19	**< 0.001**	0.29	1090.85	176.87
Lignin/N ratio	-0.55	**< 0.001**	0.28	1092.93	178.95
C/N ratio	-0.31	**< 0.001**	0.26	1096.65	182.67
RNC	3.10	**< 0.001**	0.25	1098.80	184.82
Cellulose	-0.09	**< 0.001**	0.11	1124.26	210.28
RCC	-0.31	**< 0.001**	0.08	1129.30	215.32
Hemicellulose	-0.25	**< 0.001**	0.08	1129.75	215.77
SRL	-0.13	**< 0.01**	0.07	1131.57	217.59
D	25.72	ns	0.00	1140.26	226.28
RTD	-7.62	ns	0.00	1140.47	226.49
Lignin	0.00	ns	0.00	1141.23	227.25

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

Tableau S6
Model selection on relationships between each root trait and particulate organic C (POC) according to aictab and lmer functions. Data included soil samples from all distances from a stem and all soil depths (n=150).

Root trait	**Estimate**	***P***	**R^2**	**AICc**	**ΔAICc**
Log_e (RLD)	1.40	< **0.001**	0.68	321.25	0.00
Log_e (RMD)	1.26	**< 0.001**	0.62	341.47	20.21
Soluble compounds	0.03	**< 0.001**	0.26	414.12	92.87
C/N ratio	-0.04	**< 0.001**	0.22	420.86	99.61
Lignin/N	-0.07	**< 0.001**	0.19	424.43	103.18
RNC	0.40	**< 0.001**	0.19	424.54	103.29
Cellulose	-0.02	**< 0.001**	0.15	430.17	108.92
Hemicellulose	-0.04	**< 0.01**	0.09	437.16	115.91
RCC	-0.05	**< 0.01**	0.09	437.75	116.50
RTD	-3.00	**< 0.05**	0.03	444.08	122.83
D	7.04	ns	0.02	445.62	124.37
SRL	-0.01	ns	0.02	445.71	124.45
Lignin	0.00	ns	0.00	447.32	126.07

AICc: Akaike Information Criterion, D: average root diameter, RCC: root [carbon], RLD° root length density, RMD: root mass density, RNC: root [nitrogen], RTD: root tissue density and SRL: specific root length. Numbers in bold indicate a significant correlation at $P < 0.05$.

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