UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

COMPOSANTE SOUTERRAINE DE LA VULNÉRABILITÉ DES ARBRES À LA SÉCHERESSE : EFFET DE LA MICROTOPOGRAPHIE ET DE LA DISPONIBILITÉ EN EAU SUR LA BIOMASSE ET LA PRODUCTION DE RACINES FINES EN FORÊT TEMPÉRÉE

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

CAC	Caryer cordiforme (*Carya cordiformis*)
DOY	Jour de l'année (« Day of year »)
ERS	Érable à sucre (*Acer saccharum*)
SP	Période de récolte (« Sampling Period »)
SRL	Longueur racinaire spécifique (« Specific Root Length »)
TPI	Indice de position topographique (« Topographic Position Index »)

RÉSUMÉ

À l'échelle globale, l'intensité et la durée des sécheresses sont amenées à augmenter avec les changements climatiques, favorisant l'apparition de stress hydrique, l'un des principaux facteurs de mortalité des forêts. Les études sur la réponse des arbres à la sécheresse se concentrent principalement sur les parties aériennes et peu sur les parties souterraines, bien que les racines assurent la fonction vitale du prélèvement en eau. Dans l'optique de mieux comprendre la vulnérabilité des arbres à la sécheresse, ce projet vise à déterminer l'effet de la microtopographie et de la disponibilité en eau sur les racines fines d'arbres matures en forêt tempérée. Nous avons étudié 1) comment la microtopographie influence la croissance (production et biomasse), la distribution verticale et la morphologie (longueur racinaire spécifique) des racines fines de deux espèces d'arbres en milieu naturel et 2) comment ces traits racinaires répondent à une expérience d'assèchement. Pour ce faire, les racines fines de deux espèces représentatives de la Vallée-du-Haut-Saint-Laurent, l'érable à sucre et le caryer cordiforme, ont été récoltées sur des arbres en position microtopographique de monticule et de creux, pendant cinq mois en 2017. La moitié des arbres ont été soumis à une expérience d'exclusion des précipitations à partir du mois d'août. Des données sur la production et la biomasse en racines fines à différentes profondeurs ont été obtenues respectivement à l'aide de chambres de croissance et de carottes de sol. Pour les deux espèces, la production en racines fines en profondeur (20-40 cm) et la biomasse racinaire étaient significativement plus faibles en creux qu'en monticule, avec une différence de longueur moyenne observée de 43% et 16% respectivement. L'érable à sucre a produit significativement plus de racines en profondeur que le caryer cordiforme avec une différence de longueur moyenne observée de 42%. La microtopographie avait toutefois un effet plus important que l'espèce sur la longueur de biomasse globale et sur la production de racines fines en profondeur. L'exclusion des précipitations n'a pas eu d'effet sur la production et a conduit à une faible diminution de la biomasse globale. Ces résultats illustrent l'acclimatation différentiée du système racinaire des arbres face à la microtopographie, avec un système racinaire plus développé pour les arbres de monticules que pour les arbres de creux, ce qui pourrait jouer un rôle crucial dans leur réponse à la sécheresse.

Mots-clés : racines fines, microtopographie, sécheresse, *Acer saccharum*, *Carya cordiformis*.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Problématique

Depuis quelques décennies, les conditions climatiques à l'échelle du globe connaissent de nombreux changements en raison de l'augmentation de la concentration des gaz à effet de serre. Les projections des modèles climatiques montrent que les évènements extrêmes tendent à être plus fréquents, plus intenses et de plus longue durée, dans de nombreuses régions du monde (Groupe d'experts intergouvernemental sur l'évolution du climat et al., 2013), le sud du Québec n'y faisant pas exception (Ouranos, 2015). À l'échelle globale, l'intensité et la durée des sécheresses sont amenées à augmenter avec les changements climatiques (Trenberth et al., 2013). Plusieurs définitions du terme sécheresse existent selon le champ d'intérêt, mais de manière générale, celle-ci correspond à une période aux conditions météorologiques plus sèches que la normale (Van Loon, 2015). Les températures moyennes au Québec ont augmenté de 1 à 3°C entre 1950 et 2011 et la tendance se poursuit (Ouranos, 2015). Dans le sud de la province, les scénarios climatiques projettent des conditions plus sèches pendant l'été (Ouranos, 2015), avec une réduction de 20 à 40% de l'humidité du sol à l'horizon 2080 (Houle et al., 2012). Cette réduction est entre autres occasionnée par un prélèvement accru en eau par la végétation, causé par l'allongement de la saison de croissance (Logan et al., 2011) et l'augmentation de la demande évaporative de l'atmosphère en réponse aux températures plus élevées (Breshears et al., 2013 ; Eamus et al., 2013).

Les événements de sécheresse peuvent entraîner des conditions de stress hydrique chez les plantes, lequel a été identifié comme un des principaux facteurs explicatifs du déclin global des forêts (Allen et al., 2010). Un arbre connaît un stress hydrique lorsque la quantité d'eau disponible dans le sol devient insuffisante au maintien de ses activités métaboliques. Au Canada, ces conditions de stress ont été associées à une croissance réduite et une mortalité accrue dans la forêt boréale (Hogg et al., 2002 ; Huang et al., 2010 ; Peng et al., 2011). L'impact du stress hydrique sur la forêt tempérée canadienne n'a pas été documenté jusqu'à maintenant, mais des études ont fait état des effets délétères de la sécheresse sur la forêt tempérée européenne et nord-américaine (Bréda et al., 2006 ; Martin-Benito et Pederson, 2015). Le risque de mortalité accrue des arbres face à la sécheresse est une source d'inquiétude sur les plans économiques, sociaux et environnementaux. Il devient donc important de mieux comprendre comment réagiront les écosystèmes forestiers aux conditions futures auxquelles ils seront exposés, ainsi que le rôle que joueront les différents facteurs abiotiques et biotiques. De telles connaissances favoriseront une gestion territoriale pouvant inclure des mesures d'adaptation tant du point de vue de l'aménagement forestier que de la conservation des écosystèmes. Cependant, étudier la vulnérabilité des forêts est complexe et comporte plusieurs défis. La compréhension des phénomènes de déclin à l'échelle du paysage passe en tout premier lieu par une compréhension à l'échelle de l'individu.

1.2 Mécanismes de mortalité des arbres

Différents facteurs prédisposent les arbres d'un peuplement à la vulnérabilité à la sécheresse : les facteurs d'exposition et les facteurs de sensibilité (Figure 1.1). Dans le cadre de ce projet, la sensibilité dépend des facteurs propres à l'espèce tandis que les facteurs d'expositions sont des facteurs liés à l'environnement de développement (site) et ses fluctuations dans le temps (aléas). La combinaison des facteurs de sensibilité et d'exposition définira l'impact qu'aura un aléa climatique sur un arbre. La vulnérabilité à cet impact variera selon la capacité d'adaptation de l'individu, qui comprend sa plasticité phénotypique et la variabilité génétique intraspécifique.

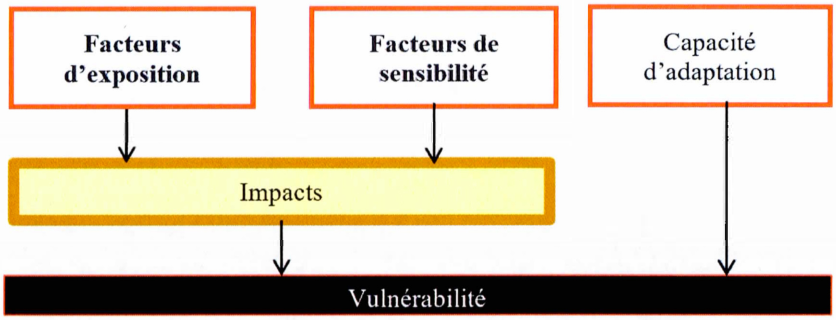

Figure 1.1. Vulnérabilité des arbres à la sécheresse à l'échelle de l'individu.

Les arbres peuvent répondre différemment à des conditions de stress hydrique, notamment en ce qui concerne le fonctionnement hydraulique et le contrôle des stomates (Aubin et al., 2007 ; Bréda et al., 2006). En situation de sécheresse, le fort lien entre la petite quantité d'eau restante et les particules de sol ainsi que la forte demande évaporative accentue la baisse de potentiel hydrique au sein de la plante. Si l'eau dans les vaisseaux est soumise à une tension trop importante, cela peut entraîner un phénomène de cavitation, parfois fatal pour l'arbre (Brodersen et al., 2013 ; Cochard et al., 2002). Afin de minimiser le risque de cavitation, l'arbre peut fermer ses stomates. Cependant, cela limite ensuite les échanges de gaz et l'acquisition de CO2 indispensable à la photosynthèse ce qui entraîne une carence en carbone. L'arbre doit alors arriver à un compromis entre minimiser le risque de cavitation et obtenir le CO2 nécessaire à son développement (Simonneau et al., 2014). Face à ce compromis, les espèces peuvent adopter un caractère isohydrique ou anisohydrique. Le caractère isohydrique consiste en une fermeture rapide des stomates face à un stress hydrique afin de conserver le potentiel hydrique du xylème constant. Un caractère anisohydrique consiste à maintenir les stomates ouverts malgré la baisse du potentiel hydrique afin de privilégier la photosynthèse (Lovisolo et al., 2010). Une espèce donnée peut également jongler entre ces caractères (Klein, 2014). La mortalité des arbres est rarement induite par un bref épisode de sécheresse (Nishimura et al., 2007), mais, de manière générale, on associe une sécheresse de longue durée à des mortalités par carence en carbone, et une sécheresse très intense à des mortalités par embolie (Aubin et al., 2007 ; McDowell et al., 2008) (Figure 1.2).

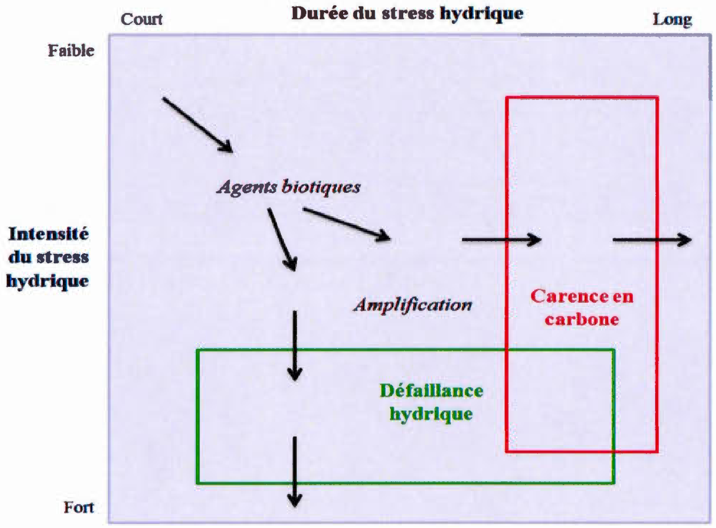

Figure 1.2 : Deux mécanismes sous-jacents de la mortalité des arbres par la sécheresse, tiré de McDowell et al. (2008).

Les sécheresses peuvent également affecter indirectement les forêts en les rendant plus susceptibles à des attaques par les pathogènes et les insectes (Anderegg et al., 2015 ; McDowell et al., 2008 ; Millar et Stephenson, 2015).

1.3 Facteurs de sensibilité à la sécheresse

Dépendamment de l'espèce à laquelle ils appartiennent, les arbres présentent des traits propres qui les rendent plus ou moins sensibles au stress hydrique. Les études mettent en évidence deux grandes stratégies mises en place par les espèces pour lutter contre la sécheresse : tolérer ou éviter le stress hydrique (Brunner et al., 2015). Les espèces plus tolérantes au stress ont la capacité de synthétiser des solutés et protéines afin de diminuer leur potentiel osmotique et maintenir une turgescence des tissus alors que l'eau est limitée (Claeys et Inze, 2013). Les espèces privilégiant les stratégies d'évitement équilibrent leurs pertes et leurs apports en eau. La limitation des pertes peut se faire par une fermeture contrôlée des stomates et une utilisation interne de l'eau plus efficace (Aubin et al., 2016). L'augmentation des apports en eau nécessite une optimisation du prélèvement par les racines. Ainsi, les espèces avec un ratio de biomasse hypogée vs épigée plus important et des racines plus profondes présentent une plus forte résistance à la sécheresse (Kozlowski et Pallardy, 2002). Enfin, face à des sécheresses prolongées, le stockage de carbone non structurel chez certaines espèces est un véritable atout pour prévenir la mortalité par carence en carbone (O'Brien et al., 2014). L'utilisation seule des traits d'une espèce, souvent mesurés dans des conditions environnementales spécifiques, ne permet pas de prédire avec exactitude la réponse de l'espèce dans des conditions différentes (Albert et al., 2011). En effet la variation intraspécifique est à considérer et est peu étudiée dans la littérature (Albert et al., 2011). Ce biais limite ainsi la compréhension des réponses des individus aux conditions de stress hydrique.

1.4 Facteurs d'exposition à la sécheresse

Les espèces présentent des traits propres qui leur permettent de répondre différemment à des périodes de sécheresse, mais la vulnérabilité d'un individu à la sécheresse varie fortement selon les conditions de sites (Abrams et al., 1998). Les caractéristiques granulométriques du sol et les facteurs physiographiques, comme la microtopographie, conditionnent fortement l'exposition des arbres à la sécheresse par leur influence sur la disponibilité en eau du sol ainsi que sur les phénomènes d'évapotranspiration (Calvet, 2003). Le potentiel matriciel du sol est fortement lié à la texture puisque, selon la taille des particules de sol, la liaison avec les molécules d'eau sera plus ou moins forte (Wang et al., 2009). En effet, la liaison des molécules d'eau avec des particules grossières, comme le sable, est moins forte qu'avec des particules fines, comme l'argile. Ainsi, un sol sableux facilite le drainage et a une faible capacité de rétention de l'eau. Au contraire, un sol argileux peut emmagasiner de plus grandes quantités d'eau, mais une plus grande partie demeure inaccessible pour les plantes en raison des fortes liaisons avec les particules de sol (Wang et al., 2009). La microtopographie, c'est-à-dire la topographie à une échelle fine, a aussi une influence sur la disponibilité en eau dans le sol. Elle se caractérise par la présence d'élévations, des monticules, et de dépressions, des creux, de petites amplitudes. L'humidité du sol est inversement corrélée à l'élévation du terrain à faible échelle (Born et al., 2015 ; Simmons et al., 2011). Cette plus faible disponibilité en eau pour les plantes dans les zones de monticules pourrait occasionner un stress hydrique accru à cette position microtopographique. L'étude de ces facteurs sur le stress hydrique en milieu naturel comporte une difficulté importante puisqu'ils covarient souvent ensembles. Par exemple, la concentration des sols en argile est généralement plus importante dans les zones sans pente ou avec une topographie concave, menant ainsi à la formation de cuvettes d'accumulation d'eau (Brubaker et al., 1993). De plus, d'un point de vue topographique, les zones de bas de pente présentent généralement des sols d'épaisseur plus importante que les zones de pente ou de haut de pente, et sont plus concentrées en éléments fins (Brubaker et al., 1993 ; Enoki et al., 1996).

