Collège Doctoral du Languedoc-Roussillon

THÈSE

Pour obtenir le grade de

Docteur

Délivré par Université Montpellier 2

Préparée au sein de l'école doctorale SIBAGHE
Et de l'unité de recherche AMAP ; IEES Paris

Spécialité : Ecosystèmes et Sciences Agronomiques

Présentée par Jean-Luc Maeght

L'influence de la variabilité climatique sur l'enracinement superficiel et profond d'arbres adultes en plantation: Les cas de l'hévéa (*hevea brasiliensis*) et du teck (*tectona grandis*) sous contraintes hydriques en Asie du sud-est.

Soutenue le 16 septembre 2014 devant le jury composé de

D. Alexia Stokes, DR , INRA (AMAP)	Directrice de thèse
D. Alain Pierret, CR, IRD (iEES-Paris)	Co-directeur de thèse
D. Mark Bakker, IR, INRA (Bordeaux Sciences Agro)	Rapporteur
D. Mathieu Javaux, Professeur, UCL Louvain	Rapporteur
D. Lionel Dupuy, CR, Hutton ac, UK	Examinateur
D. Jean-Luc Chotte, DR , IRD (Eco&Sol)	Président du jury

UNIVERSITÉ MONTPELLIER 2
SCIENCES ET TECHNIQUES

Quand tu arrives en haut de la montagne, continue de grimper.
Dix « on dit » ne valent pas ce que j'en vois !
Quand on est tout seul, il faut faire attention à ses pensées, quand on est en groupe il faut faire attention à ses paroles.
(Proverbes Laotiens)

Si la science évolue, c'est souvent parce qu'un aspect encore inconnu des choses se dévoile soudain.
(François Jacob)

Il suffit de nommer la chose pour qu'apparaisse le sens sous le signe.
(Léopold Sédar Senghor)

Un petit pas de plus et c'est un nouvel horizon qui s'ouvre.
Plus on prend le temps de regarder, plus on découvre de choses !

(Mon expérience)

Remerciements / Acknowledgements

First I would like to thank Alain Pierret, co–advisor of this research and all members and colleagues of IRD who gave me the desire and the means to work in the fascinating and obscure world of roots. Without them this work would not have been possible. I would also like to thank Corentin Clement for his help at all levels of this work during the past two years.

My thanks also goes out to my supervisor Alexia Stokes who accepted to support my work in an unusual context, with my double status as student and engineer at the IRD. I also thank warmly all the members of my thesis committee for their expert advice and patience. This is for Mr. Christian Dupraz, Mr. Thierry Fourcaud, Mr. Philippe Hinsinger, Mr. Christophe Jourdan, Mr. Xavier Raynaud and Mr. Loïc Pages.

I also want to thank the rapporteurs and jury members for accepting to join us at the end of this work. I thank them for their interest, their patient reading and for their defence of this thesis.

I would like to express my recognition to the Thai authorities (Land Development Department) and to the Laotian authorities (National Agriculture and Forestry Research Institut) for allowing this research on their soil, and to those responsible for IRD who provided me with the opportunity to complete this thesis.

I don't forget my family. I could have started with you, Sylvia, Elina, Loan and Solene who accompany me every day. I am infinitely grateful for your patience throughout this long journey devoted to successive research on literature, field works and time devoted to the writing of these pages. You were sometimes rightly jealous of this adventure, due to how much time I devoted to it. Thank you again for your patience...

Thank you for another great family formed by friends, colleagues from Thailand, Laos and many other nationalities. Thank you for your support and your perseverance during this long period of collecting data that's been difficult to access. The list is long and I can't mention you all. I thank especially Mr. Oloth, Santimaitrie, Wor, Thum, Supat, Mathilde, Mathieu, Lee, Phap, Louis, Ki, Bounsamaï, Loon, Ley, Sommay, Amendine, and Mr.Tan. I can assure you that these periods of joint activities will remain in my memory as rich experiences and I hope to have the opportunity to work with you again.

Thank you to Mr. Boris Rewald of Forest Ecology, Department of Vienna and Dylan Fischer faculty at Evergreen, USA for their support and advice.

I finally pay tribute to the many authors of the research I have discovered throughout this work and particularly the work done by Dr. Lore Kutschera (1917-2008) and Dr. John E. Weaver (1884-1956). Two remarkable and tireless scientists behind many original works, which demonstrate that with patience, perseverance and thoroughness, many aspects of root system description, are possible. They remain to me my models.

Résumé

L'influence de la variabilité climatique sur l'enracinement superficiel et profond d'arbres adultes en plantation: Les cas de l'hévéa (*hevea brasiliensis*) et du teck (*tectona grandis*) sous contraintes hydriques en Asie du sud-est.

Mots clefs :

Arbre adulte, plantation, Hévéa, Teck, racine, racine fine, racine profonde, dynamique racinaire, variabilité climatique, sécheresse, sol, eau, stock de carbone, environnement.

Le système racinaire, lien essentiel entre la plante et le sol quoi qu'essentiellement invisible, reste encore aujourd'hui peu étudié dans son ensemble. Les plantes étant ancrées au sol via leur système racinaire, leurs facultés d'adaptation et de survie sont donc très dépendantes de leurs capacités à savoir tirer profit de l'espace qui les entoure, notamment par l'intermédiaire de leur système racinaire. Certains arbres font néanmoins partie des plus grands et plus anciens êtres vivants de la planète, preuve s'il en est de leur capacité d'adaptation au milieu dans lequel ils poussent et aux changements environnementaux pouvant survenir dans le temps. Dans le cas des plantations, les contraintes anthropiques imposées se heurtent parfois aux limites de cette formidable capacité d'adaptation. Ces situations particulières offrent autant d'opportunités d'études que nous avons exploitées pour améliorer notre compréhension des nombreux paramètres susceptibles d'influencer le fonctionnement du système racinaire.

Pour appréhender un milieu aussi complexe, nous avons dû faire des choix tant du point de vue de la définition des objectifs visés que de celui des outils à développer et à leur mise en œuvre. Les travaux développés dans la première partie de cette thèse font l'objet de deux articles publiés et se concentrent sur une revue bibliographique des connaissances sur l'enracinement profond. Le rôle vital du système racinaire pour la plante est ainsi mis en avant ainsi que ses fonctions dans le continuum sol-plante-atmosphère. Son rôle essentiel, souvent sous-estimé dans le stockage du carbone, est également abordé. Les différentes techniques permettant d'accéder aux systèmes racinaires *in situ* sont passées en revue et nous

présentons la technique du puits d'accès que nous avons utilisé pour observer les racines jusqu'à 5 mètres de profondeur. Nous avons également développé nos propres outils de prise de vue par l'intermédiaire de scanner à plat ainsi qu'un outil d'analyse d'images (IJ_Rizo) aujourd'hui disponible en ligne.

Dans la deuxième partie du mémoire, nous nous consacrons à l'étude du système racinaire de l'hévéa adulte (*Hevea brasiliensis*) dans le nord-est de la Thaïlande. Premier producteur mondial de caoutchouc naturel, la Thaïlande a fortement développé ses plantations d'hévéas allant jusqu'à étendre son exploitation au-delà de sa zone climatique naturelle, dans des zones à fortes contraintes hydriques. Dans ce contexte, nous avons étudié la saisonnalité et la dynamique des racines fines pendant trois ans ainsi que leur contribution au cycle du carbone. Nous avons pu mettre en évidence la continuité de la dynamique racinaire indépendamment des périodes de défoliation mais en lien avec la saisonnalité de la pluviométrie. Nous avons également pu caractériser la faible différenciation de la dynamique racinaire de 0 à 4,5 mètres de profondeur dans un tel contexte.

La troisième partie de la thèse concerne l'étude du teck (*Tectona grandis)*, espèce endémique d'Asie du Sud-Est, et notamment du Laos dans la région de Luang Prabang. Le développement de sa culture sous forme de plantations mono-spécifiques se poursuit depuis les années 80. En appliquant la technique d'exclusion de pluie pendant 2 ans sur des arbres d'une plantation d'une vingtaine d'années, nous avons observé l'influence du régime de précipitations sur l'enracinement. Un arrêt pratiquement total de croissance des racines en surface et en profondeur a ainsi été mis en évidence. Nous concluons, dans le cas d'espèces à une forte dépendance à la ressource en eau de surface, à un impact direct sur l'état physiologique et une stagnation de la croissance des troncs. Certains individus ont démontré une capacité d'adaptation en modifiant leur cycle de foliation / défoliation accompagné d'une reprise de la croissance des troncs lors de la deuxième année du régime de sécheresse imposé. Nous avons également démontré l'importance de l'enracinement fin pour le stockage du carbone qui, dans ce contexte, représente plus de 45 % du carbone total, soit environ le double des données publiées dans la littérature.

Les données obtenues pour les espèces étudiées dans ce mémoire pourront être utilisées pour la modélisation de scenarios simulant le changement climatique et le changement d'usage des terres.

Abstract

Effects of climate variability on shallow and deep root growth of mature rubber (Hevea brasiliensis) and teak (Tectona grandis) trees in South East Asian plantations

Keywords:

Adult trees, plantation, rubber trees , teak trees, root, fine root, deep root, root dynamics, climate variability, drought, soil, water, carbon stock environment.

The root system is essential but essentially invisible. It is a vital link between the plant and the soil but remains largely unstudied as a whole. Plants are anchored to the soil through their root system; their adaptation and survival abilities are highly dependent on their ability to learn to take advantage of the space that surrounds them. Certain trees are nevertheless some of the largest and oldest living species on the planet- evidence of their ability to adapt to changes in their environment. Within managed anthropogenic constraints, particular species are vulnerable. It is clear that a wide range of parameters are likely to influence the root system and its operation, which offers many entry points to improve our understanding of a root's capacity for expansion, its dynamics, its role within the plant itself and within the soil plant atmosphere continuum. Available data on the extent and dynamics of plant roots includes several thousand references. However, the vast majority of these observations were made within the first meter of the soil profile. Data acquisition for the fine and/or deep roots is currently limited by constraints of time and financial resources. To overcome this lack of information, while trying to assess root dynamics under different environmental conditions, many models have been developed. However, it is still difficult to describe the complexity of root development in the community and to integrate its "plasticity".

In this context, any study to understand the root systems must continuously provide access to new information. To understand such a complex environment, we must work toward

establishing a definition of objectives and the tools necessary to develop and implement them. The work developed in the first part of this thesis is the subject of two articles and focuses on a literature review about deep roots. The vital role of the root system for the plant is well highlighted, as is its impact as a link within the atmosphere. We discuss the role of deep roots in carbon storage, which is critical and often underestimated. The different techniques for accessing the root systems in situ are also considered, and we present our access technique for observing the roots down to depths of five meters. We have also developed tools for shooting through a flatbed scanner and image analysis (IJ_Rizo) now available online.

In the second part of the thesis, we focus on the study of root systems of adult rubber trees (Hevea brasiliensis L. RRIM 600) in the northeast of Thailand. The world's largest producer of natural rubber, Thailand has greatly expanded its acreage to extend its operations beyond its natural climate zone, into areas of high water stress. In this context, we studied the seasonality and dynamics of fine roots for three years and their contribution to the carbon cycle. We were able to highlight the continuity of root dynamics during independent periods of defoliation, yet link these to the seasonality of rainfall. We were also able to characterize the low differentiation of root dynamics at 0 to 4.5 m of depth in this context.

The third part of the thesis concerns the study of teak particular to the region of Luang Prabang, Laos, where its development in the form of mono-specific plantations has continued since the 1980's. By applying the rain exclusion technique for 2 years on a plantation of twenty-year-old trees, we observed the influence of precipitation patterns. During the period of water stress, an almost total cessation of root growth, at the surface and significant depths, has been highlighted. We conclude that in the case of species with a high dependence on water resources there is a direct impact on the physiological state and stagnated trunk growth. Some individuals have demonstrated an ability to adapt by changing their foliation/defoliation cycle, accompanied by a resumption of trunk growth during the second year of imposed drought. We also demonstrated the importance of rooting as a means of carbon storage, which in this context represents more than 45% of total carbon- roughly double the amount published in other literature.

The data obtained for the species studied in this paper can be used for modelling scenarios simulating climate change and changing land use.

Table des matières

Remerciements / Acknowledgements 5

Résumé 7

Abstract 9

Liste des figures (hors articles): 13

Liste des photos : 14

Liste des annexes : 14

Liste des valorisations réalisées relatives aux thèmes traités dans la thèse. 15
Articles scientifiques 15
Chapitre de livres ou d'ouvrages de vulgarisation scientifique 15
Contributions à des congrès internationaux 15

Introduction générale 17
I.1 Racines profondes : faits, structure et interactions 20
I.1.1 Enracinement profond réalité et particularité *20*
I.1.2 Fonction des racines et rôles dans les processus de l'écosystème *27*
I.2 En conclusion, l'enracinement profond: Où en sommes-nous ? 35
I.3 Objectifs de la thèse 37
I.4 Références 39

Chapitre 1 : Revue de la littérature 45
1.1 Introduction 46
1.1.1 Références *50*
1.2 How to study deep roots – and why it matters: Article publié dans Frontiers in Plant Science, 2013 51
1.3 Conclusion 65

Chapitre 2 : L'hévéa dans le Nord-Est de la Thaïlande: éclairage sur la dynamique de l'enracinement de l'hévéa dans un contexte déficitaire en eau; implications pour la production de latex 67
2.1 Introduction 68
2.2 Differentiation of life spans of *Hevea brasiliensis* roots along a 4.5m deep soil profile in North East Thailand: article prévu pour Plant & Soil 71
2.3 Conclusion 91
2.3.1 Références *95*

Chapitre 3: *Tectonas grandis L* : Capacité d'adaptation à des propriétés édaphiques et climatiques fortement contrastées. 97
3.1 Introduction 98
3.1.1 Références *107*
3.2 Impact of near total throughfall exclusion on the above- and below-ground physiology of mature teak trees (*Tectonas grandis, L*) in Northern Laos: Article prévu pour New Phytologist 111
3.3 Conclusion 137
3.3.1 Dispositif expérimental : *137*

3.3.2 Connaissances apportées : *142*
3.3.3 Références *144*

Chapitre 4: Discussion, conclusion et perspectives **145**
4.1 Discussion générale 146
4.1.1 Les contraintes hydriques *146*
4.1.2 Le stockage de carbone *151*
4.1.3 Modélisation et perspectives *152*
4.1.4 Les recommandations agronomiques *154*
4.2 Conclusion générale *155*
4.3 Perspectives de recherches 156
4.4 Références *157*

5. Références Globales **161**

Annexes **181**
Annexe I: Logiciel personnalisé pour acquisition automatisée 181
Annexe II a: IJ_Rhizo : an open-source software to measure scanned images of root samles ; Article publié dans Plant & Soil, 2013 183
Annexe II b: IJ Rhizo: Supplementary section 193

Liste des figures (hors articles):

Figure 1: Enracinement maximum pour différentes espèces en (m), regroupé par biomes (Canadell et al. 1996) ____ *21*
Figure 2: Kuchera 1960 ____ *22*
Figure 3: Weaver 1927 ____ *22*
Figure 4: Structure des tiges, des racines de surface et des racines de profondes pour quatre espèces d'arbres (McElrone et al. 2004) ____ *25*
Figure 5: Rôles et fonction des racines dans les écosystèmes terrestres ____ *27*
Figure 6: Répartition globale des flux et forme de séquestration du carbone dans la biosphère terrestre (Esser G., Kattge J. and Sakalli A., 2011) ____ *30*
Figure 7: Processus décrivant l'influence des racines dans de nombreux modèles traitant de la végétation (Woodward 2000) ____ *34*
Figure 8: Description schématique du dispositif du puits d'accès et des fenêtres pour la prise d'images avec scanner à plat adaptés (Maeght & al. 2011) ____ *47*
Figure 9: Représentation de la boite d'accès (Rhizo-Box) permettant d'insérer à 45° un scanner plat pour la prise d'image sous rizières inondées (Maeght et al. 2007) ____ *48*
Figure 10 : A droite : image scannée de racines de teck prise dans une boite d'accès. A gauche : résultat du traçage des racines à l'aide des outils du logiciel libre Gimp. ____ *49*
Figure 11: localisation géographique et climatique de l'expérimentation sur l'hévéa ____ *70*
Figure 12: Localisation des arbres atteints de "barc necrosis" sur la parcelle; classement des arbres par diamètre (Do et al., 2011) ____ *95*
Figure 13: Distribution géographique naturelle du teck Asie ____ *103*
Figure 14: Coupes transversales de bois juvénile (à gauche) et de bois adulte ou bois parfait (à droite) (Bath et al., 2001) ____ *104*
Figure 15: Densités et circonférences des arbres de la zone d'étude avec en bleu, la zone de contrôle, en rouge la zone d'exclusion de pluie et en vert la zone irriguée; les disques de couleurs classifient les arbres en fonction de leur diamètre ____ *104*
Figure 16: Topographie de la zone d'étude, position des arbres et localisation des appareils de mesures. ____ *106*
Figure 17: Relation entre la taille des fichiers en format JPEG et la longueur des racines en mm réalisée sur plus de 1200 images ____ *142*

Liste des photos :

Photo 1: Plantation de teck au-dessus d'une paroi d'excavation au nord du Laos (A. Pierret) 17
Photo 2 : Prospection de racines profondes dans une grotte à 12 m de profondeur au Laos (A. Pierret , 2010). 45
Photo 3 : Insertion et positionnement d'un scanner plat pour la prise d'images racinaires sous plantation de teck (Maeght et al., 2012) 49
Photo 4: Dispositif de puits dans la plantation d'hévéas en saison sèche de la région de Buriram au nord-est de la Thaïlande (J.-L. Maeght) 67
Photo 5: Dispositif d'acquisition de données dans le puits et des capteurs sur un hévéa 70
Photo 6: Plantation d'hévéas en début de refoliation après défoliation totale (J.-L. Maeght) 93
Photo 7: Pratique de la saignée (D. Nandris) 94
Photo 8: Encoche en perte de production (D. Nandris) 94
Photo 9 : Hévéa en production (D. Nandris) 94
Photo 10 : Hévéa ne produisant plus de latex (D. Nandris) 94
Photo 11: Plantation de teck sur notre site d'étude 97
Photo 12: Teck âgé approximativement de 600 ans, mesurant 55 m de haut et 8 m de diamètre, dans la forêt de Pyin Oo Lwin, Myanmar (Myint 2009) 103
Photo 13 : Assemblage photos illustrant la zone d'exclusion de pluie avec tranchées, toiture et puits d'accès en profondeur 105
Photo 14: Tranchées en cours de réalisation (2.5 m de profondeur): mise en place des bâches d'étanchéités et rebouchages après collecte de racines 106
Photo 15: Jupe évitant l'écoulement de l'eau de pluie le long des troncs. 141
Photo 16: Dispositif de passerelles en bambous permettant d'effectuer les mesures au-dessus de la toiture. 141
Photo 17: Couverture foliaire dans la zone de contrôle (à gauche) et la zone isolée (à droite) à la même date 143
Photo 18: Feuilles récoltées en fonction des traitements. De haut en bas: zone irriguée, zone isolée, zone de contôle 144
Photo 19: 26-3-12-TB1-30, boite de surface, zone de contrôle, mars 2012 144
Photo 20: 26-4-12-TB1-30, boite de surface, zone de contrôle, avril 2012 144
Photo 21: Effet du brulis sous plantation de tecks adultes dans la région de Luang Prabang 145

Liste des annexes :

Annexe I : Logiciel personnalisé pour acquisition automatisée 181
Annexe II a: IJ_Rhizo: an open-source software to measure scanned images of root samles; Article publié dans Plant & Soil, 2013 183
Annexe II b: IJ Rhizo : Supplementary section 193

Liste des valorisations réalisées relatives aux thèmes traités dans la thèse.

Articles scientifiques

1. **Jean-Luc Maeght,** Boris Rewald and Alain Pierret. (2013) How to study deep roots – and why it matters. Frontiers in plant science 4:299. doi: 10.3389/fpls.2013.00299.
2. Pierret & Santimaitree Gonkhamdee & Christophe Jourdan & **Jean-Luc Maeght** (2013) IJ_Rhizo: an open-source software to measure scanned images of root samples. Plant Soil 373; 351-539. doi:10.1007/s11104-013-1795-9
3. Ayutthaya S.I.N., Do Frédéric, Pannangpetch K., Junjittakarn J., **Maeght Jean-Luc**, Rocheteau Alain, Cochard H. Water loss regulation in mature Hevea brasiliensis : effects of intermittent drought in the rainy season and hydraulic regulation. Tree Physiology, 2011, 31, p. 751-762. ISSN 1758-4469 doi : 10.1093/treephys/tpr058
4. Ayutthaya S. I. N., Do Frédéric, Pannengpetch K., Junjittakarn J., **Maeght Jean-Luc**, Rocheteau Alain, Cochard H. Transient thermal dissipation method of xylem sap flow measurement : multi-species calibration and field evaluation. Tree Physiology, 2010, 30 (1), p. 139-148. ISSN 0829-318X. doi : 10.1093/treephys/tpr020
5. **Maeght Jean–Luc**, Luely Nortourlee, F. Reboul-salze, Emmanuel Bourdon, Oloth. Sengtaheuanghoung, Bounsamay Soulileuth, Christian Hartmann, Alain Pierret. Khon Kaen AGR 39 : 291-294 (2011) Environmental impact of understorey management in Teak tree (Tectona grandis L.) plantations: A case study from Luang Prabang, Lao PDR.
6. Do Frédéric, Pierret Alain, Couteron Pierre, Lesturgez G., Boithias Laurie, Isarangkool Na Ayutthaya S., Junjittakarn J., Gonkhamdee S., **Maeght Jean-Luc**, Hartmann Christian, Nandris Daniel. Spatial distribution of Hevea brasiliensis trunk phloem necrosis within a plot : aggregation but no evidence of constraint on cumulated growth. Forest Pathology, 2010, 15 p. ISSN 1439-0329, Doi: 10.1111/j.1439-0329.2010.00640.x
7. Gonkhamdee S., **Maeght Jean-Luc**, Do Frédéric, Pierret Alain. Growth dynamics of fine Hevea brasiliensis roots along a 4.5-m soil profile. Khon Kaen Agriculture Journal, 2009, 37, p. 265-278.

Chapitre de livres ou d'ouvrages de vulgarisation scientifique

1. Pierret Alain, Hartmann Christian, **Maeght Jean-Luc**, Pagès Loïc. Biotic regulation : plants. In : Ritz K. (ed.), Young I. (ed.) Architecture and biology of soils : life in inner space. Wallingford : CAB International, 2011, p. 86-102. ISBN 9781845935320;

   http://bookshop.cabi.org/default.aspx?site=191&page=2633&pid=2183.

Contributions à des congrès internationaux

1. **Maeght, J.-L**., Henry des Tureaux, T., Sengtaheuanghoung, O., Stokes, A., Ribolzi, O., and Pierret, A. (Dundee 2012). Drought effect on teak tree (Tectona grandis) roots on carbon inputs and water uptake in a deep soil of northern Laos. in Roots to the Future 8th Symposium of the International Society of Root Research. Orale présentation.
2. Ivan Pietro, Catherine Roumet, John Kim, Alexia Stokes and the **Ecosfix Consortium**, (2012) ECOSFIX – Ecosystem services provided by root systems, in Roots to the Future 8th Symposium of the International Society of Root Research. Dundee 2012 Poster
3. **Maeght, J.-L.,** Pierret A. and Ecosfix consortium Ecosfix - Ecosystem Services of Roots – Hydraulic Redistribution,Carbon Sequestration and Soil Fixation; Journée Laos française de la recherche 19-21 11 2012.
4. **Maeght Jean Luc**, Santimaitree Gonkhamdee, Frédéric C. DO and Alain Pierret, International conférence Perth australie 10-2011. Poster : Fine root lenght and turnover : how much does soil depth matter ? A case study of rubber trees (hévéa brasiliensis) in NE Thailand.

Introduction générale



Photo 1: Plantation de teck au-dessus d'une paroi d'excavation au nord du Laos (A. Pierret)

La résilience des plantes face aux changements environnementaux, d'origine naturelle ou anthropique, est un paramètre important pour leur survie. Dans le contexte actuel de changement global, les plantes comme tous les êtres vivants, s'adaptent et mettent en œuvre des stratégies d'adaptation pour assurer leur survie face aux modifications de leur milieu. Malgré des moyens de déplacement limités, les plantes figurent pourtant parmi les êtres vivants les plus âgées qui peuplent la planète. Certaines plantes sont ainsi parvenues à développer des capacités d'adaptation remarquables ayant permis, notamment dans le cas des arbres les plus âgés, de vivre plusieurs milliers d'années! A titre d'exemple, le plus ancien *Pinus Longaeva* connu aux Etats-Unis est âgé de plus de 5000 ans. Parmi les arbres clonaux, l'âge d'un *Picea abies* en Suède a été évalué à 9500 ans. Le système racinaire relie la plante à la lithosphère; quoiqu'essentiellement invisible, il joue très certainement un rôle majeur dans la réponse de la plante aux contraintes environnementales. La capacité d'extension de ce système permettant l'exploitation des ressources est donc un élément essentiel à la vie de la plante. En retour, le système racinaire peut aussi avoir un impact sur son environnement direct et sur l'écosystème dont il fait parti par les liens qui les associe.

Du point de vue agronomique, le contexte agricole hérité de la « révolution verte » semble atteindre ses limites, notamment dans les pays en développement où les coûts liés à l'achat des intrants (engrais, produits phytosanitaires) deviennent prohibitifs et réduisent fortement les marges brutes de production. La « révolution doublement verte » avec le développement de nouveaux systèmes de culture, basés sur une utilisation raisonnée des services écosystémiques, reste à inventer et à mettre en place. Dans ce contexte, l'utilisation combinée de fonctions physiologiques complémentaires par le biais de l'association temporelle et spatiale d'espèces végétales représente une voie dont le potentiel demeure, pour l'essentiel, encore inexploité. Les services environnementaux peuvent potentiellement être tirés par l'association des caractéristiques complémentaires du système racinaire de différentes espèces, en particulier au niveau de l'utilisation des ressources en eau et du stockage du carbone, et pourraient ainsi apporter des réponses inédites dans l'optique du développement de pratiques agricoles et forestières durables.

Une meilleure connaissance de l'enracinement revêt, dans cette perspective, une importance nouvelle puisqu'elle est susceptible de contribuer à l'émergence de réponses durables face aux enjeux sociaux et environnementaux auxquels nous sommes aujourd'hui confrontés. De

nombreux obstacles restent encore à franchir car, bien que les informations disponibles sur les systèmes racinaires des plantes soient relativement conséquentes et regroupent plusieurs milliers de références, elles ne concernent, dans leur grande majorité, que des observations réalisées sur substrats artificiels ou en serres. D'autres études ont lieu en milieu naturel mais se limitent le plus souvent à la surface des profils de sol, étudiant quelques dizaines de centimètres du sol, n'atteignant que rarement le premier mètre. Pour autant, dans la plupart des cas, cette limite n'est pas liée à l'absence de racines plus profondes. Les travaux présentés dans ce mémoire tentent d'élucider les raisons qui ont favorisé jusqu'ici une vision « superficielle » de l'enracinement et d'apporter notre vision de l'enracinement dans sa globalité, en prêtant une attention particulière aux racines profondes.

Dans ce contexte, cette thèse propose tout d'abord de donner une vue globale des possibilités d'existence de l'enracinement profond et les implications majeures liées à la présence de racines profondes dans différents compartiments des écosystèmes. Cette première approche sur les questions fondamentales nous permet d'établir un état des connaissances et de mettre en relief les objectifs que nous souhaitons atteindre ici.

Sur la base d'une revue critique de la littérature, la première partie de la thèse fait l'état des connaissances sur l'enracinement profond. Cette étude bibliographique est complétée par une synthèse des techniques de terrain existantes pour étudier et mesurer les racines. Cette partie est présentée sous forme d'un article publié en 2013 dans Frontiers in Plant Science et intitulé « How to study deep roots – and why it matters ». Nous présentons ensuite l'outil d'analyse d'images que nous avons développé et validé pendant nos travaux. Cet outil fait l'objet d'un article publié dans Plant and Soil est intitulé « IJ_Rhizo: an open-source software to measure scanned images of root samples ». Plus technique, cet article figure dans son intégralité en annexe. Apres cette approche théorique et technique, les deuxième et troisième parties de cette thèse portent sur deux études de cas.

La deuxième partie est consacrée à l'étude de la dynamique de l'enracinement de l'hévéa en plantation dans une zone déficitaire en pluie du nord-est de la Thaïlande. Cette étude est présentée sous forme d'un article en préparation qui sera proposé dans la revue Plant and Soil: « Differentiation of life spans of *Hevea brasiliensis* roots along a 4.5m deep soil profile in North East Thailand».

La troisième partie est consacrée à une expérimentation d'exclusion de pluie dans une plantation de tecks au nord du Laos. Elle a pour but de mettre en évidence les conditions d'accès à l'eau et les capacités d'adaptation à la sécheresse de cet arbre originaire de la région et à forte valeur commerciale. L'article en préparation correspondant à ce travail et qui s'intitule «Impact of near total throughfall exclusion on the above- and below-ground physiology of mature teak trees (*Tectonas grandis, L*) in Northern Laos» sera proposé à la revue New Phytologist.

Finalement, nous concluons par une analyse critique des différents travaux présentés et une mise en perspective des conclusions auxquels nos travaux ont permis d'aboutir.

I.1 Racines profondes : faits, structure et interactions

En préambule au développement des différentes études présentées dans cette thèse, nous présentons les éléments clefs qui nous ont déterminés à développer des recherches sur l'enracinement profond, notamment sur l'ampleur de son existence, les propriétés particulières de la morphologie des racines profondes et leurs rôles dans les écosystèmes.

I.1.1 Enracinement profond réalité et particularité

a) Les racines profondes sont-elles anecdotiques ?

Les sols profonds sont très répandus dans le monde entier (Richter and Markewitz 1995). Ils représentent autant de sols potentiellement favorables à l'enracinement profond, ce que confirment Canadell et al. (1996) dans la Figure 1.

Pourtant, les racines profondes sont le plus souvent considérées comme peu répandues. Ceci est donc d'autant plus paradoxal si l'on considère que plus de 90 % des 11 biomes terrestres, classés par R. B. Jackson et al., (1996) présentent des espèces de plantes avec une profondeur d'enracinement maximale moyenne de plus de 2 m. Ces données montrent également que la profondeur d'enracinement maximale moyenne de 290 espèces de ces 11 biomes est de 4,6 ±

0,5 m . En termes de superficie, cette profondeur d'enracinement peut donc être rencontrée sur plus de 120 millions de km^2.

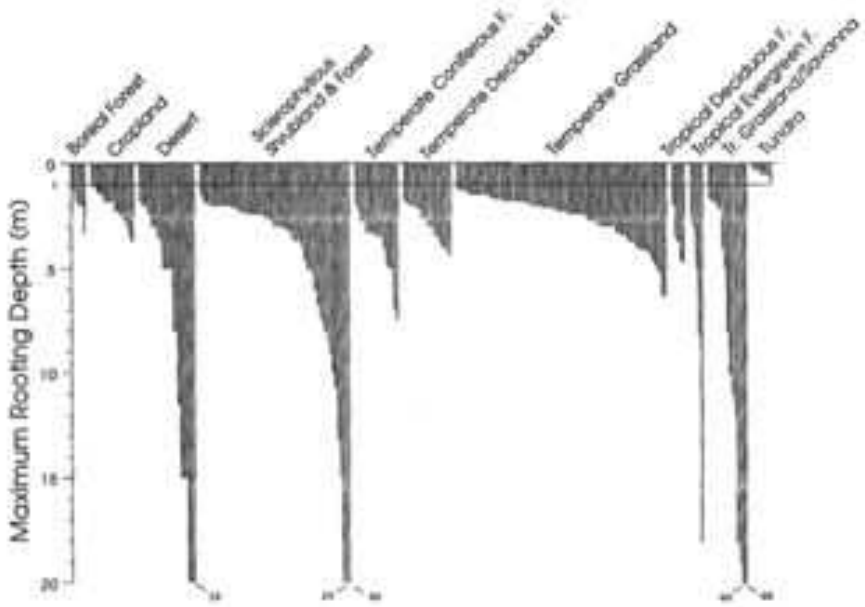


Figure 1: Enracinement maximum pour différentes espèces en (m), regroupé par biomes (Canadell et al. 1996)

b) Effort de recherche

L'effort de recherche visant à améliorer nos connaissances sur l'enracinement profond a été inégal dans le temps. Un regain d'intérêt se manifeste depuis quelques années (15 à 20 ans) après des premiers travaux très détaillés plus anciens que l'on peut retrouver chez quelques auteurs tels que McDougall, (1916); Weaver et al. (1927) et Kutschera, (1960). Ces auteurs ont menés des travaux d'une extrême minutie comme l'illustrent les Figure 2 et Figure 3.

De nos jours, la littérature récente démontre la mobilisation de bon nombre d'équipes face à la nécessité d'aborder l'enracinement dans son ensemble. Des progrès existent mais restent encore limités à des volumes restreins (Javaux et al. 2011; Lobet et al. 2014).

Dans plusieurs études de la première moitié du 19e siècle, les auteurs (Meyer and Anderson 1939; Weaver 1927) ont démontré l'ampleur remarquable de la variabilité dans les niveaux de profondeur des racines des cultures annuelles et pérennes. L'importance décisive du sol et

sous-sol dans le développement des racines profondes est également soulignée. La capacité de nombreuses espèces végétales à développer des racines profondes et en abondance a été mis en évidence par des fouilles manuelles minutieuses, menées en l'absence de forte contraintes de temps (Dittmer 1937; Kutschera 1960). Phillips (1963) a rapporté les observations faites dans une mine à ciel ouvert montrant les racines de légumineuses vivaces (*Cercidium microphyllum Prosopis juliflora et palo verde*), avec des espèces présentant des croissances racinaires atteignant 63 m de profondeur. Les racines de mesquite (*Prosopis spp* .), un arbuste du désert, ont également été trouvées jusqu'à 53 m sous la surface du sol (Stone and Kalisz 1991).

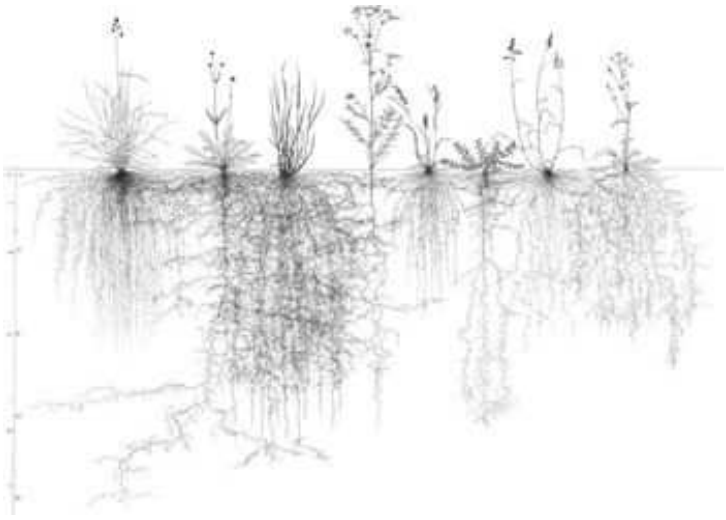


Figure 2: Kuchera 1960

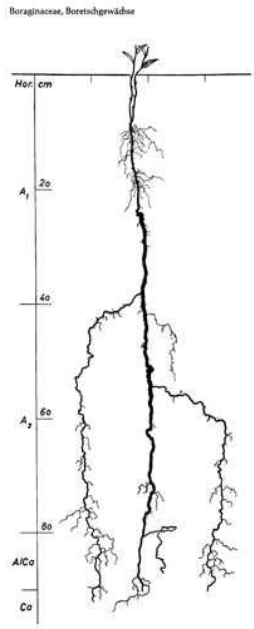


Figure 3: Weaver 1927

Pour autant, l'idée que le système racinaire se développe essentiellement dans les couches superficielles est si communément admise que de nombreux manuels actuels parlent des racines profondes comme étant de faible importance. En 2002, Schenk and Jackson, ont réalisé une méta-analyse de 1300 études. Après analyse des profils de racines, il a constaté que moins de 10% des études des systèmes racinaires reposent sur des prélèvements faits

jusqu'à la profondeur d'enracinement maximum des plantes. Dans ce contexte, certains auteurs s'accordent pour mentionner qu'il est de la plus haute importance de remédier à cette lacune si nous voulons répondre avec précision aux questions liées à l'absorption d'eau, au stockage du carbone et aux cycles biogéochimiques (Rumpel and Kögel-Knabner 2011; Schenk 2002). De même, les tentatives de modélisations des systèmes racinaires doivent nécessairement s'appuyer sur des données réelles pour leur calibration; de telles données sont à l'évidence encore trop peu disponibles aujourd'hui.

Au-delà de la question de leur présence et de leur abondance, le rôle et l'influence des racines profondes sur leur environnement doivent être éclaircis avant de pouvoir déterminer leur importance dans le fonctionnement des écosystèmes terrestres. Parmi ces questions essentielles, nous pouvons citer : (i) Les racines profondes ont-elles des rôles et des caractéristiques spécifiques ? (ii) Quels sont les impacts potentiels des racines profondes sur les processus de l'écosystème ? (iii) Peut-on utiliser des espèces à racines profondes pour améliorer les rendements des cultures ou renforcer leur résistance à des contraintes fortes notamment sur la ressource hydrique ?

Pour répondre à ces questions et proposer de nouvelles pistes de recherche, nous devons d'abord comprendre les processus sous-jacents, moteurs de la croissance des racines profondes et de leur fonctionnement. S'il est conceptuellement simple de mesurer la profondeur d'enracinement réelle des plantes, cela représente néanmoins le plus souvent une entreprise techniquement complexe. Il est par ailleurs particulièrement difficile de comprendre et d'expliciter les raisons et les conséquences du développement des racines en profondeur.

c) Des structures particulières

Les racines sont généralement classées de manière assez approximative en fonction de leurs diamètres (fines, moyennes, grossières, etc…) ou de leur localisation dans le sol (superficielles, peu profondes et profondes). Ces classifications ne sont pas exactement fondées sur une justification fonctionnelle ou physiologique (Zobel 2005).

Le classement général de racines en fonction de leur diamètre est empiriquement (et approximativement) lié à leurs différences fonctionnelles. Les plus grosses racines sont généralement considérées comme des vecteurs de transfert de l'eau à longue distance entre le système racinaire et les parties aériennes de la plante. Les racines fines sont plus spécifiquement dédiées à des fonctions locales, telles que l'absorption d'eau et de nutriments. Cependant, comme le souligne Zobel (2005), la classification des racines fines comme rapportée dans la littérature par Großkopf (1950) ou Kreutzer (1961) manque de cohérence en ce qui concerne les propriétés physiologiques et la variabilité des diamètres. La plupart des racines sont généralement considérées comme «grossières» lorsque leur diamètre est >2 mm ou parfois > 5 mm, mais la justification d'un tel seuil reste floue et n'est pas consensuelle.

Les structures et fonctions des racines peuvent varier dans les différentes parties du système racinaire d'une même plante, mais cette variabilité dépend probablement du type fonctionnel de l'ensemble du système racinaire étudié. Par exemple, les racines latérales peu profondes du pin possèdent des cellules du xylème à paroi mince avec de grandes lumières, favorisant l'absorption rapide de l'eau. Pour la même espèce, les cellules du xylème des racines verticales sont à paroi épaisse avec de petites lumières (Marciszewska and Tulik 2013). Dans ce cas, l'absorption d'eau est moins efficace, mais la racine elle-même est plus résistante mécaniquement au poids de l'arbre situé directement au-dessus (Chaffey 2013; Fayle 1968).

La structure des tissus végétaux et le diamètre des vaisseaux, diffèrent entre les tiges, les racines de surfaces et les racines profondes (Figure 4). Plus les racines sont profondes, plus le diamètre des vaisseaux est large (McElrone et al., 2004).

Cette même étude (McElrone et al., 2004) a également mesuré l'anatomie du xylème, ainsi que la vulnérabilité à la cavitation et la conductivité hydraulique spécifique, pour quatre espèces d'arbres à croissance lente et résistantes à la sécheresse (*Juniperus ashei , Bumelia lanuginosa , Quercus fusiformis et Quercus sinuata*). Ces recherches ont montré que les racines recueillies dans des grottes jusqu'à 20 m de profondeur diffèrent sensiblement de leurs homologues moins profondes. Avec de plus grands vaisseaux du bois et une conductivité hydraulique plus élevée, les racines profondes réduisent la résistance à l'écoulement et l'absorption d'eau profonde est maximisée. Mais cela se fait au prix d'une plus grande vulnérabilité à la cavitation. Le débit d'eau à travers le xylème des racines ligneuses est généralement sans restriction dans les deux sens de la redistribution (Schulte 2006). Des

observations de l'ultrastructure des racines de la forêt boréale de conifères d'espèces Pinacée révèlent que la vulnérabilité à la cavitation est liée à l'épaisseur des membranes et à la position en profondeur des racines (Hacke and Jansen 2009). Néanmoins, plus de travail est nécessaire pour évaluer si ces corrélations existent dans d'autres groupes taxonomiques et s'ils varient selon le type de racines et/ou leur position dans le système racinaire.