1.5 Acclimatation du système racinaire aux conditions de site

Dans une forêt, les propriétés du sol, de microclimat et de la microtopographie sont très variables à une échelle fine. Les plantes peuvent mettre en place différentes stratégies de développement pour exploiter localement cette hétérogénéité et diminuer le risque de stress. Le système racinaire en particulier peut faire preuve d'une grande plasticité dans le moment de sa croissance, sa densité et sa capacité d'absorption (Meier et Leuschner, 2008b). Ainsi, la plasticité phénotypique des racines permet à des arbres d'une même espèce, soumis à des conditions climatiques identiques, de présenter des systèmes racinaires différents selon leur position microtopographique et leur accès à l'eau (Fan et al., 2017 ; Guevara et al., 2010). En effet, il a été maintes fois observé que le ratio de biomasse hypogée vs épigée (root to shoot ratio en anglais) change en fonction de la fertilité et de la disponibilité en eau du sol (Bloom et al., 1985) et donc indirectement avec la microtopographie (Anschlag et al., 2008 ; Enoki et al., 1996).

Bien que la littérature soit assez pauvre quant aux données racinaires, comparativement à ce qu'elle fournit sur les organes aériens, certains consensus émergent quant à la distribution, la production et la biomasse racinaire. La fertilité du sol joue un rôle important vis-à-vis de la biomasse racinaire des arbres. Des études en forêt tempérée ont montré une relation négative entre la fertilité du sol (estimée par l'azote disponible) et la biomasse racinaire (Keyes et Grier, 1981 ; Vogt et al., 1987). Différentes études ont montré que l'ajout de nutriments, tels que l'azote, le phosphore, le potassium, le calcium et le magnésium, stimule la croissance racinaire des arbres (Fahey et Hughes, 1994 ; Pregitzer et al., 1993). La réponse des arbres à la fertilisation varie toutefois selon l'espèce (Leuschner et al., 2004). La distribution des racines varie également selon la profondeur, la structure et la texture du sol (Bréda et al., 1995 ; Lucot et Bruckert, 1992). Les racines fines sont le centre d'intérêt étant donné que c'est à ce niveau que s'effectue le prélèvement en eau (avec l'aide de la symbiose avec les champignons mycorhiziens) et de nombreux articles démontrent qu'en forêt feuillue tempérée leur densité diminue en fonction de la profondeur (Bédéneau et Auclair, 1989 ; Bouten et al., 1992 ; Bréda et al., 1995 ; Lucot et Bruckert, 1992) à partir d'une profondeur de 20 cm (Lucot et Bruckert, 1992). De plus, Bréda et al. (1995) ont montré que la distribution racinaire était latéralement homogène dans le premier mètre de profondeur de sol, dans une couronne de trois mètres autour du tronc dans le cas d'un peuplement de chênes en Europe. La densité de racines dans chaque couche de sol est inversement corrélée avec la stabilité structurale (i.e. sensibilité des sols à l'érosion hydrique), qui dépend fortement de la concentration en argile (Bréda et al., 1995). En effet, les racines ne peuvent pas pénétrer dans un sol trop dense et ainsi, dans le cas de sols argileux, la pénétration racinaire est presque inexistante (Veihmeyer et Hendrickson, 1948). Une accumulation de racines peut alors s'observer généralement juste au-dessus de la couche argileuse (Bouten et al., 1992). On peut donc s'attendre à ce que la densité racinaire soit plus importante en position de monticules où les sols sont moins argileux et la stabilité structurale est moindre. La production en racines fines a lieu tout au long de saison de croissance et est un phénomène très variable avec les années, car elle dépend fortement des caractéristiques de sol, mais ne semble pas présenter un patron de réponses clair aux fluctuations climatiques de températures et précipitations (Côté et al., 1998). Au cours d'une année, un à deux pics majeurs de production sont souvent observés. Dans le cas d'un seul pic, celui-ci s'observe au printemps ou à l'été. Dans le cas de deux pics, le premier apparaît au printemps et le second à la fin de l'été ou à l'automne (Santantonio et Hermann, 1985). En termes de biomasse, la grande importance des racines fines dans le prélèvement de l'eau s'illustre par le fait que 81 % du total de la biomasse racinaire se compose de racines de moins de deux millimètres de diamètre (considéré comme le diamètre maximum pour les racines fines dans la plupart des articles) (Bréda et al., 1995). En moyenne, la biomasse en racine fine est plus importante sur les monticules ce qui illustrerait la plasticité morphologique de l'espèce à exploiter l'hétérogénéité de l'environnement comme suggéré par Enoki et al. (1996). La différence de biomasse racinaire entre creux et monticules est exacerbée par une nappe phréatique généralement très haute à la sortie du printemps qui limite le développement racinaire en profondeur dans les positions de creux. Les racines se développent peu et se concentrent en surface afin d'éviter la zone d'anoxie (absence de dioxygène) (Fan et al., 2017).

1.6 Réponse du système racinaire à une sécheresse

Beaucoup d'études ont été menées pour tenter de comprendre la réponse des arbres à la sécheresse. Encore une fois, ces études ont pour la plupart porté sur les parties aériennes de l'arbre, mais peu sur les parties souterraines, bien que les prélèvements d'eau soient effectués au niveau racinaire. De plus, les conditions de site, telles que la topographie, sont rarement prises en compte dans l'étude de la réponse à la sécheresse. Pour comprendre les défis d'acclimatation de l'appareil racinaire en situation de stress hydrique, il est important pour commencer de bien comprendre comment la disponibilité en eau varie dans les sols. L'eau est plus disponible en surface qu'en profondeur au début de la saison de croissance due à la recharge printanière. Plus tard dans la saison de végétation, alors que le sol devient plus sec, le prélèvement en eau se fait de plus en plus profondément (Bréda et al., 1995 ; Nepstad et al., 1994). Lors de sécheresse, le compartiment le plus profond devient alors la zone de prélèvement la plus importante alors que la densité en racine y est plus faible (Bréda et al., 1995 ; Rambal, 1984). C'est pourquoi les jeunes plantes au système racinaire peu développé en profondeur sont souvent exposées à une défaillance hydrique (Luo et Chen, 2013 ; Sparks et Black, 1999).

Les arbres ont développé des stratégies d'évitement au niveau racinaire pour faire face au stress hydrique. Lorsque l'on aborde la question de stratégie d'évitement du stress hydrique, il est important de bien distinguer les réponses d'un système racinaire adapté à un climat aride (où les périodes de faible disponibilité en eau sont récurrentes) et les réponses à une sécheresse (au cours desquelles la disponibilité en eau diminue de façon imprévue sous la normale). En effet, les arbres en zone aride ont évolué afin de privilégier le prélèvement en eau par rapport à la captation de la lumière. Ils présentent alors généralement un ratio de biomasse hypogée vs épigée plus important et un système racinaire plus développé en profondeur que les arbres de zone plus tempérée avec une distribution plus ou moins égale des précipitations dans l'année (Choat et al., 2012 ; Hartmann, 2011). De manière similaire, les arbres en zone aride ont généralement une plus forte longueur racinaire spécifique (SRL, ratio de longueur sur la masse sèche de racines fines) que les arbres en milieu tempéré, ce qui traduit un caractère exploratoire pour maximiser l'acquisition en eau (Chen et al., 2013 ; Comas et al., 2012). La réponse à une sécheresse occasionnelle en climat tempéré est différente et consiste à des modifications rapides dans la distribution, la croissance et la morphologie des racines fines. Du point de vue de la distribution verticale, les études ont montré un développement des racines en profondeur en réponse à un stress hydrique en milieu tempéré (Joslin et Wolfe, 2003 ; Persson et al., 1995 ; Torreano et Morris, 1998). Du point de vue de la croissance et de l'accumulation de biomasse, le ratio de biomasse hypogée vs épigée tend à augmenter lors de conditions de sécheresse (Aspelmeier et Leuschner, 2006 ; Zang et al., 2014) bien que cette dernière entraine en termes absolus une diminution de biomasse en racines fines (Anderegg, 2012 ; Chenlemuge et al., 2013 ; Gaul et al., 2008 ; Hertel et al., 2013). Sous des conditions de stress modéré, la production en racines fines est stimulée pour augmenter l'efficacité du prélèvement en eau (Gaul et al., 2008 ; Leuschner et al., 2001 ; Meier et Leuschner, 2008a ; Zang et al., 2014). Cependant, quand le stress s'intensifie, cette production diminue et finit par cesser (Konôpka et al., 2007 ; Meier et Leuschner, 2008b ; Zang et al., 2014). Enfin, d'un point de vue morphologique, les sécheresses occasionnelles ne semblent pas impacter le SRL (Hertel et al., 2013 ; Meier et Leuschner, 2008b ; Ostonen et al., 2007). Enfin, il est important de ne pas étudier séparément les traits racinaires, propres à l'espèce, et les caractéristiques environnementales dans une étude de vulnérabilité à la sécheresse. C'est en étudiant leurs interactions qu'il sera possible d'évaluer les avantages que les traits confèrent réellement aux arbres afin de lutter contre le stress hydrique.

1.7 Objectif de l'étude

Face à la sécheresse, la position microtopographique de creux offre un plus fort taux d'humidité du sol et apparaît comme un micro-refuge hydrique pour les arbres (Born et al., 2015 ; McLaughlin et al., 2017). Toutefois, des taux de mortalité des arbres plus élevés ont été observés dans les dépressions que sur des élévations (Simmons et al., 2011). Comme souligné, la biomasse racinaire des arbres de creux se concentrerait dans les couches superficielles du sol. La faible densité racinaire en profondeur pourrait ainsi rendre les arbres de creux plus vulnérables à des épisodes de sécheresse que les arbres de monticules. Dans l'optique de mieux comprendre la vulnérabilité des arbres à la sécheresse, ce projet vise à déterminer l'effet de la microtopographie et de la disponibilité en eau sur les racines fines d'arbres matures en forêt tempérée.

CHAPITRE II

TREE FINE ROOT PRODUCTION AND STANDING CROP DIFFER ACCORDING TO MICROTOPOGRAPHY

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Abstract

Water stress is one of the primary drivers of forest mortality at the global scale and with climate change, an increase in drought duration and severity is expected. Given the challenge of in situ root measurements, ecological processes in the rhizosphere have been much less studied than aboveground processes, even though they play a crucial role in the response of trees to drought. Environmental factors at a very local level, such as microtopography, may exert a strong influence on soil water availability during the growing season, but how these factors affect in turn fine root development, and thus the sensitivity of trees to drought, remains, poorly known. We studied 1) how microtopography influences fine root growth (standing crop and daily production), vertical distribution and morphology (specific root length) for two tree species in natural forest stands and 2) how these root traits respond to water limitations. We replicated an experiment in 16 sites in the temperate forest of southern Quebec, Canada, where four sugar maple (*Acer saccharum*) and four bitternut hickory *(Carya cordiformis*) mature trees were selected in each site, half in pits and half in mounds. To simulate drought conditions, we performed a rainfall exclusion with plastic covers at half of the sampled trees for three months. We used growth chambers to monitor fine root daily production at the base of each tree through the summer of 2017 and we used soil cores to measure the fine root standing crop. For both species, the fine root production in the deeper soil layer (20-40 cm) and the standing crop were significantly lower in pits than in mounds, with respectively a 43% and 16% reduction in terms of observed length. Sugar maple produced significantly more fine roots in the deeper soil layer (20-40 cm) than bitternut hickory, with a 42% difference between the two species in terms of length. While effect sizes of tree species and microtopography were both important, microtopography had a greater influence on the overall standing crop length and the fine root production at deep soil layers. The water exclusion experiment did not affect fine root production and led to a slight reduction in the standing crop, despite a moderate but statistically significant reduction in soil water content and potential. These results highlight the distinct acclimation of the fine root system of trees to microtopography, which could play a crucial role regarding the response of trees to drought.

Keywords: fine root daily production, fine root standing crop, microtopography, rainfall exclusion, temperate forests, fine root growth chamber, *Acer saccharum*, *Carya cordiformis*.

2.1 Introduction

Drought severity and duration are projected to increase with climate change at the global scale. Although methodological issues still need to be addressed to enhance our level of confidence in projections in regards to droughts (Seneviratne et al., 2012 ; Trenberth et al., 2013), an increase in dry conditions is expected in many regions of the world, including North America (Dirmeyer et al., 2013 ; Houle et al., 2012). Soil moisture drought, defined as a deficit in the root-zone soil moisture (Van Loon, 2015), has led to increased mortality and reduced growth for trees of boreal (Peng et al., 2011) and temperate forests (Bréda et al., 2006 ; Brzostek et al., 2014 ; Martin-Benito and Pederson, 2015). Climatic scenarios point towards an intensification of the problem in coming years (Charney et al., 2016 ; Girardin et al., 2016). As a result, there has been growing research to understand ecological processes controlling drought sensitivity in order to inform forestry adaptation strategies (Chaves et al., 2003 ; D'Orangeville et al., 2018 ; Hamanishi and Campbell, 2011 ; Phillips et al., 2016).

The fine root system is responsible for water and nutrient uptake and is a key determinant of the drought sensitivity of trees (Phillips et al., 2016). This sensitivity can be described as the short-term physiological response of trees to drought. While recent work has helped elucidate aboveground factors influencing drought sensitivity (Hoffmann et al., 2011 ; McDowell et al., 2008), belowground factors have been much less studied given challenges associated with root measurements in the field. Studies have highlighted two main strategies that trees have developed to avoid damage to cellular functions when facing water limitations: 1) tolerate dehydration and 2) avoid stress from low water potentials (Brunner et al., 2015). On the one hand, trees adopting a drought tolerance strategy develop protective solutes and proteins to decrease osmotic potential of cells and maintain turgor in water-limited conditions (Claeys and Inze, 2013). On the other hand, trees adopting a drought avoidance strategy act to balance water loss and uptake by the tree, either by reducing water losses through stomatal closure or by enhancing water uptake through roots. The present study focuses on the root system and the role it could play in a drought avoidance strategy.

When assessing drought avoidance mechanisms, a clear distinction should be made between the response to arid climatic conditions vs. unpredictable drought events. Under an arid climate, trees have evolved to prioritize water uptake over light interception and thus generally have higher root-to-shoot ratios and deeper root systems than species adapted to temperate conditions (Allen et al., 2010 ; W. Chen et al., 2013 ; Choat et al., 2012 ; Comas et al., 2012 ; Hartmann, 2011 ; West et al., 2012). Vegetation growing under a water-limited climate also evolved to a greater specific root length (SRL, ratio of fine root length to dry mass) (Brunner et al., 2015 ; W. Chen et al., 2013 ; Comas et al., 2012, 2013). Indeed, the SRL describes the trade-off between resource acquisition and conservation (Weemstra et al., 2016) as a large SRL favors resource acquisition by increasing the volume of soil explored and the surface area of roots in contact with the soil. Under a temperate climate, droughts are unpredictable events and the response of vegetation goes through short-term modifications of the growth (standing crop and production), morphology (SRL) and vertical distribution of the fine root system. In terms of vertical distribution, an expansion of the root system towards deeper soil horizons has been observed for trees growing under a temperate climate and subject to water limitations (Joslin and Wolfe, 2003 ; Persson et al., 1995 ; Torreano and Morris, 1998). In terms of growth, research shows that drought triggers a shift in resource allocation that favors roots rather than shoots in trees. The root-to-shoot ratio tends to increase when facing water limitations (Aspelmeier and Leuschner, 2006 ; Zang et al., 2014) although drought still causes a reduction in the fine root biomass of trees (Anderegg, 2012 ; Chenlemuge et al., 2013 ; Gaul et al., 2008 ; Hertel et al., 2013). Under moderate water limitations, fine root production generally increases as young roots are more efficient at water uptake (Gaul et al., 2008 ; Leuschner et al., 2001 ; Meier and Leuschner, 2008a ; Zang et al., 2014). As the water limitations become severe, fine root production decreases and ultimately stops (Konôpka et al., 2007 ; Meier and Leuschner, 2008b ; Zang et al., 2014). In terms of morphology, the SRL appears relatively insensitive to drought (Hertel et al., 2013 ; Meier and Leuschner, 2008b ; Ostonen et al., 2007) although insight from arid ecosystems suggests that water limitations favor a higher SRL.

Environmental factors controlling soil water availability exert a strong influence on the sensitivity of trees to drought, with recent work suggesting that local site conditions have a greater impact than species on the response of trees (D'Orangeville et al., 2018 ; Martin-Benito and Pederson, 2015). For example, soil moisture conditions prevailed over species-specific differences to explain variations in the drought resistance of trees at the continental scale (Gazol et al., 2017). Environmental factors also play a key role on root development, thus also affecting the sensitivity of trees to drought. In fact, Weemstra et al. (2016) have argued that a root-economic spectrum is ill-suited to understand root trait coordination and instead, they proposed a multidimensional root trait framework that takes into account environmental constraints on root development such as water and nutrient availability as well as soil chemistry and structure. In forests, environmental factors such as soil properties, microclimates and microtopography vary widely at small scale (J. Chen et al., 1999), thus having the potential to influence root development. However, we still lack a clear understanding of how these site characteristics shape root development and influence drought sensitivity. For example, microtopography locally influences soil moisture in forests and mounds (i.e. small-scale topographic elevations with a convex shape) are generally drier than pits (i.e. small-scale topographic depressions with a concave shape). Indeed, mounds are generally made up of soil of a smaller particle size than pits (Fan et al., 2017), which reduces the soil's water retention capacity. Additionally, the slope of mounds favors drainage (Wang et al., 2009) which also limit soil water retention. Microtopography influence on seedling establishment has long been studied (Anschlag et al., 2008 ; Born et al., 2015 ; Cornett et al., 1997 ; Messier and Kimmins, 1992) but very little information is available on its influence on the root development of mature trees.

The objectives of this research are to understand 1) how microtopography influences fine root growth vertical distribution and morphology for bitternut hickory (*Carya cordiformis*) and sugar maple (*Acer saccharum),* two North American temperate tree species and 2) how these root properties respond to drought.

(1) Given its influence on soil moisture, we hypothesize that microtopography will influence the fine root system of trees. On the one hand, we expect that mounds, with a convex microtopography that favors drainage, will have a lower water availability than pits during the growing season. On the other hand, we expect trees in mounds to have a more extensive fine root system (larger daily production, larger standing crop, larger SRL, greater rooting depth) than in pits. This would illustrate different acclimations of the fine root system to micro-environmental conditions, that could potentially reduce the vulnerability to drought by enabling trees in mounds to avoid water deficits.

(2) We hypothesize that water stress will lead to an overall reduction of the fine root daily production and standing crop of trees. Based on hypothesis 1, we expect a larger reduction in pits than in mounds given that trees in mounds are better prepared to face water limitations with their more extensive root system than pits.

2.2 Materials and methods

2.2.1 Study area

This study took place in the region of Vallée-du-Haut-Saint-Laurent in southern Quebec, Canada (Fig. 2.1). In proximity to the Saint-Lawrence River, a wide plain is found with a maximum elevation of 40 m and going further inland, two small hills, Covey Hill (343 m) and Rigaud (220 m), can be found. The natural bedrock of the region is mainly composed of dolomitic complexes and sandstone. The area close to the Saint-Lawrence River is covered by marine deposits and they are replaced by morainal deposits as the distance from the river increases (Delage and Gangloff, 2007 ; Gagné, 2010 ; Meilleur et al., 1992, 1994). The area has been highly impacted by human activities since the beginning of the 19th century and it resulted in a fragmented landscape (Bouchard and Domon, 1997 ; Meilleur et al., 1992). Agriculture prevails in the region (53% of land cover), with isolated forest patches scattered across the landscape (26% of land cover). The region is part of the sugar maple-hickory bioclimatic domain (Grandtner, 1966) and forests are mainly composed of hardwood and mixed stands (56% and 25% respectively) (Gagné, 2010). The region is characterized by a humid continental climate according to the updated Köppen-Geiger Classification (Peel et al., 2007). The average annual temperature is 6.7°C (Environment Canada, station 7025745, years 1981-2010) with large variations throughout the year, ranging from an average temperature of -9.3°C in January to 20.9°C in July. Precipitations are evenly distributed throughout the year and the average annual precipitation is 965 mm (17% as snow). In the year 2017, when the study was conducted, the spring was exceptionally wet with rainfall between April and June reaching 382 mm compared to an average of 257 over the 1981-2010 period. At the opposite, rainfall recorded in September was relatively low (35 mm) compared to the 1981-2010 average (91 mm). The average temperature from May to November (14.5°C) was relatively similar to the long-term average (14.1°C) reported in previous years.

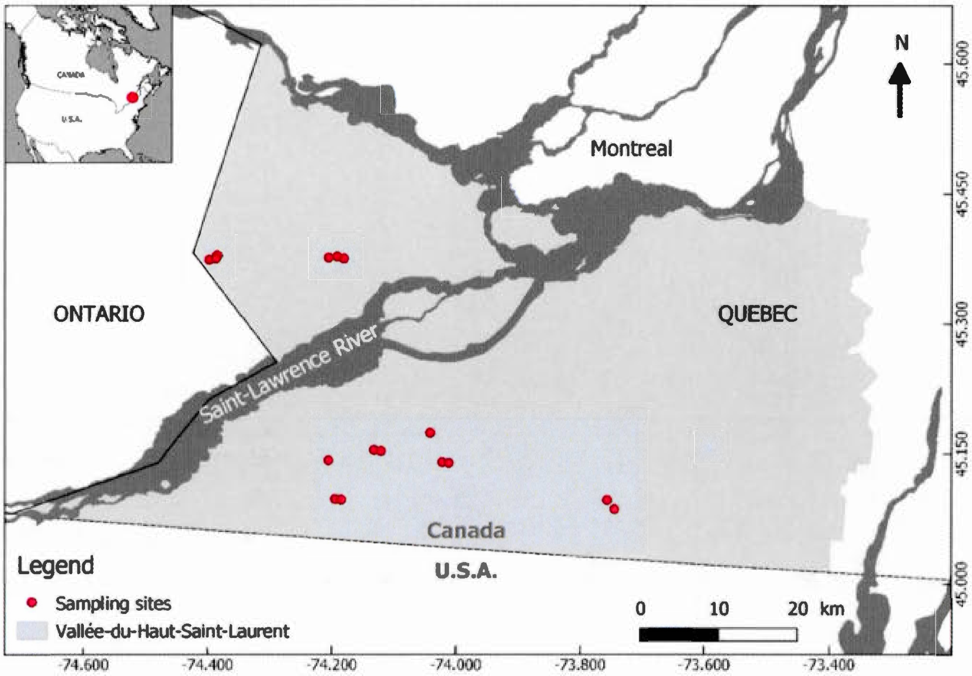


Figure 2.1: Location of the 16 sampling sites in the study area, Vallée-du-Haut-Saint-Laurent, Quebec, Canada.

2.2.2 Experimental design

Our study focused on the fine root system of two deciduous tree species commonly found in the region: the bitternut hickory (*Carya cordiformis*) and the sugar maple (*Acer saccharum*). Sugar maple is the dominant tree species in the study area and is found in association with other species like bitternut hickory (Brisson et al., 1988). We selected 16 sampling plots throughout the study region (Fig. 2.1, Annex A) in mature forest tracts (patch size >26 ha) with no sign of recent disturbances and a sufficient number of trees of the two studied species. Study sites had to exhibit a distinct pit-and-mound microtopography. To guide site selection, we assessed microtopographic patterns using a map of the topographic position index (TPI). The TPI reflects the mean difference in elevation between a focal point (the cell center) and the points at the end of equidistant radii. That map was obtained using a fine scale (resolution = 50 cm) digital elevation model derived from LiDAR data and then computing the TPI for each cell. For this computation, we used eight radii (45° between two adjacent radii) of 8 m long. Sampling plots also had to be located on morainic surficial deposits with moderate soil drainage. A first list of candidate sites was visited and validated based on species composition and site ecological classification to limit environmental variability. An additional criterion for site selection was ease of access given sites had to be visited numerous times during the summer and a final selection was conducted to retain 16 sites.

At each site, we selected four mature trees (20 cm $\leq$ Diameter at Breast Height $<$ 45 cm) for each of the two studied species (sugar maple and bitternut hickory). Half of them were located in pits (small-scale topographic depression, pit depth of about 2 m) and half of them in mounds (small-scale topographic elevation, minimum mound height of 2 m). Microtopography has often been studied in the context of tree fall pits and mounds. Instead, in our study, we focused on trees at the top or bottom of small ridges and multiple trees could be found on the same pit or mound. We measured the microtopographic position of trees by calculating the difference in elevation between the base of each tree and six points located at 8 m from it in six directions (60° between two adjacent radii). A positive total of these differences corresponded to a mound position, and inversely, a pit position.

To simulate the effect of drought conditions, we installed a rainfall exclusion device on half of the trees for each site. To do so, we followed the method designed by Belien et al. (2012) and we set up transparent polyethylene canvas covering a 3.65 m radius around each selected tree. During the exclusion device installation, we made sure to tightly wrap the canvas at 1.2 to 1.5 m high to the trunk, so the stem flow would be intercepted. We tightened the edge of the canvas at different points around the tree to ensure a smooth and continuous flowing surface. We installed this rainfall exclusion device at the end of July 2017 such that it was operational from day of year (DOY) 220 to 312. We conducted this experiment under a BACI (Before-After Control Impact) design. This approach let us compare data before and after the impact, using impacted trees paired with control trees (Smith, 2014). Each site was visited four times during the study period, twice before and twice after the rainfall exclusion device installation, to collect data on the fine root system and the soil moisture: the first sampling period spanned from DOY 186 to 205 (median = 195), the second from DOY 206 to 219 (median = 212), the third from DOY 234 to 242 (median = 238) and the fourth from DOY 292 to 312 (median = 302).

We sampled fine roots (defined as roots measuring less than 1 mm in diameter) at the base of each tree to characterize three root traits: growth (measured through the daily production and standing crop), vertical distribution and morphology (measured through the SRL). We measured fine root daily production using in situ growth chambers, also referred to as root ingrowth-core (Addo-Danso et al., 2016), dug in June (DOY 157 to 172). At a distance from the base of the tree equivalent to two thirds of the tree crown, we dug a 40 cm deep and 60 cm wide chamber in the ground. We cleaned and leveled the profile surface of the chamber that faced the tree and removed all visible fine roots from it (Fig. 2.2). We installed a 40 cm deep and 35 cm wide fiberglass fly screen (mesh of 1 mm) on the cleaned profile. We then installed a corrugated plastic panel at 2.5 cm from the fly screen and filled the gap between the profile covered with the screen and the corrugated plastic panel with fine wet sand (0.1 mm < diameter < 0.25 mm). This constituted a growth chamber of a volume of 3.5 L (40 cm X 35 cm X 2.5 cm) where fine roots can grow freely. This design was highly inspired by rhizotron technology (Côté et al., 1998), but with a greater collecting surface (area of the screen = 1400 cm^2). We collected fine roots in the growth chambers twice in 2017, before and after the rainfall exclusion (second and fourth sampling periods). Each time, we collected fine roots at four depths in the chamber (0-10, 10-20, 20-30, 30-40 cm) which provided information about the vertical distribution of fine root daily production.

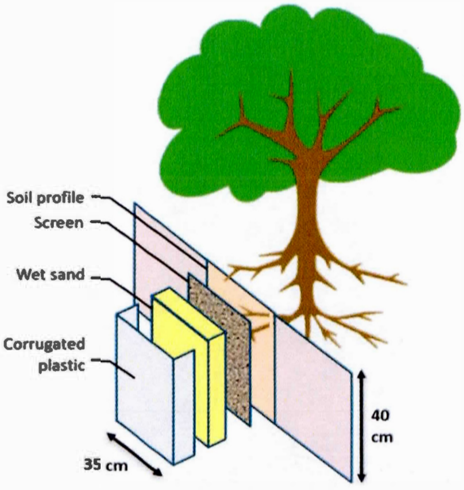


Figure 2.2: Experimental set up of the growth chamber installed at the base of each tree to measure fine root daily production.

To measure the fine root standing crop, we extracted soil cores three times during the summer: at the first two sampling periods, before the rainfall exclusion, and at the fourth sampling period, after rainfall exclusion. For each sampling period, we used cylinders (diameter = 5 cm) to collect soil cores at depths of 0-20 cm and 20-40 cm at a distance of 2 to 2.5 m from selected trees. Samples were dried in a forced-air oven at 60°C for 12 hours and then immersed in water to facilitate the separation of roots from the soil (Bonzon and Picard, 1969). We then sieved the samples to extract fine roots.