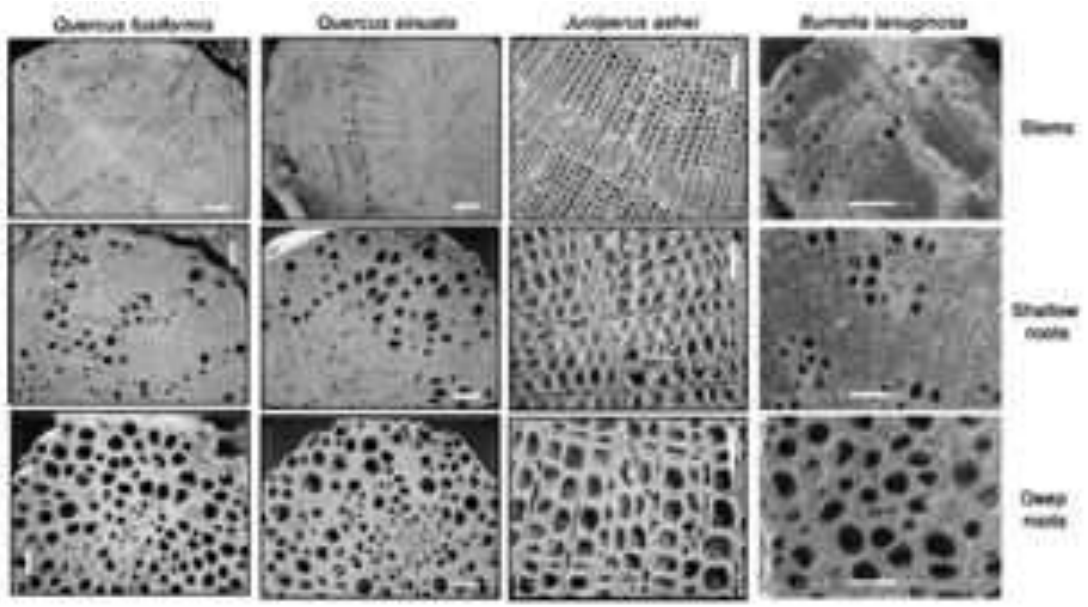


Figure 4: Structure des tiges, des racines de surface et des racines de profondes pour quatre espèces d'arbres (McElrone et al. 2004)

La combinaison de mesures expérimentales des caractéristiques hydrauliques des racines de maïs (*Zea mays L.*) avec la distribution des racines simulées a montré qu'à une profondeur de 1 m, 80% des racines latérales du maïs ont atteint leur capacité maximale de transport d'eau au bout de 100 jours (Pierret et al. 2006). Cependant, cette capacité maximale n'a été atteinte que dans 10 % des racines les plus profondes, responsables du transfert d'eau à longue distance à partir du point d'origine des racines. Watt et al. (2008) ont également mis en évidence que la plupart des racines les plus profondes des céréales ont un faible débit d'eau axial. Si l'existence de ces points de résistance majeurs au transfert d'eau à longue distance est une règle générale chez les espèces herbacées, ce phénomène pourrait représenter une limitation importante de la contribution des racines profondes à l'absorption de l'eau. Rewald et al. ont décrit en 2011 des fonctions physiologiques différentes en fonction des ordres des

racines ayant des densités de tissus variables chez *Citrus volkameriana*. Bien que les racines hautement conductrices soient impliquées dans les interactions entre la végétation et les eaux souterraines profondes, il est peu probable que ce soient les organes d'absorption à travers lesquels l'eau du sol est extraite en profondeur. Au contraire, comme l'a suggéré McElrone et al. (2004), de vastes réseaux de racines fines absorbantes doivent surement exister en amont de ces collecteurs profonds. L'analyse récente de Lobet et al. (2014) décrit les mécanismes racinaires contribuant à l'extraction de l'eau en zone sèche et met en avant les possibilités d'extraction d'eau profonde pouvant être mises à profit dans des conditions agronomiques spécifiques.

d) Dynamique et stratégie de croissance - vie et survie de la plante

Pourquoi les plantes sont-elles amenées à développer un enracinement profond ? Quels sont les éléments moteurs de ce développement en profondeur et dépendent-ils des mêmes éléments qui régissent le développement des racines en surface ? Nous voilà ici face à de nouvelles questions pour lesquelles nous cherchons dans cette thèse à trouver des éléments de réponse. Nous faisons l'hypothèse que les croissances des racines profondes et peu profondes ne sont pas nécessairement simultanées, et que le fonctionnement des racines profondes ne dépend pas nécessairement de la dynamique des racines peu profondes, même si les deux populations sont liées physiquement. Par exemple, dans les systèmes forestiers sous-alpin, la croissance des racines de surface a été minime durant les mois d'hiver (avec un manteau neigeux de 2 m), tandis que les racines des mêmes arbres à 40 cm de profondeur poussent durant la même période de plusieurs centimètres par mois (Mao et al. 2013).

En termes d'approvisionnement en eau, les racines profondes peuvent être critiques pour la survie des plantes pérennes et annuelles. Une contribution, même marginale, de l'absorption d'eau profonde participe à la survie des plantes pendant les périodes de sécheresses (Markewitz et al. 2010). A long terme, cette hypothèse semble cohérente avec les résultats d'une récente méta-analyse (Choat et al., 2012) qui montre que 70 % des 226 espèces forestières de 81 sites à travers le monde ne fonctionnent qu'avec 1 MPa de marge de « sécurité » hydraulique contre le stress et les effets irréversibles de la sécheresse. Cette faible tolérance au stress hydrique pourrait expliquer le dépérissement massif des forêts, suite au

changement climatique, phénomène récemment observé dans de nombreux écosystèmes de la zone tempérée (Allen et al. 2010).

On peut s'interroger sur les raisons liées à cette marge très faible notamment en lien avec les capacités que peuvent avoir les plantes à gérer au mieux leur développement racinaire, leur assurant ainsi le minimum vital de ressources. En parallèle, que sait-on des possibilités des différentes espèces à s'adapter aux changements du milieu et à quel rythme peuvent-elles le faire ? Des expérimentations spécifiques sur plantes adultes pourraient apporter des éléments de réponses à ces questions

I.1.2 Fonction des racines et rôles dans les processus de l'écosystème

Les échanges et interactions liés au développement des racines profondes se trouvent au centre de nombreux mécanismes et ont un impact à plusieurs niveaux de l'écosystème terrestre. La Figure 5 ci-dessous schématise ces phénomènes, au travers des principaux rôles et fonctions liés aux racines.

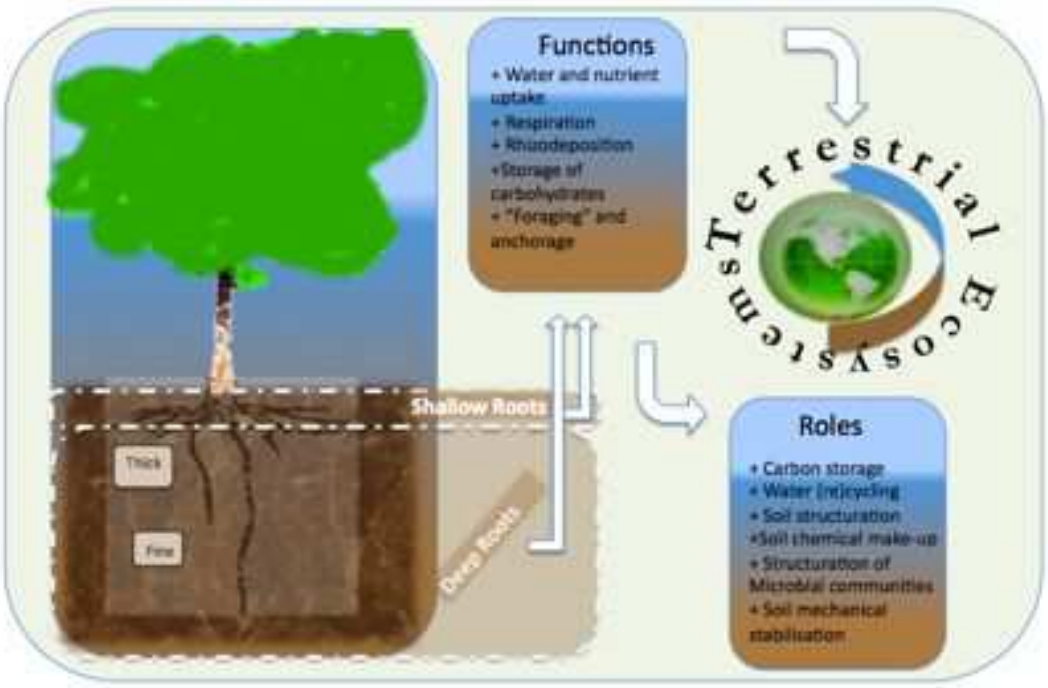


Figure 5: Rôles et fonction des racines dans les écosystèmes terrestres

a) Impacts des racines sur la physique du sol

Les racines peuvent être considérées comme des ingénieurs du sol au travers de leurs différentes fonctions et rôles (Figure 5). Certains effets de la croissance des racines et de leur développement sur les propriétés physiques du sol sont bien documentés, en particulier dans l'étude proposée par Angers and Caron (1998) et résumés plus récemment par Pierret et al. (2011). L'un des changements les plus importants dans la structure du sol lié à la croissance des racines est la création de macropores continus. De tels macropores sont souvent associés à la pénétration active de racines dans les couches du sol de densité apparente élevée. La capacité des racines à perforer le sol varie en fonction des espèces (Bengough et al. 1997; Pierret et al. 2011a; Pierret et al. 1999) avec par exemple un plus grand potentiel de pénétration pour les dicotylédones par rapport aux monocotylédones. (Materechera et al. 1991)

La présence des racines et des canaux radiculaires augmente l'infiltration de l'eau dans le sol. Les racines grossières dans les horizons plus profonds du sol favorisent l'infiltration de l'eau et réduisent le risque de ruissellement induit par la saturation des horizons peu profonds lors de pluies de fortes intensités (Jost et al., 2012). La croissance des racines dans le sol structuré ou compacté peut influencer la conductivité hydraulique du sol (Nobel and Cui, 2010). Les conséquences d'une infiltration accrue sont diverses pour la structure du sol, sa stabilité, les procédés chimiques et de l'activité microbienne (Ghestem et al., 2011) et ont en partie été modélisées (Dupuy et al., 2005a; Dupuy et al., 2007; Tobin et al., 2007). Les arbres à racines profondes réduisent les écoulements latéraux de subsurface et favorisent l'absorption d'azote dans les couches profondes du sol, ce qui représente un moyen efficace et durable de réduire les pollutions diffuses (Wang et al., 2011). L'architecture des racines contribue à la résistance au cisaillement du sol (Fan and Chen, 2010).

b) La microbiologie du sol

Les racines des plantes ont une plasticité leur permettant de répondre rapidement aux changements de l'environnement local. Cette plasticité dépend en partie de la présence de

microorganismes du sol, tels que les bactéries et les mycorhizes (Hodge et al. 2009). Il existe une association mesurable entre le nombre de bactéries et la densité d'enracinement, et par conséquent, un impact potentiel de la profondeur d'enracinement sur la propagation et la survie des communautés microbiennes du sol (Pankhurst et al. 2002; Pierret et al. 1999; Troxler et al. 2012).

En se basant sur la description de Hiltner en 1904 et la définition proposée par Hinsinger en 1998, il n'y a aucune raison pour que l'on ne puisse pas qualifier le sol autour des racines profondes de « sol rhizosphérique ». Pourtant peu d'études abordent ce thème de recherche. Le sol inclus dans la rhizosphère a des propriétés sensiblement différentes de celles du reste du volume du sol, en raison principalement de l'exsudation racinaire qui affecte localement les teneurs en eau (Carminati and Vetterlein 2012) et éléments nutritifs (Hinsinger et al. 2009). En profondeur la rhizosphère joue un rôle important. Markewitz et al. (2010) indiquent qu'environ 40 % des précipitations terrestres totales transitent dans le « faible» volume de sol de la rhizosphère autour des racines des plantes, avant d'être transpiré, ce qui en fait une des régions les plus actives hydrauliquement de la biosphère (Bengough 2012). L'action physique des racines, en conjonction avec l'activité biologique dans la rhizosphère et les spécificités physico-chimiques qu'elle induit, permettent d'établir des canaux relativement stables, ou macropores (Ghestem et al. 2011). Ces canaux peuvent être riches en nutriments (Watt et al. 2008) et fournir un milieu favorable pour les micro-organismes (Pankhurst et al. 2002). De nouvelles racines peuvent se développer à travers ces macrospores, surtout dans les sols résistants à la pénétration, qui sont souvent présents dans les couches plus profondes du sol (White and Kirkegaard 2010).

c) Le stockage du carbone

L'analyse précédente sur le développement des racines en profondeur nous conduit à nous interroger sur le carbone du sol. Ce carbone est principalement du à la présence de racines et sa teneur augmente avec la profondeur du sol (Rasse et al. 2005). Le stock en carbone du sol représente plus du double de celui de l'atmosphère (Kell 2012). Il y a probablement plus de carbone dans le sol profond que ce qui est actuellement pris en compte et les processus sous-jacents à la séquestration de matière organique et au stockage de carbone sont encore

largement méconnus (Schmidt et al. 2011) et sujets à débat (Vogel et al. 2014). Le système racinaire représente donc l'un des puits de carbone le moins bien caractérisé et son rôle dans la répartition des flux et du stock de carbone au niveau de la biosphère terrestre reste à préciser dans une très large mesure (Esser et al. 2011; Körner 2011) (Figure 6). La capacité d'absorption des sols en carbone et sa pérennité sont liées à la teneur en argile, la minéralogie, la stabilité structurelle, la position dans le paysage, les régimes d'humidité et de température, et la capacité à former et retenir des micro-agrégats stables (Biology et al. 2006; Kalliokoski and Pennanen 2010; Vogel et al. 2014; Vogel et al. 2005).

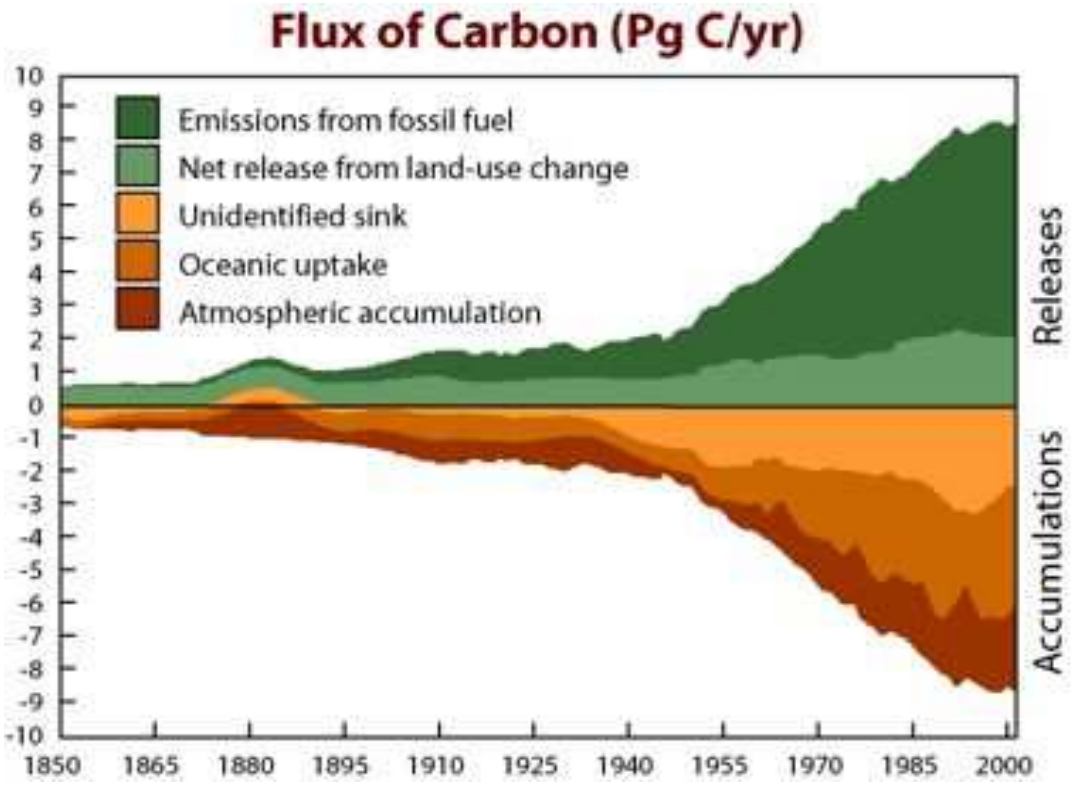


Figure 6: Répartition globale des flux et forme de séquestration du carbone dans la biosphère terrestre (Esser G., Kattge J. and Sakalli A., 2011)

Nous ne savons que peu de choses sur la longévité des racines en profondeur. Il semble cependant que la longévité des racines fine (0,1-2,0 mm de diamètre) soit très variable selon les espèces considérées et peuvent varier de quelques jours à plus de 1000 jours. Par exemple, la longévité des racines de *Pinus sylvestris* (1120 jours) est supérieure aux racines de *Picea*

abies et *Betula pendula (922 jours)* dans la même forêt de Suède (Hansson et al. 2013). Des travaux sont donc nécessaires dans ce domaine.

d) Les services environnementaux

Les services écosystémiques rendus par les racines pourraient être utilisées pour concevoir des solutions d'ingénierie afin d'améliorer la stabilité des pentes et de réduire le risque de rupture de pente, comme suggéré par Normaniza et al. (2007) avec *Leucaena leucocephala*. Les racines peuvent également être considérées comme des ingénieurs du sol en raison de leur influence sur les propriétés du sol. Cependant, les mécanismes spécifiques permettant l'utilisation de ce potentiel d'un point de vue technique sont encore mal compris. L'abondance des racines fines peut être considéré comme un des indicateurs de la durabilité des écosystèmes forestiers (Bakker 1999). Il en est de même dans certains agrosystèmes de savane ouest africains où le système pérenne arbustif sous forme de jachère peut être une possibilité d'amélioration de la conservation de ces milieux très fragiles (Manlay et al. 2002). Il existe donc de nombreux éléments suggérant que le transfert de carbone dans le sol par les racines des plantes joue un rôle primordial dans la régulation des réponses des écosystèmes aux changements climatiques et pourrait même être utilisé pour l'atténuer (Bardgett 2011). Une meilleure connaissance de l'extension des systèmes racinaires est aussi un élément clef afin d'améliorer la productivité et la durabilité des systèmes agricoles (De Smet et al. 2012).

e) Ascenseur hydraulique

Alors que nombreux mécanismes susceptibles de déboucher sur une « ingénierie de la racine » restent à élucider, certaines fonctions comme celui de « filet de sécurité » assuré par le système racinaire (Bergeron et al. 2011), semblent mieux établies. Étant les organes les plus éloignés des feuilles, les racines profondes sont, en théorie, plus coûteuses à construire (Fitter et al. 2000) que les racines superficielles. Mais cela pourrait être compensé par le fait qu'elles agissent comme un filet de sécurité en matière de protection contre le stress, par exemple face à la sécheresse et au lessivage des nutriments. Reste à évaluer l'importance effective de ce filet de sécurité dans divers écosystèmes. Des racines profondes peuvent aussi être « opportunistes », puisant dans des réserves d'eau et de nutriments à des profondeurs largement inaccessibles aux racines superficielles.

Quelques peupliers hybrides, plantés en intercalaires par rapport à d'autres cultures dans l'est du Canada, sont en mesure de récupérer l'eau et les éléments nutritifs lessivés au-delà de la zone d'enracinement des cultures voisines dans les couches plus profondes du sol. Ces ressources peuvent être retournées à la zone d'enracinement des cultures via la redistribution hydraulique à court terme et par la chute de litière sur le long terme. Ce processus a été désigné comme un « filet de sécurité » par Bergeron et al. en 2011. Plusieurs études réalisées dans les systèmes de culture en couloirs, sous climat tempéré, ont montré que les racines des arbres peuvent réduire considérablement le lessivage des nitrates vers les eaux souterraines (Allen, 2004; Bergeron et al., 2011; Zamora, Jose, & Napolitano, 2009). L'efficacité d'un tel filet de sécurité est principalement influencée par (i) l'espèce d'arbre, qui détermine à la fois l'absorption racinaire et la litière, (ii) les caractéristiques physiques et hydrologiques du sous-sol et ses propriétés chimiques (Tittonell, 2005), et (iii) la variabilité interannuelle des précipitations (Dougherty et al. 2009). Le filet de sécurité des racines profondes pourrait aussi aider à atténuer la propagation de contaminants tels que la bactérie *Escherichia coli* dans les eaux souterraines (Dougherty et al. 2009). Cependant, nous ne savons toujours pas si toutes les espèces d'arbres ou de plantes ont le potentiel pour redistribuer l'eau et les nutriments des couches profondes du sol vers les couches superficielles, ou si seulement certaines espèces adaptées à la vie dans des environnements arides ou semi-arides en sont capables. En outre, il est incomparablement plus aisé de démontrer l'ascenseur hydraulique dans les climats secs ; il y a donc davantage d'études dans ces conditions climatiques, ce qui ne signifie pas que ce sont les seules conditions où ces phénomènes existent. Des études récentes font le point sur la capacité des racines à extraire l'eau des sols secs (Lobet et al. 2014). Dans ce contexte, nous pouvons nous demander si toutes les espèces profondes ont le potentiel de redistribuer l'eau des couches profondes du sol à d'autres moins profondes.

Un lien direct entre le fonctionnement de la plante, la racine et le climat a été étudié par Lee et al. (2005) dans une étude sur la redistribution hydraulique par les arbres d'Amazonie. Lee et al. (2005) ont constaté que l'absorption d'eau par les racines à une profondeur de 5-11 m augmente la transpiration de 40% pendant la saison sèche. Les auteurs ont attribué ce phénomène à la redistribution hydraulique. D'après les résultats d'une modélisation de Lee et al. en 2005, un tel transfert d'eau profonde vers l'atmosphère affecterait les cycles saisonniers de températures de l'Amazonie et d'autres régions soumises à la sécheresse. Cette information suggère un lien entre les fonctions des racines de la plante et le climat. Dans ces écosystèmes,

de petites quantités d'eau déplacées par RH (redistribution hydraulique) peuvent être importantes pour la survie des plantes. RH aide la plante dans différentes fonctions critiques: maintenir les racines fines, les hyphes mycorhiziens, et le contact racine - sol. Elle contribue également à la prévention d'embolie, et donc pour une population importante et à l'échelle du paysage, peut influencer l'hydrologie sur le long terme (Neumann and Cardon, 2012).

Bien que l'existence de la redistribution hydraulique ait été établie dans un large éventail de conditions biophysiques, elle n'est pas toujours liée à la densité du profil racinaire (Javaux et al. 2013) ; on dispose cependant de très peu d'éléments fiables sur les volumes d'eau effectivement mobilisées et redistribués (Moreira et al., 2003; Neumann and Cardon, 2012).

f) Apports et limites des modèles de simulation

La capacité des plantes à optimiser leur développement racinaire, notamment pour ce qui est de l'accès à l'eau et aux nutriments, complique grandement la tâche des modélisateurs. Il reste très difficile de prédire les raisons qui conduisent à un enracinement plus ou moins profond.

Les outils de modélisations peuvent apporter une aide précieuse à la compréhension des processus en lien avec l'enracinement. Mais encore une fois ces efforts de recherches sont fortement concentrés sur l'enracinement superficiel. Les outils de modélisation interviennent dans de très nombreux domaines dont nous pouvons citer ici quelques exemples: la croissance racinaire (Collet et al., 2006; Doussan et al., 2003; Pagès et al. 2012) l'ancrage dans le sol (Danjon and Reubens 2008; Dupuy et al. 2005b; Reubens et al. 2007), le développement des racines en lien avec les ressources en eau (Doussan et al. 1998; Draye et al. 2010; Javaux et al. 2008; Lobet et al. 2014; Pierret et al. 2007; Pierret et al. 2006) et minérales (Darrah et al. 2006; Dunbabin et al. 2003; Ho et al. 2004; McMurtrie et al. 2012a; McMurtrie et al. 2012b).

L'enracinement est également intégré dans les modélisations des changements globaux (Woodward and Osborne, 2000; Figure 7). Dans la revue proposée par ces auteurs, seule une catégorie de modèles sur quatre prend en compte la croissance, l'architecture et l'acquisition des ressources liées aux racines. Il ne semble pas y avoir de modèle prenant largement en compte l'enracinement profond. Pourtant, c'est surement dans les modèles étudiant l'évolution des changements de végétation et leur impact à grande échelle que celui-ci devrait

d'avantage être pris en compte. A ce jour, les modèles proposés par différents auteurs étudient l'impact sur la compétition racinaire (Collet et al. 2006), les contraintes environnementales (Draye et al., 2010; Fatahi et al., 2010) mais ne sont généralement pas en mesure de faire la distinction entre les effets des racines profondes et celles de surface à quelques exception près (Doussan et al. 2003b). Cependant certains auteurs tentent de modéliser la profondeur racinaire en fonction des biomes terrestres (Kleidon and Heimann 1998), des stratégies liées aux espèces et des impacts sur la ressource en eau à de grandes échelles (Schenk, 2008a; Schenk, 2008b), malgré des limitations importantes au niveau des jeux de données disponibles. Comme nous avons pu le voir, des distinctions existent entre racines superficielles et profondes mais semblent difficiles à modéliser.

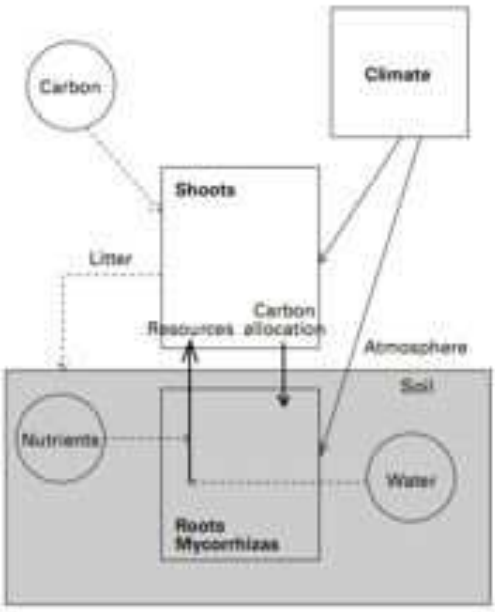


Figure 7: Processus décrivant l'influence des racines dans de nombreux modèles traitant de la végétation (Woodward & 0sborne 2000)

Les espèces enracinées superficiellement prélèvent moins d'eau de la zone saturée comparativement aux espèces enracinées profondément. Ceci induit une grande contribution à la transpiration par la zone saturée et il en résulte un usage plus important des nappes phréatiques profondes sous une végétation dominée par des espèces profondément enracinées (Laio et al. 2009; Ridolfi et al. 2006) .

Le besoin d'utiliser des données pour calibrer et améliorer la modélisations du prélèvement hydrique par les racines a été mis en avant par plusieurs auteurs, notamment Buss et al. (2005); force est de constater que ce constat est encore d'actualité aujourd'hui, surtout pour les modélisations à large échelle.

I.2 En conclusion, l'enracinement profond: Où en sommes-nous ?

Au cours de cette synthèse bibliographique, nous avons donné un aperçu des champs scientifiques en lien direct et indirect avec l'enracinement profond. Si la distinction entre racines superficielles et racines profondes est souvent mentionnée, il ne se dégage pas pour autant une définition claire autour de cette distinction. Il apparait cependant que les sols profonds sont largement présents sur la planète et que les plantes semblent avoir les moyens de les explorer et de les exploiter dans leur globalité en fonction des contraintes auxquelles elles sont soumises. Les plantes ont également démontré leurs capacités à croître sur substrat rocheux (Schwinning 2010).

Le recours très fréquent à une différenciation entre racines profondes et racines superficielles en l'absence d'une définition scientifique ou d'un consensus clair sur la définition de ces deux catégories rend l'interprétation des résultats publiés délicats. De plus, les études menées se limitent le plus souvent aux horizons superficiels induisant un biais dans l'interprétation du rôle et de l'importance des racines profondes. Il parait donc essentiel de commencer par dégager une définition claire de ces deux catégories. Sur cette base, une analyse de la littérature permettra probablement de dégager une vision plus cohérente concernant la réalité et les connaissances visant spécifiquement les racines profondes.

De très nombreuses études sur l'enracinement existent, mais la part consacrée à l'étude des systèmes racinaires dans leur globalité reste proportionnellement très faible. Est-ce par désintérêt lié au rôle secondaire généralement attribué aux racines profondes? De nombreuses zones d'ombre existent encore sur ce sujet. Plus clairement, les difficultés liées à l'acquisition des données de terrain pourraient être un frein majeur, que ce soit pour des raisons financières, de temps ou techniques. L'absence de données suffisantes sur l'enracinement profond limite les possibilités d'interprétation des mesures elles-mêmes, et dans bien des cas, rend impossible une analyse globale des systèmes étudiés. Les données existantes montrent

cependant clairement le rôle majeur joué par les racines profondes pour l'accès à l'eau, dans le stockage du carbone et dans une certaine mesure également, sur la réhabilitation des environnements dégradés.

Les modèles de simulation de prélèvement de l'eau et des nutriments par les racines tentent de reproduire leur fonctionnement. La plasticité du système racinaire et sa capacité d'adaptation au milieu particulier dans lequel il se développe restent néanmoins très complexes à cerner et comportent beaucoup d'inconnues. Les modèles restent encore trop tributaires de ces nombreuses zones d'ombres et l'absence de données disponibles suffisantes rend difficile leur validation, en particulier dans les compartiments profonds. L'effet « boite noire » est souvent présent et peut conduire à utiliser l'enracinement en profondeur comme une variable d'ajustement. Il en est de même pour les modèles architecturaux qui voudraient décrire une plante dans son ensemble et donc proposer des modèles complets notamment en ce qui concerne les ressources en carbone. Les même difficultés se rencontrent également à plus grande échelle dans les études cherchant à décrire le fonctionnent des écosystèmes. Force est de constater que le grand potentiel de développement et d'amélioration des modèles de simulation disponibles aujourd'hui est limité par le manque de données de qualité sur l'enracinement dans les compartiments profonds.

Au regard de ce vaste champ d'études, de sa complexité et des nombreuses questions encore peu abordées, nous définissons ci-dessous les objectifs et limites des travaux que nous avons réalisé dans le cadre de cette thèse.

I.3 Objectifs de la thèse

- Au travers d'une revue approfondie de la littérature, nous cherchons à définir ce qui est qualifié d'enracinement profond afin de cerner « l'objet » de notre étude. Nous faisons un point sur l'importance du rôle physiologique des racines pour la plante à travers leur rôle sur l'approvisionnement en eau et en nutriments, et leur impact sur le milieu dans lequel elles se développent. Nous tentons également d'apporter un éclairage sur l'importance de l'enracinement profond dans les écosystèmes terrestres et de son influence sur l'environnement.

- Nous faisons un point sur les techniques disponibles aujourd'hui pour étudier l'enracinement profond car c'est un élément souvent cité comme limitant l'avancée des recherches. Il est donc de fait aussi déterminant pour nos propres études. Nous présentons les techniques applicables sur le terrain et celles développées dans nos travaux. Nous cherchons à faire un comparatif de ces méthodes tant sur ce qu'elles peuvent apporter que sur leurs inconvénients.

- De plus en plus souvent, l'étude des systèmes racinaire passe part des techniques de prises d'images qu'il faut ensuite analyser. Nous cherchons à valider l'outil d'analyse d'images nommé « IJ_Rhizo » que nous avons utilisé au cours de nombreuses séries d'analyse d'images. Nous le comparons à un autre logiciel commercial afin de s'assurer de la qualité des mesures obtenues.

- Nous étudions ensuite sur le terrain la dynamique de l'enracinement superficiel et profond. Ces études doivent contribuer à apporter des éléments de réponses aux lacunes de nos connaissances actuelles et permettre d'améliorer notre compréhension globale de la dynamique des systèmes racinaires. Notre attention porte plus spécifiquement sur les contraintes hydriques et le stock du carbone, deux éléments liés à des enjeux environnementaux majeurs aussi bien en terme de production que de conservation. Pour réaliser ces études, nous avons choisi deux modèles contrastés: une plantation d'hévéas

(*Hevea brasilensis*) dans le nord-est de la Thaïlande et une plantation de tecks (*Tectona grandis* L) au nord du Laos.

A : Le modèle Hévéa (*Hevea brasilensis*) :

L'étude porte sur une plantation d'hévéas dans une zone climatique marginale au point de vue pluviométrique pour cette espèce et, de ce fait, soumise à de fortes contraintes hydriques. Notre objectif durant les 3 ans de l'étude a été d'étudier la dynamique du système racinaire en continu jusqu'à 4,5 m de profondeur et de faire le lien avec la pluviométrie et les périodes de défoliation.

B- Le modèle du teck (*Tectona grandis* L) :

A l'inverse du cas précédent, l'étude porte sur une plantation de tecks dans sa zone endémique. Une installation d'exclusion de pluie a permis de réduire artificiellement l'accès à l'eau de surface d'un échantillon d'individus et de comparer son comportement à un échantillon témoin pendant 2 ans. L'objectif premier est d'étudier les zones de prélèvements d'eau de cet arbre à travers le profil de sol et la stratégie mise en œuvre au niveau racinaire pour accéder à cette ressource. L'objectif secondaire est d'étudier la capacité de résistance et d'adaptation de cette espèce à de fortes contraintes hydriques. Nous cherchons également à quantifier le plus précisément possible le stock de carbone contenu dans les racines.

I.4 Références

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). *A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests*. *Forest Ecology and Management* (Vol. 259, pp. 660–684). doi:10.1016/j.foreco.2009.09.001

Allen, S. C., Jose, S., Nair, P. K. R., Brecke, B. J., & Ramsey, C. L. (2004). Competition for 15 N-labeled fertilizer in a pecan (Carya illinoensis K . Koch) -cotton (Gossypium hirsutum L .) alley cropping system in the southern United States, 151–164.

Angers, D. A., & Caron, J. (1998). Plant-inducted changes in soil structures: Processes and feedbacks. *Biogeochemistry*, *42*(1-2), 55–72. doi:10.1023/A:1005944025343

Bakker, M. R. (1999). Fine-root parameters as indicators of sustainability of forest ecosystems. *Forest Ecology and Management*, *122*(1-2), 7–16. doi:10.1016/S0378-1127(99)00028-6

Bardgett, R. D. (2011). *Plant-soil interactions in a changing world. F1000 biology reports* (Vol. 3, p. 16). doi:10.3410/B3-16

Bengough, a. G. (2012). Water Dynamics of the Root Zone: Rhizosphere Biophysics and Its Control on Soil Hydrology. *Vadose Zone Journal*, *11*(2). doi:10.2136/vzj2011.0111

Bengough, A. G., Croser, C., & Pritchard, J. (1997). *A biophysical analysis of root growth under mechanical stress* (pp. 155–164). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Bergeron, M., Lacombe, S., Bradley, R. L., Whalen, J., Cogliastro, A., Jutras, M.-F., & Arp, P. (2011). Reduced soil nutrient leaching following the establishment of tree-based intercropping systems in eastern Canada. *Agroforestry Systems*, *83*(3), 321–330. doi:10.1007/s10457-011-9402-7

Biology, G. C., Hole, W., Isoto, E., Nuclear, E., Box, P. O., Nazare, A., … Berkeley, P. (2006). Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration, 217–229. doi:10.1111/j.1365-2486.2005.01063.x

Buss, H. L., Bruns, M. A., Schultz, M. J., Moore, J., Mathur, C. F., Brantley, S. L., … North, G. B. (2005). The coupling of biological iron cycling and mineral weathering during saprolite formation, Luquillo Mountains, Puerto Rico Hydraulic lift - Water efflux from upper roots improves effectiveness of water-uptake by deep roots Variation in leaf structure and. *Geobiology*, *3*(4), 247–260. doi:10.1007

Canadell, J., Jackson, R., Ehleringer, J., Mooney, H., Sala, O. E., & Schulze, E.-D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia*, *108*, 583–595.

Carminati, A., & Vetterlein, D. (2012). Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. *Annals of Botany*, (2010), 1–14. doi:10.1093/aob/mcs262

Chaffey, N. (2013). Secondary Growth of Tree Roots: Cytoskeletal Perspectives. In L. Taylor & Francis Group (Ed.), *Plant roots: the hidden half* (pp. 1–19).

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., … Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*(7426), 752–5. doi:10.1038/nature11688

Collet, C., Löf, M., & Pagès, L. (2006). Root System Development of Oak Seedlings Analysed using an Architectural Model. Effects of Competition with Grass. *Plant and Soil*, *279*(1-2), 367–383. doi:10.1007/s11104-005-2419-9

Danjon, F., & Reubens, B. (2008). *Assessing and analyzing 3D architecture of woody root systems , a review of methods and applications in tree and soil stability , resource acquisition and allocation*. *Topology* (pp. 1–34). doi:10.1007/s11104-007-9470-7

Darrah, P. R., Jones, D. L., Kirk, G. J. D., & Roose, T. (2006). *Modelling the rhizosphere: a review of methods for "upscaling" to the whole-plant scale*. *European Journal of Soil Science* (Vol. 57, pp. 13–25). doi:10.1111/j.1365-2389.2006.00786.x

De Smet, I., J. White, P., Bengough, a. G., Dupuy, L., Parizot, B., Casimiro, I., … Bennett, M. (2012). *Analyzing Lateral Root Development: How to Move Forward*. *the Plant Cell Online* (pp. 1–7). doi:10.1105/tpc.111.094292

Dittmer, H. J. (1937). A quantitative study of the roots and root hairs of a winter rye plant (Secale cereale). *American Journal of Botany*, *24*, 417–420.

Dougherty, M. C., Thevathasan, N. V., Gordon, A. M., Lee, H., & Kort, J. (2009). *Nitrate and Escherichia coli NAR analysis in tile drain effluent from a mixed tree intercrop and monocrop system*. *Agriculture, Ecosystems & Environment* (Vol. 131, pp. 77–84). doi:10.1016/j.agee.2008.09.011

Doussan, C., Pagès, L., & Pierret, A. (2003a). Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. *Agronomie*, *23*(5-6), 419–431. doi:10.1051/agro:2003027

Doussan, C., Pagès, L., & Pierret, A. (2003b). Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. *Agronomie*, *23*(5-6), 419–431. doi:10.1051/agro:2003027

Doussan, C., Vercambre, G., & Pagés, L. (1998). Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption—Distribution of axial and radial conductances in maize. *Annals of Botany*, *81*, 225–232. Retrieved from http://aob.oxfordjournals.org/content/81/2/225.short

Draye, X., Kim, Y., Lobet, G., & Javaux, M. (2010). Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. *Journal of Experimental Botany*, *61*(8), 2145–55. doi:10.1093/jxb/erq077

Dunbabin, V., Diggle, A., & Rengel, Z. (2003). *Is there an optimal root architecture for nitrate capture in leaching environments ? Soil Science*. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Dupuy, L., Fourcaud, T., & Stokes, A. (2005). A Numerical Investigation into the Influence of Soil Type and Root Architecture on Tree Anchorage. *Plant and Soil*, *278*(1-2), 119–134. doi:10.1007/s11104-005-7577-2

Dupuy, L., Fourcaud, T., Stokes, A., & Danjon, F. (2005). A density-based approach for the modelling of root architecture: application to Maritime pine (Pinus pinaster Ait.) root systems. *Journal of Theoretical Biology*, *236*(3), 323–34. doi:10.1016/j.jtbi.2005.03.013

Dupuy, L. X., Fourcaud, T., Lac, P., & Stokes, A. (2007). *A generic 3D finite element model of tree anchorage integrating soil mechanics and real root system architecture*. *Am. J. Bot.* (Vol. 94, pp. 1506–1514). doi:10.3732/ajb.94.9.1506

Esser, G., Kattge, J., & Sakalli, A. (2011). *Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere*. *Global Change Biology* (Vol. 17, pp. 819–842). doi:10.1111/j.1365-2486.2010.02261.x

Fan, C., & Chen, Y. (2010). *The effect of root architecture on the shearing resistance of root-permeated soils*. *Ecological Engineering* (Vol. 36, pp. 813–826). Elsevier B.V. doi:10.1016/j.ecoleng.2010.03.003

Fatahi, B., Khabbaz, H., & Indraratna, B. (2010). Bioengineering ground improvement considering root water uptake model. *Ecological Engineering*, *36*(2), 222–229. doi:10.1016/j.ecoleng.2008.12.027

Fayle, D. C. . (1968). *Radial growth of tree roots.* (Univ Toron., pp. 1–183). Toronto.

Fitter, A., Hodge, A., & Robinson, D. (2000). Plant response to patchy soils. In Hutchings. (Ed.), *A. J. A. Stewart, E. A. John, and M. J. Hutchings,* (pp. 71–90).

Ghestem, M., Sidle, R. C., & Stokes, A. (2011). *The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability*. *BioScience* (Vol. 61, pp. 869–879). doi:10.1525/bio.2011.61.11.6

Großkopf, W. (1950). *Bestimmung der charakteristischen Feinwurzel-Intensitäten in ungünstigen Waldbodenprofilen und ihre ökologische Auswertung.* (Haller.).