We washed fine roots collected from both protocols (daily production and standing crop) with water and then scanned them between two glass panes at a resolution of 600 dpi. Fine roots were then dried in a forced-air oven at 60°C for 24 hours and weighted (Mettler Toledo Balance, precision +/-1 mg). We processed scanned images with the WinRHIZO software (Arsenault et al., 1995) to obtain the length of fine roots. Using these measurements, we computed the SRL as the ratio between the total length and dry weight of each sample.

To quantify the effect of the rainfall exclusion on soil moisture, we measured the soil volumetric water content and soil water potential at each of the four sampling periods at fixed locations. For each tree, we measured the soil water content at depths of 15 cm and 35 cm at a distance of 1 and 3 m north and south from the tree base (total of eight measurements per tree per site visit) with a portable soil moisture probe (FieldScout TDR 100, Spectrum Technologies Inc., precision +/- 0.1 $m^3 \cdot m^{-3}$). These measurements provided information about the amount of water stored in the soil, but not about its availability to plants, which is better assessed with soil water potential measurements. Using tensiometers (Irrometer company Inc., model SR, precision +/- 2 kPa), we measured soil water potential at depths of 15 and 45 cm at each of the four sampling periods. To do so, we drilled at the beginning of the study, two holes that match length and diameter of tensiometers in the soil, between the growth chamber and the tree. We drilled them at approximately 20 cm from the growth chamber and we covered them with rocks in-between site visits. For each measurement, tensiometers were left for at least one hour in the soil to allow the potential to equilibrate between the soil and the tensiometer. During transportation between sites and trees, the ceramic tip of tensiometers was submerged in water.

When creating the growth chambers, we collected soil samples at depths of 10 and 30 cm, in order to conduct particle size analysis (i.e. two soil samples per tree). For each site, we measured in the laboratory the particle size distribution of the soil samples pooled per depth and microtopography (i.e. four analyses per site) using the hydrometer procedure (Kroetsch and Wang, 2008). We evaluated stone content visually at the base of each tree on the field with a stone content diagram (Rowell, 1994).

2.2.3 Statistical analysis

To determine whether the clay content (n = 64) and stone content (n=128) differed between microtopographic positions (pit vs. mound) and depth (10 cm vs. 30 cm; effect tested only for the clay content), we used general linear mixed models (GLMM) with a beta distribution (link = logit), which is adapted to analyze response variables expressed as proportions (Ferrari et Cribari-Neto, 2004). The site was included into the model as a random effect to take into account the autocorrelation between trees on the same site. We used a GLMM with a beta distribution (link = logit) for soil water content, and with a negative binomial distribution (link = log) for soil water potential, to assess the influence of microtopography (pit vs. mound), tree species (sugar maple vs. bitternut hickory), soil depth and rainfall exclusion (control vs. exclusion) on soil moisture. Given soil water potentials are expressed as negative values, we performed the analysis on absolute values. Given our BACI design, the main effect of rainfall exclusion treatment is of little interest in our model and we evaluated the effect of the rainfall exclusion on soil moisture by assessing the significance of the interaction between the sampling period (SP1, SP2, SP3 and SP4) and the rainfall exclusion treatment. To evaluate if this rainfall exclusion effect is similar between microtopographic positions, we included the three-way interaction sampling period x rainfall exclusion treatment x microtopography. For both soil water content and potential, the tree identifier nested within site nested within date was included as random variables.

We then conducted two analyses on the same dataset to answer our two hypotheses about the effect of microtopography and rainfall exclusion on the fine root system. Due to convergence issues, we did not use one model to test the two hypotheses. We used GLMMs to assess the effect of the rainfall exclusion on the daily production and standing crop variables (fine root length, mass and SRL). We observed over-dispersed frequency distributions for the length (n = 896) and mass (n = 896) of daily production. As such, we rounded values to the nearest integer and used a negative binomial distribution (link = log) to analyze these two response variables. When assessing the effect of rainfall exclusion on the daily production, we included the number of days between sampling periods (log transformed) as an offset variable to take the time lapse differences between samplings at each site into account. The offset variable makes model adjustments while being constrained to have a regression coefficient of 1 (Hilbe, 2011). We used a GLMM with a gamma distribution (link = log) to describe the SRL (n = 758) of daily production and to describe the length (n = 725), mass (n = 725) and SRL (n = 725) of standing crop. Given our BACI design, we evaluated the effect of the rainfall exclusion by assessing the significance of the interaction between the sampling period and the rainfall exclusion treatment. Moreover, to evaluate if this effect is depth, microtopography or species dependent, we included three-way interactions (sampling period x rainfall exclusion treatment x depth, sampling period x rainfall exclusion treatment x microtopography and sampling period x rainfall exclusion treatment x species). Finally, tree identifier nested within site was included as random variable for all analyses. We did not include sampling period as a random variable because it was included as a fixed variable. We evaluated the effect of the microtopography, species and depth on fine root production (length, mass, and SRL) and standing crop (length, mass and SRL) in a different analysis. We used the same distributions than previously. In the models, we included two-way interactions depth x microtopography and depth x species. We included the number of days between sampling periods (log transformed) as an offset variable for the models of length and mass of daily production. Tree identifier nested within site nested within sampling period was included as random variable. When microtopography and species significantly influenced fine root production or standing crop, we compared their relative effect size by computing Cohen's d estimates (Cohen, 1988). We performed all the GLMMs with the R package glmmTMB (Berg et al., 2017).

2.3 Results

2.3.1 Effect of microtopography on soil physical properties and moisture

Across our study sites, soil clay content increased with depth ($P < 0.001$, Annex B). Microtopography significantly influenced the soil texture: mounds had a lower clay content than pits (P = 0.004, Annex B), especially at a greater depth (P = 0.0498, Annex B). For example, the clay content of pits was on average twice that of mounds at a 30 cm depth (23% for pits vs. 12% for mounds, Fig. 2.3a). Stone content was higher in mounds than in pits (P <0.001, Annex B), with an average content of 22% in mounds compared to 11% in pits (Fig. 2.3b).

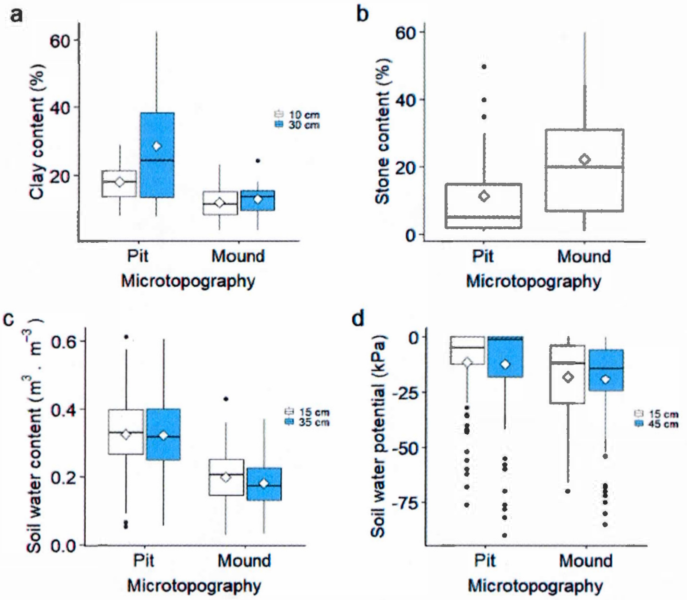


Figure 2.3: Differences in the soil a) clay content, b) stone content, c) soil water content ($m^3 \cdot m^{-3}$) and d) soil water potential (kPa) of pits and mounds. The diamond is the mean, the central line is the median, edges of the box represent the interquartile range, whiskers represent extreme values that are not considered outliers and points represent outliers.

Throughout the summer, measurements at depths of 10 and 30 cm show that soil water content was significantly lower in mounds than in pits (P <0.001, Annex C), with an average of 0.2 $m^3 \cdot m^{-3}$ in mounds compared to 0.3 $m^3 \cdot m^{-3}$ in pits (Fig. 2.3c). Similarly, measurements at depths of 15 and 45 cm show that soil water potential was lower in mounds than in pits (P <0.001, Fig. 2.3d, Annex D). In addition, both soil water content and potential decreased slightly with depth (water content: $P < 0.001$; water potential: $P < 0.001$, Fig. 2.3, Annex C, Annex D). Overall, water content was lower for sugar maple than bitternut hickory ($P = 0.030$, Annex C) but water potential, which describes water availability from a biological standpoint, was similar ($P = 0.721$, Annex D).

2.3.2 Effect of rainfall exclusion on soil moisture, fine root daily production and standing crop

Looking at the pseudo-R^2, our models assessing the effects of the rainfall exclusion on the length and mass of the fine root daily production (Annex E) explained 54% of variance (fixed factors 31%) and 50% of variance (fixed factors 28%), respectively. Our models assessing the effects of the rainfall exclusion on the length and mass of the fine root standing crop (Annex F) explained a greater proportion of variance, respectively 68% (fixed factors 58%) and 62% (fixed factors 54%). Explanatory variables in our models describing the SRL of the daily production or standing crop (Annex E, Annex F) did not explain more than 10% of variance. Given such a small proportion, we could not make any conclusions on the effect of the rainfall exclusion on the SRL of the fine root production and standing crop.

According to the weather station (7025745), total rainfall throughout the study period cumulated 118 mm before the installation of the rainfall exclusion device, at the end of the second sampling period, and 240 mm afterwards (Fig. 2.4). The rainfall exclusion experiment significantly reduced soil water content at the fourth sampling period (DOY = 302: $P < 0.001$, Fig. 2.4, Annex C) and soil water potential at the third and fourth sampling periods (DOY = 238: $P = 0.007$; DOY = 302: $P = 0.005$, Fig. 2.4, Annex D). For example, the rainfall exclusion reduced soil water content on average by about 0.10 $m^3 \cdot m^{-3}$ at the fourth sampling period (Fig. 2.4b). While the reduction in soil water content was similar at both depths, we observed a larger reduction in soil water potential near the surface: we observed an average reduction of 29 kPa at 15 cm compared to 18 kPa at 45 cm (Fig. 2.4c). Overall, soil moisture reduction due to rainfall exclusion experiment was similar between pits and mounds in terms of water content (sampling period 3: P = 0.244; sampling period 4: P = 0.283, Annex C) and water potential (sampling period 3: P = 0.579; sampling period 4: P = 0.232, Annex D).

Even though the rainfall exclusion experiment reduced the soil water content and water potential, it did not significantly influence the fine root production, whether described in terms of length, mass or SLR (see Annex E for coefficient estimates and p-value for each predictor). This lack of effect holds whatever the depth, the species or the microtopography considered. In contrast, the length and mass of the standing crop were significantly reduced after the rainfall exclusion experiment (interaction treatment x 4th sampling period: P = 0.047, mass: P = 0.011, Annex F). Between the second and fourth sampling periods, the average length of the fine root standing crop increased from 1794 cm·dm^{-3} to 1886 cm·dm^{-3} for control trees while it decreased from 1780 cm·dm^{-3} to 1625 cm·dm^{-3} for trees with rainfall exclusion (Fig. 2.5). Similarly, we observed a small decrease in the standing crop mass for trees with rainfall exclusion (891 mg·dm^{-3} before exclusion and 840 mg·dm^{-3} after exclusion) while it increased for control trees (886 mg.dm^{-3} to 925 mg·dm^{-3}, Fig. 2.5). This decrease in the standing crop mass of rainfall restricted trees was species-dependent; it was more important for bitternut hickory than for sugar maple (interaction treatment x species x sampling period 4: P = 0.041, Annex F, Fig. 2.5c-d).

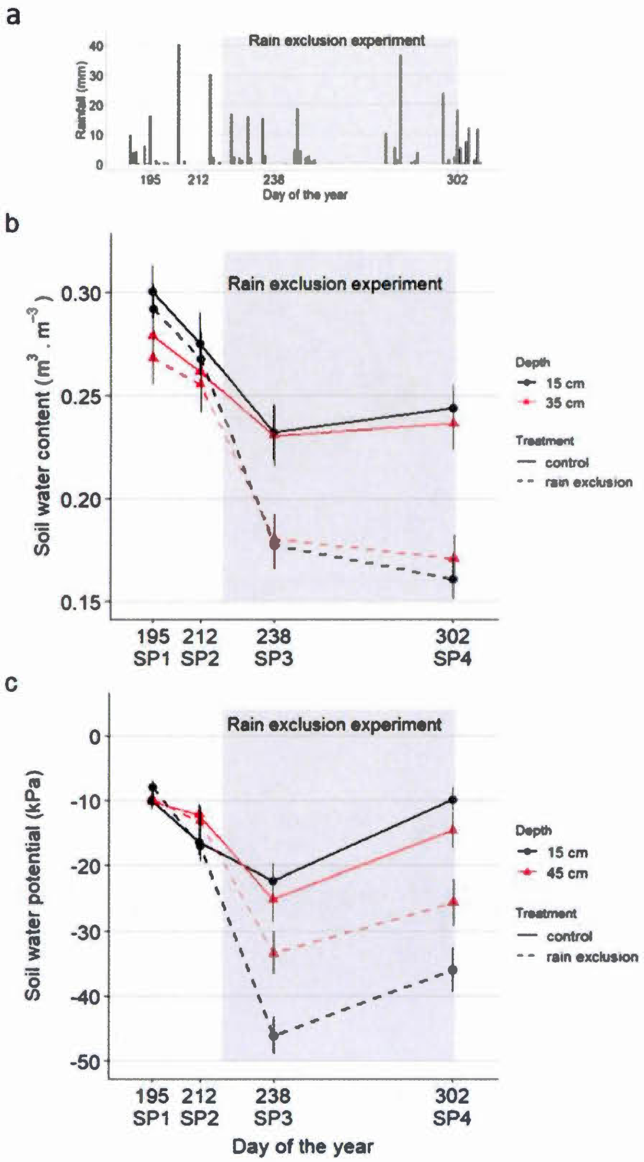


Figure 2.4: a) Daily precipitation at the nearest meteorological station during the study period and changes in b) soil water content and c) soil water potential, with and without rainfall exclusion at the four sampling periods (SP1, SP2, SP3 and SP4, represented by the median day of year).