Hacke, U. G., & Jansen, S. (2009). *Embolism resistance of three boreal conifer species varies with pit structure. The New phytologist* (Vol. 182, pp. 675–86). doi:10.1111/j.1469-8137.2009.02783.x

Hansson, K., Helmisaari, H.-S., Sah, S. P., & Lange, H. (2013). Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. *Forest Ecology and Management*, *309*, 58–65. doi:10.1016/j.foreco.2013.01.022

Hiltner, P. (1904). Über neuere ehrfahrungen und problem auf dem gebiet der bodenbakteriologie unter besonderer berücksichtigung der grundüngung und brache. *Arb.Dtsch.Landwirt. Ges.*, *98*, 59–78.

Hinsinger, P. (1998). How Do Plant Roots Acquire Mineral Nutrients? Chemical Processes Involved in the rhizosphere. *Adavances in Agronomy*, 225,265. doi:10.1016/S0065-2113(08)60506-4

Hinsinger, P., Bengough, a. G., Vetterlein, D., & Young, I. M. (2009). *Rhizosphere: biophysics, biogeochemistry and ecological relevance*. *Plant and Soil* (Vol. 321, pp. 117–152). doi:10.1007/s11104-008-9885-9

Ho, M. D., Mccannon, B. C., & Lynch, J. P. (2004). *Optimization modeling of plant root architecture for water and phosphorus acquisition*. *Journal of Theoretical Biology* (Vol. 226, pp. 331–340). doi:10.1016/j.jtbi.2003.09.011

Hodge, A., Berta, G., Doussan, C., Merchan, F., & Crespi, M. (2009). Plant root growth, architecture and function. *Plant and Soil*, *321*(1-2), 153–187. doi:10.1007/s11104-009-9929-9

Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. a., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, *108*(3), 389–411. doi:10.1007/BF00333714

Javaux, M., Couvreur, V., Vanderborght, J., & Vereecken, H. (2013). Root Water Uptake: From Three-Dimensional Biophysical Processes to Macroscopic Modeling Approaches. *Vadose Zone Journal*, *12*(4). doi:10.2136/vzj2013.02.0042

Javaux, M., Draye, X., Doussan, C., Vanderborght, J., & Vereecken, H. (2011). Root Water Uptake: Toward 3-D Functional Approaches. In *Encyclopedia of Agrophysics* (Encycloped., pp. 717–722). doi:10.1007/978-90-481-3585-1_224

Javaux, M., Schröder, T., Vanderborght, J., & Vereecken, H. (2008). Use of a Three-Dimensional Detailed Modeling Approach for Predicting Root Water Uptake. *Vadose Zone Journal*, *7*(3), 1079. doi:10.2136/vzj2007.0115

Jost, G., Schume, H., Hager, H., Markart, G., & Kohl, B. (2012). *A hillslope scale comparison of tree species influence on soil moisture dynamics and runoff processes during intense rainfall*. *Journal of Hydrology* (Vol. 420–421, pp. 112–124). doi:10.1016/j.jhydrol.2011.11.057

Kalliokoski, T., & Pennanen, T. (2010). *Belowground interspecific competition in mixed boreal forests : fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients*. *Plant and Soil* (pp. 73–89). doi:10.1007/s11104-009-0177-9

Kell, D. B. (2011). Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. *Annals of Botany*, *108*(3), 407–18. doi:10.1093/aob/mcr175

Kell, D. B. (2012). Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: why and how. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1595), 1589–97. doi:10.1098/rstb.2011.0244

Kleidon, A., & Heimann, M. (1998). A method of determining rooting depth from a terrestrial biosphere model and its impacts on the global water and carbon cycle. *Global Change Biology*, *4*(3), 275–286. doi:10.1046/j.1365-2486.1998.00152.x

Körner, C. (2011). The grand challenges in functional plant ecology. *Frontiers in Plant Science*, *2*, 1. doi:10.3389/fpls.2011.00001

Kreutzer K. (1961). Wulzelbildung jungen Waldbaume auf Pseudogleybi. *Iden. Forstwis. Cent. Bf*, *80*(11-12), 356–392.

Kutschera, L. (1960). *Wurzelatlas mitleleuropaïsher Ackerunkräuter und Kulturpflanzen. Verlag Pub., Franckfurt am Main*. Verlag Pub., Franckfurt am Main. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Laio, F., Tamea, S., Ridolfi, L., D'Odorico, P., & Rodriguez-Iturbe, I. (2009). *Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics*. *Water Resources Research* (Vol. 45). doi:10.1029/2008WR007292

Lee, J.-E., Oliveira, R. S., Dawson, T. E., & Fung, I. (2005). *Root functioning modifies seasonal climate. Proceedings of the National Academy of Sciences of the United States of America* (Vol. 102, pp. 17576–81). doi:10.1073/pnas.0508785102

Lobet, G., Couvreur, V., Meunier, F., Javaux, M., & Draye, X. (2014). Plant Water Uptake in Drying Soils. *Plant Physiology*. doi:10.1104/pp.113.233486

Manlay, R. J., Kairé, M., Masse, D., Chotte, J., Ciornei, G., & Floret, C. (2002). Carbon , nitrogen and phosphorus allocation in agro-ecosystems of a West African savanna I . The plant component under semi-permanent cultivation, *88*, 215–232.

Mao, Z., Bonis, M., & Rey, H. (2013). Which processes drive fine root elongation in a natural mountain forest ecosystem? *Plant Ecology & ….* Retrieved from http://www.tandfonline.com/doi/abs/10.1080/17550874.2013.788567

Marciszewska, K., & Tulik, M. (2013). Hydraulic Efficiency and Safety of Xylem Sap Flow in Relation to Water Stress in Woody Plants, 1–32. doi:10.5772/56656

Markewitz, D., Devine, S., Davidson, E. A., Brando, P., & Nepstad, D. C. (2010). Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. *The New Phytologist*, *187*(3), 592–607. doi:10.1111/j.1469-8137.2010.03391.x

Materechera, S. a., Dexter, a. R., & Alston, a. M. (1991). *Penetration of very strong soils by seedling roots of different plant species*. *Plant and Soil* (Vol. 135, pp. 31–41). doi:10.1007/BF00014776

McDougall, W. B. (1916). *The Growth of Forest Tree Roots*. *American Journal of Botany* (Vol. 3, pp. 384–392). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

McElrone, A. J., Pockman, W. T., Martinez-Vilalta, J., & Jackson, R. B. (2004). Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist*, *163*(3), 507–517. doi:10.1111/j.1469-8137.2004.01127.x

McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. a, & Norby, R. J. (2012a). Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging. *Ecology and Evolution*, *2*(6), 1235–50. doi:10.1002/ece3.266

McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. A., & Norby, R. J. (2012b). Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging. *Ecology and Evolution*, *2*(6), 1235–50. doi:10.1002/ece3.266

Meyer, B. S., & Anderson, D. B. (1939). *Plant Physiology*. (B. and Co, Ed.). Bridgebort: Braunworth and Co,.

Moreira, M. Z., Scholz, F. G., Goldstein, G., & Franco, A. C. (2003). *Hydraulic lift in a neotropical savanna* (pp. 573– 581). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Neumann, R. B., & Cardon, Z. G. (2012). The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *The New Phytologist*, *194*(2), 337–52. doi:10.1111/j.1469-8137.2012.04088.x

Nobel, P. S., & Cui, M. (2010). *Hydraulic Conductances of the Soil , the Root-Soil Air Gap , and the Root : Changes for Desert Succulents in Drying Soil*. *Changes* (Vol. 43, pp. 319–326). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Normaniza, O., Faisal, H. A., & Barakbah, S. S. (2007). *Engineering properties of Leucaena leucocephala for prevention of slope failure* (Vol. 2, pp. 215–221). doi:10.1016/j.ecoleng.2007.11.004

Pagès, L., Bruchou, C., & Garré, S. (2012). Links Between Root Length Density Profiles and Models of the Root System Architecture. *Vadose Zone Journal*, *11*(4). doi:10.2136/vzj2011.0152

Pankhurst, C. E., Pierret, A., Hawke, B. G., Kirby, J. M., Aitkenvale, P. M. B. P. O., Qld, T., & Box, G. P. O. (2002). Microbiological and chemical properties of soil associated with macropores at different depths in a red-duplex soil in NSW Australia. *Plant and Soil*, *238*(1), 11–20. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Phillips, W. S. (1963). Depth of Roots in Soil. *Ecology*, *44*(2), 424. doi:10.2307/1932198

Pierret, A., Doussan, C., Capowiez, Y., Bastardie, F., & Pagès, L. (2007). *Root Functional Architecture: A Framework for Modeling the Interplay between Roots and Soil*. *Vadose Zone Journal* (Vol. 6, p. 269). doi:10.2136/vzj2006.0067

Pierret, A., Doussan, C., & Pagès, L. (2006). *Spatio-temporal Variations in Axial Conductance of Primary and First-order Lateral Roots of a Maize Crop as Predicted by a Model of the Hydraulic Architecture of Root Systems*. *Plant and Soil* (Vol. 282, pp. 117–126). doi:10.1007/s11104-005-5373-7

Pierret, A., Hartmann, C., Maeght, J., Pagès, L., & Growth, R. (2011). *Biotic Regulation : Plants*. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Pierret, A., Moran, C. J., & Pankhurst, C. E. (1999). *Differentiation of soil properties related to the spatial association of wheat roots and soil macropores* (Vol. 200660, pp. 51–58). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Rasse, D. P., Rumpel, C., & Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, *269*(1-2), 341–356. doi:10.1007/s11104-004-0907-y

Reubens, B., Poesen, J., Danjon, F., Geudens, G., & Muys, B. (2007). *The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review*. *Trees - Structure and Function* (Vol. 21, pp. 385–402). doi:10.1007/s00468-007-0132-4

Rewald, B., Ephrath, J. E., & Rachmilevitch, S. (2011). *A root is a root is a root? Water uptake rates of Citrus root orders. Plant, cell & environment* (Vol. 34, pp. 33–42). doi:10.1111/j.1365-3040.2010.02223.x

Richter, D. D., & Markewitz, D. (1995). How Deep Is Soil? *BioScience*, *45*(9), 600–609. doi:10.2307/1312764

Ridolfi, L., D'Odorico, P., & Laio, F. (2006). *Effect of vegetation–water table feedbacks on the stability and resilience of plant ecosystems*. *Water Resources Research* (Vol. 42, p. W01201). doi:10.1029/2005WR004444

Rumpel, C., & Kögel-Knabner, I. (2011). Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant and Soil*, *338*(1-2), 143–158. doi:10.1007/s11104-010-0391-5

Schenk, H. (2002). *The global biogeography of roots*. *Ecological monographs* (Vol. 72, pp. 311–328). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Schenk, H. J. (2008a). Soil depth, plant rooting strategies and species' niches. *The New Phytologist*, *178*(2), 223–5. doi:10.1111/j.1469-8137.2008.02427.x

Schenk, H. J. (2008b). The Shallowest Possible Water Extraction Profile: A Null Model for Global Root Distributions. *Vadose Zone Journal*, *7*(3), 1119. doi:10.2136/vzj2007.0119

Schenk, H. J., & Jackson, R. B. (2002). *Rooting depths , lateral root spreads and below-ground / above-ground allometries of plants in water-limited*. *Journal of Ecology* (pp. 480 – 494). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. a., … Trumbore, S. E. (2011). *Persistence of soil organic matter as an ecosystem property. Nature* (Vol. 478, pp. 49–56). doi:10.1038/nature10386

Schulte, P. (2006). *Water flow through junctions in Douglas-fir roots*. *Plant, Cell & Environment* (Vol. 29, pp. 70–6). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Schwinning, S. (2010). *Ecohydrology Bearings - Invited Commentary The ecohydrology of roots in rocks* (Vol. 245, pp. 238–245). doi:10.1002/eco

Stone, E. L., & Kalisz, P. J. (1991). On the maximum extent of tree roots. *Forest Ecology and Management*, *46*(1-2), 59–102. doi:10.1016/0378-1127(91)90245-Q

Tittonell, P., Vanlauwe, B., Leffelaar, P. A., & Giller, K. E. (2005). *Estimating yields of tropical maize genotypes from non-destructive , on-farm plant morphological measurements*. *Response* (Vol. 105, pp. 213–220). doi:10.1016/j.agee.2004.04.002

Tobin, B., Čermák, J., Chiatante, D., Danjon, F., Di Iorio, a., Dupuy, L., … Spanos, I. (2007). *Towards developmental modelling of tree root systems*. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* (Vol. 141, pp. 481–501). doi:10.1080/11263500701626283

Troxler, J., Svercel, M., Natsch, A., Zala, M., Keel, C., Moënne-Loccoz, Y., & Défago, G. (2012). *Persistence of a biocontrol Pseudomonas inoculant as high populations of culturable and non-culturable cells in 200-cm-deep soil profiles*. *Soil Biology and Biochemistry* (Vol. 44, pp. 122–129). doi:10.1016/j.soilbio.2011.09.020

Vogel, J., Bronson, D., Gower, S. T., & Schuur, E. A. G. (2014). The response of root and microbial respiration to the experimental warming of a boreal black spruce forest. *Canadian Journal of Forest Research*, 140505143419008. doi:10.1139/cjfr-2014-0056

Vogel, J. G., Valentine, D. W., & Ruess, R. W. (2005). Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. *Canadian Journal of Forest Research*, *35*(1), 161–174. doi:10.1139/x04-159

Wang, Y., Zhang, B., Lin, L., & Zepp, H. (2011). *Agroforestry system reduces subsurface lateral flow and nitrate loss in Jiangxi Province, China*. *Agriculture, Ecosystems & Environment* (Vol. 140, pp. 441–453). doi:10.1016/j.agee.2011.01.007

Watt, M., Magee, L., & McCully, M. (2008). *Types, structure and potential for axial water flow in the deepest roots of fieldâ€ grown cereals*. *New Phytologist* (Vol. 178, pp. 135–46). doi:10.1111/j.1469-8137.2007.02358.x

Weaver, J. E. (1927). *Root development of vegetable crops*. Springer. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Weaver, J. E., Bruner, W. E., & Weaver, R. J. (1927). *VEGETABLE CROPS BY*. *Development* (pp. 1–7). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

White, R. G., & Kirkegaard, J. A. (2010). The distribution and abundance of wheat roots in a dense, structured subsoil--implications for water uptake. *Plant, Cell & Environment*, *33*(2), 133–48. doi:10.1111/j.1365-3040.2009.02059.x

Woodward, F. I., & Osborne, C. P. (2000). The representation of root processes in models addressing the responses of vegetation to global change. *New Phytologist*, *147*, 223–232. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Zamora, D. S., Jose, S., & Napolitano, K. (2009). *Competition for 15N labeled nitrogen in a loblolly pine–cotton alley cropping system in the southeastern United States*. *Agriculture, Ecosystems & Environment* (Vol. 131, pp. 40–50). doi:10.1016/j.agee.2008.08.012

Zobel, R. (2005). *Primary and secondary root systems. Roots and Soil Management : interactions between roots and the soil* (p. 2005). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Chapitre 1 :

Revue de la littérature



Photo 2 : Prospection de racines profondes dans une grotte à 12 m de profondeur au Laos (A. Pierret , 2010).

1.1 Introduction

Ce chapitre, publié sous forme d'article dans la revue Frontiers in Plant Science et intitulé « How to study deep roots – and why it matters » (doi :10.3389/fpls.2013.00299), est consacré à une revue approfondie de la littérature traitant de l'enracinement profond. Nous y proposons une définition consensuelle de ce qui est généralement qualifié d'enracinement profond, en nous appuyant sur une synthèse très large des études proposées par la littérature. Nous faisons le point sur l'importance du rôle physiologique de ces racines pour la plante à travers leurs rôles dans l'approvisionnement en eau et en nutriments dans les différents horizons du sol. Nous étudions également l'impact des racines profondes sur le milieu dans lequel elles se développent, que ce soit au niveau de leurs actions sur la physique, la géochimie et la microbiologie du sol. Nous apportons un éclairage sur l'importance de l'enracinement profond dans les écosystèmes terrestres notamment pour ce qui est du stockage du carbone et de son influence sur l'environnement.

Dans la deuxième partie de cet article nous réalisons un point sur les techniques disponibles aujourd'hui pour étudier l'enracinement profond. Nous présenterons les techniques applicables sur le terrain et celles développées puis testées lors de la réalisation de nos travaux. Nous faisons un comparatif de ces méthodes listant leurs atouts et inconvénients.

La littérature invoque souvent les difficultés d'accès aux racines profondes comme un facteur limitant l'avancée des recherches. Face à cette réalité, nous devons faire preuve d'imagination et souvent innover pour à la fois rationaliser l'effort nécessaire pour accéder aux données sur les racines profondes et maximiser la quantité et la qualité des données récoltées. Chaque étape est concernée : l'accès visuel aux racines, la prise d'images, le traçage du réseau racinaire et l'analyse des images obtenues.

Au fil de nos expérimentations et des expériences passées, nous avons développé la technique du puits d'accès (Figure 8), présentée dans l'article ci-dessous. Nous avons adapté la méthode des boites d'accès ou « Rhizo_Box » de McDougall (1916) sous différentes formes (Figure 9 et Photo 3). Nous avons testé la méthode du scanner plat et sa robustesse pendant plusieurs mois afin de nous assurer de la qualité du matériel utilisé et de son adaptation aux conditions

difficiles de terrain. Le modèle de scanner choisi a été testé lors d'une expérimentation automatisée avec prises d'images toutes les heures pendant 6 mois. Nous avons adapté un programme fonctionnant sous OS Windows permettant de gérer cette prise d'images simultanée sur plusieurs scanners. Le programme développé nous permet de choisir plusieurs paramètres dont, par exemple, la sélection de la définition des images en DPI, le recadrage d'une zone particulière ou encore le choix du rythme de mesures. Plus d'informations sont disponibles dans l'annexe I sur ce logiciel que je tiens à la disposition des personnes intéressées.



Figure 8: Description schématique du dispositif du puits d'accès et des fenêtres pour la prise d'images avec scanner à plat adaptés (Maeght & al. 2011)

Les images scannées doivent ensuite être analysées afin d'en retirer les informations sur les longueurs et diamètres racinaires. Pour y arriver, il est nécessaire d'identifier visuellement

chaque racine sur les images produites et de les tracer manuellement pour les rendre identifiables par un logiciel d'analyse d'image.

Pour réaliser ces travaux nous utilisons des fonctionnalités proposées par le logiciel libre d'édition et retouche d'image Gimp (http://www.gimp.org/about/introduction.html). La procédure suivie a été décrite dans un guide interne assurant un traitement standardisé et cohérant des images. Nous obtenons des tracés racinaires que nous pouvons ensuite analyser (Figure 10).

Nous avons ensuite développé et validé l'outil d'analyse d'images nommé « Ij_Rhizo » que nous avons utilisé au cours de nombreuses séries d'analyses. Nous l'avons comparé à un autre logiciel commercial afin de nous assurer de la qualité des mesures obtenues. Ces travaux sont publiés dans l'article intitulé « IJ_Rhizo : an open-source software to measure scanned images of root samples » dans la revue Plant and Soil (doi :10.1007/s11104-013-1795-9) et présenté en annexes II a et II b. Suite à la publication de cet article, l'outil open source a été mis à disposition de la communauté scientifique. Il est aujourd'hui disponible sur une plateforme collaborative avec d'autres outils destinés aux études sur les racines en suivant ce lien : http://www.plant-image-analysis.org/software/IJ_Rhizo.

Nous espérons ainsi apporter des éléments de réponses et des pistes d'action face aux nombreuses interrogations et contraintes techniques limitant aujourd'hui la recherche sur les racines profondes.

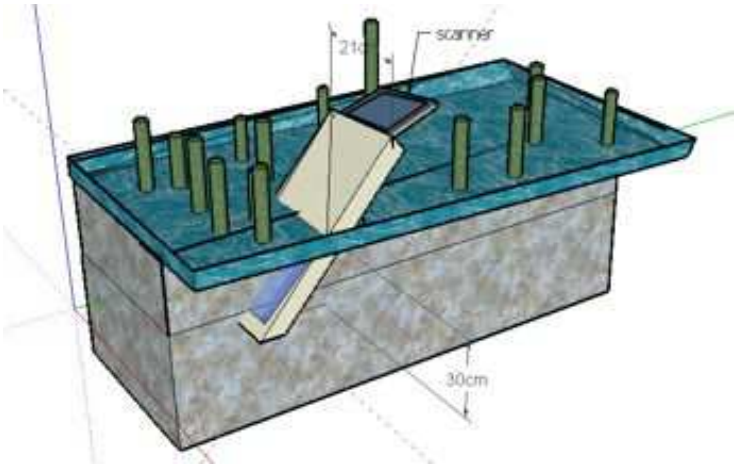


Figure 9: Représentation de la boite d'accès (Rhizo-Box) permettant d'insérer à 45° un scanner plat pour la prise d'image sous rizières inondées (Maeght et al. 2007)



Photo 3 : Insertion et positionnement d'un scanner plat pour la prise d'images racinaires sous plantation de teck (Maeght et al., 2012)

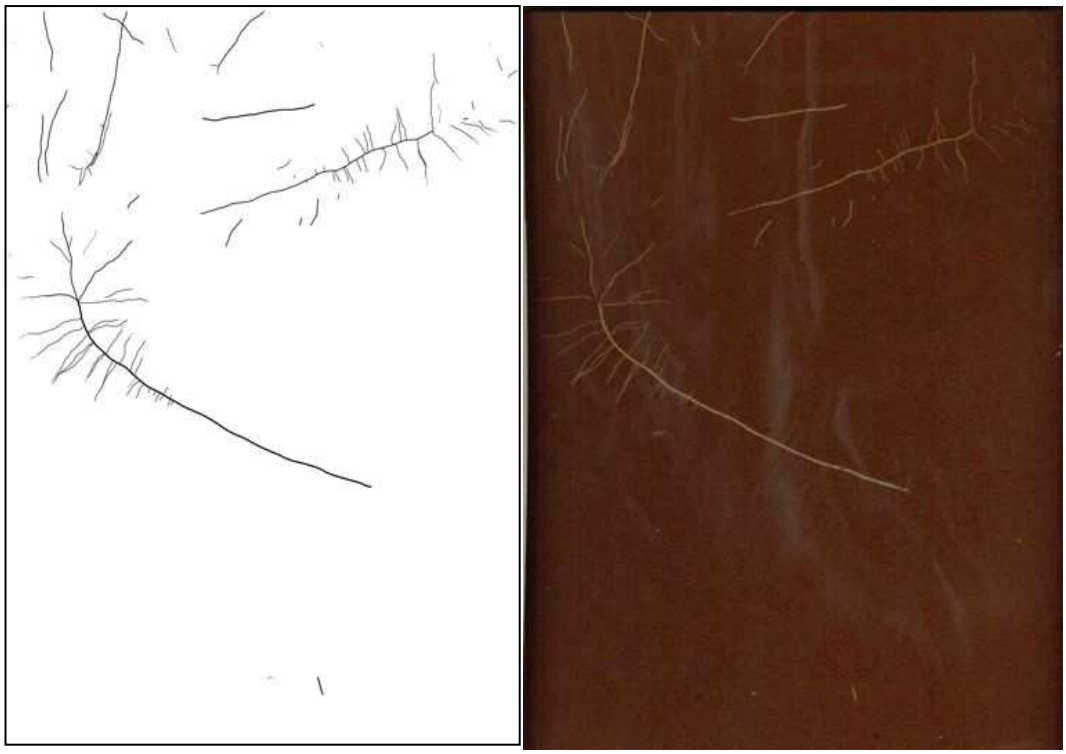


Figure 10 : A droite : image scannée de racines de teck prise dans une boite d'accès. A gauche : résultat du traçage des racines à l'aide des outils du logiciel libre Gimp.

1.1.1 Références

Maeght, J. ., Nortourlee, L., Reboul-salze, F., Bourdon, E., Sengtaheuanghoung, O. Soulileuth, .B, Hartmann, C., & Pierret, A. (2011). Environmental impact of understorey management in Teak tree (Tectona grandis L.) plantations: A case study from Luang Prabang, Lao PDR. *Khon Kaen AGR*, *39*, 291–294.

Maeght, J. L., Henry des Tureaux, T., Sengtaheuanghoung, O., Stokes, A., Ribolzi, O., & Pierret, A. (2012). Drought effect on teak tree (Tectona grandis) roots on carbon inputs and water uptake in a deep soil of northern Laos. In *Roots to the Future 8th Symposium of the International Society of Root Research*.

Maeght, J.-L., Pierret, A., Sanwangsri, M., & Hammecker, C. (2007). Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand. In *International Conference Rhizosphere 2, 26-31 August 2007, Montpellier, France.* (pp. 26–31). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

McDougall, W. B. (1916). *The Growth of Forest Tree Roots. American Journal of Botany* (Vol. 3, pp. 384–392). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

1.2 How to study deep roots – and why it matters: Article publié dans Frontiers in Plant Science, 2013

frontiers in
PLANT SCIENCE

REVIEW ARTICLE
published: 13 August 2013
doi: 10.3389/fpls.2013.00299

How to study deep roots—and why it matters

Jean-Luc Maeght[1]*†, Boris Rewald[2†] and Alain Pierret[1]

[1] *Joint Research Unit Biogéochimie et Ecologie des Milieux Continentaux, IRD, Vientiane, Laos*
[2] *Forest Ecology, Department of Forest and Soil Sciences, University of Natural Resources and Life Science, Vienna, Austria*

Edited by:
Shimon Rachmilevitch, Ben Gurion University of the Negev, Israel

Reviewed by:
Dirk Vanderklein, Montclair State University, USA
Heather R. McCarthy, University of Oklahoma, USA

****Correspondence:***
Jean-Luc Maeght, Unité Mixte de Recherche 211, Biogéochimie et Ecologie des Milieux Continentaux, IRD-NAFRI, BP 5992 Vientiane, Lao PDR
e-mail: jean-luc.maeght@ird.fr
† Joint first authors.

The drivers underlying the development of deep root systems, whether genetic or environmental, are poorly understood but evidence has accumulated that deep rooting could be a more widespread and important trait among plants than commonly anticipated from their share of root biomass. Even though a distinct classification of "deep roots" is missing to date, deep roots provide important functions for individual plants such as nutrient and water uptake but can also shape plant communities by hydraulic lift (HL). Subterranean fauna and microbial communities are highly influenced by resources provided in the deep rhizosphere and deep roots can influence soil pedogenesis and carbon storage.Despite recent technological advances, the study of deep roots and their rhizosphere remains inherently time-consuming, technically demanding and costly, which explains why deep roots have yet to be given the attention they deserve. While state-of-the-art technologies are promising for laboratory studies involving relatively small soil volumes, they remain of limited use for the *in situ* observation of deep roots. Thus, basic techniques such as destructive sampling or observations at transparent interfaces with the soil (e.g., root windows) which have been known and used for decades to observe roots near the soil surface, must be adapted to the specific requirements of deep root observation. In this review, we successively address major physical, biogeochemical and ecological functions of deep roots to emphasize the significance of deep roots and to illustrate the yet limited knowledge. In the second part we describe the main methodological options to observe and measure deep roots, providing researchers interested in the field of deep root/rhizosphere studies with a comprehensive overview. Addressed methodologies are: excavations, trenches and soil coring approaches, minirhizotrons (MR), access shafts, caves and mines, and indirect approaches such as tracer-based techniques.

Keywords: deep roots, biogeochemical and ecological functions, root measure

INTRODUCTION

Studies on below-ground ecosystem processes are relatively rare compared to those dealing with above-ground traits of plants; roots and the rhizosphere being "hidden" in the soil (Smit et al., 2000), their observation and study relies on deploying special methodologies that are generally time-consuming and often costly. Even though methodologies to study belowground processes have significantly improved and the number of studies addressing roots has increased in recent decades, studies on roots remain mostly confined to the uppermost soil horizons. While Canadell and colleagues (1996) highlighted the potential influence of "deep roots" on many ecosystem processes nearly two decades ago, information about the actual importance of deep roots in terms of plant and ecosystem functioning, (global) water cycles and biogeochemistry remains scarce. This situation appears to be related to two major factors: (i) technological and economical limitations, i.e., the absence of tools to measure roots with sufficient throughput and standardization at affordable costs (Böhm, 1979; Vogt et al., 1996; Smit et al., 2000), and (ii) the widespread assumption that deep roots are a rather marginal component of plants. Even though deep roots may, in most cases, represent a relatively small fraction of the overall root system biomass, they likely fulfill much more essential functions than commonly accepted; an increasing number of studies clearly indicate that "looking deeper" is essential to increase our understanding of plant ecophysiology, but also of community ecology and geochemical cycles (Harper and Tibbett, 2013; see below). This review highlights the increasing importance and impact of deep roots in environmental research and provide some guidance to future research.

In this context, this review elaborates on the physiological and ecological significance of deep roots before providing a detailed overview on methods to study deep roots. Addressed methodologies are (i) excavations, trenches and soil coring approaches, (ii) minirhizotrons (MRs), (iii) access shafts, (iv) caves and mines, and (v) indirect approaches such as tracer-based techniques.

THE CHALLENGE OF DEFINING DEEP ROOTS AND MEASURING ROOTING DEPTHS

Factors that drive root growth and root system expansion are known from a diversity of field and laboratory observations. Previous publications have described the genetic control of root

traits such as length, branching and root hair formation [see references in Kell (2011)]; however, the mechanistic details, resulting in different root system phenotypes, are often unknown [but see e.g., Kato et al. (2006) for "root growth angle"]. With regard to genetic control, some root systems were found to develop rapidly: *Pinus radiata* and *Robinia pseudoacacia* roots reached a depth of 2.5 and 3.7 m after 4 years respectively (Stone and Kalisz, 1991). Similarly, Christina et al. (2011) reported that roots of Eucalypt trees could progress downward at rates of 0.55 m month^{-1}, 9–10 months after planting. Beside genetics, root architecture is controlled by hormonal influences from the plant (e.g., Santner et al., 2009) and soil organisms, and by the environment.

Due to the fact that soils are the most complex of all environments (Fitter et al., 2000) and nutrients are often strongly bound to the soil matrix (Strong et al., 1999), soil resources are inherently patchy and poorly available to organisms. In turn, plants have evolved complex strategies to forage for soil resources; root growth and root system development correspond to the allocation of assimilates to individual root apices capable of independent, yet coordinated at the plant level, morphological and physiological responses to their immediate environment. In view of the major influence of soil patchiness on root growth, it is not unexpected that spatial rooting patterns are highly variable. Indeed, one major confounding factor that often precludes accurate estimation of rooting depth is the inherent variability of root distributions (e.g., Nicoullaud et al., 1995). Further, even when this variability is taken into account, sampling depths are often decided arbitrarily and set to values that are too shallow to allow reliable estimates of rooting depth (Schenk and Jackson, 2002).

However, studies focusing on rooting depth have clearly shown that woody plants are, on average, more deeply rooted than herbaceous ones (e.g., Shalyt, 1952; Baitulin, 1979; Kutschera and Lichtenegger, 1997; Schenk and Jackson, 2002). According to Canadell et al. (1996), the rooting depths of herbaceous plants, shrubs and trees are globally in the magnitude order of 2.6 ± 0.1 m, 5.1 ± 0.8 m, and 7.0 ± 1.2 m, respectively. Many trees (*Eucalyptus spp*) and shrubs in arid areas are very deep rooted, with woody legumes such as *Acacia,* and *Prosopis* reaching depths of 20 m and even extremes such as 50–60 m (Stone and Kalisz, 1991). Canadell et al. (1996) have pointed out that tropical savannah is the biome with the deepest mean rooting depth (15 ± 5 m) and also has the deepest recorded root system (i.e., 68 m; Jennings, 1974). However, even in evergreen tropical forests a number of tree species have deep root systems (>8 m), which enable them, e.g., to survive periodic droughts (see below).

Thus, aside from genetic control and the physiological needs of each single species, external physical or biochemical factors influence the root development. Indeed, Harper et al. (1991) proposed to define root system architecture (RSA) as an evolutionary response to the spatio-temporal variability of resource availability and the corresponding constraints to growth. Some studies suggested that maximum rooting depth is mostly limited by water tables or by subsoil characteristics that prevent rooting (Cannon, 1949; Stone and Kalisz, 1991; Stone and Comerford, 1994) while others demonstrated that trees can grow roots well beyond the subsoil into the weathered bedrock (Schwinning, 2010) and/or maintain active roots below the mean water table (Wardle et al., 2004; Laio et al., 2009), e.g., by carrying and releasing oxygen under water-logged conditions (Justin and Armstrong, 1987; Shimamura et al., 2007). Thus at least some plants can modify the soil properties in their immediate vicinity (Hodge et al., 2009) to allow for deeper root system placement. However, according to Schenk (2008), roots grow as shallow as possible and as deep as necessary in response to the required water supply. Despite providing a rational explanation for the development of deep roots under a range of environmental conditions, this approach overlooks other major root functions such as nutrient foraging (see below) and plant anchorage. In addition, some experiments conducted under favorable environments (with no water or nutrient constraints, no anchoring hindrances) evidenced substantial root systems (Passioura and Wetselaar, 1972), which contradicts the former statement and confirms the generic value of the concept of a plastic root growth (Hodge, 2006).

Given this inherent plastic nature of root system development and the resulting variability of rooting patterns, there is currently no consensus on the definition of "deep root." Based on a global review of 565 root profiles, Schenk and Jackson (2002) derived average rooting profiles for 15 terrestrial biomes including all latitudes; the average of these 15 profiles indicates that soil depths of 1.1, 0.7, and 0.4 m correspond to cumulated root proportions of 95, 90, and 80%, respectively. Schenk and Jackson (2002) also found that the median sampling depth for root profiles was 0.88 m. Based on these figures, and notwithstanding species-specific or functional definitions, we therefore propose here to qualify "deep roots" in general as roots growing at soil depths of at least 1 m.

PHYSICAL, BIO-CHEMICAL, AND ECOLOGICAL FUNCTIONS OF DEEP ROOTS

While it is impossible to attribute most traits and functions exclusively to shallow or deep roots, some distinctions can be made in their specialization and their impact on the environment. The main ecological and geochemical impacts of deep roots are highlighted in this first part of the review and key processes are visually summarized in **Figure 1**.

THE ROLE OF DEEP ROOTS IN WATER UPTAKE AND REDISTRIBUTION

Water uptake is one of the key functions of deep root systems, especially in the driest and rockiest environments. Stone and Kalisz (1991) identified more than 30 species of trees that develop roots over long distances and can access deep water tables. Water storage in bedrock may also be of global importance: plants that experience soil moisture deficits might keep expanding their root systems in the weathered bedrock (Schwinning, 2010), an hypothesis supported by findings that shallow-soil endemic plants developed the special ability to explore large rock surface areas, which increases their chance to locate and explore cracks in the underlying rock (Poot and Lambers, 2008; Schenk, 2008). For example, evergreen forests in Northeastern Pará state in Brazilian Amazonia maintain transpiration during the up to 5-month dry periods by absorbing water from the soil to depths >8 m (Nepstad et al., 1994). Similar, most deciduous species in dry monsoon forests of South and Southeast Asia form new leaves 1–2 months

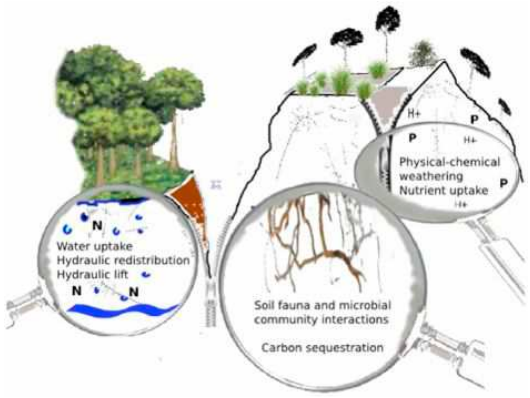


FIGURE 1 | Summary of major impacts of deep roots on the subsoil and deep roots' functions, i.e., water uptake and hydraulic redistribution, nutrient uptake, physical–chemical weathering and C sequestration, and deep root-fauna and -microbial interactions. See text for further information.

before the first monsoon rains, during the hottest and driest part of the year, which indicates that climate is not the principal determinant of their vegetative phenology which most likely depends on deep rooting (Elliott et al., 2006). More surprisingly, significant contributions of deep root to plant water uptake appears not to be restricted to water-limited environments; for example, Dawson and Ehleringer (1991) found that mature riparian trees hardly used readily available stream water and derived most of their water supply from ground water at much greater depth.

It has been argued that under pronounced seasonal arid climates deep roots favor hydraulic lift (HL), also termed hydraulic redistribution (HR; Burgess et al., 1998; Burgess, 2000), i.e., the nocturnal transfer of water by roots from moist to dry regions of the soil profile. In addition to the effects on water uptake, HL and HR can indirectly influence the availability of some nutrients (Snyder et al., 2008; see below). The process of HL was probably first described by Breazeale (1930) and received much attention since the late 1980's (Richards and Caldwell, 1987; Caldwell and Richards, 1998). HL is known to predominantly-while not exclusively-occur in deep rooted vegetation of biomes such as savannahs and shrublands, mobilizing water resources down to depths of 20 m (Bleby et al., 2010). HL and HR have been reported to provide benefits for mixed species stands/intercrops in many different biomes (Peñuelas and Filella, 2003; Goldstein et al., 2008; Zapater et al., 2011) and as a consequence, to have an impact on ecosystem functioning (Horton and Hart, 1998; Oliveira et al., 2005). With regard to agro-ecosystems, HL could contribute to develop more efficient intercropping systems (Mulia and Dupraz, 2006; Malézieux et al., 2009) with positive plant–plant interactions at best acting as a "water-safety net" (Sekiya et al., 2010). Thus, it has been proposed that breeding and engineering efforts aimed at facilitating water redistribution could eventually be used to boost yields in intercropping/agroforestry systems (Burgess, 2010).

In a wider perspective, the impact of deep roots on hydrological cycles could indirectly influence regional climates; Kleidon and Heimann (2000) concluded that deep-rooted vegetation is an important part of the tropical climate system and that without considering deep roots, the present-day surface climate cannot be simulated adequately. As many tree species of tropical forests establish a link between groundwater and the atmosphere, the presence or absence of un-degraded tropical forest reportedly influences regional climate (Bruijnzeel, 2004). In summary, there is diverse, yet consistent evidence that deep roots play a major role in plant water uptake, soil water availability and the water cycle at various scales from the rhizosphere to whole catchments (Bengough, 2012)

DEEP ROOTS AND NUTRIENT UPTAKE

RSA, i.e., the spatial distribution and morphology of roots, root physiology and symbiotic interactions affect the ability of plants to access nutrients. The occurrence of deep-rooted plants, especially in (semi-) arid ecosystems, is classically explained in regard to water uptake (see above). However, McCulley et al. (2004) collected evidence suggesting that water uptake at depth can be limited, even under arid conditions. Furthermore, they found that some nutrients had comparable if not larger plant available pools in deeper soil layers; for example, P weathering (see below) is usually greater in deep soil layers than in the topsoil (Sverdrup et al., 2002). These results, in addition to data on strontium (Sr) uptake from deep soil horizons, suggest that deep soils in (semi-) arid regions may be more significant nutrient sources than commonly believed (He et al., 2012). In addition, HR could mobilize nutrients within the soil and supply those to roots through mass flow or diffusion (McCulley et al., 2004; Lambers et al., 2006; Da Silva et al., 2011). While data on the contribution of deep roots on nutrient uptake in other ecosystems such as highly weathered tropical soils is still scarce (Hinsinger et al., 2011), it is generally believed that deep(er) root systems are important for the uptake of mobile nutrients such as potassium (K) but also nitrogen (N). While an increase in roots length in the topsoil will not increase uptake due to overlapping depletion zones (Andrews and Newman, 1970), deep roots can significantly expand the soil volume accessible for uptake and thus, e.g., increase the N-uptake fraction (McMurtrie et al., 2012). Differences in N depletion due to differences in rooting depth are of special interest for environmental protection; N in deep soil layers is more prone to leaching than N in shallow soil horizons (Thorup-Kristensen and Nielsen, 1998; Thorup-Kristensen, 2001). While, due to the high mobility of nitrate, high root densities may not be needed to enable plants to deplete specific soil areas (Robinson, 1991; Robinson et al., 1996), a linear relationship was found between root density and ^{15}N uptake from different depths (Kristensen and Thorup-Kristensen, 2004). In addition, early root growth to deeper soil horizons has been found to be important because N depletion of deep soil can be slower than N uptake in shallow soil horizons (Strebel et al., 1989), cited after (Thorup-Kristensen, 2001). For trees, Laclau et al. (2010) demonstrated that 6 m-deep roots of *Eucalyptus* spp. limited nutrient losses through deep drainage, following clear-cutting of previous tropical vegetation. While Kristensen and Thorup-Kristensen (2004, 2007)

indicate that different N use efficiencies of crops depend more on species-specific differences in root development over time and space than on differences in N uptake physiology of roots, Göransson et al. (2006, 2007, 2008) found differences in the nutrient uptake capacities, i.e. root physiology, between shallow- (5 cm) and deeper-growing (50 cm) oak roots. While such differences were not found for beech and spruce, and P uptake of oak, estimates of fine root distribution alone may thus not reflect the uptake capacity of all nutrients and all tree species with sufficient accuracy (Göransson et al., 2008). Similar differences in root uptake potentials between shallow and deep roots under tropical conditions have been found for *Eucalyptus* spp. (Da Silva et al., 2011; Laclau et al., 2013). Interestingly, Pregitzer et al. (1998) found declining root respiration rates with increasing soil depth in Sugar maple. In summary, the previous studies indicate that deep rooting species such as oak, Sugar maple and *Eucalyptus* may have evolved different physiological uptake strategies in deep and shallow soil horizons, possibly optimizing uptake efficiency in terms of carbon costs by functional specialization [see also discussion in Da Silva et al. (2011)] under reduced competition. Future studies on the physiological properties of deep roots are imperative for a better understanding of the functional specialization of nutrient uptake by fine roots in general and the development of improved nutrient uptake models in specific.