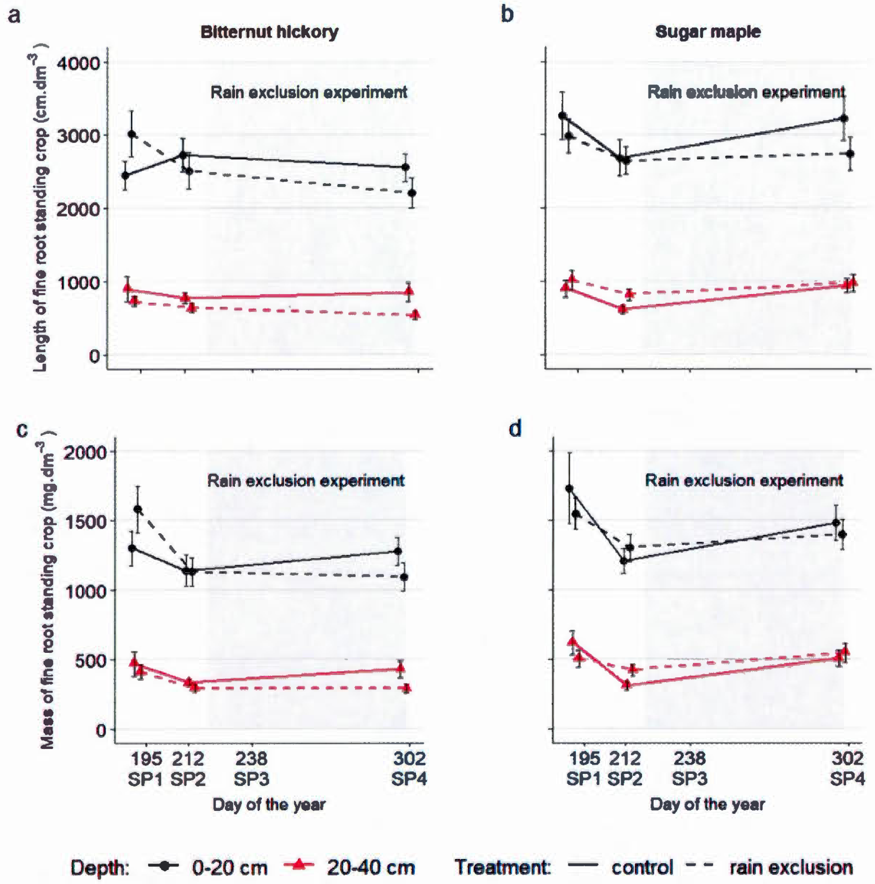


Figure 2.5: Average length and mass of the fine root standing crop for bitternut hickory (a,c) and sugar maple (b,d) with and without rainfall exclusion at 0-20 cm and 20-40 cm deep at the four sampling periods (SP1, SP2, SP3 and SP4, represented by the median day of year). The shaded area represents the period when rainfall exclusion was performed. Error bars represent the standard error. No data for SP3.

2.3.3 Effect of microtopography on fine root daily production and standing crop

When testing the effects of microtopography, tree species, soil depth, rainfall exclusion and their interactions on the fine root system, we found that the rainfall exclusion had no significant influence and, as such, we removed this predictor from the models. Based on the pseudo-R^2, our models explained 54% (fixed factors = 31%) and 50% (fixed factors = 30%) of the variance in the length and mass of fine root production. Models describing variation in the length and mass of the fine root standing crop explained 70% (fixed factors = 56%) and 68% (fixed factors = 50%) of variance. Once again, as was the case in our models assessing the effect of the rainfall exclusion, models describing the SRL of the daily production or standing crop did not explain more than 10% of the variance and we focused our analyses on the fine root mass and length.

We found that microtopography significantly influenced the fine root daily production, but only at greater depths (Table 2.1). Indeed, the length of fine root daily production was on average 43% lower for pits than for mounds at depths between 20 and 40 cm (Fig. 2.6a). Similarly, the mass of fine root daily production was on average 58% lower for pits than for mounds at the 30-40 cm depth (Fig. 2.6b). The fine root standing crop was lower for pits than for mounds, but, unlike fine root daily production, this effect was not depth-dependent (Table 2.2). Overall, the length of the fine root standing crop was on average 16% lower for pits than for mounds (Fig. 2.6c). Similarly, the mass of fine root standing crop was on average 14% lower for pits than for mounds (Fig. 2.6d).

Daily fine root production and standing crop decreased with the soil depth (Table 2.1, Table 2.2). For example, the length of daily fine root production reached an average of 1.99 $\text{cm}\cdot\text{dm}^{-2}\cdot\text{d}^{-1}$ at 0-10 cm depth compared to an average of 0.54 $\text{cm}\cdot\text{dm}^{-2}\cdot\text{d}^{-1}$ at 30-40 cm depth, which means four times more. As for the standing crop, its length reached an average of 2741 $\text{cm}\cdot\text{dm}^{-3}$ at 0-20 cm depth and an average of 800 $\text{cm}\cdot\text{dm}^{-3}$ at 20-40 cm depth. Mass of fine root daily production and standing crop followed the same pattern as length.

Table 2.1: Generalized linear mixed model describing the length (cm·dm^{-2}·d^{-1}) and mass (mg·dm^{-2}·d^{-1}) of the fine root daily production as a function of soil depth (0-10, 10-20, 20-30 and 30-40 cm), tree species (sugar maple and bitternut hickory), and microtopography (pit and mound).

	Length of fine root daily production Negative binomial distribution (link=log)				Mass of fine root daily production Negative binomial distribution (link=log)			
Predictors	*Estimates*	*Confidence interval*	*Z-value*	*P-Value*	*Estimates*	*Confidence interval*	*Z-value*	*P-Value*
Intercept (Depth 0-10, Pit, Bitternut hickory)	0,335	0,089 – 0,582	2,663	**0,008**	-0,786	-1,021 – -0,551	-6,553	**<0,001**
Depth 10-20 cm	-0,013	-0,246 – 0,220	-0,106	0,915	0,076	-0,158 – 0,311	0,638	0,524
Depth 20-30 cm	-0,785	-1,056 – -0,515	-5,684	**<0,001**	-0,439	-0,708 – -0,169	-3,189	**0,001**
Depth 30-40 cm	-2,177	-2,535 – -1,819	-11,912	**<0,001**	-1,937	-2,300 – -1,573	-10,441	**<0,001**
Mound	0,205	-0,041 – 0,452	1,634	0,102	0,103	-0,138 – 0,343	0,836	0,403
Sugar maple	0,067	-0,178 – 0,312	0,535	0,593	0,069	-0,170 – 0,308	0,567	0,571
Depth 10-20 cm * Mound	0,009	-0,246 – 0,265	0,071	0,943	0,07	-0,194 – 0,334	0,516	0,606
Depth 20-30 cm * Mound	0,467	0,182 – 0,752	3,209	**0,001**	0,273	-0,018 – 0,564	1,836	0,066
Depth 30-40 cm * Mound	0,874	0,512 – 1,235	4,737	**<0,001**	0,811	0,443 – 1,179	4,317	**<0,001**
Depth 10-20 cm * Sugar maple	0,105	-0,151 – 0,360	0,803	0,422	0,063	-0,201 – 0,326	0,467	0,641
Depth 20-30 cm * Sugar maple	0,335	0,053 – 0,617	2,328	**0,02**	0,185	-0,102 – 0,473	1,262	0,207
Depth 30-40 cm * Sugar maple	0,517	0,163 – 0,871	2,863	**0,004**	0,528	0,166 – 0,891	2,858	**0,004**

Table 2.2: Generalized linear mixed model describing the length (cm·dm^{-3}) and mass (mg·dm^{-3}) of the fine root standing crop as a function of depth (0-20, and 20-40 cm), tree species (sugar maple and bitternut hickory) and microtopography (pit and mound).

	Length of fine root standing crop Gamma (link=log)				Mass of fine root standing crop Gamma (link=log)			
Predictors	*Estimates*	*Confidence interval*	*Z-value*	*P-Value*	*Estimates*	*Confidence interval*	*Z-value*	*P-Value*
Intercept (Depth 0-20, Pit, Bitternut hickory)	7,738	7,626 – 7,850	135,488	**<0,001**	7,027	6,867 – 7,186	86,392	**<0,001**
Depth 20-40	-1,27	-1,392 – -1,149	-20,556	**<0,001**	-1,278	-1,403 – -1,152	-19,963	**<0,001**
Mound	0,167	0,055 – 0,279	2,92	**0,003**	0,125	0,015 – 0,234	2,223	**0,026**
Sugar maple	0,117	0,005 – 0,230	2,055	**0,04**	0,137	0,027 – 0,247	2,446	**0,014**
Depth 20-40 * Mound	-0,039	-0,179 – 0,101	-0,548	0,583	0,079	-0,065 – 0,224	1,077	0,281
Depth 20-40 * Sugar maple	0,045	-0,095 – 0,185	0,633	0,527	0,121	-0,024 – 0,265	1,638	0,101

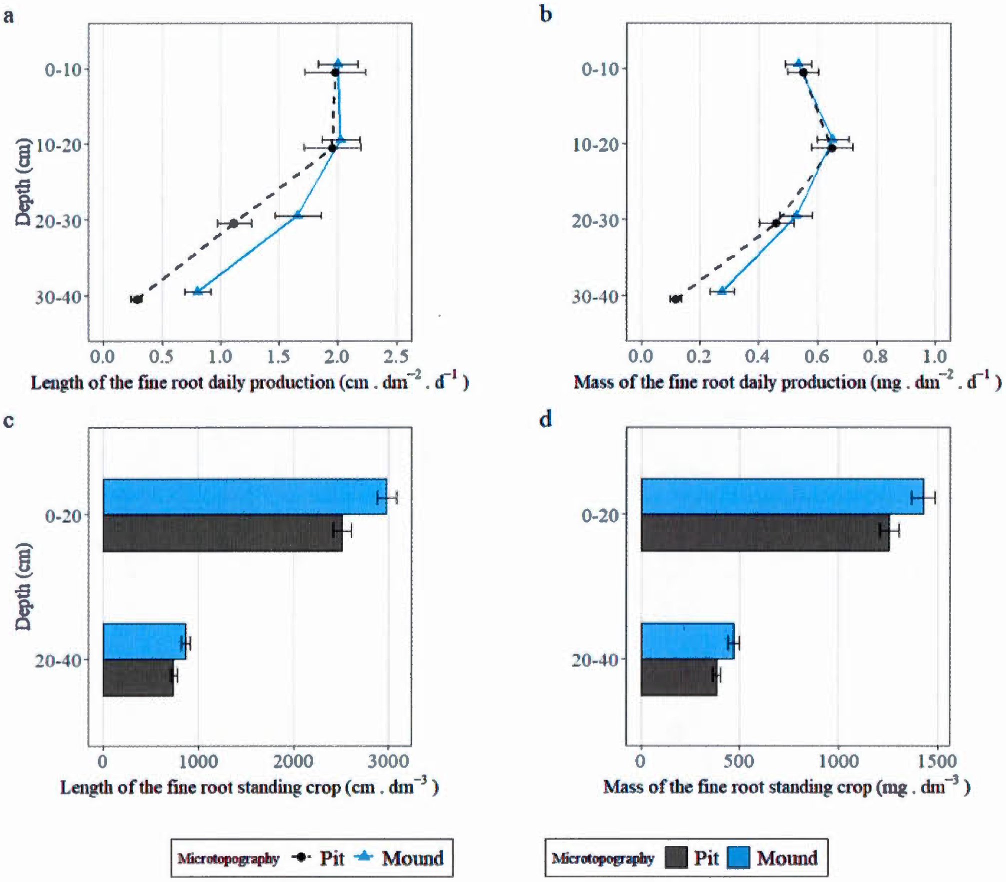


Figure 2.6: a) Length and b) mass of the fine root daily production at four depths (0-10, 10-20, 20-30, 30-40 cm) and c) length and d) mass of the fine root standing crop at two depths (0-20 and 20-40 cm) in pits and mounds. Error bars represent the standard errors.

We measured a SRL of 36.9 m·g^{-1} in mounds and 32.2 m·g^{-1} in pits for fine root daily production, and of 21.1 m·g^{-1} in mounds and 22.3 m·g^{-1} in pits for standing crop (Annex G). However, as our models (Annex E, Annex F) describe only a very low proportion of the variance of the SRL of the daily production and standing crop, we could not assess statistically the effects of depth, species or microtopography on this variable.

2.3.4 Effect of tree species on fine root daily production and standing crop

Overall, the length and mass of the daily fine root production were not significantly different between the two tree species (Table 2.1). However, the interaction between species and depth was significant, indicating that sugar maple produced more fine roots (length and mass) at greater depth than bitternut hickory (Table 2.1). The length of fine root daily production was on average 42% lower for bitternut hickory than for sugar maple at depths between 20 and 40 cm (Fig. 2.7a). Similarly, the mass of fine root daily production was on average 36% lower for bitternut hickory than for sugar maple at the 30-40 cm depth (Fig. 2.7b). The fine root standing crop (length and mass) was slightly higher for sugar maple than for bitternut hickory, with no interaction with depth (Table 2.2). Overall, fine root standing crop was on average 13% and 16% lower for bitternut hickory than for sugar maple, for length and mass respectively (Fig. 2.7c-d).

We measured a SRL of 35.4 $m \cdot g^{-1}$ for sugar maple and 34.1 $m \cdot g^{-1}$ for bitternut hickory for fine root daily production, and a SRL of 20.5 $m \cdot g^{-1}$ for sugar maple and 22.9 $m \cdot g^{-1}$ for bitternut hickory for standing crop (Annex G). However, as mentioned above, our models only describe a low proportion of the variance of the SRL of fine root daily production and standing crop and we could not assess statistically the effects of species on this variable.