PHYSICAL–CHEMICAL WEATHERING BY DEEP ROOTS

Growing roots tend to follow pores, channels and preferentially explore soil less dense than the bulk soil (Moran et al., 2000); as woody roots grow radially, they expand in volume and exert enormous pressure on the surrounding soil (Misra et al., 1986). In contrast to roots in uppermost soil horizons, growth pressure by deep roots cannot be relieved by upward displacement but by soil compaction, reducing for example, porosity and subsequently hydraulic conductivity and aeration and thus biogeochemical functioning. Even relatively consolidated, un-weathered rocks are susceptible to the physical effects of deep roots: rock wedging results when growing roots expand at joints or fractures and the pressure can accelerate chemical dissolution of minerals (Richter and Markewitz, 1995; Richter and Walthert, 2007). It has been known for decades that roots exert physical–chemical weathering actions on their environment (Meyer and Anderson, 1939), and that such processes are decisive for the mobilization of nutrients. Roots influence the ionic concentrations in their immediate environment and are also involved in other interactions due to the root exudates in the rhizosphere (Hinsinger, 1998). While such processes have almost exclusively been studied in top soils, it is certainly valid to consider that they also prevail in deep soil layers (Richter and Markewitz, 1995). Indeed, it was shown that fine roots at a soil depth of 1 m could balance chemical adversity in natural soil (Richter and Walthert, 2007). Carboxylate exudation by deep roots can contribute accessing poorly soluble iron phosphate in arid zones (He et al., 2012). As deep roots directly influence the depth distribution of soil carbon dioxide and acidity, there is no doubt that they play an active role in the physical–chemical weathering of mineral material and thus contribute to pedogenesis, but the precise biogenic effects of deep roots remain to be clarified (Richter and Markewitz, 1995).

INFLUENCE OF ROOTING DEPTH ON C BIOGEOCHEMISTRY

Despite their low carbon (C) content, subsoil horizons contribute to more than half of the total soil C stocks, and therefore need to be considered in the global C cycle (Harrison et al., 2011; Koarashi et al., 2012; Harper and Tibbett, 2013). Soil organic carbon (SOC) has three main origins: plant root growth including exudates, dissolved organic carbon (DOC) transport and bioturbation (Rumpel and Kögel-Knabner, 2011). While the relative importance of each source is dependent on, for example, climate, soil and vegetation types, the general importance of roots for soil C sequestration (Kell, 2011) is underlined by the fact that the root-derived C has a high potential to be stabilized long-term. Beside other stabilizing factors (Rumpel and Kögel-Knabner, 2011), roots are often more recalcitrant than topsoil litter (Abiven et al., 2005; Rasse et al., 2005). The deposition and fate of C from deep roots (and their associated biota, see below) has rarely been examined in detail (Clemmensen et al., 2013; Harper and Tibbett, 2013). Furthermore, root C fluxes to deep soil layers are poorly understood mainly due to uncertainties associated with the measurement of total root C input, i.e., sloughing of root cells during growth, root exudates and root turnover. Because subsoil horizons with low C concentrations may not yet be saturated in SOC, it has been suggested that they may have the potential to sequester SOC through increasing C input by turnover of deep roots and DOC following preferential flow pathways such as root pores (Lorenz and Lal, 2005; Rumpel and Kögel-Knabner, 2011). The dynamics of deep SOC is largely controlled by interactions with soil minerals (Koarashi et al., 2012), and as both processes are highly influenced by deep roots (see above), future studies are urgently needed, including estimates on C changes in deep soil profiles in response to land-use changes such as de-/reforestation or the disappearance of specific deep-rooted plant species. Further studies on deep roots will significantly improve information on root-derived C, which is needed to accurately describe critical processes like net primary production and carbon storage from ecosystem to global scales and under recent and future climates (McCormack et al., 2013).

IMPACT OF DEEP ROOTS ON SOIL FAUNA AND MICROBIAL COMMUNITIES

Fauna diversity was described as declining from the shallow toward the deep subterranean habitats (Culver and Pipan, 2009), however it is still widely unknown how deep roots influence the vertical distribution of soil fauna. While it is well known that fauna in the uppermost soil horizons and litter layers utilize roots for feed, it was also shown that deep plant roots are the major energy source, and provide shelter and cocoon-building material for troglobionts, i.e., invertebrates restricted to subterranean environments (Howarth et al., 2007; Silva et al., 2011; Novak and Perc, 2012). Both living and dead roots are used, providing resources for a wide diversity of cave organisms, including root-feeders, scavengers, and predators (Howarth, 1983). Freckman and Virginia (1989) showed that in some ecosystems the majority of nematodes, and thus herbivory, may occur at soil depths rarely studied. Because deep roots can directly or indirectly support the fauna, the loss of deep-rooted plants in general or of specific species will affect subterranean animals–as far as eliminating

host root-specific animal (Reboleira et al., 2011). Knowledge on deep root-fauna interactions is thus decisive for development of conservation strategies in ecosystems and to understand root herbivory. While Silva et al. (1989) claimed that deep-rhizosphere micro-arthropod fauna is a reduced subset of the fauna of shallow soil horizons, Novak and Perc (2012) stated that the division of soil fauna into shallow and deep communities is a global pattern, at least in karst ecosystems with deep-rooted vegetation. While caves might represent very special ecosystems, the concentrations of organic matter and bioavailable nutrients usually decrease with soil depth; thus, in deep soil horizons the rhizosphere is "an oasis of resources compared with the [bulk soil]" (Richter and Walthert, 2007). For example, the fungal biomass in forest bulk soil decreased steadily by three orders of magnitude from the soil surface to 2.5 m depth whereas the fungal biomass in the rhizosphere remained relatively constant between depths of 0.4–2.5 m and was higher than in bulk soil (Richter and Walthert, 2007), illustrating the impact of roots on the depth distribution of fungal biomass. Furthermore, fungal species community compositions can change with depth too, i.e., different species or fungal functional groups form mycorrhizal symbioses with deep roots than with shallow roots (e.g., Rosling et al., 2003; Clemmensen et al., 2013). While it is known that the diversity of microorganisms is typically decreasing with depth and the community composition is changing (Eilers et al., 2012), high levels of bacterial biomass were found to remain down to 8 m depth in prairie soils (Dodds et al., 1996); it is thus currently unknown which roles deep roots play for soil microbial communities in detail. However, because deeper occurring microbes may have a greater influence on soil formation processes than their counterparts in shallow soil horizons, due to their proximity to soil parent material (Buss et al., 2005) and a critical influence on longer-term soil carbon sequestration (Rumpel and Kögel-Knabner, 2011), further studies including the rhizosphere of deep roots are imperative. A first indication of the importance of deep roots on bacterial communities is given by Snider et al. (2009), who observed complex interaction between deep roots and bacterial communities, some bacteria from the soil overlaying the cave being introduced by the roots while deep roots could acquire bacteria from the cave walls.

In general, the distributions of root-associated biota through the soil profile remains poorly understood, as most studies focus on communities in shallow soil horizons. This emphasizes the importance of future research into faunal, fungal and microbial communities adapted to the deep root zone, enhancing understanding of subterranean ecology and ecosystem functioning (Cardon and Whitbeck, 2007).

DIRECT AND INDIRECT METHODS TO STUDY DEEP ROOTS

In this second part of the review we highlight the most important methods to access and to study deep roots directly and visually (**Figures 2–6**) and discuss their main advantages and shortcomings (**Table 1**). More precisely, we present four methodological groups: (i) excavations, trenches and soil coring

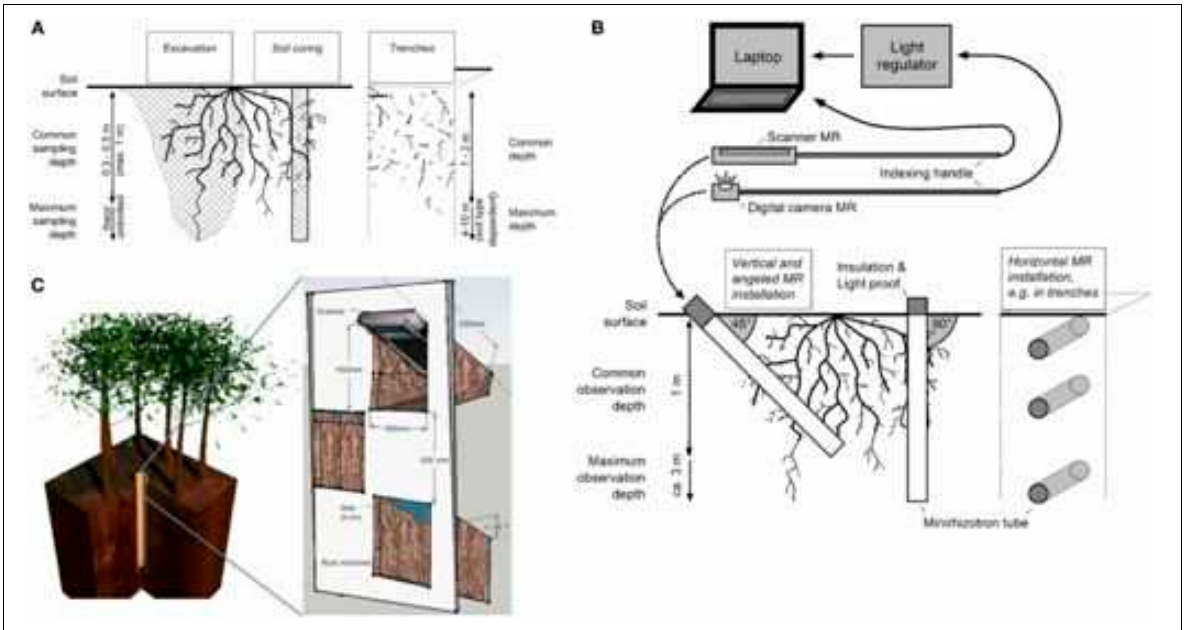


FIGURE 2 | (A–C) Illustrations of some direct field methods to access (deep) root systems. **(A)** Excavation, soil coring and soil trenching techniques. **(B)** Minirhizotron (MR) techniques with image acquisition devices (i.e., Digital Camera or Scanner MR) and different options to install the MR tubes, i.e., angled or vertical from the soil surface or horizontally from trenches. **(C)** Schematic view of the access shafts technique. Left: Location of the well in relation to a tree row (vertical projection). Right: Side view of the soil volume excavated for angled root window installation. See text for further information.



FIGURE 3 | Root mapping and collection in a trench (4 m deep) in Thailand (Maeght, 2009).



FIGURE 4 | Root sampling from an excavation (7 m deep) in Lao PDR (Maeght, 2009).



FIGURE 5 | Root scanning in access shaft (5 m deep) in Lao PDR (Maeght, 2012).

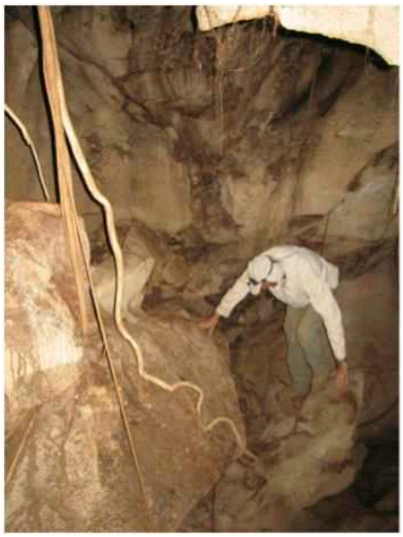


FIGURE 6 | Cave prospection (12 m deep) for root studies in Lao PDR (Pierret, 2010).

approaches, (ii) MRs, (iii) access shafts, and (iv) caves and mines. In addition, a short overview on (v) indirect approaches such as tracer studies is given.

EXCAVATION, TRENCHES, AND CORING APPROACHES

Despite advances in root studies in the last five decades, the most common methods used to obtain data on root distribution and structure have not changed substantially: excavation and coring techniques are still and by far the preferred methods. Recently, the term "shovelomics" was establish (Trachsel et al., 2010) to qualify simple but effective approaches to determine root phenotypes including maximum rooting depth. Excavation methods include manual digging and up-rooting, the use of various mechanical devices, explosives, and high pressure water or air (Weaver, 1919; Stoeckeler and Kluender, 1938; Mitchell and Black, 1968; Newton and Zedaker, 1981; Rizzo and Gross, 2000). Coring can be conducted manually by pushing or hammering sampling equipment into the soil using various devices from simple, sharpened steel augers to advanced cryogenic devices for sampling wetland soil (Cahoon

Table 1 | Main advantages and disadvantages of direct (i.e. mechanical, visual) methods to access and to study deep roots.

Method	Realistic replication per plot	Key benefits	Disadvantages
Excavation	Very few (∼1–2)	3D information, possibility of mapping root systems layer by layer (root biomass). Root samples can be analysed further (e.g. for root morphology, to digitize the coarse root system)	Fine roots are often omitted. Very destructive and very labor intensive for bigger plants
Trenching	Few (<3)	Vertical and horizontal information (2D, root counting). Possibility to take root and soil samples and to install MR tubes and other measurement gear	Difficulty to establish deep trenches without reinforcements. Limited time of usability. Destructive and labor intensive
Soil coring	Many (>10–20)	Vertical information (fine root biomass). Root samples can be analysed further (e.g. for root morphology). Easy to replicate in stone-free soils. Minor plot disturbance	Requires a large number of samples. Moderate destructive and labor intensive rinsing. Logistically difficult if machine drilled
Minirhizotrons	Average (5–8)	Continuous, vertical information (fine root length density, root dynamics). Relatively easy to replicate in stone-free soils. Minor plot disturbance	Difficult set-up into deep soil layers ("gap formation"). Time lag before first measurement. Limited length of commercial tubes (<3 m). Expensive imaging equipment. Very labor intensive analysis and logistically difficult if machine drilled
Access shafts	Few (<3)	Continuous, vertical information (fine root length density, root dynamics). Possibility to manipulate/sample roots and soil at different depths. Sufficient space for additional measurements/devices	Adaptation depends on soil type and local geography. Moderate plot disturbance and very labor intensive. Logistically difficult for enforcement delivery
Mines and caves	Not controllable	Can provide cost-efficient access to the greatest depth. Intrinsic potential to study root-cave animal/microbe interactions. Sufficient space to install (sap-flow) sensors	Not a "normal" soil environment. Difficulties in identifying the parent plant taxa/individual from the root. Replication not controllable. Often difficult to enter

Description of key benefits is based on one replicate per method.

et al., 1996; Rewald and Leuschner, 2009). In addition, vehicle-mounted or hand-held mechanical devices have been developed to take soil cores in the field, especially to greater depth or with larger diameters (see Kornecki et al., 2008 and references within). An overview on the historical use of coring and excavation methods for root studies can be found in Böhm (1979).

While commonly used, most excavation and trenching approaches (**Figures 2A**, **3**, **4**) are limited to the first meter and reach only occasionally soil depths of two meters and below (Wearver, 1915; Eamus et al., 2002; Silva and Rego, 2003; Dauer et al., 2009; De Azevedo et al., 2011). While commercial trench diggers, e.g., for sewer placement, can easily be used to excavate at greater soil depth (e.g., 5 m), the stability of unsupported side walls, which depends on soil type and moisture levels (Vanapalli and Oh, 2012), is the major obstacle limiting pit/trench depth. However, occasionally several meters deep trenches can be established (**Figure 3**). The cost of establishing deep trenches lead many researchers to use available soil profile-walls, created by road cuts, exposed at stream cut-banks or after landslides, to determine vertical rooting pattern (Canadell et al., 1999; Silva and Rego, 2003). Common analyses at all profile-walls are root counts and estimationsL of the root length density RLD; "trench profile" technique (Van Noordwijk et al., 2000) and the determination of maximum rooting depth. While some innovations such as radiotracers (Abbott and Fraley, 1991; see below) or digital imaging (Dauer et al., 2009) have been introduced, overall profile-walls are used to quantify roots by soil location in a similar manner since the end of the 19th century (Weaver and Bruner, 1927 and references within). In contrast, excavations (**Figure 2A**) give full biomass per individual and often allow taking photographs/3D-scans of whole (coarse) root systems (Wagner et al., 2010)–providing valuable data on the vertical and horizontal root system distribution. However, because excavations, especially of larger plants, are particularly labor intensive, they are frequently restricted to the analysis of the upper soil layers, omitting deep roots of mature plants, and/or to low sample numbers (Cameron, 1963; Silva and Rego, 2003; Fang et al., 2012).

Soil coring approaches (**Figure 2A**) are suitable to obtain estimates of root length and mass, and root morphology beside data on root distribution. However, root coring is also often restricted to the uppermost soil layers because the majority of fine roots can be found in the first 0.3–0.5 m of soil. In addition, the occurrence of stones or boulders or high soil densities can prevent the use of simple and cheap manual coring tools for sampling of deep roots. However, corers have occasionally been taken to a much

greater soil depth with technical help; for example Virginia et al. (1986) took samples down to the water table at 5–6 m depth in the Sonoran Desert, and Ritson and Sochacki (2003) sampled roots down to six meters with a motor driven corer to determine the root biomass of *Pinus pinaster* in Australia. Rarely much greater soil depths are explored by machine drilling of cores (<20 m, Carbon et al., 1980; <34 m, Dalpé et al., 2000). At moderate depths, soil coring was found to be a more efficient option for fine root distribution mapping than trenching (Dauer et al., 2009) but this advantage might not hold for deeper soil horizons. Upscaling from core data to stand level root biomasses is in general only possible if sample numbers are sufficiently high due to heterogeneous root distribution (see above). For deep roots this might be especially problematic because of the low biomass of deep roots and their even more heterogeneous distribution; thus, high sample numbers are essential for deep root sampling by soil coring (Bengough et al., 2000).

MINIRHIZOTRON TECHNIQUES

Non-destructive methods for studying root systems, rhizotrons, "root windows" and MRs have the advantage of allowing the repeated observation of particular locations in the soil profile. The techniques also permits visualization of very small roots, and occasionally hyphae, through the transparent observation windows/tubes. The MR method was probably first used by Bates (1937); Bates, and described again later (Waddington, 1971; Vos and Groenwold, 1983; see Rewald and Ephrath, 2013 for a recent review). This method is now widely used in multiple fields of root research, such as studies on root distribution and root demography, and interaction between roots and root-soil (organisms) (Poelman et al., 1996; Majdi et al., 2005). Setting up MR tubes in the field requires the use of a soil corer (Hummel et al., 1989) or manual auger (Kage et al., 2000), and can be technically complex depending on the nature of the soil (e.g., smearing of walls with high clay content, presence of gravels preventing progress, lack of cohesiveness in sandy soils or in water saturated soils, etc.). Nevertheless, some researchers have successfully installed MR tubes in rocky soil (Phillips et al., 2000) and in wetlands (Iversen et al., 2011). MR tube installation from the soil surface (vertical or angled; **Figure 2B**) rarely occurs beyond the first meter of the soil profile, due to the above-mentioned difficulties encountered during installation (Rewald and Ephrath, 2013). For soil with higher bulk densities and to access greater depths, researchers need to use portable mechanical drilling devices or tractor-mounted auger systems (Brown and Upchurch, 1987; Kloeppel and Gower, 1995). Furthermore, the length of commercially available transparent observation tubes (norm: 2 m long, max. length: approx. 3 m) presents a constraint for continuous tube installation to greater depth. This problem is partially circumvented by researchers by installing MR tubes horizontally in rhizo-lysimeters or from trenches (**Figure 2B**). However, because of the workload such attempts have been extremely rare; examples are the field-based rhizo-lysimeter complex of Charles Sturt University, Australia (Eberbach et al., 2013) and MR tube installation in 8 m deep trenches in a plantation of eucalypt trees in Brazil (Hinsinger et al., 2012).

The MR method permits calculation of fine-root length production, mortality and turnover (Trumbore and Gaudinski, 2003); the same fine-root segments can be monitored over their lifetime and pictures are stored in a database for processing (Rewald and Ephrath, 2013). However, the conversion of MR data, i.e., RLD, to root biomass requires the simultaneous collection of root cores to develop correlations. Compared to excavated roots and repeated coring approaches, the MR technique allows relatively continuous segregation of live and dead root since image sequences that span the life-time of roots are acquired (but see Rewald and Ephrath, 2013). However, it has been documented that one major limitation of MR studies with regard to the assessment of root turnover is that they over-sample the smaller and more dynamic lower-order roots (Guo et al., 2008).

A common limitation of the MR technique (Johnson et al., 2001) is the difficulty in obtaining good contact between the tube and the soil; in many soil types gaps form in some places along the tube, creating artificial conditions for root growth. This problem is suggested to aggravate with increasing drilling depth ("off-centered") and the use of machine drilling which creates less precisely sized holes than manual hammering. In conclusion, MR tubes installed from the soil surface rarely reach much more down than one meter because this is the depth to which manual installation is often possible. The installation of deep horizontal MR tubes, e.g., in trench profiles, is difficult due the limited space for using an auger and inserting tubes, and laborious due to the additional trenching. However, the most serious limitations to the MR technique seem to be the initial costs of hard- and software and the time lag until soil and root dynamics come back to steady state conditions after tube installation. Furthermore, while labor costs for tube installation and picture capturing are relatively moderate, image analysis can become very time consuming and sufficient resources have to be scheduled for these purposes.

ACCESS SHAFTS

The access shaft (or access well) observation technique (**Figures 2C**, **5**) is a recent evolution and combination of the different techniques for root observation described in Böhm (1979) and in the two previous method sections of this review. The access well method provides safe access to deep soil observation locations, by means of ladders affixed to the well's wall. Depths of several meters, typically between 5 and 10 m depending on soil conditions, can be investigated. Building the well can take about a week and the walls are reinforced with concrete tubes or other materials (Maeght et al., 2012), distinguishing this techniques from trenches. Importantly, wells maximize the accessible soil depth: volume of displaced soil ratio, compared to other types of excavations.

Similar to MR techniques, access shafts allow direct observation of root growth dynamics using adapted "root windows" through which roots can be observed at regular time intervals. Using an access-well and a window scanner technique, following a procedure similar to that described by Maeght et al. (2007), root growth dynamics and root turnover could be monitored at 0.5 m soil depths increments down to 4.5 m in a rubber tree plantation in NE Thailand (Gonkhamdee et al., 2009). The number

of root windows should be adapted to the well depth; windows should be geometrically arranged to allow for complete observation of the profile without compromising the strength of the reinforcing structure. Each root window includes a specifically designed glass frame supporting, on its upper side, a piece of 10 mm thick glass (∼ 25 × 30 cm) pressed against the soil at a 45° angle (**Figure 2C**; Maeght et al., 2012). On the frame's lower side, two guide rails allow the insertion of a standard flatbed scanner; the images can be analysed analogue to pictures from MR tubes and similar constrains to data analysis apply (see above). However, the advantage of the access shafts method is that it provides physical access to deep soil horizons for (manipulative) research, e.g., to measure microbiological activities, and nutrient and water uptake *in situ*. Access shafts also allow the installation of various sensors at soil depths that have not been investigated in greater detail, examples are special devices for imaging the dynamics of soil pH as influenced by roots (e.g., optodes, Blossfeld et al., 2011) or NIR/VIS portable spectrometry analysis (Nakaji et al., 2008).

CAVES AND MINES

Deep roots of trees and shrubs are regularly found in caves and mine shafts (Cannon, 1960, cited after Stone and Kalisz, 1991; Stone, 2010). However, such observations have most often been mentioned in the literature as curiosities. Only in the last decade caves have been used more systematically for studies on roots. In 1999, Jackson et al. used 21 different deep caves (5–65 m deep) in the Edwards Plateau, USA to study the community composition below ground and maximum fine root depth of six dominant tree species (Jackson et al., 1999). They linked deep roots to each species and individual DNA sequence variation of the internal transcribed spacer (ITS) and inter-simple sequence repeats (ISSR) (Rewald et al., 2012), and found that all six tree species grew roots below 5 m, and at least four of the six reached a depth of 18 m. Similarly, Howarth et al. (2007) determined species composition of deep roots in Hawaiian lava tube caves with DNA sequence variation and related root taxa to cave arthropod fauna. In more recent years, the caves utilized by Jackson et al. (1999) were frequently used for further studies, e.g., to compare the hydraulic parameters of deep vs. shallow roots and to determine the water flux thru deep roots (McElrone et al., 2004, 2007; Bleby et al., 2010). In Europe, Filella and Peñuelas (2003) studied tree access to deep water sources and the possibility of HL from the deep roots of one *Pinus nigra* tree. They enriched the deep roots with deuterium by accessing them from a cave at 8 m depth, showing that, in this Mediterranean forest and during the dry summer, *P. nigra* trees accessed a deep water source and recycled it via HL. In Australia, Doody and Benyon (2011) installed sap-flow sensors on *P. radiata* roots, extending through a limestone cave to an unconfined aquifer 14 m below the surface, to quantify the contribution of deep roots to whole plant water uptake (>22%). Thus, caves can provide access to intact, functioning deep roots and several research groups have taken advantage of these natural access tunnels to deep roots in the past. While research in caves of mesic areas has been conducted (e.g., McElrone et al., 2004; Novak and Perc, 2012), results of root-specific studies are overwhelmingly available for deep roots in (karst) caves of (semi-) arid ecosystems. Aside from questions of maximum rooting depth and species community composition below ground, research mainly addressed root hydraulics and water flux patterns *in situ*. The abundance of caves and the unique environment of caves are two factors limiting the broad use of this technique, especially for studies of deep root functioning in "normal" soil environments and for quantifying deep roots.

INDIRECT APPROACHES FOR THE OBSERVATION DEEP ROOTS

Quite a few indirect approaches have been used to study and quantify the role of deep roots in plant species and on the environment; while this is outside the focus of this review we will give an overview on some of them in the following.

To assess differences in uptake capacity between different soil depths, *tracers* can be injected at different depths for later recovery in the biomass; the amount of tracer in plant biomass is related to the uptake from each depth (Lewis and Burgy, 1964). Tracer element can be either radioactive or stable isotopes, or analogous elements. Analogous are chemical elements, which are similar to specific nutrient ions, thus uptake, and integration into biomass works the same way as the nutrient (e.g., Sr^{2+} instead of Ca^{2+}). Some factors must be considered to successfully use tracers: (i) the application method must label the respective soil horizon uniformly and dilution effects must be predictable, (ii) the root-available amount of tracer must be predictable with respect to competing processes such as microbial immobilization and soil adsorption, and (iii) the uptake capacity of the tracer by roots, compared to (other) nutrients (i.e., discrimination factor), should be known under different soil properties (after Göransson et al., 2006, modified).

Electrical capacitance has been proposed as a means to estimate root mass based on the premise that the equivalent parallel resistance-capacitance of the electrical circuit formed by the interface between soil water and plant root surfaces is proportional to the overall amount of active roots present. Good correlations between root capacitance and root mass were obtained for young plants (Chloupek et al., 2006). However, the relative influence of deep vs. shallow roots on root electrical capacitance remains unclear (Herrera et al., 2012).

Electrical resistivity tomography (ERT) can be used to monitor soil water movement in large volumes of soil. A field study with 3-month-old maize showed that this technique could be used to non-destructively quantify in 2-D, root water uptake as well as preferential infiltration and drainage under plant rows (Michot, 2003). More recently, ERT was used as part of an experiment set up in a mature tropical forest in eastern Amazonia to demonstrate greater depletion of soil water in the 11–18 m depth increment of a throughfall exclusion plot compared with a control in the experiment (Davidson et al., 2011). These authors used a soil water content measure obtained with a TDR probe to convert soil apparent electrical resistivity values to soil water contents. Despite its sensitivity to soil characteristics, which can affect its performance, ERT is an effective means to obtain, non-destructive, indirect information about root functioning at considerable soil depths.

Soil moisture measurements, assessing soil moisture changes over time, represent an indirect way to detect signs of root activity namely water uptake. For example, based on soil moisture measurements, Calder et al. (1997) found clear evidence of water uptake down to a soil depth of 7.5 m under three species of plantation trees. Based on an analysis of water balance changes in a crop sequence with lucerne, Dunin et al. (2001) estimated an apparent root extension for lucerne 2–2.5 m beyond that of annual crops. Similar, simple rainfall and groundwater monitoring can be used to relate the survivorship/transpiration of some species in arid systems to the plant's ability to tap water from permanent water tables, which are sometimes located at depths of 18 m or more (Rawitscher, 1948).

CONCLUSION AND OUTLOOK

Although the literature does not include, by far, as many references on deep roots as it does on shallow roots, the available information has clearly demonstrated that deep roots are common and of pivotal importance for plant functioning, subterranean biocenosis and many biogeochemical cycles and associated ecosystem services such as pedogenesis, soil carbon sequestration and moisture regulation in the lower troposphere. We hope that this review will lead to a sustained interest on deep roots and the deep rhizosphere in the future; while it remains difficult to define "deep roots" in an absolute manner, there is a pressing need to reassess current root sampling and monitoring schemes, to avoid introducing bias in future assessments of root system traits. Because no methodologies exist today to characterize the entire RSA of mature plants at once, particularly not for large-sized organisms such as trees, the methods presented in this review need to be improved further. Clever combinations of techniques, such as access shafts, must be developed toward reaching deeper soil horizons at lower costs—allowing for more frequent "deep-root"-studies. While we predict that research on deep roots and the deep rhizosphere will remain laborious in the years to come, the crucial knowledge gained in regard to plant and ecosystem functioning by "looking deeper" will leave us no choice, especially not in times of increasing climate change.

ACKNOWLEDGMENTS

Jean-Luc Maeght would like to thank Dylan Fischer for his recommendation of studies on using minirhizotrons in the field and his contribution to this section of the manuscript. We also are deeply grateful to the National Agriculture and Forestry Research Institute (NAFRI) of Laos, the French Agence Nationale de la Recherche (project Ecosfix, ANR-2010-STRA-003) and the French Institute for Research for Development (IRD) for providing the enabling environment and financial resources.

REFERENCES

Abbott, M. L., and Fraley, L. (1991). A review: radiotracer methods to determine root distribution. *Environ. Exp. Bot.* 31, 1–10.

Abiven, S., Recous, S., Reyes, V., and Oliver, R. (2005). Mineralisation of C and N from root, stem and leaf residues in soil and role of their biochemical quality. *Biol. Fertil. Soils* 42, 119–128. doi: 10.1007/s00374-005-0006-0

Andrews, R. E., and Newman, E. I. (1970). Root density and competition for nutrients. *Oecol. Plant* 5, 319–334.

Baitulin, I. O. (1979). *Kornevaja Sistema Rastenij Aridnoj Zony Kazakhstana.* [Root Systems of Plants of the *Arid Zone* of Kazakhstan]. Alma-Ata: Nauka.

Bates, G. H. (1937). A device for the observation of root growth in the soil. *Nature* 139, 966–967.

Bengough, A. G. (2012). Water dynamics of the root zone: rhizosphere biophysics and its control on soil hydrology. *Vadose Zone J.* 11. doi: 10.2136/vzj2011.0111

Bengough, A. G., Castrignano, A., Pagès, L., and van Noordwijk, M. (2000). "Sampling strategies, scaling, and statistics," in *Root Methods*, eds A. L. Smit, A. G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin, and S. C. van de Geijn (Berlin; Heidelberg: Springer), 147–173. doi: 10.1007/978-3-662-04188-8_533

Bleby, T. M., McElrone, A. J., and Jackson, R. B. (2010). Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant Cell Environ.* 33, 2132–2148. doi: 10.1111/j.1365-3040.2010.02212.x

Blossfeld, S., Gansert, D., Thiele, B., Kuhn, A. J., and Lösch, R. (2011). The dynamics of oxygen concentration, pH value, and organic acids in the rhizosphere of Juncus spp. *Soil Biol. Biochem.* 43, 1186–1197. doi: 10.1016/j.soilbio.2011.02.007

Böhm W. (1979). *Methods of Studying Root Systems*. Berlin: Springer.

Breazeale, J. F. (1930). Maintenance of moisture-equilibrium and nutrition of plants at and below the wilting percentage. in Ariz. *Agric. Exp. Stn. Tech. Bull.* 29, 137–177.

Brown, D. A., and Upchurch, D. R. (1987). Minirhizotron observation tubes: methods and applications for measuring rhizosphere dynamics. *ASA Spec. Publ.* 50, 15–30.

Bruijnzeel, L. A. (2004). Hydrological functions of tropical forests: not seeing the soil for the trees. *Agric. Ecosyst. Environ.* 104, 185–228. doi: 10.1016/j.agee.2004.01.015.

Burgess, S. S. O. (2010). Can hydraulic redistribution put bread on our table. *Plant Soil* 341, 25–29. doi: 10.1007/s11104-010-0638-1

Burgess, S. S. O. (2000). Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Ann. Bot.* 85, 215–224. doi: 10.1006/anbo.1999.1019

Burgess, S. S. O., Adams, M. A., Turner, N. C., and Ong, C. K. (1998). The redistribution of soil water by tree root systems. *Oecologia* 115, 306–311. doi: 10.1007/s004420050521

Buss, H. L., Bruns, M. A., Schultz, M. J., Moore, J., Mathur, C. F., Brantley, S. L., et al. (2005). The coupling of biological iron cycling and mineral weathering during saprolite formation, Luquillo Mountains, Puerto Rico. *Geobiology* 3, 247–260.

Cahoon, D. R., Lynch, J. C., and Knaus, R. M. (1996). Improved cryogenic coring device for sampling wetland soils. *J. Sedement. Res.* 66, 1025–1027.

Calder, I. R., Rosier, P. T. W., Prasanna, K. T., and Parameswarappa, S. (1997). Eucalyptus water use greater than rainfall input - possible explanation from southern India. *Hydrol. Earth Syst. Sci.* 2, 249–255.

Caldwell, M. M., and Richards, J. H. (1998). Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113, 151–161.

Cameron, R. (1963). A study of the rooting habits of rimu and tawa in pumice soils. *N.Z. J. For.* 8, 771–785.

Canadell, J., Djema, A., Lopez, B., Lioret, F., Sabaté, S., Siscart, D., et al. (1999). Structure and dynamics of the root system. *Ecol. Stud.* 137, 47–59.

Canadell, J., Jackson, R. B., Ehleringer, J. B., Mooney, H. A., Sala, O. E., and Schulze, E.-D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595. doi: 10.1007/BF00329030

Cannon, W. A. (1949). A tentative classification of root systems. *Ecology* 30, 542.

Cannon, H. L. (1960). The development of botanical methods of prospecting for uranium on the Colorado Plateau. *U.S. Geol. Surv. Bull.* 1085-A, 1–50.

Carbon, B. A., Bartle, G. A., Murray, A. M., and Macpherson, D. K. (1980). The distribution of root length, and the limits to flow of soil water to roots in a dry sclerophyll forest. *For. Sci.* 26, 656–664.

Cardon, Z. G., and Whitbeck, J. L. (2007). *The Rhizosphere: An Ecological Perspective*. London: Elsevier.

Chloupek, O., Forster, B. P., and Thomas, W. T. B. (2006). The effect of semi-dwarf genes on root system size in field-grown barley. *Theor. Appl. Genet.* 112, 779–786. doi: 10.1007/s00122-005-0147-4

Christina, M., Laclau, J.-P., Gonçalves, J. L. M., Jourdan, C., Nouvellon, Y., and Bouillet, J.-P. (2011). Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. *Ecosphere* 2, 1–10. doi: 10.1890/ES10-00158.1

Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., et al. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339, 1615–1618. doi: 10.1126/science.1231923

Culver, D. C., and Pipan, T. (2009). *The Biology of Caves and Other Subterranean Habitats*. Oxford, New York: University Press.

Dalpé, Y., Diop, T., Plenchette, C., and Gueye, M. (2000). Glomales species associated with surface and deep rhizosphere of *Faidherbia albida* in Senegal. *Mycorrhiza* 10, 125–129. doi: 10.1007/s005720000069

Da Silva, E. V., Bouillet, J.-P., De Moraes Gonçalves, J. L., Junior, C. H. A., Trivelin, P. C. O., Hinsinger, P., et al. (2011). Functional specialization of *Eucalyptus* fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. *Funct. Ecol.* 25, 996–1006. doi: 10.1007/s10531-011-0057-5

Dauer, J. M., Withington, J. M., Oleksyn, J., Chorover, J., Chadwick, O. A., Reich, P. B., et al. (2009). A scanner-based approach to soil profile-wall mapping of root distribution. *Dendrobiology* 62, 35–40.

Davidson, E., Lefebvre, P., and Brando, P. (2011). Carbon inputs and water uptake in deep soils of an eastern Amazon forest. *For. Sci.* 57, 51–58.

Dawson, T., and Ehleringer, J. (1991). Streamside trees that do not use stream water. *Nature* 350, 335–337.

De Azevedo, M. C. B., Chopart, J. L., and de Medina, C. C. (2011). Sugarcane root length density and distribution from root intersection counting on a trench-profile. *Sci. Agric.* 1, 94–101. doi: 10.1590/S0103-90162011000100014.

Dodds, W., Banks, M., and Clenan, C. (1996). Biological properties of soil and subsurface sediments under abandoned pasture and cropland. *Soil Biol. Biochem.* 28, 837–846. doi: 10.1016/0038-071700057-0

Doody, T. M., and Benyon, R. G. (2011). Direct measurement of groundwater uptake through tree roots in a cave. *Ecohydrology* 4, 644–649. doi: 10.1002/eco.152

Dunin, F., Smith, C., Zegelin, S., and Leuning, R. (2001). Water balance changes in a crop sequence with lucerne. *Aust. J. Agric. Res.* 52, 247–261. doi: 10.1071/AR00089

Eamus, D., Chen, X., Kelley, G., and Hutley, L. (2002). Root biomass and root fractal analyses of an open Eucalyptus forest in a savanna of north Australia. *Aust. J. Bot.* 50, 31–41. doi: 10.1071/breakBT01054

Eberbach, P. L., Hoffmann, J., Moroni, S. J., Wade, L. J., and Weston, L. A. (2013). Rhizo-lysimetry: facilities for the simultaneous study of root behaviour and resource use by agricultural crop and pasture systems. *Plant Methods* 9:3. doi: 10.1186/1746–4811-9-3

Eilers, K. G., Debenport, S., Anderson, S., and Fierer, N. (2012). Digging deeper to find unique microbial communities: the strong effect of depth on the structure of bacterial and archaeal communities in soil. *Biol. Chem.* 50, 58–65. doi: 10.1016/j.soilbio.2012.03.011

Elliott, S., Baker, P., and Borchert, R. (2006). Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecol. Biogeogr.* 15, 1–10. doi: 10.1016/j.soilbio.2012.03.011

Fang, S., Clark, R., and Liao, H. (2012). "3D quantification of plant root architecture *in situ*," in *Measuring Roots - An Updated Approach*, ed S. Mancuso (Berlin: Springer), 135–148.

Filella, I., and Peñuelas, J. (2003). Indications of hydraulic lift by Pinus halepensis and its effects on the water relations of neighbour shrubs. *Biol. Plantarum* 47, 209–214. doi: 10.1023/B:BIOP.0000022253.08474.fd

Fitter, A., Hodge, A., and Robinson, D. (2000). "Plant response to patchy soils," in *The Ecological Consequences of Environ- Mental Heterogeneity*, eds M. J. Hutchings, E. A. John, and A. J. A. Stewart (Oxford: Blackwell Science), 71–90.

Freckman, D. W., and Virginia, R. A. (1989). Plant-feeding nematodes in deep-rooting desert ecosystems. *Ecology* 70, 1665–1678. doi: 10.2307/1938101

Goldstein, G., Meinzer, F. C., Bucci, S. J., Scholz, F. G., Franco, A. C., and Hoffmann, W. A. (2008). Water economy of Neotropical savanna trees: six paradigms revisited. *Tree Physiol.* 28, 395–404. doi: 10.1093/treephys/28.3.395

Gonkhamdee, S., Maeght, J. L., Do, F., and Pierret, A. (2009). Growth dynamics of line Heavea brasiliensis roots along a 4.5-m soil profile. *Khon Kaen Agric. J.* 37, 265–276.

Göransson, H., Fransson, A.-M., and Jönsson-Belyazid, U. (2007). Do oaks have different strategies for uptake of N, K and P depending on soil depth. *Plant Soil* 297, 119–125. doi: 10.1007/s11104-007-9325-2

Göransson, H., Ingerslev, M., and Wallander, H. (2008). The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature *Quercus robur*, *Fagus* sylvatica and *Picea abies* stands. *Plant Soil* 306, 129–137. doi: 10.1007/s11104-007-9524-x

Göransson, H., Wallander, H., Ingerslev, M., and Rosengen, U. (2006). Estimating the relative nutrient uptake from different soil depth of *Quercus robur*, *Fagus sylvatica* and *Picea abies* (L.) Karst. *Plant Soil* 286, 87–97. doi: 10.1007/s11104-006-9028-0

Guo, D., Li, H., Mitchell, R. J., Han, W., Hendricks, J. J., Fahey, T. J., et al. (2008). Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytol.* 177, 443–456. doi: 10.1111/j.1469-8137.2007.02242.x

Harper, R. J., and Tibbett, M. (2013). The hidden organic carbon in deep mineral soils. *Plant Soil* 368, 641–648. doi: 10.1007/s11104-013-1600-9

Harper, J. L., Jones, M., and Sackville Hamilton, N. R. (1991). "The evolution of roots and the problems of analyzing their behaviour," in *Plant Root Growth: An Ecological Perspective*, ed D. Atkinso (Oxford: Blackwell Scientific Publications), 3–22.