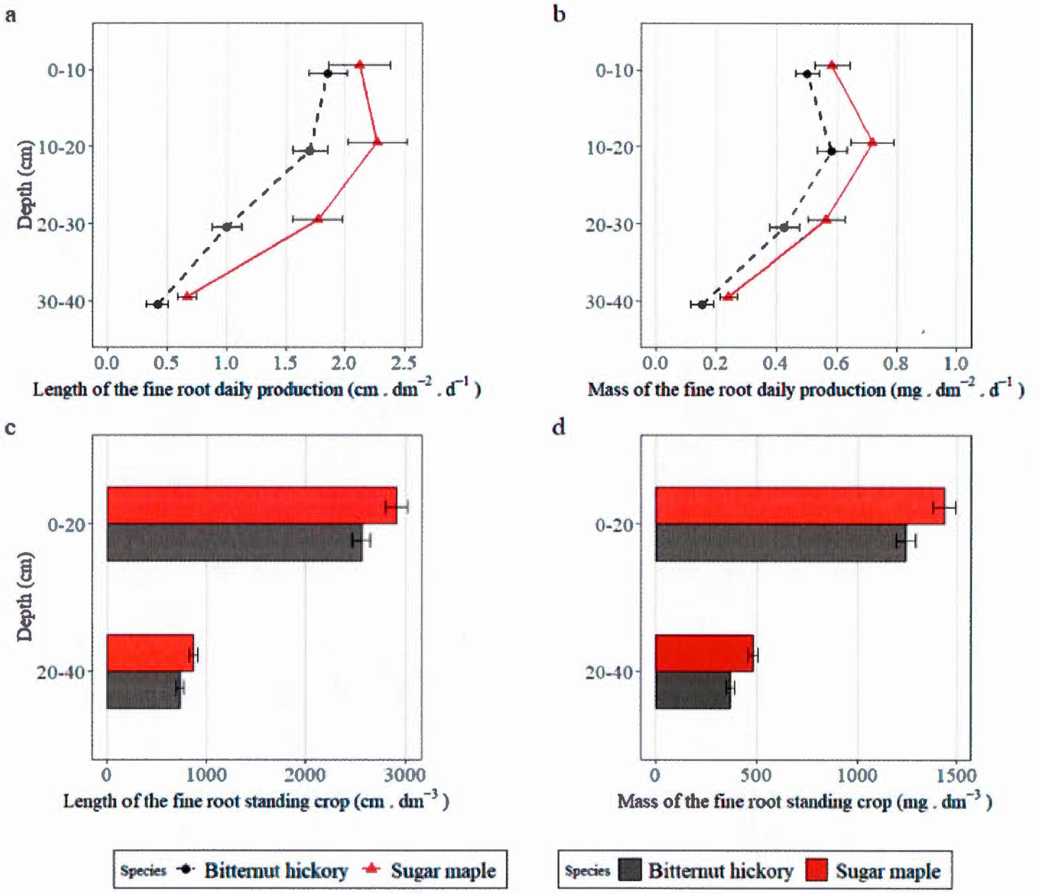


Figure 2.7: a) Length and b) mass of the fine root daily production at four depths (0-10, 10-20, 20-30, 30-40 cm) and c) length and d) mass of the fine root standing crop at two depths (0-20 and 20-40 cm) for sugar maple and bitternut hickory. Error bars represent the standard errors.

Table 2.3 presents the effect size of microtopography and tree species using Cohen's d index. Regarding the length of the standing crop, the effect size of microtopography (d index = 2.93) was greater than tree species (d index = 2.06). However, we observed the opposite for the mass of the standing crop thus making it impossible to identify the strongest effect on standing crop. As for the fine root daily production, the effect size of microtopography was greater than tree species both in terms of length and mass.

Table 2.3: Effect size of microtopography and tree species on the fine root standing crop and daily production using Cohen's d estimate.

		Cohen's d for microtopograpy	**Cohen's d for tree species**
Standing crop	*Length*	2.93	2.06
	Mass	1.53	1.68
Daily production (20-30 cm)	*Length*	5.11	3.00
	Mass	3.03	2.03
Daily production (30-40 cm)	*Length*	6.24	3.26
	Mass	5.37	3.41

2.4 Discussion

2.4.1 Mounds reduce water availability because of their shape and their soil properties

Our results showed that soil moisture was greater in pits than in mounds (Fig. 2.3c-d), thus supporting the first part of hypothesis 1 regarding the effect of microtopography on soil moisture. A similar pattern has been observed in both temperate (Beatty, 1984 ; Yeakley et al., 1998) and tropical forests (Born et al., 2015) where tree fall mounds have been shown to create heterogeneous conditions in terms of soil moisture. This is consistent with the convex shape of mounds that enhances drainage while the concave shape of pits favors water accumulation. Indeed, pits tend to delay runoff and favor infiltration thus leading to higher soil moisture (Valtera and Schaetzl, 2017). Moreover, the higher stone content in mounds (Fig. 2.3b) can also decrease the infiltration rate (Brakensiek and Rawls, 1994). Analyses of soil texture showed a greater clay content in pits than in mounds (Fig. 2.3a) which also explains the greater soil moisture in pits as fine textured soils have a larger water holding capacity. This accumulation of clay in pits is linked to microtopography as the soil erosion process leads to the accumulation of fine particles downslope. (Enoki et al., 1996 ; Pachepsky et al., 2001). Unlike most studies that compared the volumetric water content of pits and mounds, we performed soil water potential measurements with tensiometers, which allow us to assess soil water availability. Soil water potential measurements describe water availability from a biological standpoint by integrating the effect of the soil texture as water molecules bond more strongly to fine clay particles than to coarse sand particles. Overall, our results show that soil water availability during the summer was greater in pits than in mounds (Fig. 2.3d).

2.4.2 Microtopography influences fine root growth but not morphology

Table 2.4 summarizes the effect of variables of interest considered in the present study on fine root growth and morphology. First and foremost, results of this study concern the effect of microtopography. Fine root growth was greater in mounds than in pits as shown by both in-depth daily production (Fig. 2.6a-b) and standing crop (Fig. 2.6c-d) measurements, thus supporting hypothesis 1 regarding the effect of microtopography on the fine root system. We observed this effect despite the fact that stony soils, such as those found in mounds, might limit root development (Poesen and Lavee, 1994). Many studies have shown that mounds create favorable conditions for seed germination and sapling establishment in temperate forests (Šamonil et al., 2016 ; Simon et al., 2011) while very little work has been done on the effect of microtopography on fine root development of mature trees, thus offering little comparison to the present work. Still, on a larger scale, Enoki et al. (1996) compared the fine root standing crop at various topographic positions over a 60 m long hillside of a black pine plantation and, similar to our results, the fine root standing crop at upslope sites was greater than at downslope sites.

Table 2.4: Summary of the effect of microtopography, tree species and rainfall exclusion on the fine root system. The letter (d) indicates a depth dependent relationship and thus an influence on root vertical distribution.

		Effect of microtopography and species			
		Pit	Mound	*Bitternut Hickory*	*Sugar maple*
Environmental conditions	**Variable**				
Water availability	Soil water potential	+	–	=	=
Root trait category	**Variable**				
Growth	Standing crop	–	+	–	+
	Daily production	– (d)	+ (d)	– (d)	+ (d)
Morphology	SRL of standing crop	=	=	=	=
	SRL of daily production	=	=	=	=

In our study, greater fine root growth in mounds concurred with a lower water availability (Fig. 2.3d). One potential explanation could be that trees in mounds, develop a more extensive root system to avoid water limitations, similar to a drought avoidance strategy observed for trees adapted to arid climatic conditions (W. Chen et al., 2013 ; Comas et al., 2012 ; Hartmann, 2011). Other factors could also explain the more extensive root system of trees in mounds than in pits. Given our study was conducted during a particularly wet year, fine root growth in pits could also have been limited by the water table depth, which we found to be particularly high at the first sampling period. In a global synthesis of root observations, Fan et al. (2017) showed that the rooting depth is strongly related to the topographic position and roots in poorly drained valley bottoms were constrained by the water table depth and tended to be shallow and wide. Indeed, the accumulation of meltwater in pits could lead to saturated conditions that limit root development given anoxic conditions (Fan et al., 2017). Finally, soil texture also varied with microtopography and we observed a greater clay content in pits (Fig. 2.3a) which might have restricted fine root growth. A clayey soil is very compact, and roots cannot grow in a soil too dense (Veihmeyer and Hendrickson, 1948). As a result, root density tends to decrease with soil structural stability which is strongly related to clay content (Bréda et al., 1995) and an accumulation of roots tends to occur above clay layers (Bouten et al., 1992).

Although this study focused on assessing the effect of microtopography on various fine root traits, we did not assess if these traits translate into a competitive advantage for trees. In dry years, we could expect pits to have a greater water availability than mounds, which would minimize the exposure to water stress. For example, pits can offer a hydrologic microrefugia for vegetation to withstand dry periods (McLaughlin et al., 2017). On the other hand, by investing in the growth of their fine root system, trees in mounds may be better equipped to withstand water limitations. Indeed, Valtera and Schaetlz (2017) suggested that trees in mounds could potentially extend their root system to pits and have the double benefit of tapping the pit water supply during dry periods while the mound portion of their root system can avoid periods of prolonged wetness associated with pits. This could explain the presence of larger trees in mounds than in pits, as shown for sugar maple (Šamonil et al., 2016) and European beech (Šebková et al., 2012). Overall, more research is needed to understand how the interacting influence of microtopography on soil moisture and fine root development influences the resistance of trees to drought.

While we found growth traits (standing crop, daily production) to be significantly influenced by microtopography, fine root morphology was not. Indeed, the SRL of both the standing crop and daily production did not vary between mounds and pits despite differences in water availability. Differences in water availability between pits and mounds may not be strong enough to generate differences in SRL of fine roots.

Moreover, as explanatory variables in our models did not explain a large proportion of the SRL variance, other factors that we did not measure may explain a more important role than microtopography. The important difference between the SRL values of production and standing crop we observed could be explained by younger roots on average in growth chambers.

Our mean standing crop values for mass (1341 $mg.dm^{-3}$ at 0-20 cm deep and 427 $mg.dm^{-3}$ at 20-40 cm deep) and length (2741 $cm.dm^{-3}$ at 0-20 cm deep and 800 $cm.dm^{-3}$ at 20-40 cm deep) are in line with other studies using soil cores which give us confidence in our work. For example, Bauhus and Messier (1999) and Rytter (1999) found a length of standing crop below 5000 $cm \cdot dm^{-3}$ for deciduous trees which is comparable to the range of values we observed. Moreover, Jackson et al. (1997) found an average mass of fine root standing crop of 1470 $mg.dm^{-3}$ and an average length of 1800 $cm.dm^{-3}$ for temperate deciduous forest. However, we could not find any study using soil pit to evaluate fine root production which makes it difficult to compare our production values to other results. Regarding SRL, once again, our values are comparable to those in other studies. Bauhus and Messier (1999) found SRL values of fine roots from deciduous trees between 18 and 36 $m \cdot g^{-1}$ for standing crop and between 24 and 56 $m \cdot g^{-1}$ for production via ingrowth cores.

2.4.3 Species influences fine root growth and vertical distribution but to a lesser degree than microtopography

Few studies have analyzed the root system in mature mixed forests, and therefore little is known about the variation between species, especially regarding fine root production. In our study, we observed differences at the species level, with a larger daily production at greater depths (20-30 and 30-40 cm) and a larger standing crop for sugar maple than for bitternut hickory. In terms of similarities, both species have a similar maximum trunk growth rate (Burns and Honkala, 1990 ; Comas and Eissenstat, 2004), with a larger accumulation of biomass for bitternut hickory at a young age (Doyon et al., 1998).

From the start, we would thus expect root growth rates of similar magnitudes between the two species. Both species are also characterized by fine roots of thin diameter (W. Chen et al., 2018) thus facilitating root exploration similarly for sugar maple and bitternut hickory. In terms of differences, the two species have developed different symbiosis with mycorrhizae. Sugar maple is colonized intracellularly by arbuscular mycorrhizal fungi (AM) and bitternut hickory is colonized extracellularly by ectomycorrhizal fungi (EM) (W. Chen et al., 2018 ; Comas et al., 2014). These differences could generate differences in architectural root characteristics as branching intensity or extension (Comas and Eissenstat, 2009). EM mycorrhizae extend further in the soil than AM mycorrhizae (Querejeta et al., 2007). As a result, trees associated with EM mycorrhizae, like bitternut hickory, may rely more on fungi development than fine roots development (Comas and Eissenstat, 2009). This could be an explanation for the species-level differences observed in our study.

The present study showed that local environmental conditions, in this case microtopography, had a greater influence on fine root production at medium depth (20-40 cm) than tree species (Table 2.3). This finding agrees with Weemstra et al. (2016) who argued against an exclusive focus on root traits, without any consideration on environmental conditions, when studying belowground resource strategies. Both climatic and soil conditions have been shown to play an important role in mediating drought (D'Orangeville et al., 2018 ; Phillips et al., 2016), with in fact, mean species values of aboveground traits being poor predictors of drought sensitivity in temperate forests (D'Orangeville et al., 2018). Overall, we still have a limited understanding of the belowground trait variations across environmental gradients (Laliberté, 2017) and this study helped address this gap by showing that microtopography is an important driver of fine root growth and vertical distribution at the local scale. We calculated that the microtopographic effect on daily production was stronger than the species effect (Table 2.3). We cannot conclude about standing crop because microtopographic effect appears stronger for the length and species effect appears stronger for the mass.

2.4.4 Rainfall exclusion reduced soil moisture but not sufficiently to produce major stress

Our rainfall exclusion experiment successfully reduced the soil water content and potential (Fig. 2.4). However, the response of fine roots to this stress was weak. Overall, the standing crop decreased slightly, and we observe a reduction between control trees and trees with rainfall exclusion of 13% and 10% for length and mass respectively (Fig. 2.5), supporting in part hypothesis 2, while the daily production was not impacted. While we observed a modest reduction in the standing crop, we observed no differences between pits and mounds which does not support hypothesis 2. Under drought conditions, a decrease in standing crop is typically observed in boreal (Cudlin et al., 2007) and temperate forests (Anderegg, 2012 ; Cudlin et al., 2007 ; Konôpka et al., 2007 ; Meier and Leuschner, 2008a). The effect of drought on the fine root daily production has been less studied, but a few studies have observed a decrease in temperate forests under severe stress (Konôpka et al., 2007 ; Zang et al., 2014). In the present study, the rainfall exclusion experiment only induced a mild stress. Indeed, the soil potential reached an average of -45 kPa at the third sampling period, far from the permanent wilting point (-1500 kPa). The wet spring 2017 led to an important accumulation of water in the soil, which could have attenuated the effect of the rainfall exclusion experiment. Moreover, we only measured the response of fine roots over a short period, immediately after the rainfall exclusion although drought-induced damage to tree organs may lead to long-term responses (Anderegg, 2012 ; Bréda et al., 2006). A five months study might have been too short to observe a strong signal. (Asbjornsen et al., 2018). Short term rainfall exclusion experiments lasting less than four years are relatively common, and more research is needed to understand the long-term response to drought (Asbjornsen et al., 2018 ; Hoover et al., 2018).

2.4.5 Limitations of the study

In the present study, we sampled roots at a distance equivalent to two thirds of the tree crown from the base of the tree. An important assumption of this study is that fine roots belong to trees selected based on their microtopographic position (mound or pit) and species (bitternut hickory or sugar maple). As such, samples may also include fine roots from understory vegetation or adjacent trees. While we cannot link fine roots to selected trees in terms of species, we are confident that a major proportion of them were from the tree we sampled as the soil pits was closer to it than any other trees.

Although a better understanding of belowground processes is essential to determine the response of forests to drought, sampling of fine roots remains a challenging task. In this study, we measured the fine root standing crop using soil cores. This method has been used for decades (Yuan and Chen, 2012) but it remains a laborious task especially on stony soils. Moreover, the small sampling volume does not necessarily reflect the spatial heterogeneity, although we minimize this by collecting several cores per tree. Despite certain limitations, sampling the standing crop with soil cores remained the best compromise given the time and resources of the study as this approach remains more precise than indirect methods based on allometry (Addo-Danso et al., 2016 ; Vogt et al., 1998).

We measured the fine root production using a growth chamber, a method widely used given its low cost and ease of deployment in the field. However, with this sampling method, we created injuries on roots and our measurements could have been impacted. Like all studies using this method, we also assumed that the soil disturbance had a minimal effect on root production. We used sand to fill in growth chambers, a medium facilitating root growth but not representative of surrounding soil conditions (Vogt et al., 1998). This is a common issue with growth chambers but using sand as a fill-in medium highly facilitates root sampling and processing thus improving accuracy. The use of minirhizotrons has been recommended to study fine root production (Addo-

Danso et al., 2016). While soil disturbance is indeed reduced with the use of minirhizotrons, this method remains expensive and could not be implemented given the large number of trees (n = 128) in the present study. Although it is a non-destructive method, minirhizotrons only provide visual data and it is difficult to identify the dead roots. The user also has to convert the minirhizotron data to root biomass measures (Ahrens et al., 2014 ; Lukac, 2012) which was not necessary with our growth chamber. The fine root growth chamber that we specifically designed for this study had a volume of assessment that was way greater than what has been used in most of the other studies in the literature using a similar system (Côté et al., 1998), which give us a certain confidence in the values obtained for characterizing fine root daily production. As fine root turnover may be very fast (Hendrick and Pregitzer (1993) found a mortality rate between 0.25 and 0.41 % per day during the growing season for sugar maple), we are aware that a portion of the production may not have been captured because of the sampling frequency we used (9 weeks between sampling in average) and that those numbers are probably an underestimation.

We performed the rainfall exclusion experiment over a 3.65 m radius around trees. However, lateral roots of trees can spread more than 10 m around trees (Schenk and Jackson, 2002). The construction of trenches would have minimized water subsidies from roots extending beyond the rainfall exclusion but would have disturbed root development, which was our main variable of interest.

Finally, a study focusing only on fine roots does not inform us on the health status of trees and a "whole-tree approach" would be more relevant to consider advantages and disadvantages of root traits in case of water stress. Droughts may also occur successively for several years and a longer-term experiment would be necessary to better understand the response of trees.

2.5 Conclusion

To our knowledge, this study is the first one to link microtopography to fine root production and standing crop of mature trees up to a depth of 40 cm. We observed a strong relation between environmental conditions and belowground processes with trees in mounds developing a more extensive fine root system than trees in pits. Although we still do not know how root traits influence the resistance of trees to drought (Laliberté, 2017), this study is a first step in a better understanding of the interaction between environmental conditions and root traits. The importance of the effect size we observed let us suggest that different acclimations of the fine root system to micro-environmental conditions may play a crucial role in tree survival.

CHAPITRE III

CONCLUSION GÉNÉRALE

Notre étude avait pour but de mieux cerner la vulnérabilité des forêts au stress hydrique généré par les sécheresses. La compréhension de cette vulnérabilité des forêts passe par une compréhension à l'échelle de l'arbre et des mécanismes à l'origine de leur réponse au stress. Alors que la plupart des études sur le sujet portent sur les parties aériennes des arbres, la présente étude effectue une contribution importante aux connaissances actuelles en étudiant les traits racinaires, particulièrement importants pour comprendre la vulnérabilité des arbres à la sécheresse étant donné le rôle des racines fines dans le prélèvement en eau.

Dans un premier temps, cette recherche démontre l'acclimatation différentiée du système racinaire des arbres face à des conditions micro-environnementales contrastées. En effet, nous avons observé que les monticules, plus secs et moins argileux que les creux, présentaient des arbres aux systèmes racinaires plus développés (production en profondeur et biomasse plus élevées). L'effet de la microtopographie sur l'acclimatation de semis est assez étudié, mais cette recherche effectue une contribution importante en étudiant des arbres matures en milieu naturel. L'acclimatation différenciée du système racinaire selon les conditions de site pourrait influencer la résistance des arbres à la sécheresse. Des études supplémentaires sont toutefois nécessaires pour évaluer les avantages que les traits racinaires étudiés confèrent réellement aux arbres face à la sécheresse. Par son effet sur l'humidité du sol, la microtopographie influence l'exposition à la sécheresse, avec une exposition moindre attendue dans les creux que sur les monticules. L'effet combiné de la microtopographie sur l'exposition (humidité du sol) et la sensibilité (traits racinaires) des arbres à la sécheresse reste toutefois à être évaluée et s'avère une étape importante pour comprendre le rôle de la microtopographie dans la vulnérabilité des arbres à la sécheresse. En effet, les creux semblent faire office de micro-refuges hydriques, mais limitent toutefois le développement racinaire et donc pourraient, par contradiction, favoriser la vulnérabilité des arbres à la sécheresse. Par ailleurs, cette recherche s'est exclusivement concentrée sur l'étude des racines fines et il serait pertinent dans le futur de mener une évaluation plus globale de l'individu dans son ensemble (composantes aériennes et souterraines) afin de bien saisir l'effet de la microtopographie sur la vulnérabilité des arbres à la sécheresse.

Dans un deuxième temps, l'expérience d'exclusion des précipitations a permis de diminuer la teneur en eau volumétrique ainsi que le potentiel matriciel du sol, mais n'a toutefois pas permis la création d'un stress hydrique important. Cette disponibilité en eau légèrement réduite n'a eu que peu d'effet sur le système racinaire ; seule une légère diminution de la biomasse racinaire a été observée, quelle que soit la position microtopographique.

Finalement, cette étude a permis de montrer que l'érable à sucre possède un système racinaire plus développé (production en profondeur et biomasse plus élevées) que le caryer cordiforme. L'effet de la microtopographie reste cependant plus important que l'effet espèce en ce qui concerne la production de racines fines. Ces résultats soulignent l'importance des conditions environnementales dans l'étude de la vulnérabilité des arbres à la sécheresse, et ce, malgré le large intérêt porté à une approche basée sur l'étude des traits propres aux espèces (Albert et al., 2011 ; Weemstra et al., 2016). Les traits des parties aériennes des arbres constituent de faibles indicateurs de la sensibilité à la sécheresse en forêt tempérée (D'Orangeville et al., 2018) par rapport aux conditions climatiques et pédologiques (D'Orangeville et al., 2018 ; Phillips et al., 2016). Pour le moment, notre compréhension du rôle des traits racinaires dans la sensibilité des arbres à la sécheresse demeure assez limitée (Laliberté, 2017), mais cette étude pose un premier jalon en permettant une meilleure compréhension de l'interaction entre les conditions environnementales et les traits racinaires.

ANNEXE A

COORDINATES OF THE SAMPLING SITES

Table S1: Geographical coordinates of the 16 sampling sites in the study area, Vallée-du-Haut-Saint-Laurent, Quebec, Canada.

Site	Latitude	Longitude
1	45.04616	-74.21179
2	45.32613	-74.24348
3	45.13119	-74.06960
4	45.06943	-73.77539
5	45.32402	-74.23943
6	45.32411	-74.25765
7	45.10557	-74.15448
8	45.05960	-73.76269
9	45.04676	-74.21446
10	45.31196	-74.44855
11	45.09050	-74.23085
12	45.10655	-74.15833
13	45.09790	-74.04284
14	45.09863	-74.04635
15	45.31611	-74.43917
16	45.31051	-74.45145

ANNEXE B

MODELS DESCRIBING CLAY CONTENT AND STONE CONTENT

Table S2: Generalized linear mixed model describing clay content proportion as a function of soil depth (10, 30 cm) and microtopography (pit and mound).

Beta (link=logit)

Predictors	**Estimates**	**Confidence interval**	**Z-value**	**P-Value**
Intercept (Depth 10 cm, Pit)	-1,532	-1,834 – -1,230	-9,938	**<0,001**
Depth 30 cm	0,535	0,244 – 0,826	3,608	**<0,001**
Mound	-0,501	-0,839 – -0,164	-2,911	**0,004**
Mound * Depth 30 cm	-0,459	-0,919 – -0,000	-1,961	**0,0498**

Table S3: Generalized linear mixed model describing stone content proportion as a function of microtopography (pit and mound).

Beta (link=logit)

Predictors	**Estimates**	**Confidence interval**	**Z-value**	**P-Value**
Intercept (Pit)	-2,309	-2,745 – -1,873	-10,371	**<0,001**
Mound	0,905	0,664 – 1,146	7,362	**<0,001**

ANNEXE C

MODEL DESCRIBING SOIL WATER CONTENT

Table S4: Generalized linear mixed model describing soil water content proportion as a function of soil depth (15, 35 cm), tree species (ERS - sugar maple and CAC - bitternut hickory), microtopography (pit and mound), rainfall exclusion treatment (control and rain exclusion) and sampling period (SP1 – mean DOY =195, SP2 – mean DOY = 212, SP3 – mean DOY = 238 and SP4 – mean DOY = 302).

Beta (link=logit)

Predictors	**Estimates**	**Confidence interval**	**Z-value**	**P-Value**
Intercept (Depth 15 cm, SP1, Control, Pit, CAC)	-0.549	-0.780 – -0.319	-4.669	**<0.001**
Depth 35 cm	-0.051	-0.071 – -0.031	-5.018	**<0.001**
Rain exclusion	-0.045	-0.193 – 0.102	-0.603	0.547
SP2	-0.077	-0.405 – 0.251	-0.459	0.646
SP3	-0.363	-0.701 – -0.024	-2.102	**0.036**
SP4	-0.288	-0.615 – 0.039	-1.726	0.084
Mound	-0.763	-0.910 – -0.615	-10.127	**<0.001**
ERS	-0.059	-0.112 – -0.006	-2.176	**0.030**
Rain exclusion * SP2	0.016	-0.193 – 0.225	0.153	0.878
Rain exclusion * SP3	-0.201	-0.411 – 0.009	-1.874	0.061
Rain exclusion * SP4	-0.389	-0.600 – -0.179	-3.628	**<0.001**
Rain exclusion * Mound	0.049	-0.161 – 0.260	0.457	0.647
SP2 * Mound	-0.008	-0.218 – 0.201	-0.077	0.938
SP3 * Mound	0.066	-0.144 – 0.276	0.614	0.539
SP4 * Mound	0.091	-0.119 – 0.301	0.849	0.396
Rain exclusion * SP2 * Mound	0.006	-0.293 – 0.304	0.037	0.970
Rain exclusion * SP3 * Mound	-0.179	-0.481 – 0.122	-1.165	0.244
Rain exclusion * SP4 * Mound	-0.165	-0.466 – 0.136	-1.073	0.283

ANNEXE D

MODEL DESCRIBING SOIL WATER POTENTIAL

Table S5: Generalized linear mixed model describing absolute values of soil water potential as a function of soil depth (15, 45 cm), tree species (ERS - sugar maple and CAC - bitternut hickory), microtopography (pit and mound), rainfall exclusion treatment (control and rain exclusion) and sampling period (SP1 – mean DOY =195, SP2 – mean DOY = 212, SP3 – mean DOY = 238 and SP4 – mean DOY = 302).

Negative binomial (link= log)

Predictors	**Estimates**	**Confidence interval**	**Z-value**	**P-Value**
Intercept (Depth 15 cm, SP1, Control, Pit, CAC)	1.562	0.986 – 2.138	5.317	**<0.001**
Depth 45 cm	-0.192	-0.290 – -0.093	-3.819	**<0.001**
Rain exclusion	0.064	-0.434 – 0.563	0.253	0.800
SP2	0.261	-0.516 – 1.038	0.659	0.510
SP3	0.893	0.077 – 1.709	2.145	**0.032**
SP4	0.165	-0.643 – 0.972	0.400	0.689
Mound	1.224	0.781 – 1.667	5.413	**<0.001**
ERS	-0.025	-0.164 – 0.113	-0.357	0.721
Rain exclusion * SP2	-0.178	-0.851 – 0.495	-0.518	0.605
Rain exclusion * SP3	0.844	0.225 – 1.462	2.674	**0.007**
Rain exclusion * SP4	0.963	0.293 – 1.634	2.816	**0.005**
Rain exclusion * Mound	-0.211	-0.838 – 0.416	-0.659	0.510
SP2 * Mound	-0.457	-1.060 – 0.146	-1.485	0.137
SP3 * Mound	-0.502	-1.076 – 0.072	-1.713	0.087
SP4 * Mound	-0.893	-1.537 – -0.248	-2.714	**0.007**
Rain exclusion * SP2 * Mound	0.356	-0.504 – 1.216	0.811	0.417
Rain exclusion * SP3 * Mound	-0.225	-1.022 – 0.571	-0.554	0.579
Rain exclusion * SP4 * Mound	0.528	-0.338 – 1.394	1.195	0.232

ANNEXE E

MODEL DESCRIBING THE EFFECT OF RAINFALL EXCLUSION ON FINE ROOT DAILY PRODUCTION

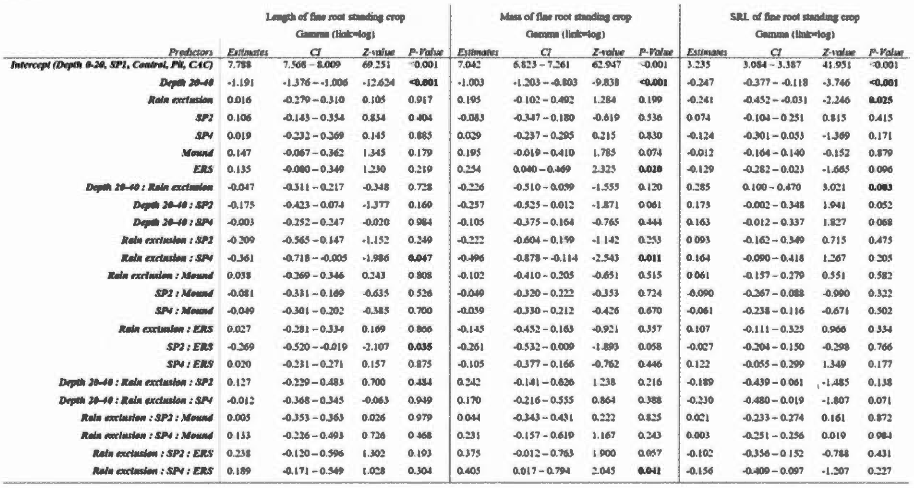
Table S6. Generalized linear mixed model describing the length ($cm\cdot dm^{-2}\cdot d^{-1}$), mass ($mg.dm^{-2}\cdot d^{-1}$) and SRL ($m\cdot g^{-1}$) of the fine root daily production as a function of soil depth (0-10, 10-20, 20-30 and 30-40 cm), tree species (ERS - sugar maple and CAC - bitternut hickory), microtopography (pit and mound), rainfall exclusion treatment (control and rain exclusion) and sampling period (SP2 – mean DOY = 212 and SP4 – mean DOY = 302).