Harrison, R., Footen, P., and Strahm, B. (2011). Deep soil horizons: contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. *For. Sci.* 57, 67–76.

He, H., Bleby, T. M., Veneklaas, E. J., and Lambers, H. (2012). Arid-zone Acacia species can access poorly soluble iron phosphate but show limited growth response. *Plant Soil* 358, 119–130. doi: 10.1007/s11104-011-1103-5

Herrera, J., Verhulst, N., and Govaerts, B. (2012). "Strategies to identify genetic diversity in root traits," in *Physiological Breeding I: Interdisciplinary Approaches to Improve Crop Adaptation*, eds M. P. Reynolds, A. J. D. Pask, and D. Mullan (Mexico, DF: CIMMYT), 97–108.

Hinsinger, P. (1998). How do plant roots acquire mineral nutrients. Chemical processes involved in the rhizosphere. *Adv. Agron.* 64, 225–265.

Hinsinger, P., Brauman, A., Devau, N., Gérard, F., Jourdan, C., Laclau, J.-P., et al. (2011). Acquisition of phosphorus and other poorly mobile nutrients by roots. Where do plant nutrition models fail? *Plant Soil* 348, 29–61. doi: 10.1007/s11104-011-0903-y

Hinsinger, P., Cloutier-Hurteau, B., Jourdan, C., and Laclau, J. P. (2012). "The roots of our soils," in *Roots to The Future 8th Symposium of the International Society of Root Research* (Dundee).

Hodge, A. (2006). Plastic plants and patchy soils. *J. Exp. Bot.* 57, 401–411. doi: 10.1093/jxb/eri280

Hodge, A., Berta, G., Doussan, C., Merchan, F., and Crespi, M. (2009). Plant root growth, architecture and function. *Plant Soil* 321, 153–187. doi: 10.1007/s11104-009-9929-9

Horton, J. L., and Hart, S. C. (1998). Hydraulic lift: a potentially important ecosystem process. *Trends Ecol. Evol.* 13, 232–235. doi: 10.1016/S0169-534701328-7

Howarth, F. G. (1983). Ecology of cave arthropods. *Annu. Rev. Entomol.* 28, 365–389. doi: 10.1146/annurev.en.28.010183.002053

Howarth, F. G., James, S. A., McDowell, W., Preston, D. J., and Imada, C. T. (2007). Identification of roots in lava tube caves using molecular techniques: implications for conservation of cave arthropod faunas. *J. Insect. Conserv.* 11, 251–261. doi: 10.1007/s10841-006-9040-y

Hummel, J. W., Levan, M. A., and Sudduth, K. A. (1989). Mini-rhizotron installation in heavy soils. *Trans. ASAE* 32, 770–776.

Iversen, C. M., Murphy, M. T., Allen, M. F., Childs, J., Eissenstat, D. M., Lilleskov, E. A., et al. (2011). Advancing the use of minirhizotrons in wetlands. *Plant Soil* 352, 23–39. doi: 10.1007/s11104-011-0953-1

Jackson, R. B., Moore, L. A., Hoffmann, W. A., Pockman, W. T., and Linder, C. R. (1999). Ecosystem rooting depth determined with caves and DNA. *Proc. Natl. Acad. Sci. U.S.A.* 96, 11387–11392. doi: 10.1073/pnas.96.20.11387

Jennings, C. M. J. (1974). *The hydrogeology of Botswana.* PhD thesis, University of Natal, South Africa, p. 873.

Johnson, M. G., Tingey, D. T., Phillips, D. L., and Storm, M. J. (2001). Advancing fine root research with minirhizotrons. *Environ. Exp. Bot.* 45, 263–289. doi: 10.1016/S0098-847200077-6

Justin, S. H. F. W., and Armstrong, W. (1987). The anatomical characteristics of roots and plant response to soil flooding. *New Phytol.* 106, 465–495. doi: 10.1111/j.1469-8137.1987.tb00153.x

Kage, H., Kochler, M., and Stutzel, H. (2000). Root growth of cauliflower (*Brassica oleracea* L. botrytis) under unstressed conditions: measurement and modelling. *Plant Soil* 223, 131–145. doi: 10.1023/A:3A1004866823128

Kato, Y., Abe, J., Kamoshita, A., and Yamagishi, J. (2006). Genotypic variation in root growth angle in rice (*Oryza sativa* L.) and its association with deep root development in upland fields with different water regimes. *Plant Soil* 287, 117–129. doi: 10.1007/s11104-006-9008-4

Kell, D. B. (2011). Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. *Ann. Bot.* 108, 407–418. doi: 10.1093/aob/mcr175

Kleidon, A., and Heimann, M. (2000). Assessing the role of deep rooted vegetation in the climate system with model simulations: mechanism, comparison to observations and implications for Amazonian deforestation. *Clim. Dynam.* 16, 183–199. doi: 10.1007/s003820050012

Kloeppel, B. D., and Gower, S. T. (1995). Construction and installation of acrylic minirhizotron tubes in forest ecosystems. *Soil Sci. Soc. Am. J.* 59, 241–243.

Koarashi, J., Hockaday, W. C., Masiello, C. A., and Trumbore, S. E. (2012). Dynamics of decadally cycling carbon in subsurface soils. *J. Geophys.* 117, G03033. doi: 10.1029/2012JG002034

Kornecki, T. S., Prior, S. A., Runion, G. B., Rogers, H. H., and Erbach, D. C. (2008). Hydraulic core extraction: cutting device for soil–root studies. *Commun. Soil Sci. Plant* 39, 1080–1089. doi: 10.1080/00103620801925588

Kristensen, H. L., and Thorup-Kristensen, K. (2004). Uptake of 15N labeled nitrate by root systems of sweet corn, carrot and white cabbage from 0.2-2.5 meters depth. *Plant Soil* 265, 93–100. doi: 10.1007/s11104-005-0696-y

Kristensen, H. L., and Thorup-Kristensen, K. (2007). Effects of vertical distribution of soil inorganic nitrogen on root growth and subsequent nitrogen uptake by field vegetable crops. *Soil Use Manage.* 23, 338–347. doi: 10.1111/j.1473-2743.2007.00105.x

Kutschera, L., and Lichtenegger, E. (1997). *Bewurzelung Von Pflanzen in Verschiedenen Lebensräumen*. Linz: Landesmuseum.

Laclau, J.-P., Ranger, J., De Moraes Gonçalves, J. L., Maquère, V., Krusche, A. V., M'Bou, A. T., et al. (2010). Biogeochemical cycles of nutrients in tropical *Eucalyptus* plantations. *For. Ecol. Manage.* 259, 1771–1785. doi: 10.1016/j.foreco.2009.06.010

Laclau, J.-P., Silva, E. a. D., Rodrigues Lambais, G., Bernoux, M., Le Maire, G., Stape, J. L., et al. (2013). Dynamics of soil exploration by fine roots down to a depth of 10 m throughout the entire rotation in Eucalyptus grandis plantations. *Front. Plant Sci.* 4:243. doi: 10.3389/fpls.2013.00243

Laio, F., Tamea, S., Ridolfi, L., D'Odorico, P., and Rodriguez-Iturbe, I. (2009). Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics. *Water Resour. Res.* 45, 1–13. doi: 10.1029/2008WR007292

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J., and Veneklaas, E. J. (2006). Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann. Bot.* 98, 693–713. doi: 10.1093/aob/mcl114

Lewis, D. C., and Burgy, R. H. (1964). The Relationship between oak tree roots and groundwater in fractured rock as determined by tritium tracing. *J. Geophys.* 69, 2579–2588. doi: 10.1029/JZ069i012p02579

Lorenz, K., and Lal, R. (2005). The depth distribution of soil organic carbon in relation to land use and management and the potential of carbon sequestration in subsoil horizons. *Adv. Agron.* 88, 35–66. doi: 10.1016/S0065-211388002-2

Maeght, J. L., Henry des Tureaux, T., Sengtaheuanghoung, O., Stokes, A., Ribolzi, O., and Pierret, A. (2012). "Drought effect on teak tree (*Tectona grandis*) roots on carbon inputs and water uptake in a deep soil of northern Laos," in *Roots to The Future 8th Symposium of the International Society of Root Research* (Dundee).

Maeght, J.-L., Pierret, A., Sanwangsri, M., and Hammecker, C. (2007). "Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand," in *International Conference Rhizosphere* (Montpellier), 26–31.

Majdi, H., Pregitzer, K., Morén, A.-S., Nylund, J.-E., and Ågren, G. I. (2005). Measuring fine root turnover in forest ecosystems. *Plant Soil* 276, 1–8. doi: 10.1007/s11104-005-3104-8

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., et al. (2009). Mixing plant species in cropping systems: concepts, tools and models. A review. *Agron. Sustain. Dev.* 29, 43–62. doi: 10.1051/agro:2007057

McCormack, M. L., Eissenstat, D., Prasad, A., and Smithwick, E. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biol.* 19, 1697–1708. doi: 10.1111/gcb.12163

McCulley, R. L., Jobbágy, E. G., Pockman, W. T., and Jackson, R. B. (2004). Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia* 141, 620–628. doi: 10.1007/s00442-004-1687-z

McElrone, A. J., Bichler, J., Pockman, W. T., Addington, R. N., Linder, C. R., and Jackson, R. B. (2007). Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant Cell Environ.* 30, 1411–1421. doi: 10.1111/j.1365-3040.2007.01714.x

McElrone, A. J., Pockman, W. T., Martinez-Vilalta, J., and Jackson, R. B. (2004). Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytol.* 163, 507–517. doi: 10.1111/j.1469-8137.2004.01127.x

McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, et al. (2012). Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging. *Ecol. Evol.* 2, 1235–1250. doi: 10.1002/ece3.266

Meyer, B. S., and Anderson, D. B. (1939). *Plant Physiology*. Bridgebort, CT: Braunworth and co.

Michot, D. (2003). Spatial and temporal monitoring of soil water content with an irrigated corn crop cover using surface electrical resistivity tomography. *Water Resour. Res.* 39, 1138. doi: 10.1029/2002WR001581

Misra, R. K., Dexter, A. R., and Alston, A. M. (1986). Maximum axial and radial growth pressures of plant roots. *Plant Soil* 95, 315–326. doi: 10.1007/BF02374612

Mitchell, P., and Black, J. (1968). Distribution of peach roots under pasture and cultivation. *Aust. J. Exp. Agric.* 8, 106–111. doi: 10.1071/EA9680106

Moran, C. J., Pierret, A., and Stevenson, A. W. (2000). X-ray absorption and phase contrast imaging to study the interplay between plant roots and soil structure. *Plant Soil* 223, 99–115. doi: 10.1023/A:1004835813094

Mulia, R., and Dupraz, C. (2006). Unusual fine root distributions of two deciduous tree species in southern France: what consequences for modelling of tree root dynamics. *Plant Soil* 281, 71–85. doi: 10.1007/s11104-005-3770-6

Nakaji, T., Noguchi, K., and Oguma, H. (2008). Classification of rhizosphere components using visible–near infrared spectral images. *Plant Soil* 310, 245–261. doi: 10.1007/s11104-007-9478-z.

Nepstad, D., de Carvalho, C., and Davidson, E. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372, 666–669. doi: 10.1038/372666a0

Newton, M., and Zedaker, S. M. (1981). *Excavating Roots With Explosives*. Corvallis, OR: Oregon State University, Forest Research Laboratory.

Nicoullaud, B., Darthout, R., Duval, O., Le Lay, D. C., and Terrasse, B. R. B. (1995). Étude de l'enracinement du blé tendre d'hiver et du maïs dans les sols argilo-limoneux de Petite beauce. *Etud. Gest. Sols* 2, 183–200.

Novak, T., and Perc, M. (2012). Duality of terrestrial subterranean fauna. *Int. J. Speleol.* 41, 181–188. doi: 10.5038/1827-806X.41.2.5

Oliveira, R. S., Dawson, T. E., Burgess, S. S. O., and Nepstad, D. C. (2005). Hydraulic redistribution in three

Amazonian trees. *Oecologia* 145, 354–363. doi: 10.1007/s00442-005-0108-2

Passioura, J. B., and Wetselaar, R. (1972). Consequences of banding nitrogen fertilizers in soil. *Plant Soil* 36, 461–473. doi: 10.1007/BF01373498

Peñuelas, J., and Filella, I. (2003). Deuterium labelling of roots provides evidence of deep water access and hydraulic lift by *Pinus nigra* in a Mediterranean forest of NE Spain. *Environ. Exp. Bot.* 49, 201–208. doi: 10.1016/S0098-847200070-9

Phillips, D. L., Johnson, M. G., Tingey, D. T., Biggart, C., Nowak, R. S., and Newsom, J. C. (2000). Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. *Soil Sci. Soc. Am. J.* 64, 761. doi: 10.2136/sssaj2000.642761x

Poelman, G., van de Koppel, J., and Brouwer, G. (1996). A telescopic method for photographing within 8×8 cm minirhizotrons. *Plant Soil* 185, 163–167. doi: 10.1007/BF02257572

Poot, P., and Lambers, H. (2008). Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology. *New Phytol.* 178, 371–381. doi: 10.1111/j.1469-8137.2007.02370

Pregitzer, K. K. S., Laskowski, M. J. M., Burton, A. J., Lessard, C., and Zak, D. R. (1998). Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiol.* 18, 665–670. doi: 10.1093/treephys/18.10.665

Rasse, D. P., Rumpel, C., and Dignac, M.-F. (2005). Is soil carbon mostly root carbon. Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356. doi: 10.1007/s11104-004-0907-y.

Rawitscher, F. (1948). The water economy of the vegetation of the Campos cerrados in southern Brazil. *J. Ecol.* 36, 237–268.

Reboleira, A. S., Borges, P., Gonçalves, F., Serrano, A., and Oromí, P. (2011). The subterranean fauna of a biodiversity hotspot region - Portugal: an overview and its conservation. *Int. J. Speleol.* 40, 23–37. doi: 10.5038/1827-806X.40.1.4

Rewald, B., and Ephrath, J. E. (2013). "Minirhizotron techniques," in *Plant Roots: The Hidden Half*, eds A. Eshel and T. Beeckman (New York, NY: CRC Press), 42.1–42.15.

Rewald, B., and Leuschner, C. (2009). Does root competition asymmetry increase with water availability. *Plant Ecol. Divers.* 2, 255–264. doi: 10.1080/17550870903022865

Rewald, B., Meinen, C., Trockenbrodt, M., Ephrath, J. E., and Rachmilevitch, S. (2012). Root taxa identification in plant mixtures – current techniques and future challenges. *Plant Soil* 359, 165–182. doi: 10.1007/s11104-012-1164-0

Richards, J., and Caldwell, M. (1987). Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 486–489. doi: 10.1007/BF00379405

Richter, A. K., and Walthert, L. (2007). Does low soil base saturation affect fine root properties of European beech (*Fagus sylvatica* L.). *Plant Soil* 298, 60–79. doi: 10.1007/s11104-007-9338-x

Richter, D. D., and Markewitz, D. (1995). How deep is soil. *Bioscience* 45, 600–609. doi: 10.2307/1312764

Ritson, P., and Sochacki, S. (2003). Measurement and prediction of biomass and carbon content of Pinus pinaster trees in farm forestry plantations, south-western Australia. *For. Ecol. Manage.* 175, 103–117. doi: 10.1016/S0378-112700121-4

Rizzo, D., and Gross, R. (2000). "Distribution of Armillaria on pear root systems and comparison of excavation techniques," in *The Supporting Roots of Trees and Woody Plants: Form, Function and Physiology*, ed A. Stokes (Dordrecht: Kluwer Academic Publishers), 305–311.

Robinson, D. (1991). "Roots and resource fluxes in plants and communities," in *Plant Root Growth: An Ecological Perspective*, ed D. Atkinson (Oxford: Blackwell Scientific), 103–130.

Robinson, D., Crop, S., and Dd, D. (1996). Resource capture by localized root proliferation: why do plants bother. *Ann. Bot.* 77, 179–186. doi: 10.1006/anbo.1996.0020

Rosling, A., Landeweert, R., Lindahl, B. D., Larsson, K.-H., Kuyper, T. W., Taylor, A. F. S., et al. (2003). Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. *New Phytol.* 159, 775–783. doi: 10.1046/j.1469-8137.2003.00829.x

Rumpel, C., and Kögel-Knabner, I. (2011). Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant Soil* 338, 143–158. doi: 10.1007/s11104-010-0391-5.

Santner, A., Calderon-Villalobos, L. I. A., and Estelle, M. (2009). Plant hormones are versatile chemical regulators of plant growth. *Nat. Chem. Biol.* 5, 301–307. doi: 10.1038/nchembio.165

Schenk, H. J. (2008). Soil depth, plant rooting strategies and species' niches. *New Phytol.* 178, 223–225. doi: 10.1111/j.1469-8137.2008.02427.x

Schenk, H. J., and Jackson, R. B. (2002). The global biogeography of roots. *Ecol. Monogr.* 72, 311–328. doi: 10.1890/0012-9615072[0311:TGBOR]2.0.CO;2

Schwinning, S. (2010). The ecohydrology of roots in rocks. *Ecohydrology* 245, 238–245. doi: 10.1002/eco.134

Sekiya, N., Araki, H., and Yano, K. (2010). Applying hydraulic lift in an agroecosystem: forage plants with shoots removed supply water to neighboring vegetable crops. *Plant Soil* 341, 39–50. doi: 10.1007/s11104-010-0581-1

Shalyt, M. S. (1950). Podzemnaja cast' nekotorykh lugovykh, stepnykh i pustynnykh rastenyi i fitocenozov. C. I. Travjanistye i polukustarnigkovye rastenija i fitocenozy lesnoj (luga) i stepnoj zon. (Belowground parts of some meadow, steppe, and desert plants and plant communities. Part I: Herbaceous plants and subshrubs and plant communities of forest and steppe zones. In Russian). *Trudy Botanicheskogo Instituta im. V.L. Komarova. Akademii nauk SSSR. Seriia III, Geobotanika* 6, 205–442.

Shimamura, S., Yoshida, S., and Mochizuki, T. (2007). Cortical aerenchyma formation in hypocotyl and adventitious roots of *Luffa cylindrica* subjected to soil flooding. *Ann. Bot.* 100, 1431–1439. doi: 10.1093/aob/mcm239

Silva, J. S., and Rego, F. C. (2003). Root distribution of a Mediterranean shrubland in Portugal. *Plant Soil* 255, 529–540. doi: 10.1023/A:1026029031005

Silva, M. S., Martins, R. P., and Ferreira, R. L. (2011). Cave lithology determining the structure of the invertebrate communities in the brazilian atlantic rain forest. *Biodivers. Conserv.* 20, 1713–1729. doi: 10.1007/s10531-011-0057-5

Silva, S., Whitford, W. G., Jarrell, W. M., and Virginia, R. A. (1989). The microarthropod fauna associated with a deep rooted legume, *Prosopis glandulosa*, in the Chihuahuan Desert. *Biol. Fert. Soils* 7, 330–335. doi: 10.1007/BF00257828.

Smit, A. L., Bengough, A. G., Engels, C., van Noordwijk, M., Pellerin, S., van de Geijn, S. C. (2000). *Root Methods: A Handbook*. Berlin: Springer.

Snider, J., Moya, M., Garcia, M. G., Spilde, M. N., and Northup, D. E. (2009). "Identification of the microbial communities associated with roots in lava tubes in new mexico an Hawai," in *Proceedings of the15th International Congress of Speleology*, Vol. 2 (Kerrville, TX), 718–723.

Snyder, K. a., James, J. J., Richards, J. H., and Donovan, L. a. (2008). Does hydraulic lift or nighttime transpiration facilitate nitrogen acquisition. *Plant Soil* 306, 159–166. doi: 10.1007/s11104-008-9567-7

Stoeckeler, J. H., and Kluender, W. A. (1938). The hydraulic method of excavating the root systems of plants. *Ecology* 19, 355–369.

Stone, E. L., and Comerford, N. B. (1994). "Plant and animal activity below the solum," in *Proceedings of a Symposium on Whole Regolith Pedology* (Minneapolis, MN), 57–74. doi: 10.2136/sssaspecpub34.c4

Stone, E. L., and Kalisz, P. J. (1991). On the maximum extent of tree roots. *For. Ecol. Manage.* 46, 59–102. doi: 10.1016/0378-112790245-Q

Stone, F. D. (2010). "Bayliss lava tube and the discovery of a rich cave fauna in tropical Australia," in *14th International Symposium on Vulcanospeleology*, (Undara Volcanic National Park, Queensland), 47–58.

Strebel, O., Duynisveld, W. H. M., and Böttcher, J. (1989). Nitrate pollution of groundwater in Western Europe. *Agric. Ecosyst. Environ.* 26, 189–214. doi: 10.1016/0167-880990013-3

Strong, D., Sale, P., and Helyar, K. (1999). The influence of the soil matrix on nitrogen mineralisation and nitrification III. Predictive utility of traditional variables and process location within the pore. *Aust. J. Soil Res.* 37, 137–149.

Sverdrup, H., Hagen-Thorn, A., Holmqvist, J., Wallman, P., Warfvinge, P., Walse, C., et al. (2002). "Biogeochemical processes and mechanisms. Developing principles and models for sustainable forestry in Sweden," in *Managing Forest Ecosystems*, Vol. 5, eds H. Sverdrup and I. Stjernquist (Dordrecht: Kluwer Academic Publishers), 91–196.

Thorup-Kristensen, K. (2001). Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant Soil* 230, 185–195.

Thorup-Kristensen, K., Nielsen, N. E. (1998). Modelling and measuring

the effect of nitrogen catch crops on the nitrogen supply for succeeding crops. *Plant Soil* 203, 79–89. doi: 10.1023/A:1004398131396

Trachsel, S., Kaeppler, S. M., Brown, K. M., and Lynch, J. P. (2010). Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant Soil* 341, 75–87. doi: 10.1007/s11104-010-0623-8

Trumbore, S. E., and Gaudinski, J. B. (2003). Atmospheric science. the secret lives of roots. *Science* 302, 1344–1345. doi: 10.1126/science.1091841

Vanapalli, S. K., and Oh, W. T. (2012). "Stability analysis of unsupported vertical trenches in unsaturated soils," in *GeoCongress 2012*, (Reston, VA: American Society of Civil Engineers), 2502–2511. doi: 10.1061/9780784412121.256

Van Noordwijk, M., Brouwer, G., Meijboom, F., Do Rosario G Oliveira, M., and Bengough, A. (2000). "Trench profile techniques and core break methods," in *Root methods*, eds A. L. Smit, A. G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin, and B. H. Van der Geijn (Berlin: Springer), 212–233.

Virginia, R. A., Jenkins, M. B., and Jarrell, W. M. (1986). Depth of root symbiont occurrence in soil. *Biol. Fert. Soils* 2, 127–130. doi: 10.1007/BF00257591

Vogt, K. A., Vogt, D. J., Palmiotto, P. A., Boon, P., and Jennifer, O. H. (1996). Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* 187, 159–219. doi: 10.1007/BF00017088

Vos, J., and Groenwold, J. (1983). Estimation of root densities by observation tubes and endoscope. *Plant Soil* 300, 295–300. doi: 10.1007/BF02143621

Waddington, J. (1971). Observation of plant roots *in situ*. *Can. J. Bot.* 49, 1850–1852. doi: 10.1139/b71-261.

Wagner, B., Gärtner, H., Ingensand, H., and Santini, S. (2010). Incorporating 2D tree-ring data in 3D laser scans of coarse-root systems. *Plant Soil* 334, 175–187. doi: 10.1007/s11104-010-0370-x

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Heikki, S., van der Putten, W. H., and Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633. doi: 10.1126/science.1094875

Wearver, J. E. (1915). A study of the root-systems of prairie plants of south eastern Washington. *Plant World* 18, 227–248.

Weaver, J. E. (1919). *The Ecological Relations of Roots*. Publication No. 286. Washington, DC: Carnegie Institu-tion of Washington

Weaver, J. E., and Bruner, W. E. (1927). *Root Development of Vegetable Crops*. New York, NY: McGraw-Hill Book Company.

Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., and Granier, A. (2011). Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees* 25, 885–894. doi: 10.1007/s00468-011-0563-9

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 21 May 2013; accepted: 20 July 2013; published online: 13 August 2013.
*Citation: Maeght J-L, Rewald B and Pierret A (2013) How to study deep roots—and why it matters. Front. Plant Sci. **4**:299. doi: 10.3389/fpls.2013.00299*
This article was submitted to Frontiers in Functional Plant Ecology, a specialty of Frontiers in Plant Science.
Copyright © 2013 Maeght, Rewald and Pierret. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

1.3 Conclusion

L'analyse globale de la littérature effectuée dans la première partie de la thèse et dans les articles publiés nous a permis de constater qu'il n'existe que peu de références sur l'étude des racines profondes comparativement à celles disponibles sur l'enracinement de surface. Cette estimation repose sur la définition que nous avons proposée pour l'enracinement profond, à savoir les racines se trouvant en dessous d'un mètre de profondeur. Les informations que nous avons recueillies démontrent cependant clairement l'existence de l'enracinement profond et son rôle essentiel pour de nombreuses plantes dans 90 % des biomes terrestres. Nous avons également mis en lumière l'importance des racines profondes par rapport à de nombreux mécanismes et interactions avec le sol, par exemple avec la ressource en eau ou encore pour le stockage du carbone ou par rapport à la chimie des sols. Encore moins d'études analysent la rhizosphère liée à cet enracinement profond et dans ce domaine, les champs exploratoires sont multiples. Ces interactions ont des impacts à différentes échelles de la biosphère sur les écosystèmes. Les mécanismes engendrés représente un fort potentiel de service écosystémique qui permettraient de tirer avantage des propriétés liées à l'enracinement profond.

Ressortent également de cette revue bibliographique les nombreuses difficultés techniques et limites liées à l'étude de l'enracinement en profondeur. Notre synthèse sur les techniques existantes met en avant les possibilités proposées par différentes méthodes classiques d'investigation. La méthode des puits d'accès que nous avons développée présente des avantages substantiels dans nos contextes d'étude. Dans bien des cas, il apparait utile, sinon nécessaire, d'associer plusieurs méthodes pour appréhender au mieux les racines profondes sur le terrain. Une telle démarche est encore très largement ouverte à de futurs développements et améliorations. Si les techniques disponibles aujourd'hui pour les études de terrain évoluent à un rythme assez modéré, il n'en est pas de même des outils d'analyse d'images. Ces derniers offrent de nouvelles possibilités grâce aux ressources informatiques toujours plus performantes. Il n'en reste pas moins qu'il est nécessaire de prêter attention aux méthodes de mesures proposées et aux modes de calcul qui y sont liés. Nous avons mis en pratique certains des points relevés ci-dessus dans la suit de nos travaux.

Les deux expérimentations de terrains conduites sur *Hevea brasiliensis* en Thaïlande et *Tectona grandis L* au Laos en plantations matures, que nous présentons sous forme d'article

dans les chapitres 2 et 3, cherchent à apporter de nouvelles informations sur la dynamique racinaire superficielle et profonde dans des environnements sous contraintes principalement de sècheresse hydrique. Elles font l'objet de développements technologiques et fournissent des données originales sur de nombreux aspects liés aux dynamiques de croissance racinaires et/ou de la plante dans son ensemble.

Chapitre 2 :

L'hévéa dans le Nord-Est de la Thaïlande: éclairage sur la dynamique de l'enracinement de l'hévéa dans un contexte déficitaire en eau; implications pour la production de latex



Photo 4: Dispositif de puits dans la plantation d'hévéas en saison sèche de la région de Buriram au nord-est de la Thaïlande (J.-L. Maeght)

2.1 Introduction

L'étude approfondie de la littérature réalisée dans la première partie de cette thèse nous a permis de mettre en avant l'importance de l'enracinement profond. Son rôle central, dans certaines conditions, pour la survie des plantes, a également pu être illustré. Les difficultés des conditions d'études souvent évoquées n'enlèvent rien à l'intérêt de celles-ci. La mise au point de différentes techniques permettant l'étude et l'analyse des mesures de croissances des racines en profondeur dans différents milieux nous a permis de nous doter d'outils adaptés aux conditions de terrain.

Dans cette deuxième partie, nous allons analyser le modèle de l'hévéa (*Hevea brasiliensis)* dans une plantation du nord-est de la Thaïlande. Des conditions climatiques favorables ont permis à la Thaïlande de développer de façon intensive la culture de l'hévéa dans la moitié sud du pays, permettant à ce pays de se hisser au rang de premier producteur mondial de caoutchouc naturel. L'attractivité du cours du caoutchouc naturel et la recherche de revenus alternatifs complémentaires ont conduit les agriculteurs du nord-est de la Thaïlande à investir à leur tour dans la plantation d'hévéas. Contrairement à la moitié sud du pays, le nord-est est soumis à une climat beaucoup moins humide avec une saisonnalité très marquée, dont une saison sèche de plus de quatre mois. La pluviométrie annuelle y est significativement inferieure, avec moins de 1400 mm de pluie par an (Figure 11), à celle de l'Amazonie, région d'origine de l'hévéa, ou à celle des zones de production privilégiées situées plus au sud en Asie. L'expansion de la culture de l'hévéa dans ces zones marginales se fait sur un sol déjà fortement dégradé suite à des déforestations massives opérées dans les années 1960 et à la succession de cultures à valeur commerciale telle que le manioc ou la canne à sucre. L'hévéa, dans ces conditions, met en moyenne 7 ans pour entrer en production alors que seuls 5 ans sont nécessaires sous de meilleures conditions climatiques. De fait, ces plantations d'hévéas se trouvent maintenant implantés durablement dans cette région.

Malgré ces contraintes, l'exploitation de l'hévéa se fait sur le même modèle de densité de plantation et les mêmes rythmes de récolte du latex que dans les zones de forte production du sud de la Thaïlande, qui elles, se situent en conditions climatiques favorables (plus de 2000 mm de pluie par an). Le rythme des saignées répétées devient donc un facteur de stress

hydrique supplémentaire qui conduit parfois à des réactions physiologiques fortes allant jusqu'à l'arrêt de la production de latex. L'arbre, dans ce milieu, a adapté son rythme physiologique avec une période de défoliation totale de plus de 2 mois pendant la saison sèche, ce qui n'est pas le cas pour la même espèce avec des apports de pluies supérieurs et mieux répartis au cours de l'année. Nous nous interrogeons donc sur la capacité de l'hévéa à produire durablement dans un tel contexte. La mobilisation des terres et la longue période d'attente avant que l'hévéa ne devienne productif rendent cet investissement considérable pour les petits producteurs. Les contraintes environnementales pourraient rendre cet investissement hasardeux.

Plusieurs expérimentations complémentaires ont été conduites sur le site de Buriram. Parmi les nombreux paramètres physiologiques suivis, des mesures de transpiration, de flux de sève et de croissance ont été faites à l'aide de capteurs et d'une centrale d'acquisition (Photo 5). Nous avons également développé une expérimentation que nous avons suivie mensuellement pendant plus de trois ans afin d'étudier en continu le long d'un profil de 4,5m de profondeur, la dynamique de l'enracinement à l'aide d'un puits d'observation et des techniques de prises d'images présentées en partie 1 de cette thèse. Nous allons analyser la dynamique du développement racinaire, notamment en relation avec les cycles de foliation et défoliation. Dans un contexte environnemental dégradé et avec des ressources en eau limitées, le coût de production des racines est potentiellement conséquent pour la plante. Nous nous sommes donc également intéressés à la durée de vie des racines produites dans les différents horizons du sol. Nous présentons dans les pages suivantes les résultats de cette étude originale sous la forme d'un article intitulé « Differentiation of life spans of Hevea brasiliensis roots along a 4,5 m deep soil profile in North East Thailand » qui sera proposé à la revue Plant & Soil.

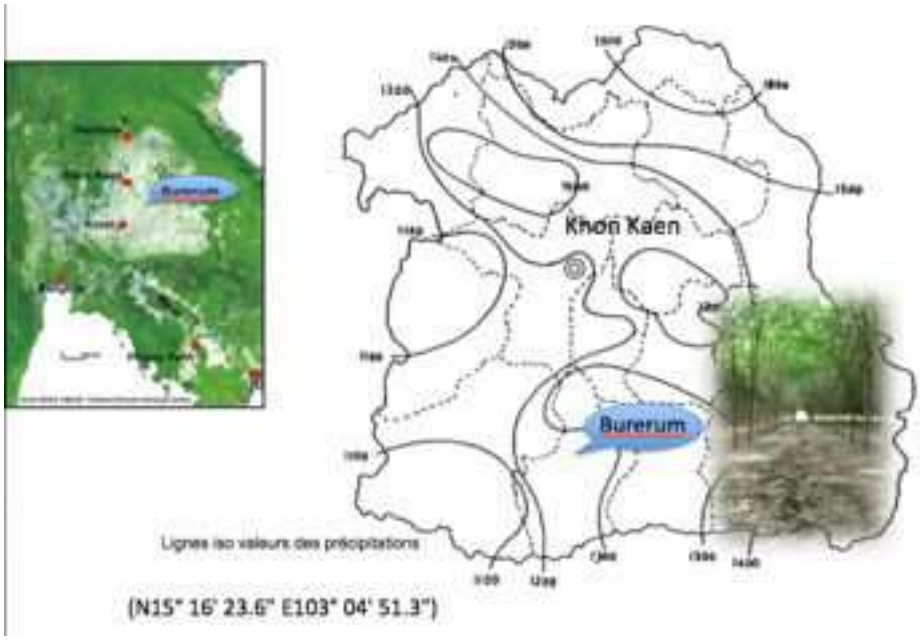


Figure 11: localisation géographique et climatique de l'expérimentation sur l'hévéa



Photo 5: Dispositif d'acquisition de données dans le puits et des capteurs sur un hévéa

2.2 Differentiation of life spans of *Hevea brasiliensis* roots along a 4.5m deep soil profile in North East Thailand: article prévu pour Plant & Soil

Differentiation of life spans of *Hevea brasiliensis* roots along a 4.5m deep soil profile in North East Thailand.

Jean-Luc Maeght[1] , Santimaitree Gonkhamdee [2], Corentin Clément [3], Supat Isarangkool Na Ayutthaya [2], Alexia Stokes [4], Alain Pierret [3].

[1] UMR Iees Paris UMR AMAP, IRD 9343Bondy cedex, France ; [2] Faculty of Agriculture, Khon Kaen University, Khon Kaen 40002, Thailand; [3]UMR Iees Paris IRD office c/o National Agriculture and Forestry Research Institute (NAFRI) P.O. ; [4] INRA, UMR AMAP,34398 Montpellier Cedex 5, France, Corresponding author ; (Jean-Luc.maeght@ird.fr)

Abstract

Perennial plants and trees experience a wide range of environmental conditions, subject to change over time due to climate variability. This phenomenon is amplified by societal and economic constraints associated with the development of plantations in marginal areas such as regions where e.g. drought conditions prevail. This is the case of the recent expansion of *Hevea Brasiliensis* plantations in North East Thailand where the climate is characterized by annual water deficit and marked seasonal drought. The tapping of trees for latex production further increases the natural water demand of trees. Root dynamics and functioning determine some of the key parameters that can contribute to tree adaptation or resilience to water stress. Studying roots development in situ, particularly at depth, remains a challenging endeavour.

The cultivation of rubber trees (*Hevea Brasiliensis)* has increased over the past 30 years, especially in marginal regions where the climate is much drier than that of the natural range of rubber trees.

The mechanism by which this species acclimates to dry hard semi-arid conditions is not known. In particular case of data concerning the growth and functioning of the root system under very dry conditions as mature rubber trees in North East Thailand where the climate is marked by annual water deficit and seasonal drought the root systems can grow more than 6.0 m deep. We hypothesize that deep roots contribute to the water demands of rubber trees and hence their resilience to very dry conditions. A root observation access-well was installed to observe root dynamics along a 4,5 m deep profile. Image-based measurements of root elongation and lifetimes of individual roots were carried out at monthly intervals for 3 years. Two contrasting patterns of roots dynamics were observed depending on soil depth. Within the first 2 m of the profile, the number of fine roots decreased with

depth and their half-live varied from 13 to 28 months. At depths of 2 to 4.5 m, the number of roots did not vary much and the half-life was surprisingly less than 10 months. Root emergence occurred throughout the year along the entire soil profile ever during the dry season. However, at depths of more than – 2.0 m, root emergence was substantial in the dry season when trees were leafless. Therefore our results show that roots at depths of -1.0 to -4.5 m sustain rubber trees during dry periods.

Keywords: Fine deep roots, *Hevea Brasiliensis,* roots lifetime, carbon storage, measurement method, drought

Introduction

. The increasing demand for natural rubber has had a direct effect on the extension of *Hevea Brasiliensis* cultivation. It is particularly the case in Thailand, the first world latex producer, where the surface area was multiplied by a factor 75 from 24 000 ha in 1980 (ACIAR 1985) to 1,8 million ha in 2008 (Carr 2011a). Cultivated rubber tree clones have been selected from the indigenous *Hevea Brasiliensis* endemic to the Amazon rainforest and now principally grow throughout the humid tropics. Due to the booming expansion of rubber tree in recent years, plantations have largely encroached on degraded soil and drought-prone areas (Carr 2011b). This is particularly true in North East Thailand (Fox and Castella 2013) where a typical monsoon climate with marked seasonality prevails (Bridhikitti 2013). In this marginal zone, the sustainability of *Hevea Brasiliensis* essentially depends on the water demand for growth and latex production (Boithias et al. 2011; Junjittakarn 2012; Rodrigo 2007) linked to two physiological phenomena, stomata resistance and transpiration (Rao et al. 1990). Other environmental constraints such as low soil fertility and low temperatures can also contribute to challenge rubber tree growth (Priyadarshan et al. 2005), especially in this zone where soils are not very fertile (Isarangkool Na Ayutthaya et al. 2011).

. These cumulative constraints are believed to contribute to the occurrence of conditions such as Tapping Panel Dryness (TPD) (Sookmark et al. 2002) or Trunk Phloem Necrosis (TPN) (Do et al. 2011) which greatly limit latex production capacities (Jacob and Krishnakumar 2006).

. As an absorption organ, roots can play a determining role with regard to a trees resilience to a range of environmental constraints, especially for water stress (Boyce 2005; Hales 1727; Kramer and Boyer 1995; Lobet et al. 2013). Fine roots are also an integrative indicator of plant response to environmental factors (Edwards et al. 2004). Fine roots of trees contribute to water extraction (Clothier et al. 2007; Pregitzer 2002; Stokes and Bakker 2013) while a variable share of water demand can be supplied by deep roots (Bleby et al. 2010; Maeght et al. 2013). The measurement of root growth and survival *in*

situ along a deep soil profile, is an approach that can bring essential information to understand how rubber trees cope in water-limited environments, and to unravel tree resilience to such constraints. However, it remains a major challenge to observe and analyse roots non destructively within the soil matrix (Virginia and Jarrell 1987), especially in deep soil layers (Elliott et al. 2006; Maeght et al. 2013; Stone and Kalisz 1991). Our knowledge of root lifespan, particularly as a function of soil depth is also quite limited (Eissenstat and Yanai 1997). The objective of this study is twofold: first to present and discuss data about fine rubber tree roots dynamics along a 4.5 m soil profile under natural drought environment and second to assess the relative importance of fine deep roots into the carbon balance.

Materials and methods

Study site and climatic conditions:

The field site (Satuck) was located at Baan Sila Khu-Muang village, Buriram province in North East Thailand (N15°1623 E103°0451.3, elevation = 150 m). The experiment was conducted in a monoclonal plot of 11 year-old clones of RRIM 600 trees, planted in 1991 at 2.5 m / 7.0 m spacing (500 – 600 tree/ha) and tapped for latex over 4 years. Taping 2d/3 1/2s (e.g. once quasi-spiral cuts every three days) is largely adapted to the local climatic conditions and usually discontinued during three to four months during the dry season.

Weather conditions in this marginal area for rubber tree cultivation are characterised by a rainy season that lasts about 6 months (from May to October), and an average annual rainfall of 1176 mm for the last ten years. The maximum leaf area index (LAI), measured using nine 1 m^2 litter traps during the defoliation period (December–January–February) (Isarangkool Na Ayutthaya et al. 2010), was estimated at 3.9 (SD 0.7). The local microclimate was monitored automatically with a Minimet weather station (Skye Instruments Ltd) attached to a data-logger recording air temperature, relative humidity, incoming short wave radiation, wind speed and rainfall at 30 minutes intervals. The reference evapotranspiration (ET0) was calculated according to Allen et al. (1998). (Fig.1)

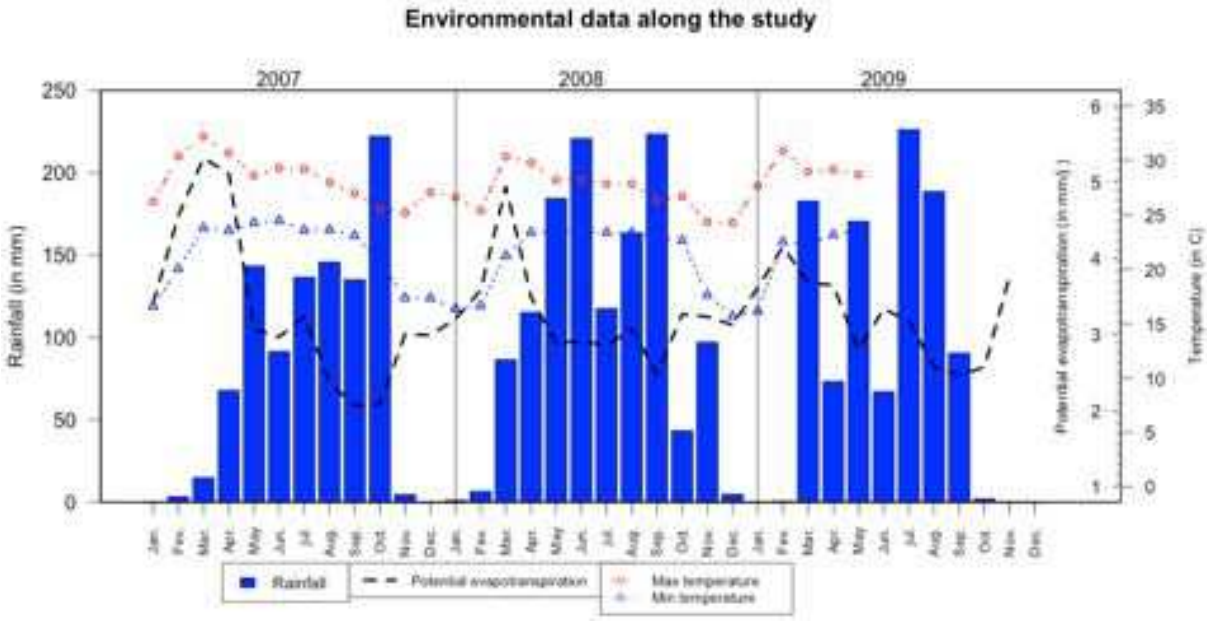


Figure 1: Rainfall, minimum and maximum temperature and potential evapotranspiration curves monitored continuously on the experimentation site over 3 years

The Buriram area is subjected to a South-East Asia Monsoon regime with heavy rainfall between March-April and September-October. Total annual rainfall during the 3 years period over which the experiment report in this paper was conducted, was 965, 1265 and 1002 mm, in 2007, 2008 and 2009, respectively. Temperatures increased during the dry season and decreased following the end of the rainy season (with a range from $^{+}$40.3°C to $^{+}$8.3 °C). Potential evapotranspiration (measured at the nearby Buriram station), follow roughly the monsoon regime, with higher evapotranspiration during the dry season and a decrease during the rainy season.

Soil conditions:

Soil at the study site is a deep loamy sand with limited water retention capacity. This soil develops on fine sand or coarse silt deposits with a homogeneous sandy loam texture throughout the profile. The Ap horizon is a 25 cm thick remant from previous cane cultivation (Hartmann et al. 2006). Clay, silt and sand contents were 100, 100 and 800 g/kg, respectively. The clay content increase with depth: from 150 g/kg in Bt1 (25-50 cm) to 200 g/kg in Bt2 (50-100 cm). The silt content is similar in all soil layers throughout the soil profile (100 g/kg) while sand decreased to 700 g/kg at a depth of 100 cm. From 100 to about 400 cm, these properties remained fairly stable. The laterite soil layer was found at a depth of 6 to 7 m, as previously observed in this region (Cawte and Boyd 2010). The water table was not found within the first 7 m of the profile. The soil is acidic with a pH ranging from 5.0 to 5.3. Soil organic carbon content is present at concentrations lower than 10g/kg in the topsoil. Typical bulk soil density is 1.55 g/cm^{-3} down to a depth of 3 m (Gonkhamdee et al. 2009). A more detailed description

of soil properties can be found in Hartmann et al. (2006) and Isarangkool Na Ayutthaya et al. (2011).

Ecophysiological measurements:

To estimate the physiological status of trees depending of edaphic and climatic constraints, leaf water potential was measured in situ immediately after leaf sampling with an Scholander-type pressure chamber (PMS 1000, PMS Instrument Company) at pre-dawn (pd) (between 5:30 and 6:15 a.m. ICT) and mid-day (md) (between 12:30 and 1:30 p.m ICT). Three replications of leaf water potential were measured on five trees at least once every month. To characterise the physiological functioning of the trees, xylem sap flow density was measured using the transient thermal dissipation method (TTD). The TTD method is based on Granier's probe (1987) and used heating power designs but uses a cyclic schedule of heating and cooling to assess a transient thermal index over a 10-min rise in temperature (Isarangkool Na Ayutthaya et al. 2010). Probes were inserted in to the trunks at 1.8 m above the soil. At this height, average sapwood area was estimated to be 1.97 X 10^{-752} m^2. Probes were inserted to a depth of 2.5 cm into the sapwood, in such a way that the whole probe was fully inside the conductive sapwood. All the probes were protected from direct sun exposition with heat reflecting material. The hourly sap flux density (Js; kg m^{-2} h^{-1}) was calculated according to the non species calibration assessed by Isarangkool Na Ayutthaya et al. (2010).

Root section:

Measurements of root growth

Root growth was studied using the access well technique described in Maeght et al. (2013). An access well (0.9 m in diameter and 4.5 m deep) was built at a distance of 1.35 m from two trees, 0.5 m aside from a tree row. The access well observation technique is a recent evolution and combination of the different techniques for root observation described in Böhm (1979) and root windows adapted from McDougall (1916). The access well method provides safe access to deep soil observation windows, by means of ladders affixed to the well's wall. Building the well takes about 3 days with 4 people. The walls are reinforced with concrete tubes thus distinguishing this technique from trenches. More importantly, wells maximize the ratio of accessible soil depth/volume of displaced soil compared to other types of excavations. Similar to Mini-Rhizotron (MR) techniques, access shafts allow direct observation of root growth dynamics using adapted "root windows". In order not to weaken the structure formed by the concrete rings, 9 windows observations were positioned in staggered rows: (with 1.0 and 0.5 m horizontal and vertical spacing's, respectively). Each root window included a specifically designed metallic frame supporting, on its upper side, a piece of 8-mm thick glass (25 x 30 cm) pressed against the soil at a 45° angle by means of two threaded rod actuators. On the frame's lower side, two guide rails allow the insertion of a standard flatbed scanner. More detail about the set

up of the root access well set be found in Gonkhamdee et al. (2009) and Maeght et al. (2013).

Images of roots were taken using a flatbed scanner (HP Scanjet 4370 Photo scanner at 200 DPI) and dedicated software which offers a convenient, faster and more accurate record than manual techniques (Kaspar and Ewing 1997; Zoon and Tienderen 1990). Roots were observed at monthly intervals during three years staring on January 2007, 6 months after setting up the access well to avoid overproduction of roots linked to the setting of the experiment as reported (Yuan and Chen 2012). Long-term observations are highly recommended to avoid the risk of over estimating fine-root turnover (Strand et al. 2008). Root growth monitoring was conducted following a procedure described in Maeght et al. (2007). Images of the soil and roots in direct contact with each window were used to estimate root length, diameter, branching intensity and most importantly, time of root appearance/disappearance (from which root turnover was inferred). We use the Gimp freeware package (www.gimp.org) to digitize roots and classified them as alive or dead. A total of more of 1500 roots distributed in 300 images were processed. Senescent roots are sometimes difficult to identify with certainty (Majdi et al. 2005). We considered as senescent roots that exhibited no elongation and/or diameter expansion between 2 to 6 successive observation dates and the colour of which turned from white to brown. The senescent roots were consider as "dead roots" when the absence of growth was persistent over 6 months with no morphological change in any direction and when the colour changed to dark brown or the root completely disappeared.

Observed differences in root life span might be related to root branching order, with lower branching order roots putatively associated with slower turnover than higher order ones but still linked to nutrient availability (Pregitzer 2002). Root half-life in the shallowest layer was significantly different than that at other soil depths ($p<0,001$), except the 2.5 m soil layer. In our case, root branching order could not be determined as root windows only occasionally offer the possibility to observe topological relationships between roots. However, root radius, which represents a crude proxy of root type, can be readily assessed from root window images, offering the possibility to check whether thick and thin roots have different dynamics.

Root length density and root biomass were measured using the coring method described by Böhm (1979). Destructive sampling was performed to estimate root length density down to a depth of 4 m. These soil samples were processed and analysed according to the protocol described in Pierret et al. (2007). Specific root length (SRL) values, i.e. the length of root per gram of dry root biomass, obtained from samples collected within the first meter of the soil profile were used to estimate the root dry biomass (RDB) distribution along the 4 m profile observed in the well, based on the following equation:

RDB[z] = RLD x [Z]/SRL eq. 1

where RDB[z] (in Mg/ha) is the root dry biomass for a depth increment [Z], RLD[z] is the root length density (m/m3), [Z] (m) the depth increment corresponding to a given RLD value and SRL is the specific root length i.e. the length of root per unit dry weight (m/g).

Image analysis of roots

For image analyses, we used the Kimura method provided by our open source tool IJ_Rhizo, an ImageJ macro (http://rsbweb.nih.gov/ij/) primarily designed to measure washed roots from soil samples (Pierret et al., 2013). ImageJ is a public domain Java image-processing program developed at the National Institutes of Health of the USA. The Kimura approach (1999) is based on discriminating each pixel of the medial axis transform (or skeleton) of each digitized root according its number of orthogonal and diagonal (vertical or horizontal) neighbours. Further details on IJ_Rhizo can be found in Pierret et al. (2013). We used IJ_Rhizo to obtain data of root length and root radius in millimetres and histogram of radius class.

Statistical analysis.

As it was not possible to replicate the access well due to time and budgetary constraints, data replication comes from different roots on the same windows, and the windows themselves at different soil depths. In this case, we consider original data from deep soil layer more important than statistical considerations to improve the understanding of the system. The number (n) of roots depends on their apparition on each window. Root longevity analyses include all roots that were present at the beginning of the observation period and that emerged subsequently. Roots that were still alive at the time of the last observation were right-censored. In an attempt to assess the effect of soil depth on root lifespan, we applied a Kaplan-Meier survival analysis (Kaplan and Meier 1958), from which we derived root survival curves and the median survival time, or root half-life. Differences in roots survivorship at different soil depths were assessed by pairwise comparisons using the log-rank test to compare survivorship of roots that emerged at different times. The time taken into account was the time from the appearance of each root to (a) an event (death) or (b) the end of the study. Thus, at the first time step of the Kaplan-Meier analysis, every layer is constituted with its total population size. The population size and number of dying roots along the study play a significant role as we will compare population of different sizes and thus individual's importance in term of statistic will differ.

Non-parametric tests were performed because data were not normally distributed. Post-hoc test on root half-life were performed using the Kruskall-Wallis test. Box plots were used to describe roots starting date and root age data are mean +- standard error. The population size and number of dying

roots along the study play a significant role as we will compare population of different sizes and thus individual's importance in term of statistic will differ.

Results

Destructives sampling of roots below 100 cm showed that while fine root length density (RLD) decreased by more than one order of magnitude from 5 to 50 cm, it declined only slightly from 50 to 150 cm and remained fairly constant at greater depths (RLD between 383 and 419 cm was 27% higher than that between 137 and 177 cm) (Fig. 2).

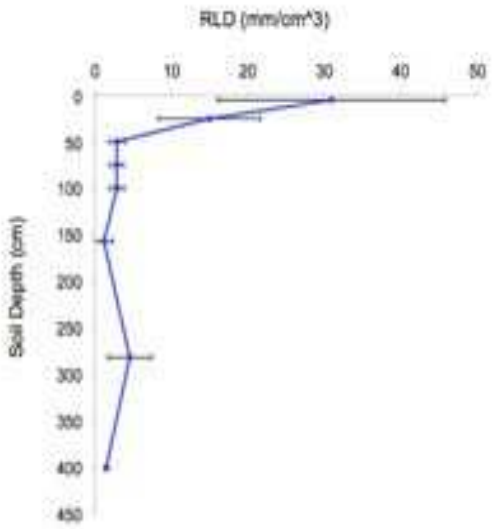


Figure 2: Mean root length density (RLD) decrease significantly with increasing soil depth but increase at 2.75 m upper to all soil level between 0.50 cm and 1.50 cm.

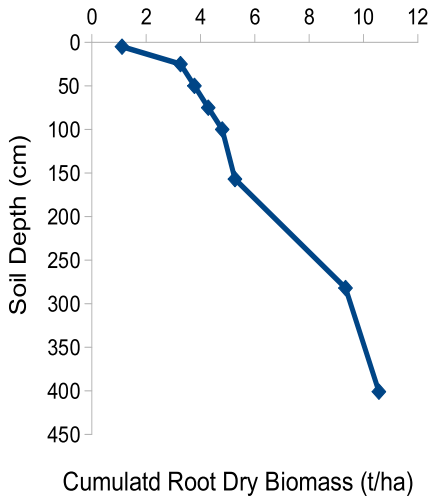


Figure 3: Cumulated fine root biomass augmented with increasing soil depth. Fifty percent of the cumulated fine root biomass was a depth of 1.0 m

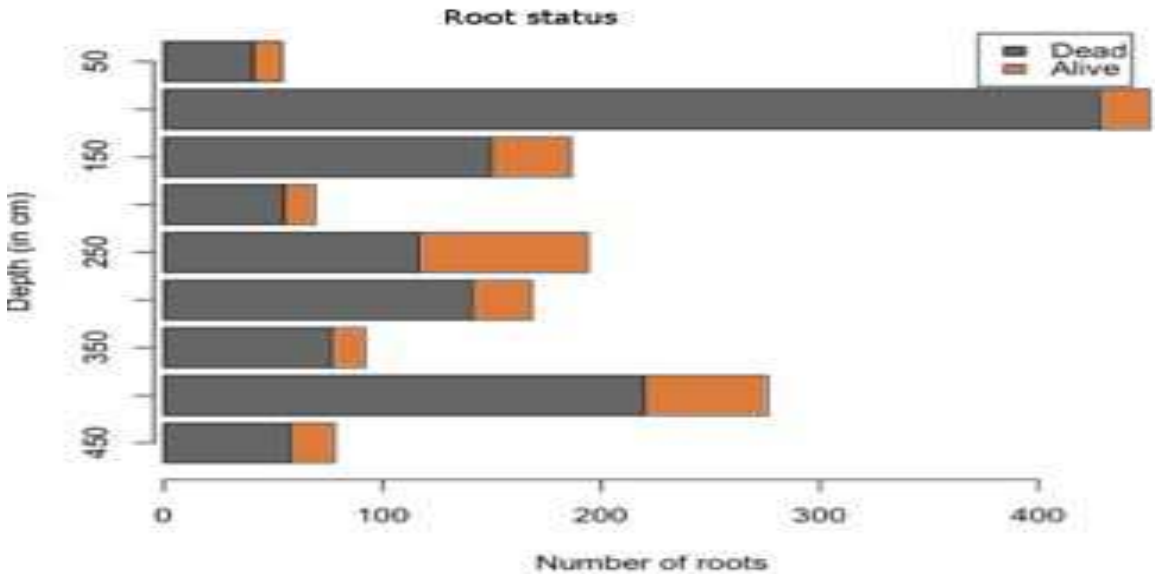


Figure 4: The number of roots present at different soil depths is greater at 1.0m and 4.0 m. Data are number of roots cumulated over 3 years per soil depth.

Individual roots were more abundant at soil depth increments of 1 and 4 m (windows data) (Fig.4). Surprisingly, the surface layer was where the smallest amount of roots was found, followed by horizons 2, 3.5 and 4.5 meters.

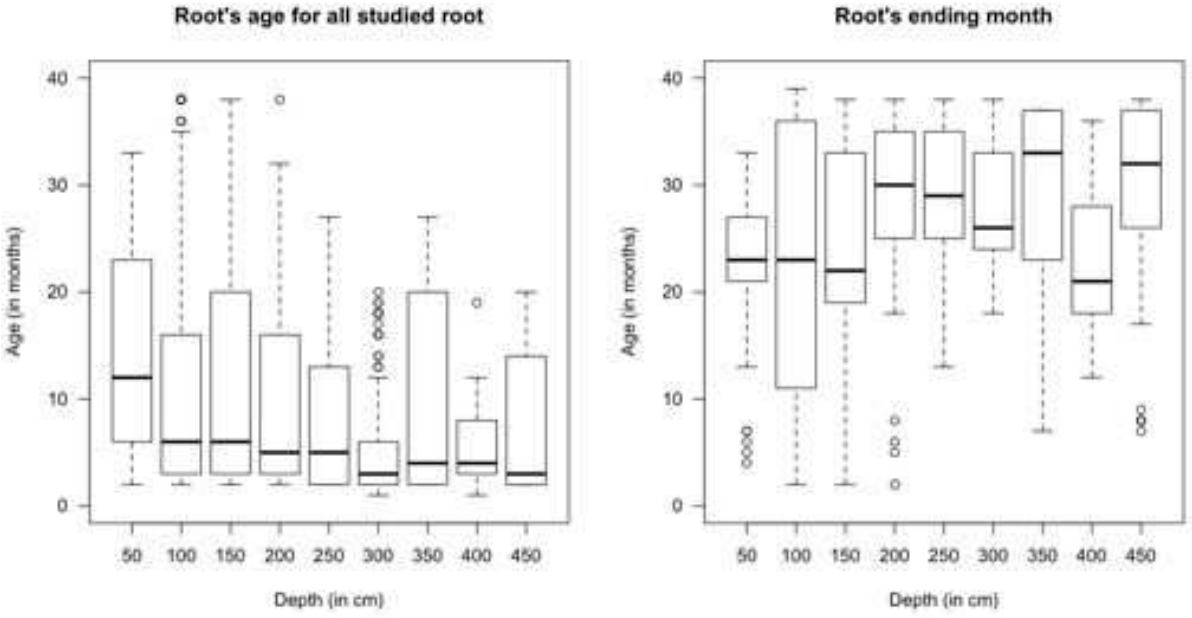


Figure 5a (left): Root age (for live and dead roots combined) per soil depth; Figure 5b (right): Mean root life-span per soil depth (From windows data).

During the course of the observation period, roots first appeared in horizons close to the soil surface and then progressively in deeper horizons (Fig. 5a). This is most likely related to the fact that roots were more abundant near the soil surface (Fig. 4) (data from coring method), which increased the probability for root growth to be observed earlier in shallow horizons. This delayed emergence of roots according to depth induces a bias regarding root life spans: the later they appeared, the more likely roots were to survive past the end of the observation period (right-censored data – Figure 5b). Roots near the soil surface (0-50 cm) had a longer life span compared to that in deeper soil layers. The longest living roots (>30 months) were found between the surface to a depth of 2m.

Roots from the shallowest soil layer had the longest half-life (16 month) a log-rank test revealed a significant effect of soil depth on root half-life values ($\chi^2_{1.8} = 89.9$ $p<0,01$).

Root half-life decreased markedly with soil depth. Deep roots between 3 and 4 m had the shortest life, with a median survival of 4 months against 6 to 8 months for the deeper and upper soil layers, respectively. A Kruskall-Wallis test did not reveal any difference in half-lives between layers 3.5, 4, 4.5 m. Globally, we identified three main trends: the 0-0.5 m soil layer where roots had a half-life of about 16 months, the 2.5-3 and 3.5-4 m layer where root half-life was 4 months and all the other soil depths with half-lives of about 7-8 months (Fig.6).

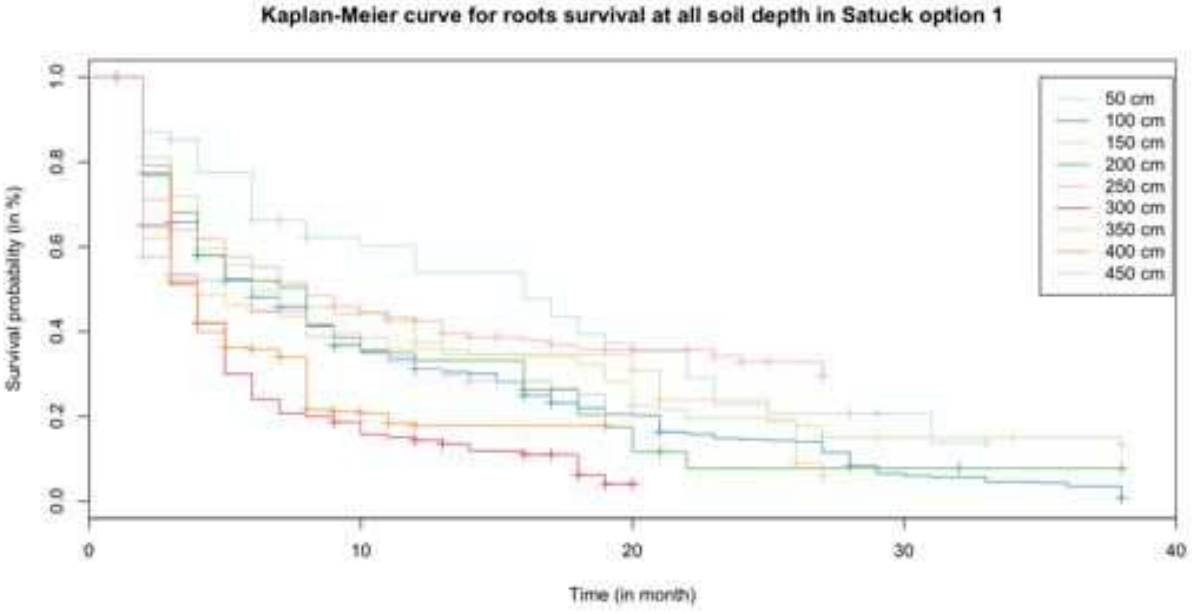


Figure 6: Root survival from a soil depth of 0.5 to 4.50 m of soil profile with estimated a Kaplan-Meier curve (Kaplan and Meier 1958).

The root radius distribution in the 0-0.5 m horizon was clearly different from that in deeper horizons (Fig. 7), with the highest proportion (> 80% in most radius classes) of thick roots with classes from 0.8 to 1.4 mm. At all the other soil depth increments, the most represented radius comprised 0.1 and 0.7 mm, with the exception of the 3.5-4.0 m increments that displayed an atypical peak at 1 mm.

The radius classes analysis, show that surface horizons (0.5 and 1.0 m) have more fine roots than in deeper horizons. It can also be seen that overall, root radius decreases gradually with soil depth.

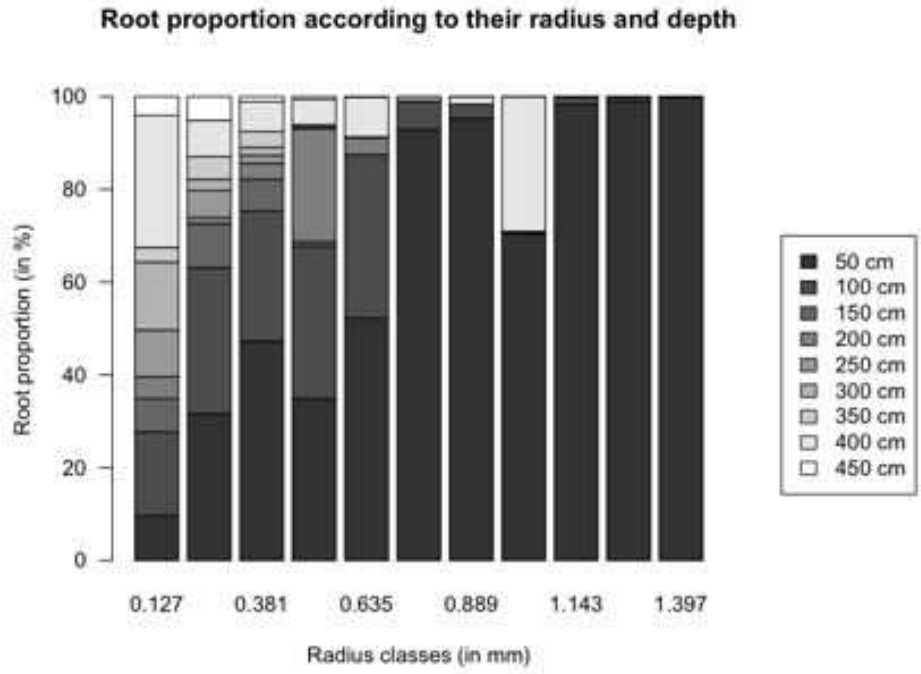


Figure 7: Root radius ratio according to soil depth from 0.0 to -4.5 m.

The 3.5 – 4.0 m horizon appears rather atypical with more roots than adjacent in horizons and a higher proportion of thick roots. However, the life span of roots in this horizon, although one of the shortest, is not significantly different than that in other soil layers. The root dynamics along the time series illustrate unusual results with mainly a greater roots appearance of roots during the second dry season. Therefore, we did take to consideration this layer in the following root dynamics analysis.

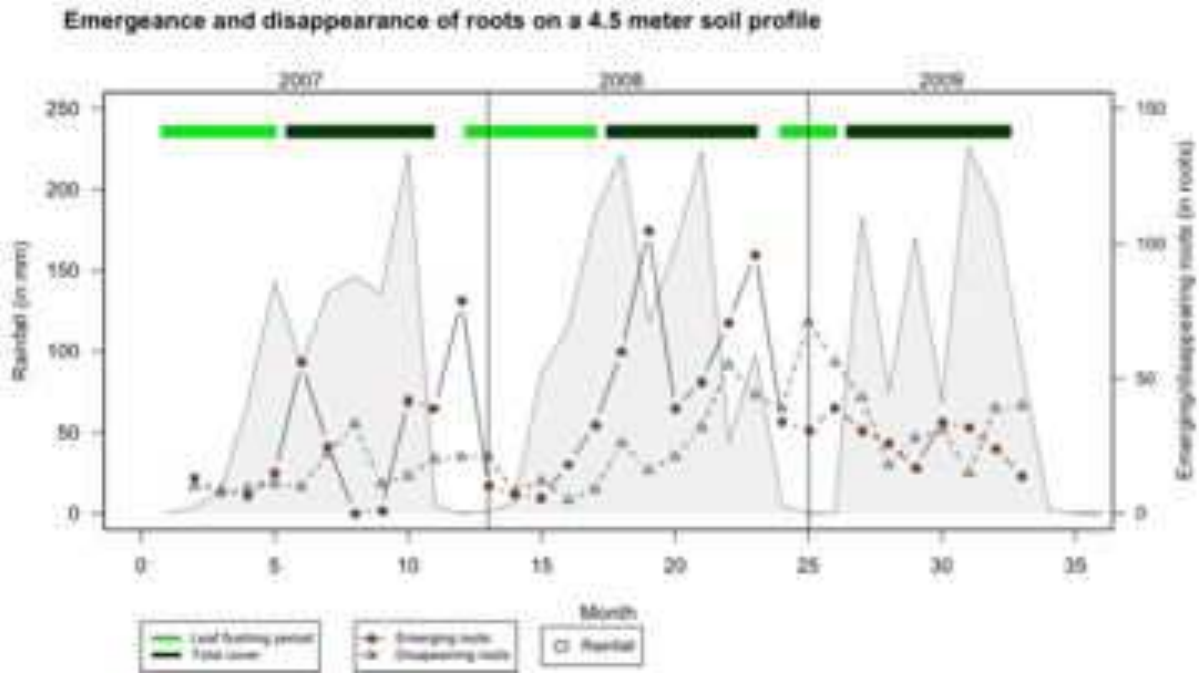
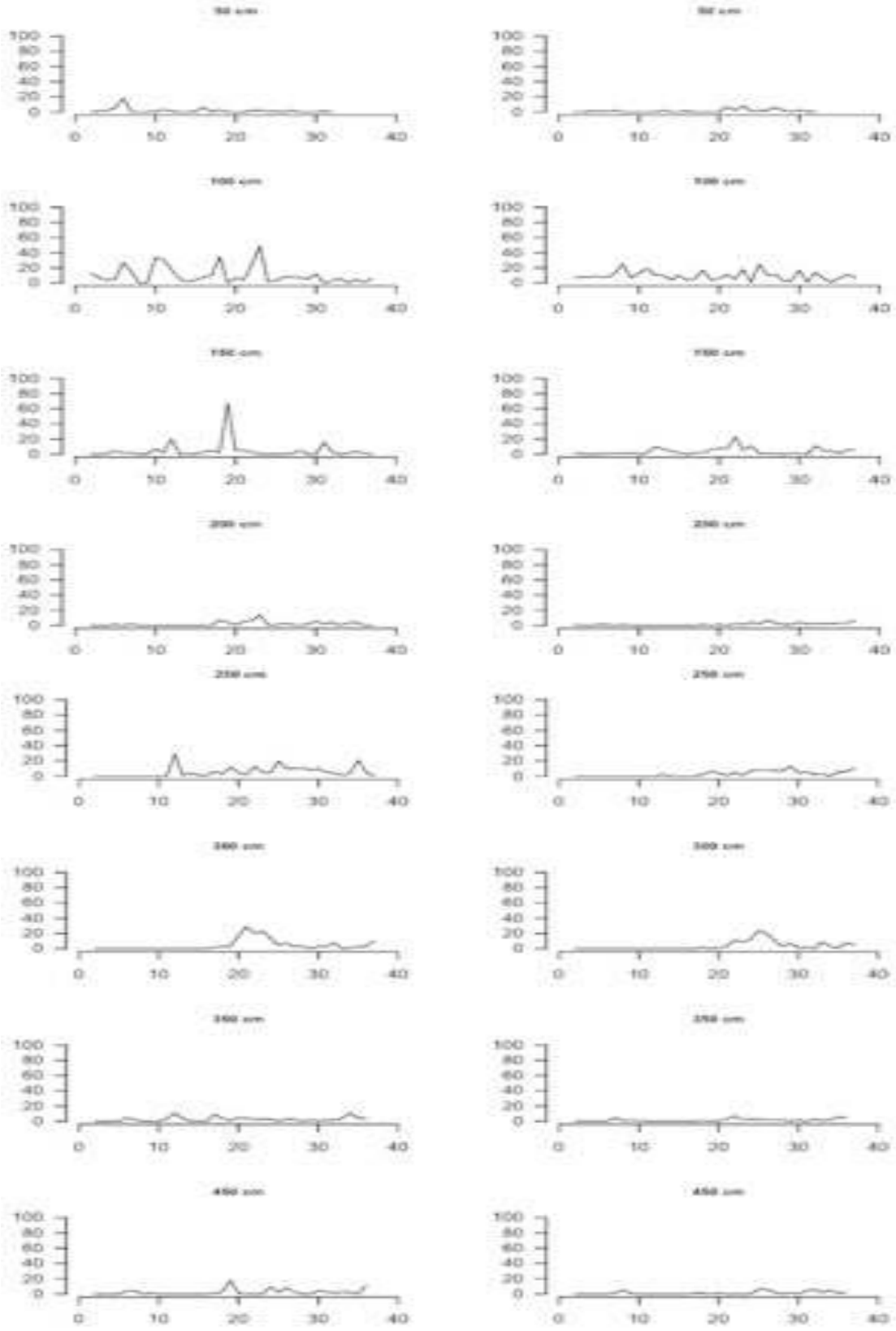


Figure 8: Root growth dynamics along the time series in a 4.5 m soil profile (cumulated data).

We computed a time series of the numbers of emerging and disappearing roots spanning the whole 3 years of the observation period. When plotted against rainfall and phenological data (Fig. 8), it appears that during the first two years of monitoring, root emergence occurred preferentially during two periods: 2 to 3 months after the onset of the rainy season and about 2 to 3 months after the end of the rainy season (Fig.9). During the first two years of the monitoring period, (1) the peak of the second episode of root emergence coincided with the time at which trees started to shed leaves, (2) root emergence was conspicuously reduced during leaf flushing (between March and May), (3) root mortality followed a pattern similar to that of root emergence, without being synchronous with it. During the second year, variations in root mortality appear to precede variations in root emergence by about one month, suggesting the existence of a mechanism for the replacement of dead roots. The last year of the monitoring period appears atypical and difficult to interpret; it did not show the same pattern and started with a 3-4 months period of marked root mortality, not compensated by root emergence.



Roots appearance Roots disappearance

Figure 9: Roots dynamic (emergence and disappearance) along the soil profile for all the root observation (36 months) (9 levels) – Number of root (y) months (x). 0 = 1 January 2007

Discussion:

The original technique combining several tools used in this experience to observe roots dynamics in situ has demonstrated its validity to collect valuable data and to contribute to improve our understanding of root dynamics. However, by using the observation window survey method (Maeght et al. 2013), we may have introduced a source of bias due to roots' shape. The technique allows a 2 dimensional observation surface when roots are growing in a 3 dimensional element. Indeed, when a root is pressed on the window, it could continue to grow against the window. We may as well just observe a section of a root that will pursue its grow further in the soil. Thus, a same root can appear several times on the same window but due to our protocol, every single piece of root is treated as an unique root. Furthermore, the death rate could have been overestimate, as a single dying root appearing in three parts on a window will be referred as a three roots losts.

During the dry season, rubber trees' responds to soil and atmospheric drought with high evapotranspiration level is a good indicator of extreme environmental conditions. It is to notice that some individuals reached the saturation level of transpiration due to the high evaporative demand (Bovard et al. 2005). In cases of rubber, this response can differ according to clones (Sangsing et al. 2004). High evaporative demands induced conservative stomata behaviour, can reduce growth and productivity in the short term but contribute to long-term survival. For the RRIM 600 clone in similar soil and atmospheric conditions, Isarangkool Na Ayutthaya et al. (2011) observed a complete cessation of growth at the onset of the dry season with high decrease in transpiration (0.4-0.3 REW). This range of values was close to other studies reviewed by Bréda et al. (2006). Similar observations are also confirmed in a recent publication from Kobayashi et al. 2014 in Cambodia. Tree density (500 – 600 tree/ha) was the same as that implemented in Southern Thailand where the annual rainfall (2000 mm) is much more compatible with the water requirements of rubber trees (Carr 2011b).

Observations made during the three years monitoring period support the hypothesis that root growth dynamics over the whole 4.5 m profile is linked, on the one hand, to the rainfall pattern and, on the other hand, to the partitioning between above-ground and below-ground carbon allocation. The third year's observation followed have distinct pattern. Different hypothesis have been made and will be discuss later.

We measure a high root establishment during the second dry season associated with a high death-rate, this could illustrate the root turn over which could be located at a similar layer or applied in different layers according to the environment conditions. We can imagine the emergences of roots at a time step, which cannot be maintained by the tree (too costly in terms of resources or changes in environmental

conditions) and thus high root emerging peaks are linked or followed by high root disappearance peaks. These observations suggest a replacement mechanism but we don't identify clearly the reason of this. This supposes a specific situation where trees seem to stop their vital function (high root emergence, short leave cycle) but are not able to maintain the fresh roots until next season. In all cases, the emergence of new roots occurs before the emergence of new leaves. This phenomenon can be considered as anticipation for the future peak of resources demands of trees on the verge to enter in a new growing and production cycle.

The specificity of the roots dynamics observed in this edaphic and climatic situation can be linked to the same specificity in the leaves growth dynamics adopted by rubber trees as a response to an unfavourable environment. As well as resources are insufficient to maintain leaves until the renewal period as usually observed in its endemic areas, rubber trees seem unable to maintain fresh roots alive until next season. The link with this necessity of adaptation can also be made with the absence of roots observation with longer live span in the deeper section of the soil profile. This confirms in our case that exogenous factors can influence root development (Harper et al. 1991; McCormack and Guo 2014). Even in deep soil layers, root live span was linked to climatic constraints and has not systematically a longer life span compared to shallow roots. The fact that the half-life of roots in the 0-0.5 m horizon is higher than in the other horizons could be related to the fact that this horizon encompasses a different population of roots than deeper horizons.

It can be inferred that fine root biomass below 100 cm could amount for more than a third of the overall fine root biomass of the trees we measured (Fig. 3). It is noteworthy that, as there is no indication that the deepest depth increment sampled for this study (i.e. 450 cm) is the maximum rooting depth of the studied trees, the total root biomass actually present below 100 cm is likely to account for more than the figure we were able to estimate. Assuming an average Specific Root Length of ~14 m/g for fine rubber tree roots (Pierret et al. 2007a), a mean organic carbon content of approximately 47% for fine rubber tree roots (Wauters et al. 2008), data gained from this study indicated that the amount of carbon stored in rubber tree roots of 0.5 mm in diameter or less, is approximately 4.5 t C ha-1 on average, which is of the same order of magnitude, although slightly higher, than values reported by Wauters et al. (2008) for coarser roots (2.5-25 mm in diameter) for a range of clones including GT1, PB217, PB235, PB260, PR255 and RRIM600 from Western Ghana and Brazil. This result has important implications since the depth range throughout which this fairly low RLD was observed is considerable. This means that an important carbon pool may have been overlooked by most studies. These results are also of the same order of magnitude as the value of 16.50 t C ha^{-1} reported by Cheng et al. (2007) for roots of all sizes, in rubber tree plantations at Hainan Island, China.

Conclusion and Outlook

Root emergence was influenced by endogenous factors and exogenous factors in relation to edaphic and climatic conditions, an original example was provided by J.M. Coulter in 1899. We observe some substantial root emergence in dry season previously to new leaves emission following by the starting point on raining season. Roots growth during the dry season during the vegetative period of trees is an original finding that contradict another study proposed by Chairungsee et al. in 2013 for the same clone species (RRIM600) in the same region. Roots emergence pattern had a strong effect on root lifespan Roots longevity was generally correlated positively with root diameter and the risk of mortality was decreasing with diameter growth (Yao et al. 2009). Fine roots turnover was more than once a year in our case in contradiction of assumption generally used in other studies (Jackson et al. 1997; Matamala and Gonza 2003; Wu et al. 2013). All these studies mention the necessity to take in account the maximum of rooting depth to understand plants/environments interaction, especially when attempting to assess the soil carbon budget in soil under tree.

Our finding concludes to more carbon sequestration as previously proposed by Brunner and Godbold (2007). This observation was previously mentioned by Nadelhoffer and Raich in1992 and Vogt et al. in 1996- who highlighted the important role of fine roots in that the amount of nitrogen returned to the soil from fine root death and decomposition equalled or exceeded that from leaf litter fall. But recently Xiong et al. 2012 indicated a show decomposition and limited release by lower roots order for subtropical trees species. Trees' roots are an essential contributor to tree adaptation in a changing environment (Brunner and Godbold 2007). The uncertainty regarding the below-ground carbon biomass values is underlined by Yuen et al. (2013). Our results thus speak in favour of more studies in this field to come up with a better assessment of root carbon storage. The realistic assessment of deep root contributions to mitigation and adaptation of trees to exogenous and endogenous constraints is still challenging.

If rubber trees have demonstrate a remarkabled capacity to adapt to unfavourable climate and environmental conditions, being able to grow and produce latex in adverse contexts, several physiological and morphological signs, including evapotranspiration saturation or high root decease rate, indicate that they have reached a limit in their adaptation capacity. More in-depth and long term studies are still needed to improve our knowledge on tree's strategy and adaptation capacity to climate variability and to fully understand key roles played by the root system in this process.

Acknowledgements

This research was funded by IRD, the French Institute for Rubber (IFC), and Michelin / Socfinco / SIPH Rubber Tree Plantations Companies. We would also like to thank all our Thai counterparts from Khon Kaen University (KKU), Land Development Department (LDD), and the owner of the plantation (Mr. Chaipat Sirichaiboonwat) who welcomed us so kindly in his plantation. The authors also wish to thanks Drs. D. Nandris and F. Do (IRD) for having contributed and for their interest in this research.

References

ACIAR (1985) Smallholder rubber production and policies. Smallhold. rubber Prod. policies. ACIAR, Adelaide, p 151

Allen RG, Pereira LS, Raes D, et al. (1998) Crop evapotranspiration - Guidelines for computing crop water requirements - FAO Irrigation and drainage paper 56 By. 1–15.

Bleby TM, McElrone AJ, Jackson RB (2010) Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant Cell Environ 33:2132–48. doi: 10.1111/j.1365-3040.2010.02212.x

Böhm W (1979) Methods of studying root systems. 188.

Boithias L, Do FC, Isarangkool Na Ayutthaya S, et al. (2011) Transpiration, growth and latex production of a Hevea brasiliensis stand facing drought in northeast Thailand: The use of the WaNuLCAS model as an exploratory tool. Exp Agric 48:49–63. doi: 10.1017/S001447971100086X

Bovard BD, Curtis PS, Vogel CS, et al. (2005) Environmental controls on sap flow in a northern hardwood forest. Tree Physiol 25:31–8.