	Length of daily fine root production Binomial negative (link=log)				Mass of daily fine root production Binomial negative (link=log)				SRL of daily fine root production Gamma (link=log)			
Predictors	*Estimates*	*CI*	*Z-value*	*P-Value*	*Estimates*	*CI*	*Z-value*	*P-Value*	*Estimates*	*CI*	*Z-value*	*P-Value*
Intercept (Depth 0-10, SP2, Control, Pit, CAC)	0.112	-0.294 – 0.518	0.543	0.587	-1.108	-1.502 – -0.714	-5.514	<0.001	3.723	3.541 – 3.905	40.024	<0.001
Depth 10-20	-0.138	-0.420 – 0.145	-0.954	0.340	0.030	-0.267 – 0.326	0.196	0.845	-0.214	-0.390 – -0.038	-2.382	**0.017**
Depth 20-30	-0.562	-0.878 – -0.246	-3.485	**<0.001**	-0.296	-0.623 – 0.032	-1.769	0.077	-0.368	-0.554 – -0.183	-3.891	**<0.001**
Depth 30-40	-1.671	-2.068 – -1.273	-8.241	**<0.001**	-1.422	-1.834 – -1.009	-6.748	**<0.001**	-0.262	-0.471 – -0.054	-2.463	**0.014**
SP4	0.030	-0.517 – 0.577	0.106	0.915	0.307	-0.067 – 0.682	1.608	0.108	-0.011	-0.262 – 0.240	-0.088	0.930
Rain exclusion	0.139	-0.234 – 0.511	0.729	0.466	0.117	-0.417 – 0.651	0.429	0.668	-0.273	-0.488 – -0.059	-2.498	**0.012**
Mound	0.929	0.559 – 1.298	4.928	**<0.001**	0.819	0.459 – 1.179	4.456	**<0.001**	0.137	-0.031 – 0.305	1.599	0.110
ERS	0.107	-0.258 – 0.471	0.573	0.566	0.068	-0.287 – 0.424	0.377	0.706	0.015	-0.150 – 0.181	0.183	0.855
Depth 10-20 : SP4	-0.063	-0.465 – 0.340	-0.305	0.761	0.219	-0.157 – 0.596	1.141	0.254	-0.009	-0.258 – 0.239	-0.074	0.941
Depth 20-30 : SP4	-0.181	-0.628 – 0.266	-0.792	0.428	0.232	-0.180 – 0.644	1.102	0.270	0.185	-0.073 – 0.443	1.404	0.160
Depth 30-40 : SP4	-0.152	-0.720 – 0.417	-0.523	0.601	0.307	-0.213 – 0.827	1.157	0.247	-0.005	-0.301 – 0.291	-0.033	0.974
Depth 10-20 : Rain exclusion	0.280	-0.083 – 0.644	1.511	0.131	-0.078	-0.494 – 0.339	-0.365	0.715	0.055	-0.187 – 0.296	0.444	0.657
Depth 20-30 : Rain exclusion	0.265	-0.140 – 0.670	1.282	0.200	-0.329	-0.791 – 0.133	-1.394	0.163	0.111	-0.142 – 0.363	0.858	0.391
Depth 30-40 : Rain exclusion	0.365	-0.142 – 0.872	1.410	0.159	-0.154	-0.742 – 0.434	-0.513	0.608	0.030	-0.247 – 0.308	0.215	0.830
SP4 : Rain exclusion	-0.133	-0.668 – 0.401	-0.488	0.625	-0.174	-0.708 – 0.360	-0.639	0.523	-0.028	-0.334 – 0.279	-0.177	0.859
SP4 : Mound	-0.550	-1.077 – -0.024	-2.049	0.041	-0.569	-0.880 – -0.258	-3.588	**<0.001**	-0.034	-0.269 – 0.201	-0.286	0.775
Rain exclusion : Mound	-0.525	-0.833 – -0.218	-3.350	**0.001**	-0.544	-1.055 – -0.034	-2.090	**0.037**	0.036	-0.152 – 0.224	0.373	0.709
SP4 : ERS	0.588	0.064 – 1.113	2.198	**0.028**	-0.131	-0.436 – 0.173	-0.845	0.398	-0.072	-0.305 – 0.160	-0.608	0.543
Rain exclusion : ERS	-0.103	-0.402 – 0.196	-0.676	0.499	0.585	0.076 – 1.093	2.255	**0.024**	0.069	-0.116 – 0.255	0.734	0.463
Depth 10-20 : SP4 : Rain exclusion	0.108	-0.420 – 0.635	0.400	0.689	0.033	-0.507 – 0.574	0.121	0.904	0.103	-0.240 – 0.446	0.588	0.557
Depth 20-30 : SP4 : Rain exclusion	0.539	-0.036 – 1.114	1.838	0.066	0.454	-0.132 – 1.040	1.518	0.129	0.045	-0.308 – 0.399	0.252	0.801
Depth 30-40 : SP4 : Rain exclusion	0.496	-0.230 – 1.222	1.338	0.181	0.423	-0.317 – 1.164	1.121	0.262	0.184	-0.208 – 0.576	0.919	0.358
SP4 : Rain exclusion : Mound	0.246	-0.194 – 0.685	1.096	0.273	0.249	-0.192 – 0.691	1.106	0.269	0.018	-0.246 – 0.282	0.136	0.892
SP4 : Rain exclusion : ERS	-0.420	-0.856 – 0.015	-1.894	0.058	-0.396	-0.835 – 0.043	-1.768	0.077	-0.001	-0.263 – 0.260	-0.010	0.992

ANNEXE F

MODEL DESCRIBING THE EFFECT OF RAINFALL EXCLUSION ON FINE ROOT STANDING CROP

Table S7: Generalized linear mixed model describing the length ($\mathrm{cm \cdot dm^{-3}}$), mass ($\mathrm{mg \cdot dm^{-3}}$) and SRL ($\mathrm{m \cdot g^{-1}}$) of the fine root standing crop as a function of soil depth (0-20 and 20-40 cm), tree species (ERS - sugar maple and CAC - bitternut hickory), microtopography (pit and mound) rainfall exclusion treatment (control and rain exclusion) and sampling period (SP1 – mean DOY =195, SP2 – mean DOY =212 and SP4 – mean DOY = 302).

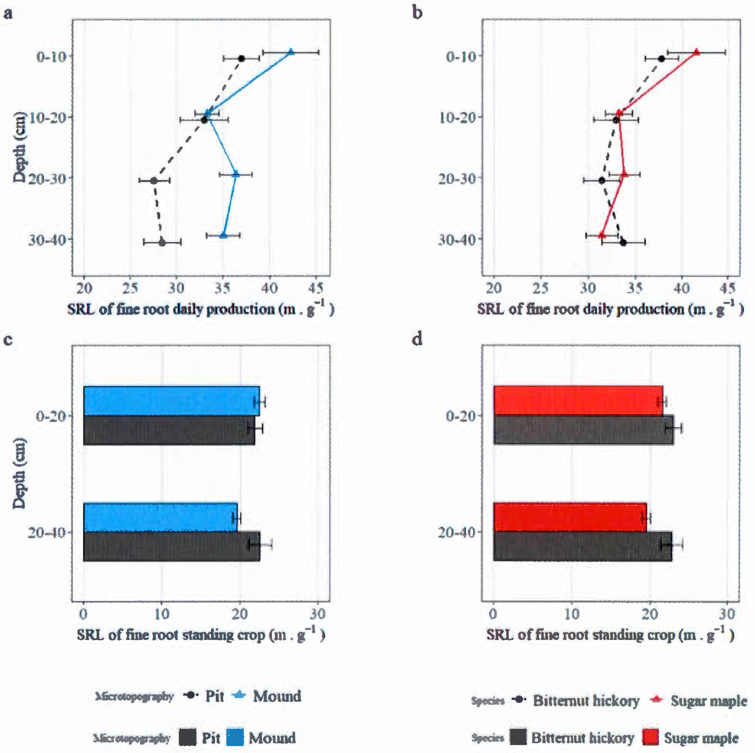


	Length of fine root standing crop Gamma (link=log)				**Mass of fine root standing crop Gamma (link=log)**				**SRL of fine root standing crop Gamma (link=log)**			
Predictors	*Estimates*	*CI*	*Z-value*	*P-Value*	*Estimates*	*CI*	*Z-value*	*P-Value*	*Estimates*	*CI*	*Z-value*	*P-Value*
Intercept (Depth 0-20, SP1, Control, Pit, CAC)	7.788	7.568 – 8.009	69.251	<0.001	7.042	6.823 – 7.261	62.947	<0.001	3.235	3.084 – 3.387	41.951	<0.001
Depth 20-40	-1.191	-1.376 – -1.006	-12.624	**<0.001**	-1.003	-1.203 – -0.803	-9.838	**<0.001**	-0.247	-0.377 – -0.118	-3.746	**<0.001**
Rain exclusion	0.016	-0.279 – 0.310	0.105	0.917	0.195	-0.102 – 0.492	1.284	0.199	-0.241	-0.452 – -0.031	-2.246	**0.025**
SP2	0.106	-0.143 – 0.354	0.834	0.404	-0.083	-0.347 – 0.180	-0.619	0.536	0.074	-0.104 – 0.251	0.815	0.415
SP4	0.019	-0.232 – 0.269	0.145	0.885	0.029	-0.237 – 0.295	0.215	0.830	-0.124	-0.301 – 0.053	-1.369	0.171
Mound	0.147	-0.067 – 0.362	1.345	0.179	0.195	-0.019 – 0.410	1.785	0.074	-0.012	-0.164 – 0.140	-0.152	0.879
ERS	0.135	-0.080 – 0.349	1.230	0.219	0.254	0.040 – 0.469	2.325	**0.020**	-0.129	-0.282 – 0.023	-1.665	0.096
Depth 20-40 : Rain exclusion	-0.047	-0.311 – 0.217	-0.348	0.728	-0.226	-0.510 – 0.059	-1.555	0.120	0.285	0.100 – 0.470	3.021	**0.003**
Depth 20-40 : SP2	-0.175	-0.423 – 0.074	-1.377	0.169	-0.257	-0.525 – 0.012	-1.871	0.061	0.173	-0.002 – 0.348	1.941	0.052
Depth 20-40 : SP4	-0.003	-0.252 – 0.247	-0.020	0.984	-0.105	-0.375 – 0.164	-0.765	0.444	0.163	-0.012 – 0.337	1.827	0.068
Rain exclusion : SP2	-0.209	-0.565 – 0.147	-1.152	0.249	-0.222	-0.604 – 0.159	-1.142	0.253	0.093	-0.162 – 0.349	0.715	0.475
Rain exclusion : SP4	-0.361	-0.718 – -0.005	-1.986	**0.047**	-0.496	-0.878 – -0.114	-2.543	**0.011**	0.164	-0.090 – 0.418	1.267	0.205
Rain exclusion : Mound	0.038	-0.269 – 0.346	0.243	0.808	-0.102	-0.410 – 0.205	-0.651	0.515	0.061	-0.157 – 0.279	0.551	0.582
SP2 : Mound	-0.081	-0.331 – 0.169	-0.635	0.526	-0.049	-0.320 – 0.222	-0.353	0.724	-0.090	-0.267 – 0.088	-0.990	0.322
SP4 : Mound	-0.049	-0.301 – 0.202	-0.385	0.700	-0.059	-0.330 – 0.212	-0.426	0.670	-0.061	-0.238 – 0.116	-0.671	0.502
Rain exclusion : ERS	0.027	-0.281 – 0.334	0.169	0.866	-0.145	-0.452 – 0.163	-0.921	0.357	0.107	-0.111 – 0.325	0.966	0.334
SP2 : ERS	-0.269	-0.520 – -0.019	-2.107	**0.035**	-0.261	-0.532 – 0.009	-1.893	0.058	-0.027	-0.204 – 0.150	-0.298	0.766
SP4 : ERS	0.020	-0.231 – 0.271	0.157	0.875	-0.105	-0.377 – 0.166	-0.762	0.446	0.122	-0.055 – 0.299	1.349	0.177
Depth 20-40 : Rain exclusion : SP2	0.127	-0.229 – 0.483	0.700	0.484	0.242	-0.141 – 0.626	1.238	0.216	-0.189	-0.439 – 0.061	-1.485	0.138
Depth 20-40 : Rain exclusion : SP4	-0.012	-0.368 – 0.345	-0.063	0.949	0.170	-0.216 – 0.555	0.864	0.388	-0.230	-0.480 – 0.019	-1.807	0.071
Rain exclusion : SP2 : Mound	0.005	-0.353 – 0.363	0.026	0.979	0.044	-0.343 – 0.431	0.222	0.825	0.021	-0.233 – 0.274	0.161	0.872
Rain exclusion : SP4 : Mound	0.133	-0.226 – 0.493	0.726	0.468	0.231	-0.157 – 0.619	1.167	0.243	0.003	-0.251 – 0.256	0.019	0.984
Rain exclusion : SP2 : ERS	0.238	-0.120 – 0.596	1.302	0.193	0.375	-0.012 – 0.763	1.900	0.057	-0.102	-0.356 – 0.152	-0.788	0.431
Rain exclusion : SP4 : ERS	0.189	-0.171 – 0.549	1.028	0.304	0.405	0.017 – 0.794	2.045	**0.041**	-0.156	-0.409 – 0.097	-1.207	0.227

ANNEXE G

EFFECT OF MICROTOPOGRAPHY AND SPECIES ON THE SRL OF FINE ROOT PRODUCTION AND STANDING CROP

Figure S1: SRL of the fine root daily production (a,b) at four depths (0-10, 10-20, 20-30, 30-40 cm) and SRL of the fine root standing crop (c,d) at two depths (0-20 and 20-40 cm) in pits and mounds, and for sugar maple and bitternut hickory. Error bars represent the standard errors.



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