Boyce KC (2005) The evolutionary history of roots and leaves. In: Elsevier C (ed) Vasc. Transp. Plants, NM Holbroo. San Diego, pp 479–500

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–644. doi: 10.1051/forest

Bridhikitti A (2013) Atmospheric aerosol layers over Bangkok Metropolitan Region from CALIPSO observations. Atmos Res 127:1–7. doi: 10.1016/j.atmosres.2013.02.008

Brunner I, Godbold DL (2007) Tree roots in a changing world. J For Res 12:78–82. doi: 10.1007/s10310-006-0261-4

Carr MK V. (2011a) The water relations of rubber (Hevea Brasiliensis): a review. Exp Agric 48:176–193. doi: 10.1017/S0014479711000901

Carr MK V. (2011b) THE WATER RELATIONS OF RUBBER (HEVEA BRASILIENSIS): A REVIEW. Exp Agric 48:176–193. doi: 10.1017/S0014479711000901

Cawte HJ, Boyd WE (2010) Laterite nodules: A credible source of iron ore in iron age northeast Thailand? Geoarchaeology 25:626–644. doi: 10.1002/gea.20326

Chairungsee N, Gay F, Thaler P, et al. (2013) Impact of tapping and soil water status on fine root dynamics in a rubber tree plantation in Thailand. Front Plant Sci 4:1–11. doi: 10.3389/fpls.2013.00538

Cheng C-M, Wang R-S, Jiang J-S (2007) Variation of soil fertility and carbon sequestration by planting Hevea brasiliensis in Hainan Island, China. J Environ Sci (China) 19:348–52.

Clothier BE, Green SR, Deurer M (2007) Preferential flow and transport in soil: progress and prognosis. Eur J Soil Sci 59:2–13. doi: 10.1111/j.1365-2389.2007.00991.x

Coulter JM (1899) Plant relation, first book of botany. 1 – 264.

Do FC, Pierret A, Couteron P, et al. (2011) Spatial distribution of Hevea brasiliensis trunk phloem necrosis within a plot: aggregation but no evidence of constraint on cumulated growth. For Pathol 41:90–100. doi: 10.1111/j.1439-0329.2010.00640.x

Edwards EJ, Benham DG, Marland LA, Fitter AH (2004) Root production is determined by radiation flux in a temperate grassland community. Glob Chang Biol 10:209–227. doi: 10.1111/j.1365-2486.2004.00729.x

Eissenstat DM, Yanai RD (1997) The Ecology of Root Lifespan Advances in Ecological Research. Advances. pp 1–60

Elliott S, Baker P, Borchert R (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. Glob Ecol … 1–10. doi: 10.1111/j.1466-822x.2006.00213.x

Fox J, Castella J-C (2013) Expansion of rubber (Hevea brasiliensis) in Mainland Southeast Asia: what are the prospects for smallholders? J Peasant Stud 40:155–170. doi: 10.1080/03066150.2012.750605

Gonkhamdee S, Maeght JL, Do F, Pierret A (2009) Growth dynamics of line Heavea brasiliensis roots along a 4.5-m soil profile. Khon kaen Agric J 37:265–276.

GRANIER A, GROSS P (1987) Mesure du flux de sève brute dans le tronc du Douglas par une nouvelle méthode thermique. Ann des Sci For 44:1–14. doi: 10.1051/forest:19870101

Hales S (1727) Vegetable staticks.

Harper JL, Jones M, Sackville Hamilton NR (1991) The evolution of roots and the problems of analyzing their behaviour. Plant root growth An Ecol. Perspect., D. Atkinso. Blackwell Scientific Publications, Oxford., pp 3–22

Hartmann C, Lesturgez G, Do FC, et al. (2006) Rubber tree Trunk Phloem Necrosis (TPN) in Northeast Thailand: 1. Investigations on soil heterogeneities linked to disease outbreak. Int. Nat. Rubber Conf. - IRRDB Annu. Meet. Ho Chi Minh City., pp 139–156

Isarangkool Na Ayutthaya S, Do FC, Pannangpetch K, et al. (2011) Water loss regulation in mature Hevea brasiliensis: effects of intermittent drought in the rainy season and hydraulic regulation. Tree Physiol 31:751–62. doi: 10.1093/treephys/tpr058

Isarangkool Na Ayutthaya S, Do FC, Pannengpetch K, et al. (2010) Transient thermal dissipation method of xylem sap flow measurement: multi-species calibration and field evaluation. Tree Physiol 30:139–48. doi: 10.1093/treephys/tpp092

Jackson RB, Mooney H a, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci U S A 94:7362–6.

Jacob J, Krishnakumar R (2006) Tapping Panel Dryness syndrome: what we know and we do not know. In: James, J.; Krishnakumar, R.; Mathew NMK (ed) Tapping Panel Dryness of Rubber Trees. Rubber Research Institute of India, pp 01–27

Junjittakarn J (2012) Short term effects of latex tapping on micro-changes of trunk girth in Hevea Brasiliensis. Aust J Crop Sci 6:65–72.

Kaplan EL, Meier P (1958) Nonparametric Estimation from Incomplete Observations. J Am Stat Assoc 53:457–481. doi: 10.1080/01621459.1958.10501452

Kaspar TC, Ewing RP (1997) ROOTEDGE: Software for Measuring Root Length from Desktop Scanner Images. Agron J 89:932. doi: 10.2134/agronj1997.00021962008900060014x

Kimura K, Kikuchi S, Yamasaki S (1999) Accurate root length measurement by image analysis. Plant Soil 117–127.

Kobayashi N, Kumagai T, Miyazawa Y, et al. (2014) Transpiration characteristics of a rubber plantation in central Cambodia. Tree Physiol 34:285–301. doi: 10.1093/treephys/tpu009

Kramer PJ, Boyer JS (1995) Roots and root systems. In: CA: Academic Press I (ed) Water Relations of Plant and Soils, P. J. Kram. San Diego, pp 116–166

Lobet G, Hachez C, Draye X (2013) Root Water Uptake and Water Flow in the Soil–Root Domain. Plant Roots Hidden Half. Inc, CRC Press, pp 24–1, 24–18

Maeght J-L, Pierret A, Sanwangsri M, Hammecker C (2007) Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand. Int. Conf. Rhizosph. 2, 26-31 August 2007, Montpellier, Fr. pp 26–31

Maeght J-L, Rewald B, Pierret A (2013) How to study deep roots—and why it matters. Front Plant Sci. doi: 10.3389/fpls.2013.00299

Majdi H, Pregitzer K, Morén A-S, et al. (2005) Measuring Fine Root Turnover in Forest Ecosystems. Plant Soil 276:1–8. doi: 10.1007/s11104-005-3104-8

Matamala R, Gonza MA (2003) Impacts of Fine Root Turnover on Forest NPP and Soil C. Science (80-) 302:1385–1387.

McCormack ML, Guo D (2014) Impacts of environmental factors on fine root lifespan. Front Plant Sci 5:1–11. doi: 10.3389/fpls.2014.00205

McDougall WB (1916) The Growth of Forest Tree Roots. Am J Bot 3:384–392.

Nadelhoffer K, Raich J (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147.

Pierret A, Doussan C, Pages L, et al. (2007a) Is impeded root growth related to the occurrence of rubber tree Trunk Phloem Necrosis (TPN)? Preliminary results from NE Thailand. IRRDB Annu. Meet. pp 489–498

Pierret A, Gonkhamdee S, Jourdan C, Maeght J-L (2013) IJ_Rhizo: an open-source software to measure scanned images of root samples. Plant Soil. doi: 10.1007/s11104-013-1795-9

Pierret A, Latchackak K, Sengtaheuanghoung O, Valentin C (2007b) Interactions between root growth , slope and soil detachment depending on land use : a case study in a small mountain catchment of Northern Laos. Plant Soil 51–64. doi: 10.1007/s11104-007-9413-3

Pregitzer K (2002) Fine roots of trees–a new perspective. New Phytol 154:267–270.

Priyadarshan PM, Hoa TTT, Huasun H, de Gonçalves PS (2005) Yielding Potential of Rubber (Hevea brasiliensis) in Sub-Optimal Environments. J Crop Improv 14:221–247. doi: 10.1300/J411v14n01_10

Rao GG, Rao PS, Rajagopal R, et al. (1990) Influence of soil, plant and meteorological factors on water relations and yield in. 175–180.

Rodrigo V (2007) Ecophysiological factors underpinning productivity of Hevea brasiliensis. Brazilian J Plant Physiol 19:245–255.

Sangsing K, Kasemsap P, Thanisawanyangkura S, et al. (2004) Xylem embolism and stomatal regulation in two rubber clones (Hevea brasiliensis Muell. Arg.). Trees - Struct Funct 18:109–114. doi: 10.1007/s00468-003-0286-7

Sookmark U, Pujade-Renaud V, Chrestin H, et al. (2002) Characterization of polypeptides accumulated in the latex cytosol of rubber trees affected by the tapping panel dryness syndrome. Plant Cell Physiol 43:1323–33.

Stokes A, Bakker MR (2013) Root Systems of Woody Plants. Plant Roots Hidden Half. Inc, CRC Press, pp 29–1, 29–18

Stone EL, Kalisz PJ (1991) On the maximum extent of tree roots. For Ecol Manage 46:59–102. doi: 10.1016/0378-1127(91)90245-Q

Strand AE, Pritchard SG, McCormack ML, et al. (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–8. doi: 10.1126/science.1151382

Virginia RA, Jarrell WM (1987) Approaches for studying the function of deep root systems. Plant response to …

Vogt KA, Vogt DJ, Palmiotto PA, et al. (1996) Review of root dynamics in forest ecosystems grouped by climate , climatic forest type and species. Plant Soil 159–219.

Wauters JB, Coudert S, Grallien E, et al. (2008) Carbon stock in rubber tree plantations in Western Ghana and Mato Grosso (Brazil). For Ecol Manage 255:2347–2361. doi: 10.1016/j.foreco.2007.12.038

Wu Y, Deng Y, Zhang J, et al. (2013) Root size and soil environments determine root lifespan: evidence from an alpine meadow on the Tibetan Plateau. Ecol Res 28:493–501. doi: 10.1007/s11284-013-1038-9

Xiong Y, Fan P, Fu S, et al. (2012) Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees. Plant Soil 363:19–31. doi: 10.1007/s11104-012-1290-8

Yao S, Merwin I, Brown M (2009) Apple root growth, turnover, and distribution under different orchard groundcover management systems. HortScience 44:168–175.

Yuan ZY, Chen HYH (2012) Indirect methods produce higher estimates of fine root production and turnover rates than direct methods. PLoS One 7:e48989. doi: 10.1371/journal.pone.0048989

Yuen JQ, Ziegler AD, Webb EL, Ryan CM (2013) Uncertainty in below-ground carbon biomass for major land covers in Southeast Asia. For Ecol Manage 310:915–926. doi: 10.1016/j.foreco.2013.09.042

Zoon FC, Tienderen PH (1990) A rapid quantitative measurement of root length and root branching by microcomputer image analysis. Plant Soil 126:301–308. doi: 10.1007/BF00012833

2.3 Conclusion

L'étude approfondie de la dynamique racinaire sur l'ensemble du profil nous a permis de mettre en évidence les rythmes d'apparition et de mortalité des racines de l'hévéa contrastés entre les deux premiers mètres de sol d'une part et le reste du profil d'autre part.

Dans les deux premiers mètres du profil, la quantité de racines émises diminue en progressant en profondeur. Ces racines s'illustrent par des durées de vie très variables, allant de 13 à 28 mois. Nous observons une durée de vie minimum plus longue que les maximums de durée de vie observés dans des forêts tropicales (4° 58' N, 117° 42' E) (Green et al. 2005). Ces forêts reçoivent 2800 mm de précipitation annuelle, ce qui représentent plus du double des précipitations reçues dans notre cas d'étude et justifie peut-être cette grande différence. Les observations proposées par Pregitzer et al. en 1993 indiquant une plus longue longévité en lien avec une plus grande humidité du sol ne se vérifient pas sur les données de notre étude.

Dans la deuxième partie du profil, entre 2 et 4,5 mètres de profondeur, la durée de vie moyenne des racines se situe autour de 10 mois et varie peu. Nous constatons donc que la durée de vie des racines dans les 2 premiers mètres du sol à tendance à être plus longue que la durée de vie des racines plus en profondeur, ce qui contraste part rapport aux tendances généralement citées, dans lesquelles la notion de profondeur se limite à quelque dizaine de centimètres.

Les observations réalisées lors des trois saisons sèches étudiées démontrent une apparition régulière de racines en l'absence de pluie dans l'ensemble du profil, ce qui contraste à nouveau avec les études de Kavanagh and Kellman (1992). Nous observons également des croissances racinaires pendant les périodes de défoliations et les données analysées démontrent que cette dynamique est d'autant plus importante en profondeur. Nous apportons ici une nouvelle information sur le découplage de phénologie entre les feuilles et les racines profondes, qui complète celui mesuré dernièrement pour les racines de surface par Chairungsee et al. en 2013 (Photo 6).

Nous n'avons que peu d'élément de comparaison sur l'étude de la dynamique de croissance des racines en profondeur notamment en saison sèche. La saignée liée à la récolte du latex a

une influence sur la dynamique racinaire de surface (Chairungsee et al. 2013). Cette saignée étant suspendue pendant la période de défoliation, nous pouvons considérer que son arrêt pourrait favoriser la croissance racinaire observée en profondeur par le biais d'une réallocation de ressource.

Les capacités de stockage du carbone dans les parties aériennes et la production de litière dans des plantations d'hévéas sont supérieures à celles des forêts naturelles présentées par Cheng et al. en 2007. Dans notre cas, le fait de tenir compte du cumul des élongations racinaires sur l'ensemble du profil double (ou multiplie) cette capacité du stockage par deux. En conséquence, nos études, dont certains résultats divergent des tendances présentées dans diverses études sur les dynamiques de racines de surfaces, plaident pour une meilleure prise en compte des données de l'enracinement profond afin de pouvoir établir des lois générales plus représentatives de la réalité. Cette meilleure prise en compte de l'enracinement profond parait d'autant plus importante pour permettre aux travaux de modélisation de simuler des scénarios prenant en compte l'ensemble des racines d'une même plante de façon réaliste.

Notre étude apporte également un éclairage sur la dynamique de l'enracinement de l'hévéa dans un contexte déficitaire en eau et sur sa capacité de production sous un rythme d'exploitation soutenu. Il est apparu que les conditions d'implantations et d'exploitations conduisent certains arbres à arrêter la production de latex (Photo 7; Photo 8;Photo 9;Photo 10). Cette réaction ne met pas en péril la vie de l'arbre car certains arbres en arrêt de production de latex démontrent des diamètres de tronc plus élevés que des arbres de même âge continuant à produire du latex (Figure 12). Ce phénomène, ajouté aux délais rallongés pour la mise en saignée des jeunes plantations (7 ans au moins dans notre cas alors que certains planteur du sud-est asiatique débute les saignées autour de 3 ans), remettent en question l'intérêt des plantations d'hévéas à forte densité dans cet environnement très contraignant en compromettant sérieusement leur rentabilité.

Dans un tel contexte, l'hévéa semble avoir atteint des limites physiologiques que les planteurs ne devraient peut-être pas franchir au risque de subir de fortes pertes d'exploitation suite à l'arrêt de production de latex sur un nombre significatif d'arbres. D'autres formes d'exploitation devraient être envisagées, avec notamment des implantations de plus faibles densités. Une autre alternative pourrait être de travailler sur des systèmes agro forestiers permettant d'assurer des revenus suffisants aux petits producteurs tout en garantissant une

durabilité du mode d’exploitation des terres. Une exploitation de l’hévéa à plus faible densité en combinaison avec des cultures annuelles permettrait de créer des conditions plus favorables à la croissance de l’hévéa, tout en garantissant des revenus alternatifs aux paysans et une moins forte dépendance au cours du marché du latex, toujours très fluctuant.

La production liée à l’agroforesterie permettrait de générer des revenus complémentaires intéressants et d’atténuer les conséquences d’une perte de revenus suite à une chute des cours. Cette démarche aurait également l’avantage de mieux préserver les sols sur lesquels sont développées les plantations d’hévéas, déjà fortement dégradés par la succession sur plusieurs années de monocultures de rente, tel que le manioc.



Photo 6: Plantation d'hévéas en début de refoliation après défoliation totale (J.-L. Maeght)



Photo 7: Pratique de la saignée (D. Nandris)



Photo 8: Encoche en perte de production (D. Nandris)



Photo 9 : Hévéa en production (D. Nandris)



Photo 10 : Hévéa ne produisant plus de latex (D. Nandris)

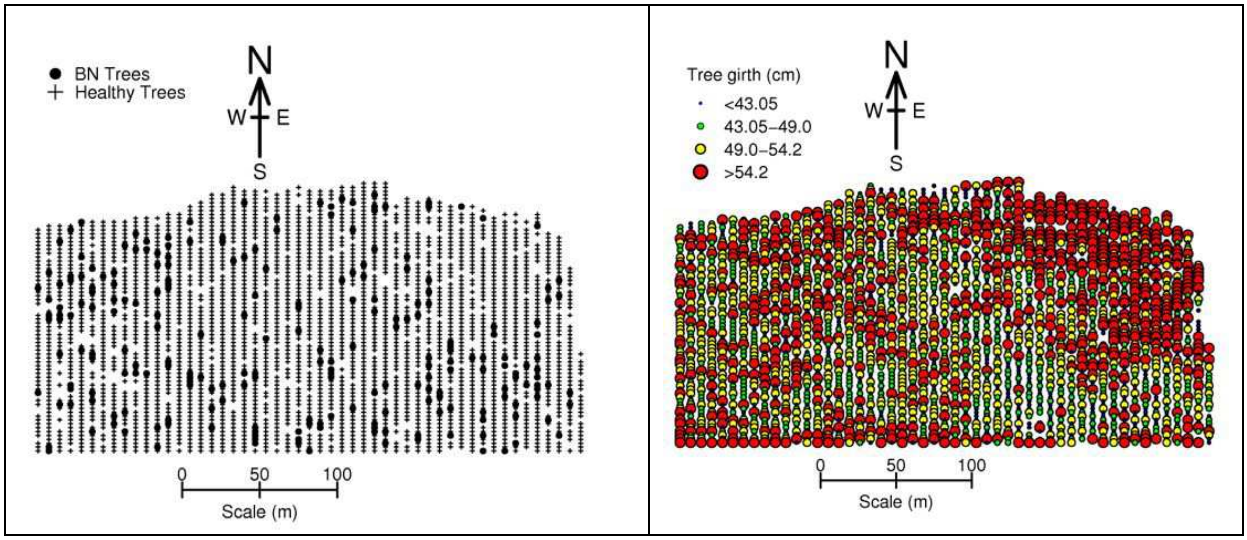


Figure 12: Localisation des arbres atteints de "barc necrosis" sur la parcelle; classement des arbres par diamètre (Do et al., 2011)

2.3.1 Références

Chairungsee, N., Gay, F., Thaler, P., Kasemsap, P., Thanisawanyangkura, S., Chantuma, A., & Jourdan, C. (2013). Impact of tapping and soil water status on fine root dynamics in a rubber tree plantation in Thailand. *Frontiers in Plant Science*, *4*(December), 1–11. doi:10.3389/fpls.2013.00538

Cheng, C.-M., Wang, R.-S., & Jiang, J.-S. (2007). *Variation of soil fertility and carbon sequestration by planting Hevea brasiliensis in Hainan Island, China. Journal of environmental sciences (China)* (Vol. 19, pp. 348–52). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Do, F. C., Pierret, A., Couteron, P., Lesturgez, G., Boithias, L., Isarangkool Na Ayutthaya, S., … Nandris, D. (2011). Spatial distribution of Hevea brasiliensis trunk phloem necrosis within a plot: aggregation but no evidence of constraint on cumulated growth. *Forest Pathology*, *41*(2), 90–100. doi:10.1111/j.1439-0329.2010.00640.x

Green, J. J., Dawson, L. a., Proctor, J., Duff, E. I., & Elston, D. a. (2005). Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. *Plant and Soil*, *276*(1-2), 23–32. doi:10.1007/s11104-004-0331-3

Kavanagh, T., & Kellman, M. (1992). Seasonal Pattern of Fine Root Proliferation in a Tropical Dry Forest. In *Biotropica* (Vol. 24, pp. 156–165). The Association for Tropical Biology and Conservation.

Pregitzer, K., Hendrick, R., & Fogel, R. (1993). The demography of fine roots in response to patches of water and nitrogen. *New Phytologist*, 575–580. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.1993.tb03905.x/abstract

Chapitre 3:

Tectonas grandis L : Capacité d'adaptation à des propriétés édaphiques et climatiques fortement contrastées.



Photo 11: Plantation de teck sur notre site d'étude

3.1 Introduction

Le teck (*Tectona grandis L.)* est une des essences de feuillues les plus prisées pour ses qualités de durabilité et son esthétique. Utilisé et apprécié depuis plus de 2000 ans en Asie comme bois de construction en raison de sa résistance exceptionnelle, il est aujourd'hui convoité dans le monde entier, entrainant une très forte demande à l'importation, notamment vers les pays européens et les Etats-Unis (Kollert and Cherubini 2012). Une autre particularité intéressante du teck est sa faculté d'adaptation qui a permis à l'homme de le planter avec succès dans des zones écologiques très diverses au delà de sa zone endémique originelle (Graudal et al. 1999).

Le teck est endémique de la région du Sud asiatique entre 10 et 25 ° de latitude nord et 0° et 10° de latitude Sud, sur une zone couvrant environ 23 millions d'hectares (Graudal et al. 1999; Pandey and Browna 2000). Il est naturellement présent en Inde, au Laos, en Thaïlande et enfin au Myanmar (Figure 13). Dans sa zone endémique, le teck est présent sous forme de peuplements mixtes dans les forêts humides et sèches d'arbres décidus à une altitude autour de 1000 m (Thein et al. 2007).

C'est en Birmanie que se trouve aujourd'hui encore la majorité des individus à l'état naturel sous forme de peuplements aménagés avec des arbres exceptionnels (Photo 12) (FAO 2010). Ces peuplements sont cependant grandement menacés (Bryant 1997). La demande mondiale pour ce bois de qualité a encouragé des abattages massifs non régulés dans la plupart des forêts et conduits à une baisse des ressources en grumes issues du milieu naturel (FAO 2011; Guizol et al. 2005). Malgré des mesures fortes de restriction de son exploitation dans son milieu naturel, le teck est aujourd'hui une espèce en danger de disparition sous sa forme de forêt naturelle (Kashio and White 1998).

Ce contexte de forte demande et de diminution des ressources naturelles a conduit au développement constant des plantations de teck dans sa zone endémique mais aussi progressivement dans toute la zone inter-tropicale. Le teck est également utilisé comme essence de reforestation sous forme de taillis, notamment en Indonésie (Bailey and Harjanto 2005). Les surfaces couvertes en plantation de teck atteignaient plus de 6 millions d'hectares en 2001 (Bhat 2004) dont plus de 80 % en Asie tropicale. Le teck a été introduit en Indonésie

il y a environ 500 ans puis a été progressivement exporté en Asie tropicale à partir de 1840 (Ross 1961), en Afrique depuis 1900 (Horne 1966), en Amérique depuis 1927 et enfin en Océanie depuis 1913. Cette dissémination anthropique du teck explique la variabilité des milieux dans lesquels il est aujourd'hui cultivé. Cette diversité met en avant la capacité d'acclimatation de cette espèce pionnière ayant pour origine le sud Asiatique. Le teck s'est donc particulièrement bien adapté dans des régions à propriétés édaphiques et climatiques contrastées de la zone intertropicale, notamment grâce à sa tolérance aux ravageurs et à sa rusticité (Alcântara and Veasey 2013). Malgré sa large zone de distribution géographique, le teck reste sensible aux variations climatiques et à la variation de la disponibilité en eau. Il est à ce titre un modèle utilisé pour des études dendroclimatiques portant sur plusieurs centaines d'années en Indonésie (Jacoby and D'Arrigo 1990) en Inde (Ram et al. 2011), en Côte d'Ivoire (Dié et al. 2012) et en Thaïlande (Pumijumnong 2012). Sa sensibilité à la ressource en eau semble avoir marqué certains traits particuliers en lien avec ses zones de cultures, comme le rapporte Nocetti et al. en 2011. Il s'agit plus particulièrement d'effets sur la croissance (Goh et al. 2013; Hidalgo et al. 1986; Jayasankar et al. 2003; Streets 1962) et sur les capacités de survie en conditions défavorables (Hidalgo et al. 1986; Madoffe and Maghembe 1988).

Le teck (*Tectona grandis L.)* est une espèce diploïde de la famille des Verbenaceae et de l'ordre des Laminales à feuilles caduques (Troup 1921) et est aussi classé dans la famille des Laminaceae (Anon 2012). Il est adapté à une très large gamme de conditions environnementales avec des pluviométries variant de 500 à 5000 mm par an (Kaosa-ard 1981) et des altitudes pouvant aller jusqu'à 1300 m (Verhaegen et al. 2010a). Ses capacités de production sont performantes sous des régimes de précipitations annuelles allant de 1250 à 3750 mm et des températures pouvant aller de 10 à 45 °C selon leur localisation (Chaix et al. 2011). Le mode d'exploitation des grumes varie selon les pays et les capacités de production sont liées à la zone d'implantation des plantations. En général, les tecks sont exploités en moyenne entre 30 et 60 ans, avec des rendements permettant des productions moyennes de 5 à 14 m^3/ha/an. Une technique d'exploitation originale par rejet après une première coupe est parfois pratiquée au Laos et au Bénin, où elle produit de bons résultats, parfois supérieurs à ceux d'une plantation classique selon Dah-Dovonon (2013). Elle repose sur les propriétés écologiques du teck et sur la capacité de son système racinaire à répondre à la demande de ressources suite à un étêtage ou à une coupe au raz du sol (Pandey and Browna 2000).

De nombreuses études sur la diversité génétique des différents génotypes du teck en fonction de leurs lieux de production ont été réalisées et d'une manière générale les résultats de ces études concluent toujours à une origine asiatique et démontre donc une large diffusion depuis son lieu d'origine (Alcântara and Veasey 2013; Verhaegen et al. 2010b). Les recherches actuelles visent essentiellement l'amélioration de la rentabilité économique et portent donc sur les rendements en fonction de la densité des plantations et sur la qualité des fibres, qui font la qualité technologique du bois. La proportion de duramen (bois parfait) peut notamment être affectée par les pratiques sylvicoles (Zobel and Van Buijtenen 1989), également l'âge du teck influence directement la qualité du bois (Figure 14). Le pourcentage de duramen augmente de façon linéaire avec le diamètre du tronc dans les jeunes plantations et atteint environ 60% autour de 30-35 ans. Au-delà de cet âge, le pourcentage de bois de cœur (duramen) ne dépend plus du diamètre du tronc (Ferguston 1934).

Dans la plupart des régions, la mise en place des plantations de teck a été soutenue financièrement par les acteurs politiques, principalement des années 1960 aux années 2000, à l'aide de mesures incitatives, variables selon les pays d'implantation. Le Laos n'échappe pas à cette règle avec la mise en place régulière de plantations de teck (May Sak en langue laotienne) depuis 1942 et une accentuation dans les années 80 (FAO 2010). Cette accélération fait suite à de nouvelles incitations visant à réduire le nombre des surfaces consacrées à l'exploitation traditionnelle des terres sous forme d'abattis-brulis au nord du Laos notamment (Sodarak 2000; Souvanthong 1995). Cette nouvelle activité correspond aussi à une forme de compte-épargne pour les communautés locales.

L'ensemble des observations rapportées ci-dessus nous amène à nous intéresser davantage à l'écologie du teck et plus particulièrement à son enracinement profond, très peu étudié. Nous faisons l'hypothèse (i) qu'il pourrait être un élément majeur à l'origine de son adaptation dans les différentes zones écologiques et donc, contribuer à son adaptation aux changements climatiques, (ii) que son rôle en tant que « filet de sécurité » peut être vital dans des conditions extrêmes de sécheresse, (iii) qu'il peut constituer une part significative du carbone stocké par chaque individu. La littérature abordant les questions de recherche liées à l'enracinement du teck reste pour le moins succincte au regard de l'étendue des recherches réalisées sur de nombreux autres points (Sarojam 2005). Sur pratiquement 5000 références regroupées sur les recherches consacrées au teck entre 1856 et 2004, seules 8 traitent partiellement du rôle des racines et une seule étudie son impact à plus d'un mètre de

profondeur. Parmi les huit références traitant de l'enracinement de surface, plusieurs mentionnent sa continuité et son existence plus en profondeur. Dans cette thèse, nous avons recherché des informations sur le rôle des racines et leur dynamique en surface pour cette espèce dans un contexte environnemental similaire. Le renouvellement et la production de biomasse de racines fines en lien avec l'importance de carbohydrate non structural comme la source majeure d'énergie pour leur production a été mise en avant part Singh et al en 1986. Elle démontre une plus grande concentration en carbohydrate non structural pour les racines des arbres plus jeunes (19 ans) par rapport à des arbres plus âgés (29 ans). La proportion de carbohydrates augmente également en rapport avec le diamètre des racines, ce qui est aussi valide pour d'autres espèces comme l'épicéa (Ford and Deans 1977). Cette concentration diminue en revanche avec la profondeur pour les racines produites entre 10 et 60 cm de profondeur (limite de l'étude réalisée par Singh and Srivastava en 1986). Les stocks de carbohydrates dans les racines varient au cours de la saison ; ils sont stockés pendant la période de pleine foliation ou les besoins liés à la croissance de l'arbre sont pourvu par la photosynthèse (Singh and R.P. Singh 1981) et sont fortement sollicités en début de saison des pluies lors de la forte production de racines fines en surface alors que les feuilles ne sont qu'à leur début d'émission.

La profondeur d'enracinement du teck semble clairement en lien avec la profondeur du sol et avec la ressource en nutriments (Drechsel et al. 1990; Schmall 1989). Les sous-sols fragmentés sont également favorables à l'implantation du teck (Combeau 1951; Lamouroux 1957) et à l'opposé, les sols compactés sont à l'origine d'une réduction de la biomasse racinaire de l'ordre de 35 % (Thomas 1989).

Pour aborder notre recherche sur les processus en jeu dans la capacité d'adaptation du teck à une faible ressource en eau, nous avons choisi de mener une expérimentation d'exclusion de pluie. Dans ce but, nous avons sélectionné une plantation de teck d'une vingtaine d'années du nord Laos (Photo 11) Nous espérons ainsi mettre en jeu la capacité d'adaptation d'un échantillon de tecks face à un changement drastique des quantités et de la localisation des ressources en eau au niveau du profil ce sol. Ces arbres, établis de longue date, bénéficient naturellement de plus de 1200 mm de pluie répartie sur 7 à 8 mois par an. Cette parcelle de petit producteur est conduite de manière traditionnelle sans intervention suite à la plantation, ce qui est représentatif des pratiques de la région (Maeght et al. 2011). Afin d'intercepter les précipitations, une toiture placée à 2,5 m du sol a été installée sur une parcelle de 100 m^2.

(Photo 13) Pour maximiser l'isolation hydraulique de cette parcelle, une tranchée de 50 cm de large et de 2,5 m de profondeur a été creusée tout autour de la parcelle. Les parois de cette tranchée ont été étanchéisé à l'aide de bâches plastiques (Photo 14) et ensuite rebouchées. Elles ont fait l'objet d'un contrôle de leur état hydrique afin de s'assurer leur imperméabilité. Par ce dispositif très restrictif, nous visons à approcher au mieux le rôle des racines profondes dans la survie des arbres face à des événements extrêmes.

Le suivi de l'expérimentation s'appuie sur un ensemble de mesures de la physiologie de l'arbre dans son ensemble, de la dynamique racinaire jusqu'à 5 mètres en continu à l'aide de la technique de puits d'accès et jusqu'à 12 mètres de manière ponctuelle. La caractérisation du sol et le suivi de sa réserve hydrique fait également l'objet de mesures précises dans le temps et dans l'espace (voir plan du dispositif : Figure 16). Du fait du poids du dispositif mis en place pour réaliser ces mesures, nous avons été contraint de limiter la surface de la zone étudiée à une centaine de mètres carrés, tout en nous assurant de la représentativité des observations. Les deux sous-parcelles, celle d'exclusion de pluie et celle de contrôle, ont été choisies à proximité afin de garantir le maximum de paramètres communs liés au milieu, à la densité et à la morphologie des arbres étudiés (Figure 15). Une troisième sous-parcelle a été par la suite délimitée: Cherchant à mettre à profit l'eau récoltée sur le toit de la zone d'exclusion, nous avons saisi cette opportunité pour suivre une troisième parcelle bénéficiant d'un apport d'eau complémentaire durant la saison des pluies. L'ensemble de l'étude, l'analyse des résultats et leurs interprétations sont présentées dans la partie suivante de ce chapitre sous la forme d'un article scientifique intitulé : **Impact of near total throughfall exclusion on the above- and below-ground physiology of mature teak trees (*Tectonas grandis, L*) in Northern Laos.** Cet article est en préparation pour la revue New Phytologist.

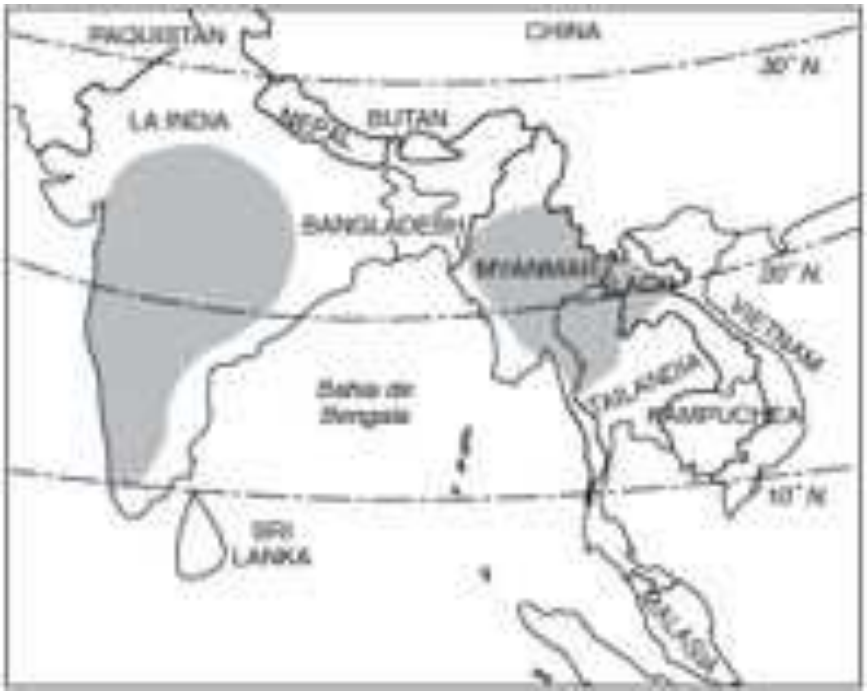


Figure 13: Distribution géographique naturelle du teck Asie



Photo 12: Teck âgé approximativement de 600 ans, mesurant 55 m de haut et 8 m de diamètre, dans la forêt de Pyin Oo Lwin, Myanmar (Myint 2009)

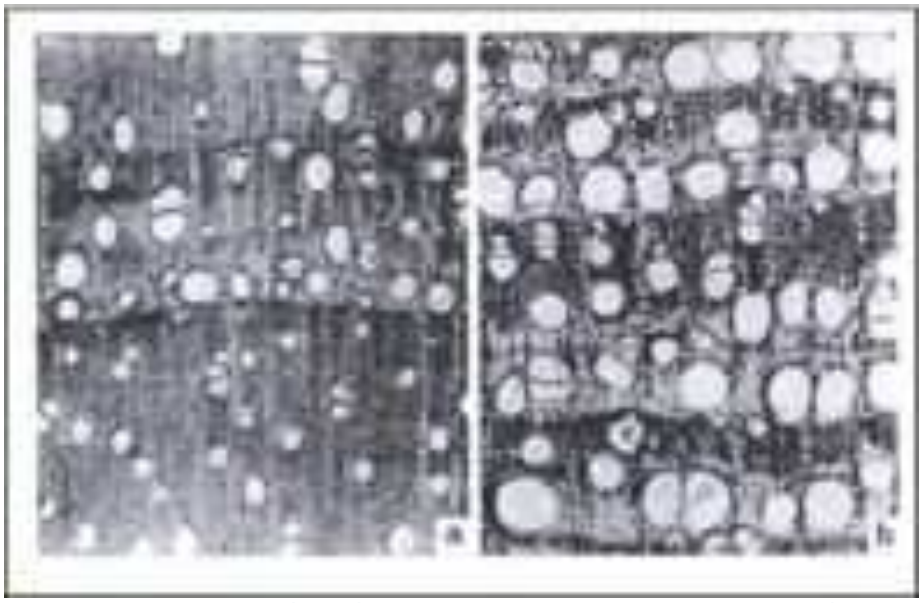


Figure 14: Coupes transversales de bois juvénile (à gauche) et de bois adulte ou bois parfait (à droite) (Bath et al., 2001)

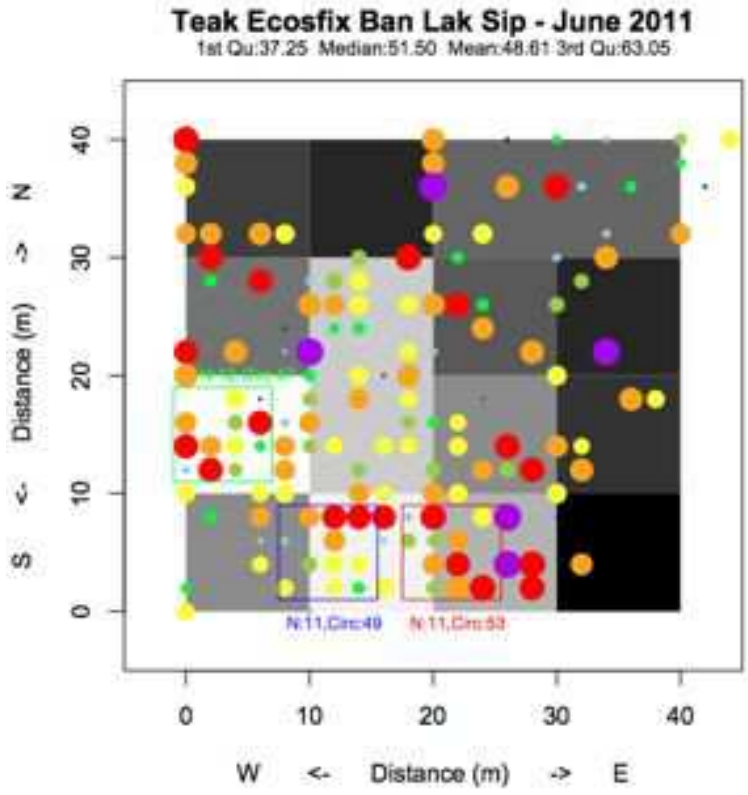


Figure 15: Densités et circonférences des arbres de la zone d'étude avec en bleu, la zone de contrôle, en rouge la zone d'exclusion de pluie et en vert la zone irriguée; les disques de couleurs classifient les arbres en fonction de leur diamètre



Photo 13 : Assemblage photos illustrant la zone d'exclusion de pluie avec tranchées, toiture et puits d'accès en profondeur



Photo 14: Tranchées en cours de réalisation (2.5 m de profondeur): mise en place des bâches d'étanchéités et rebouchages après collecte de racines

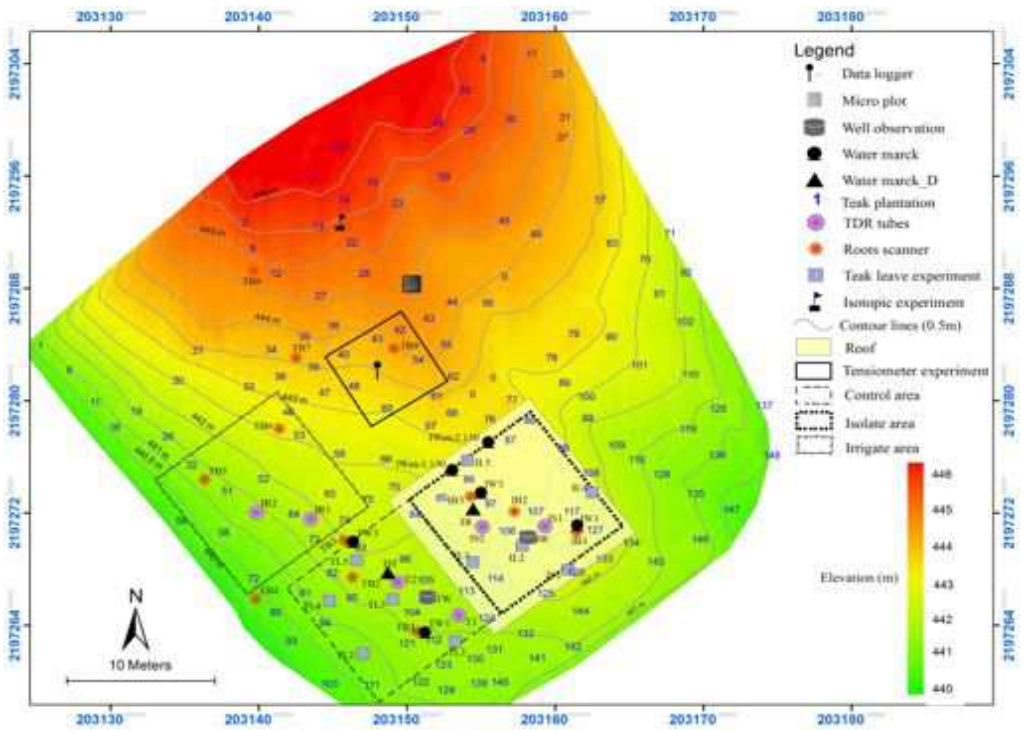


Figure 16: Topographie de la zone d'étude, position des arbres et localisation des appareils de mesures.

3.1.1 Références

Alcântara, B. K., & Veasey, E. A. (2013). Genetic diversity of teak (Tectona grandis L.F.) from different provenances using microsatellite markers. *Revista Árvore*, *37*(4), 747–758. doi:10.1590/S0100-67622013000400018

Anon. (2012). Germplasm Resources Information Network (GRIN). *USDA, ARS, National Genetic Resources Program, National Germplasm Resources Laboratory, Beltsville, Maryland*.

Bailey, J. D., & Harjanto, N. A. (2005). Teak (Tectona grandis L.) tree growth, stem quality and health in coppiced plantations in Java, Indonesia. *New Forests*, *30*(1), 55–65. doi:10.1007/s11056-004-1116-5

Bhat. (2004). Influence of provenance variation on wood properties of teak from the western chat region in india. *IAWA Journal*, *25*(March 2003), 273–282.

Bhat KM, M. H. O. (2004). Teak growers unite. *ITTO Trop Forest Update*, *14*(1), 3–5.

Bryant, R. L. (1997). *The Political Ecology of Forestry in Burma: 1824 - 1994* (pp. 1–247). Hawaï.

Chaix, G., Monteuuis, O., Garcia, C., Alloysius, D., Gidiman, J., Bacilieri, R., & Goh, D. K. S. (2011). Genetic variation in major phenotypic traits among diverse genetic origins of teak (Tectona grandis L.f.) planted in Taliwas, Sabah, East Malaysia. *Annals of Forest Science*, *68*(5), 1015–1026. doi:10.1007/s13595-011-0109-8

Combeau, A. (1951). *Observations sur les sols des Teckeraies dans la region de Sokodé. Cahier Orstom*. Lomé.

Dah-Dovonon, V. (2013). Dynamique des plantations privées de teck (Tectona grandis LF) dans le département de l'Atlantique (sud Bénin): Cas de la Commune de Tori-Bossito. *E-Journal of …*, 31–38.

Dié, A., Kitin, P., Kouamé, F. N., Van den Bulcke, J., Van Acker, J., & Beeckman, H. (2012). Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (Tectona grandis) in Ivory Coast. *Annals of Botany*, *110*(4), 861–73. doi:10.1093/aob/mcs145

Drechsel, P., Schmall, S., & W. Zech. (1990). Relationships between growth, mineral nutrition and soil properties in young Teak plantations in Bénin and Liberia. In *IUFRO-Symposium* (pp. 651–656).

FAO. (2010). *Teak resources and market assessment 2010* (pp. 1–52).

FAO. (2011). *State of the World's Forests* (pp. 1–179). Rome. Retrieved from http://www.bibliotecaflorestal.ufv.br/handle/123456789/5485

Ferguston, J. H. A. (1934). *De Dikte van Kern en spinthout van den djati (Tectona grandis L.f.) (Thickness of heartwood and sapwood of teak)* (p. 43: 1–19). Mededeelingen van het Boschbouwproefstation.

Ford, E., & Deans, J. (1977). Growth of Sitka spruce plantations: spatial distribution and seasonal fluctuations of lengths, weight and carbohydrate concentrations of fine roots. *Plant and Soil*, *47*, 463–485. Retrieved from http://link.springer.com/article/10.1007/BF00011504

Goh, D. K. S., Bacilieri, R., Chaix, G., & Monteuuis, O. (2013). Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites. *Tree Genetics & Genomes*, *9*(5), 1329–1341. doi:10.1007/s11295-013-0642-8

Graudal, L., Kjær, E., & Suangtho, V. (1999). *Conservation of genetic resources of teak (Tectona grandis) in Thailand. DFSC Series of technical notes* (p. 38). Humlebaek. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Conservation+of+genetic+resources+of+teak+(Tectonagrandis)+in+Thailand.#0

Guizol, P., Roda, J. M., Muhtaman, D. R., Laburthe, P., Fauveaud, S., & Antona, M. (2005). LE TECK JAVANAIS, ENTRE SUREXPLOITATION ET EMBARGO. *Bois et Forêts Des Tropiques*, *284*(2), 11–21. Retrieved from http://bft.revuesonline.com/article.jsp?articleId=5995

Hidalgo, E., Moreno, V., & Morales, N. (1986). Performance of 15 provenances of teak (Tectona grandis) five years after planting in Itabo, Matanzas. *Rev For Baracoa*, *16*, 65–75.

Horne, J. E. M. (1966). Teak in Nigeria. *Nigerian Information Bulletin (New Series)*, *16*.

Jacoby, G. C., & D'Arrigo, R. D. (1990). Teak (Tectona grandis L.F.), a tropical species of large-scale dendroclimatic potential. *Dendrochronologia*, *8*, 83–98.

Jayasankar, S., Sudhakara, K., & Babu, L. (2003). Provenance variation in growth, physiology, anatomical characteristics and foliar nutrient status of teak (Tectona grandis) seedlings. *J Trop For Sci*, *15*, 37–50.

Kaosa-ard, A. (1981). Teak its natural distribution and related factors. *Nat His Bull Siam Soc*, *25*, 55–74.

Kashio, M., & White, K. (1998). Teak for the future. In F. R. O. for A. and the Pacific. (Ed.), *Proceedings of the second regional seminar on teak*. Bangkok.

Kollert, W., & Cherubini, L. (2012). *Teak resources and market assessment 2010 (Tectona grandis Linn. F.)* (No. FP/47/E). *Food and Agriculture Organization, Rome*. Rome. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Teak+resources+and+market+assessment+2010R(Tectona+grandis+Linn.+F.)#0

Lamouroux, M. (1957). *Les sols de teckeraies du Togo.* Lomé.

Madoffe, S., & Maghembe, J. (1988). Performance of teak (Tectona grandis L.f.) provenances seventeen years after planting at Longuza, Tanzania. *Silvae Genet*, *37*, 175–178.

Maeght, J. ., Nortourlee, L., Reboul-salze, F., Bourdon, E., Sengtaheuanghoung, O. Soulileuth, .B, Hartmann, C., & Pierret, A. (2011). Environmental impact of understorey management in Teak tree (Tectona grandis L.) plantations: A case study from Luang Prabang, Lao PDR. *Khon Kaen AGR*, *39*, 291–294.

Myint, T. T. (2012). *A study on the sustainable management of natural teak forests in Myanmar*. Retrieved from http://repository.dl.itc.u-tokyo.ac.jp/dspace/handle/2261/54237

Nocetti, M., Rozenberg, P., Chaix, G., & Macchioni, N. (2011). Provenance effect on the ring structure of teak (Tectona grandis L.f.) wood by X-ray microdensitometry. *Annals of Forest Science*, *68*(8), 1375–1383. doi:10.1007/s13595-011-0145-4

Pandey, D., & Browna, C. (2000). *Le teck dans le monde* (Vol. 51, pp. 3–13).

Pumijumnong, N. (2012). Teak Tree Ring Widths: Ecology and Climatology Research in Northwest Thailand. *Sci., Tech. and Dev*, *31*(2), 165–174. Retrieved from http://www.researchgate.net/publication/233764422_Teak_Tree_Ring_Widths_Ecology_and_Climatology_Research_in_Northwest_Thailand/file/79e4150b5938bdf963.pdf

Ram, S., Borgaonkar, H. P., Munot, A. A., & Sikder, A. B. (2011). Tree-ring variation in teak (Tectona grandis L.) from Allapalli, Maharashtra in relation to moisture and Palmer Drought Severity Index, India. *Journal of Earth System Science*, *120*(4), 713–721. doi:10.1007/s12040-011-0090-5

Ross, P. (1961). The plant ecology of the teak plantations in Trinidad. *Ecology*, *42*(2), 387–398. Retrieved from http://www.esajournals.org/doi/abs/10.2307/1932090

Sarojam, N. (2005). *An annotated bibliography on teak: (Tectona grandis Linn. f)*. (K. F. R. Institute, Ed.) (pp. 1–461). Kerala. Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Schmall, S. (1989). *Wuchs und Ernährungszustand junger Teak-Bestände auf Vertisolen in Bénin, Westafrika.* (U. B. Diplomarbeit, Ed.). Unveröff.

Singh, K. P., & R.P. Singh. (1981). Seasonal variations in biomass and energy of small roots in a tropical dry deciduous forest. *OIKOS*, *37*, 88–92.

Singh, K. P., & Srivastava, K. (1986). Seasonal variation in the biomass and non-structural carbohydrate content of fine roots of teak (Tectona grandis L. f.) plantations in a dry tropical region. *Tree Physiology*, *1*(1), 31–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14975904

Sodarak, H. (2000). *Shifting Cultivation Practices By Hmong , Khamu and Lao ethnic categories In The Nam Nane Watershed , Nane District , Luang Phrabang province* (pp. 1–82). Vientiane.

Souvanthong, B. P. (1995). *Shifting Cultivation in Lao PDR : An overview of land use and policy initiatives*. (Shifting cultivation stabilisation office, Ed.) (pp. 1–40). Vientiane.

Streets, R. J. (1962). *Exotic trees of the British Commonwealth.* (U.K:Clarendon Press, Ed.) (pp. 712–725). Oxford.

Thein, H. M., Mamoru, K., Fukushima, M., & Minn, Y. (2007). Structure and composition of a teak-bearing forest under the Myanmar selection system: impacts of logging and bamboo flowering. In *Southeast Asian Studies* (pp. 303–316).

Thomas, T. P. (1989). *Effect of varying soil moisture and bulk density on Teak, Eucalypt and Albizia root growth* (p. 7 PP). Kerala.

Troup RS. (1921). *The SilŠiculture of Indian Trees*. (P. Agricultural Research Institute, Ed.) (pp. 697–768). Oxford University press.

Verhaegen, D., Fofana, I. J., Logossa, Z. a., & Ofori, D. (2010a). What is the genetic origin of teak (Tectona grandis L.) introduced in Africa and in Indonesia? *Tree Genetics & Genomes*, *6*(5), 717–733. doi:10.1007/s11295-010-0286-x

Verhaegen, D., Fofana, I. J., Logossa, Z. a., & Ofori, D. (2010b). What is the genetic origin of teak (Tectona grandis L.) introduced in Africa and in Indonesia? *Tree Genetics & Genomes*, *6*(5), 717–733. doi:10.1007/s11295-010-0286-x

Zobel, B. J., & , Van Buijtenen, J. P. (1989). *Wood variation. Its causes and control*. (S. V. series in wood Science., Ed.) (T. E. Time.).

3.2 Impact of near total throughfall exclusion on the above- and below-ground physiology of mature teak trees (*Tectonas grandis, L*) in Northern Laos: Article prévu pour New Phytologist

Impact of near total throughfall exclusion on the above- and below-ground physiology of mature teak trees (*Tectonas grandis, L*) in Northern Laos

Jean-Luc Maeght[1], Corentin Clément [2], Sounyaphong Phapvilay[3], Oloth Sengtaheuanghoung[4], Alexia Stokes [5], Alain Pierret [2].

[1] UMR Iees Paris UMR AMAP, IRD 9343Bondy cedex, France ; [2]UMR Iees Paris IRD office c/o National Agriculture and Forestry Research Institute (NAFRI) P.O. ; [3] IRD Project Luang Prabang Lao PDR; NAFRI, [4] The National Agriculture Forestry Institute, BP 7170 Vientiane Lao PDR [5] INRA, UMR AMAP, 34398 Montpellier Cedex 5, France, Corresponding author; Jean-Luc.maeght@ird.fr

Abstract

. We present the results of a throughfall exclusion experiment conducted in a teak tree plantation in northern Laos. This work documents the functional roles of deep versus shallow roots from teak trees and quantifies the carbon stock that corresponds to fine roots.

. Roots of 20 years-old teak trees were monitored using root windows installed at regular soil depth increments down to 4.5 m and scanned at regular time intervals, over a period of two years. Root growth dynamics under a hydraulically isolated plot were compared with a control plot. Soil water dynamics were measured, while trench techniques and a coring method were also used to quantify carbon storage. Fine roots were found down to a depth of 12 m.

. We demonstrated the influence of contrasted rainfall patterns on deep root growth dynamics and tree growth. We also found that, at specific depths increments, root dynamics are linked to local, transient changes in water availability.

. Our results suggest that fine deep roots are organs of foremost functional importance and this brings about evidence that teak trees extract deep water during critically dry periods. The presence of measurable amounts of roots deep into the soil profile further indicate that these should be taken into account when quantifying long-term carbon storage.

Key words: throughfall exclusion, drought, *Tectona Grandis L,* fine deep roots, tree physiology, carbon storage.

Introduction:

According to Craig et al. 2010, at least some of the world's forested ecosystems may already be responding to climate change and may become increasingly vulnerable in response to future warming and drought, even in environments that are not normally considered water-limited. Choat et al. (2012) showed that 70% of 226 forest species from 81 sites worldwide operate with narrow hydraulic safety margins (1 MPa) against irreversible drought stress. This is why all forest biomes are equally vulnerable to hydraulic failure regardless of their current rainfall environment (Choat et al., 2012). Drought is increasing forest die-off and natural tree mortality in many ecosystems, likely as a result of climate change (Allen et al. 2010). Changes in rainfall patterns is one cause of loss in productivity (McDowell et al., 2008) and they increase risks against ecosystem services, including the loss of sequestered forest carbon and associated atmospheric feedback (Liu et al., 2014; Craig et al., 2010).

In response to shifts in rain patterns and to increasing drought, roots are clearly playing a vital role in tree survival and adaptation. Their expansion in the soil is driven by physiological imperatives, one being acting as a safety net (Bergeron, 2011) in response to extreme conditions. Deep roots in particular, being located further away from the leaves, are acting as such when protecting against surface stress e.g. drought (Bergeron et al., 2011). The safety-net is primarily influenced by (i) the tree species, as it determines both root uptake and litter fall, and (ii) the chemical, physical and hydrological characteristics of the subsoil (Vanlauwe et al., 2005). In terms of water supply, deep roots can be critical for tree survival (Markewitz et al., 2010). Although insufficient to buffer a long-term reduction in soil moisture, deep root water uptake is nevertheless crucial for trees to survive seasonal droughts. Fifty percent of closed forest in the Brazilian Amazon depends on the active functioning of deep root systems, especially during the dry season (Nepstad et al. 1994). Although marginal in normal conditions, contribution of deep roots to water uptake becomes critical to plant survival during long-term droughts. Only a small amount of root biomass in deep soil is necessary for significant water uptake (Davidson et al., 2011). In evergreen trees growing in central Texas, deep roots at a depth of 20 m are contributing up to five times more water to transpiration compared to shallow roots during drought periods. However, this contribution was drastically reduced after rain events (Bleby et al., 2010).

Teak (Tectona grandis L.) was selected as a model to test the safety net function of deep roots in its capacity of adaptation to a wide range of environmental and ecological conditions. Teaks can be found in regions with rainfall ranging from 500 mm to 5000 mm per year (Kaosa-ard, 1981) and at altitudes of up to 1300 m (Verhaegen *et al*., 2010). Its production capacity is occurs in rainfall from 1250 mm to 3750 mm and temperatures ranging from 10 °C to 45 ° C depending on their location (Tariel, 1966;

Chaix *et al*., 2011).

Teak (*Tectona grandis L.*) is a diploid member of the Verbenaceae family and laminal deciduous order (Trope 1921) but is also classified in the family Laminaceae (Anon 2012). It is a large, deciduous tree that is dominant in mixed hardwood forests and native to the Indian and Southeast Asian zone. Teak is endemic to the region of South Asia between latitudes of 10° and 25° north and 0° to 10° south, in an area covering about 23 million hectares (Graudal et al., 1999; Pandey & Browna, 2000). In its endemic area, teak is present as mixed stands in wet and dry deciduous forests at an altitude of around 1000 m (Thein et al., 2007). Teak trees are now cultivated all around the world in sub-tropical regions. Many studies are conducted on the genetic diversity of different genotypes according to their places of production, but in general the results of these studies still conclude an Asian origin (Fofana et al., 2008; Verhaegen et al., 2010; Alcântara et Veasey, 2013). The tree species is common in northern Laos and teak tree plantations have been expanding in this region since the 1980s (Bhat, 2000). It is now widely cultivated for its durable wood. Teak trees are large trees that can measure up to 1.5 m in diameter and up to 40 m in height. Teak is a deciduous species that becomes leafless and dormant during the driest months of the year.

Teak wood is researched and appreciated for its quality and durability. High demand on the local and international market has encouraged the development of teak plantations but also the unorganized mass slaughter of natural forests, leading to a decline in teak log resources from the natural environment (Guizol et al., 2005; FAO, 2011). Despite strong measures to restrict its exploitation in its natural habitat, teak has become an endangered species in its natural form in the forest (Kashio & White, 1998). However, areas covered in teak plantation were reaching more than 6 million hectares in 2001 (Bhat & Hwan, 2004), 80 % of this being in tropical Asia.

This diversity highlights the ability for acclimation of this pioneer species originating from South Asia. The teak is particularly well suited for areas with the extremely contrasting soil and climatic properties of the tropics thanks to its tolerance to pests and hardiness (Alcântara & Veasey, 2013). Despite its large area of geographic distribution, teak remains sensitive to climate variations and change in water availability (Priya & Bhat, 1998; Arcadius *et al*., 2012). It is as such a model used for dendroclimatic studies in Indonesia (Jacoby & D'Arrigo, 1990), India (Ram et al., 2011) and Ivory Coast (Dié et al., 2012) (Bleby et al., 1963). Sensitivity to water resources seems to be a particular trait of teak trees as reported in 2011 by Nocetti et al., especially with regard to growth (Streets, 1962; Goh et al., 2013) and survival skills in adverse conditions (Hidalgo et al., 1986; Madoffe & Maghembe, 1988).

The rooting depth of teak seems clearly linked with soil depth and nutrient resource (Schmall, 1989; Drechsel et al., 1990). Fragmented soils are favourable to the establishment of teak (Combeau, 1951;

Lamouroux, 1957), while compacted soils are causing a reduction in root biomass and an increase in mortality (Thomas, 1989).

The main objectives of this study are to characterise seasonal dynamics of teak's shallow and deep fine roots and their contribution to the safety net function in an artificially imposed drought situation. To achieve our goal, we decided to conduct an experiment in the form of rainfall exclusion on adult teak trees. We hope to bring into play the adaptation capacity of individual trees facing a drastic change in the quantity and the localization of water resources availability.

We investigated the following points:

1- How will fine roots be distributed along the soil profile and how will they contribute to teak trees' adaptation to changing environment?

2- Will deep fine roots be able to play their vital role as a safety net?

3- What proportion of carbon storage is accumulated by roots of teak trees?

Materials and Methods

Field site and plant material:

The study site is located in a semi-mountainous environment, 10 km South of Luang Prabang City in Northern Lao PDR (19°50'57"N and 102°09'56"E) at an altitude of 450 m. In a plot of 1500 m^2 including 150 adult trees, we selected 3 sub-plots of 120 m^2 respectively for rainfall exclusion, irrigation and control experimentation.

Trees at our study site are 20 years old. The average girth was common to our trees is around 0.50 m and it is similar to other plantations in the same geographic zone (Maeght *et al*., 2011). The selected teak plantation is cultivated according to the most common practice in the area, i.e. at high density, with more than 1200 trees/ ha and without any clearing or thinning (Bhat *et al*., 2007). The rainfall pattern is highly seasonal with most of annual rainfall (90%) occurring during the seven months of the Asian monsoon, from April to October (Fig.1). The regional climate is marked by contrasted conditions of temperature and air moisture conditions.

The selected plantation is growing on an Ultisol (USDA soil taxonomy classification), commonly known as red clay soil, with a deep red horizon and the colour starting to change at 10 to 11 m depth. The water table was found at a depth of 16 m while setting up piezometers beside the teak plantation. The soil is characterised by a progressive transition in texture from 70 % of clay at 0.5 m, down to

15 % of clay at 11.0 m. Low density soil was measured between 1.2 (g/cm3) at the surface to 1.25 (g/cm3) at 4.0 m depth. The chemical characteristics indicated a low fertility in term of mineral nutrient availability with low CEC throughout the profile, coupled with acidic soil pH down to at least 4.5 m. A table of soil chemical analysis data, soil texture triangle and soil density is available in the supplementary material.

Experimental design:

Rainfall exclusion was achieved by installing a transparent roof 2.5 m above the soil surface over a 120 m^2 area. This roof intercepted nearly 100% of the rainfall, except for a fraction of incidental rainfall flowing along tree trunks. Due to natural tree movement, gaps appeared over time between the roof and trees. Regular maintenance was carried out and materials were replaced to seal these gaps. We also trenched the soil around the rainfall exclusion plot, down to a depth of 2.5 m and lined the walls of these trenches with polyurethane film before filling them back with the excavated soil. This design was intended to prevent roots from accessing to soil water from outside the area covered by the 120 m^2 roof, at least within the first 2.5 metres of the soil profile. These plastic-lined trenches also prevented water influx due to lateral water transport . The water intercepted by the roof installed over the rainfall exclusion plot was re-directed to the irrigated plot. In 2011 and 2012, the re-directed rainfall water represented respectively 46% and 43% of the yearly rainfall amount. We added 1421 mm of water on the irrigation plot over the two years. Not all of the yearly rainfall could be diverted to the irrigated plot because the water sprout at the lower rim particularly during high-intensity downpours and a substantial amount of water was thus discharged downstream from the rainfall exclusion plot.

Field measurements:

a) Environmental parameters

We used a Minimet weather station (Skye Instrument Company) to record weather conditions every 30 minutes. Weather parameters recorded were: rainfall, air and soil temperature, air moisture, wind speed, and the total photosynthetically active radiation (PAR). Incidental rainfall on the rainfall exclusion sub-plot was measured using an automatic rain gauge and the output recorded using a CR10X (Campbell data logger Company). An additional set of three tanks, each collecting the discharge of a narrow strip of the rainfall exclusion roof, was also used to assess the variability of the incidental rainfall over the rainfall exclusion sub-plot.

The range of field measurements conducted in both isolated and control sub-plots were similar.

However, only a limited subset of the measurements made at the two first subplots were reproduced at the irrigated sub-plot.

Soil water potential was measured every three hours using Watermark (200SS-35) soil moisture sensors (Irrometer Company) (Thomson & Armstrong, 1987; Thomson *et al*., 1996)) connected to an Irrometer water monitor terminal (900M-O-QD) as well as a Campbell CR10X data logger. A series of seven of these sensors was installed in each of the two access wells. The first two sensors were installed at soil depths of 0.5 and 1 m, while deeper sensors were positioned one metre from one another down to 5 m. Additionally, standalone Watermark sensors were set at a soil depth of 1 m in three replicates, while five other sensors were deployed at 2m increments down to a 10 m depth. Data from these standalone sensors were collected once every week.

The soil water potential range that can be measured with these devices is quite limited and does not go beyond – 2.39 x 10^5 Pa. This was a limiting factor because at some times of the year and at some depths, the soil dried up well beyond this value. However, due to their fragility and cost we could not use more powerful devices such as psychrometres.

b) Plant parameters

Leaf water potential was measured three times on three trees in the 3 sub-plots, once a month at predawn (pd) and midday (md). We used an Scholander-type pressure chamber (PMS 1000, PMS Instrument Company).

Leaf water content was measured twice during the experiment, in late September and October 2013. Ten leaves were collected in each of the three sub-plots. Leaves were stored in airtight plastic bags and brought back to the laboratory where their fresh weight was measured. Leaves were then oven-dried for 48 hours at 60 degree Celsius and dried weights were then measured.

Tree phenology dynamics were monitored every month by assessing canopy cover using semi-spherical images and by measuring leaf dimensions. Litter biomass was collected every two weeks in both the control and rainfall exclusion plots, using five square baskets covering a surface area of 1 m^2 each and oven-died for 72 hours at 60 degree Celsius.

Trees' wood production was assessed by measuring changes in tree girth at 6 months intervals during the whole duration of the experiment at diameter at breast height (DBH) in the three sub-plots. Measurement interval was extended to one year for the additional trees located outside the sub-plots within the same plantation. Each tree received a unique identification number and a mark at DBH level to limit mistake in data collection.

c) Roots measurements:

For root surface observations, we used the root box developed by Maeght et al. (2007) in conjunction with a flat bed scanner to collect root images down to a depth of 90 cm. Twelve such boxes were installed at the site, three in the rainfall exclusion sub-plot, three in the control sub-plot and another six at the periphery of the experimental subplots. For deep root observations, we used access shafts described in Maeght *et al*., (2013) which represent a recent evolution and combination of the different techniques for root observation described in Böhm (1979). Access shafts allow direct observation of root growth dynamics using adapted "root windows" through which roots can be observed and image captured at regular pace, as described by Maeght et al. (2007). We installed a 5 m deep access well in the rainfall exclusion treatment zone and a second one in the control zone, each with nine root observation windows. It took about a week to build one single well by hand digging. The walls of the wells were reinforced with concrete tubes joined together with concrete (Maeght *et al*., 2012). Root windows were installed at 0.5 m soil depth increments down to 5 m. Each root window includes a specifically designed glass frame supporting, on its upper side, a piece of 10 mm thick glass (25 × 30 cm) pressed against the soil at a 45° angle. Images for assessing root growth dynamics were taken once a month using an adapted flatbed scanner inserted in each window's supporting frame.

Fine root biomass was derived from soil samples from which roots were manually separated with washing techniques. These soil samples were either collected using an auger or along the 45 m linear trench walls (2.5 m height, 0.75 m wide) that were dug around the rainfall exclusion plot. Two manual drillings with an auger were made every year in rainfall exclusion and control sub-plots down to 11.0 or 12.0 m depth, representing the limit of our manual drill capacity. In addition, 6 complementary coring were done until 6.0 m depth in 2012.

Data analysis

Results

Rainfall:

The observed rainfall pattern is presented in Figure 1. These two years were particularly rainy. The cumulated rainfalls fall outside the 95% confidence interval of the average cumulated rainfall calculated over a 50-year period from 1950 to 2000 (Figure 2). The year 2013, with a cumulated rainfall of 1775 mm, presents the particularity of being unusually wet from the onset of the rainy season with all values from June onward above the upper confidence limit (Figure 2). The cumulated rainfall curve in 2012 exceeded the confidence interval at the end of the rainy season due to late

rainfall in November.

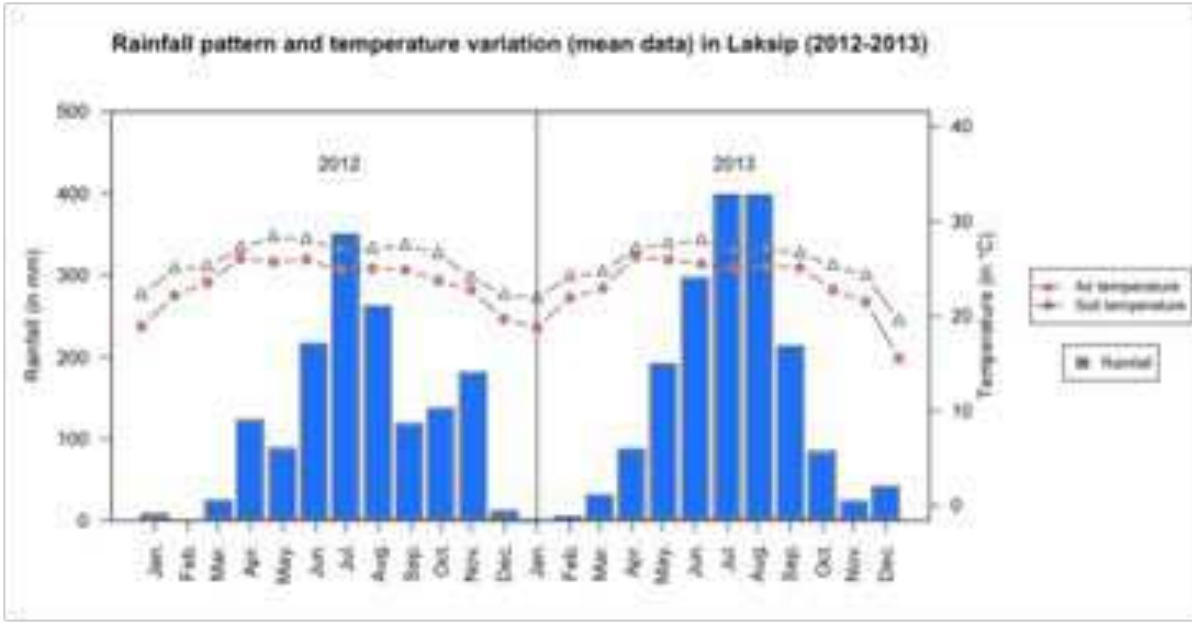


Figure 1: Meteorological data in 2012 and 2013

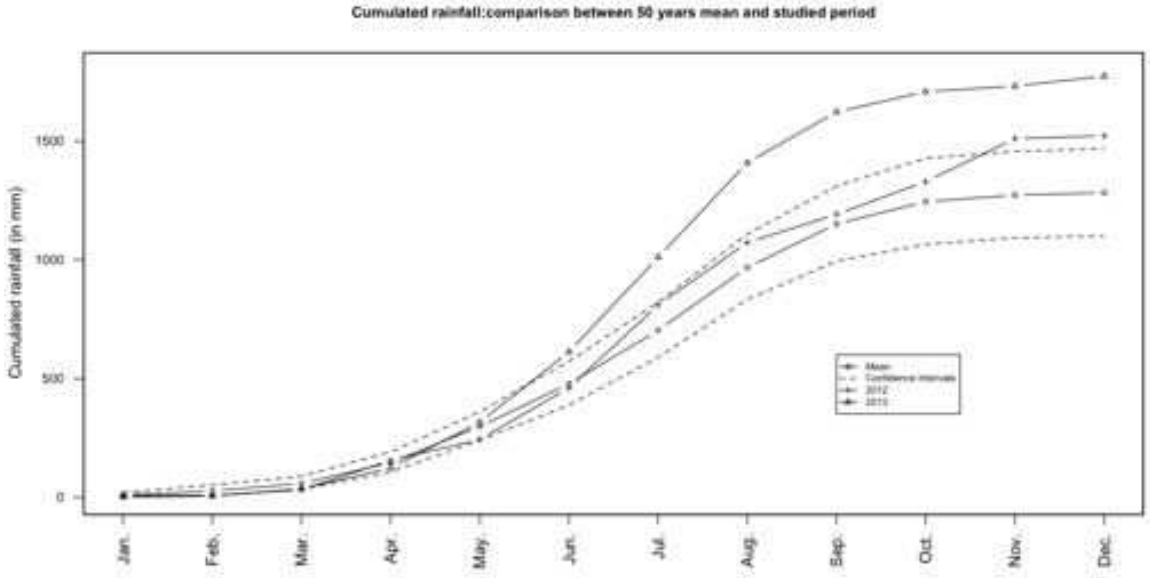


Figure 2: Yearly cumulated rainfall in 2012 and 2013 compared to the past fifty years.

Soil water potential:

The evolution of the soil water potential across the two successive years of continuous measurement in the control sub-plot is presented in Figure 3. All layers down to 4.5 m follow a drying-wetting cycle correlated to the monsoon cycle with variations of decreasing amplitude as soil depth increases. Soil

water potential within the first half-meter of the profile responded rapidly and extensively to major rainfall events and dry periods with values of soil water potential ranging from saturation to < -2.39 x 10^5 Pa (sensor's limit). At 1 m, the rewetting associated with rainfall is not as thorough and the minimum soil water potential was of the order of -1 x 10^5 Pa at the beginning of the 2013 rainy season. Deeper in the profile seasonal variations in soil water potential progressively lessen so that the driest layers during the wet season are also the wettest during the dry season for the first 1.5 m layer of soil.

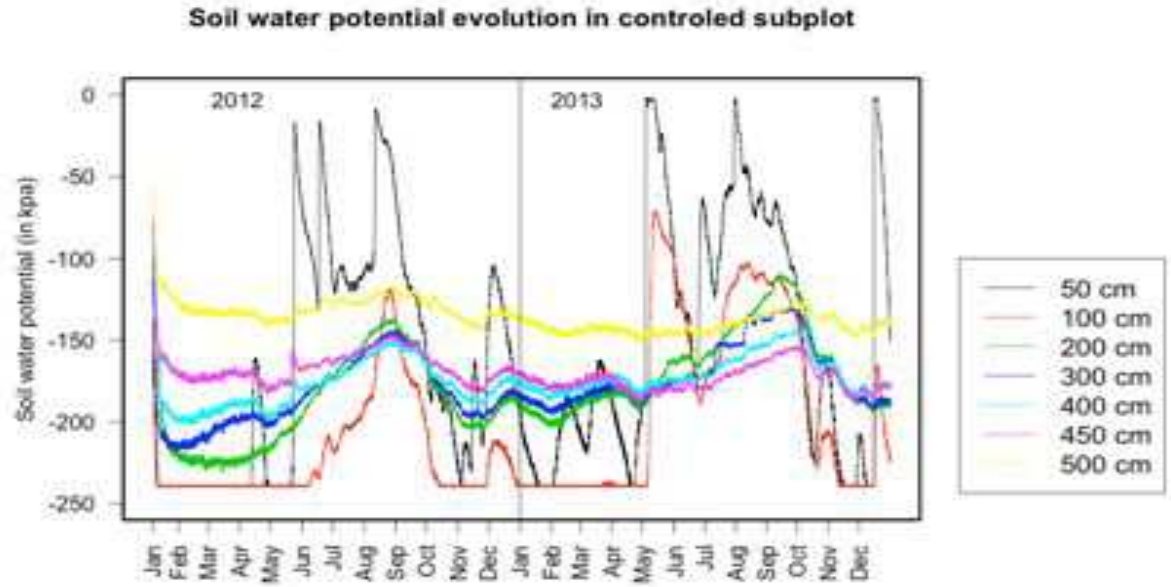


Figure 3: Soil water potential in controlled sub-plot

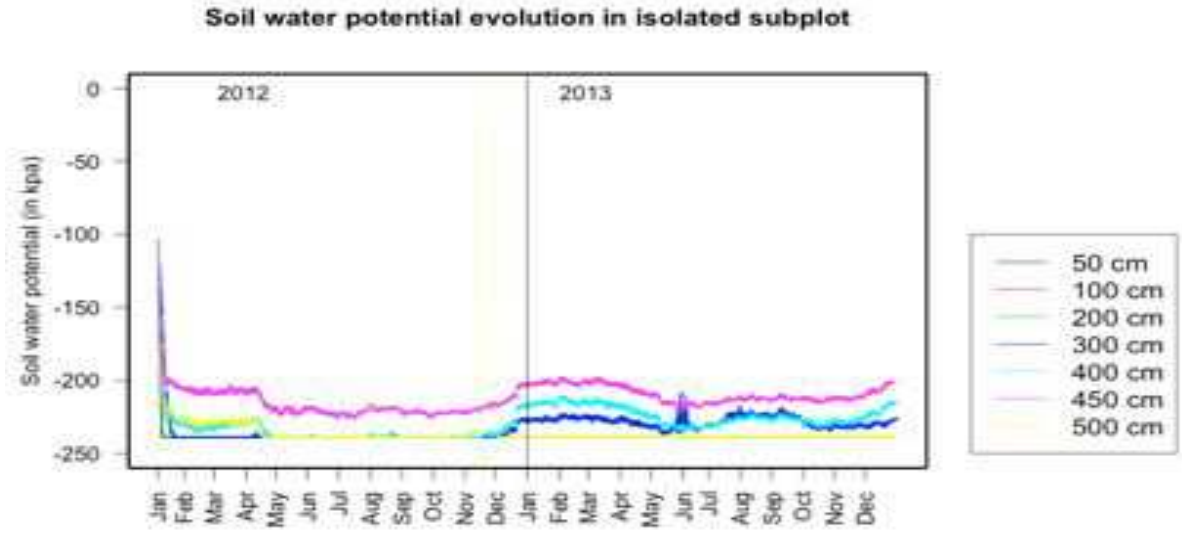


Figure 4: Soil water potential in isolated subplot

In the rainfall exclusion sub-plot, throughout the two years (Figure 4), all layers are dryer (at a more

negative soil water potential) than in the control plot. In the absence of rainfall, soil layers down to 2 m rapidly reached soil water potentials that were beyond the range accessible with the sensor and which remained as such for the entire duration of the experiment. Additionally, during the first year, all sensors but the one set at 5 m also recorded water potentials that were beyond the range of the devices. Interestingly, this reduction in soil water potential started at the onset of the 2012 rainy season. Further, soil water potential in these deep soil layers increased again towards the end of the rainy season, in December 2012, and reached a maximum towards the end of the dry season 2013. At the onset of the 2013 rainy season, soil water potential dropped in the 3 to 4.5 m horizons, but to a lesser extent than in 2012, probably due to the higher rainfall during that year which might have contributed to recharge the profile below the depth of the plastic lined trenches surrounding the sub-plot.

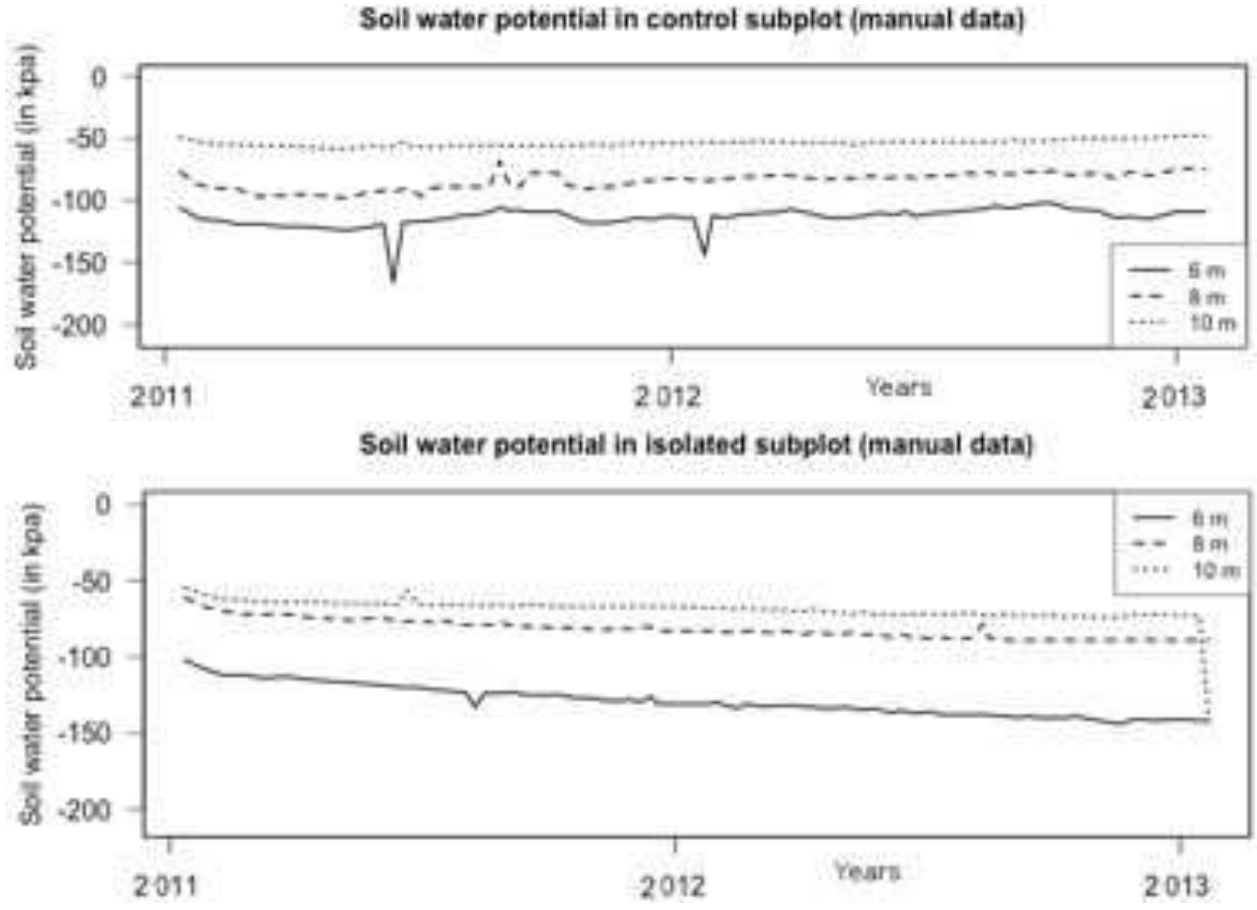


Figure 5 : Soil water potential down to 10 m (manually recorded data from 2011 to 2013)

In line with observations closer to the soil surface, in both the control and rainfall exclusion sub-plots, soil water potential in layers under 6 meters was remarkable stable over time (Figure 5). None of the sensors installed at these soil depths recorded water potential values outside the measurable range. In the control sub-plot, soil water potential was overall stable over time and set at values of about -115, -

80 and -50 x 10^5 Pa at 6, 8 and 10 m, respectively. In the rainfall-exclusion sub-plot, soil water potential was also relatively stable over time, particularly at a soil depth of 10 m. Soil water potential values also increased with soil depth. However, there was a slight but regular and significant (Theil-Sen single median linear regression, $p<2\ 10^{-16}$) decrease over the whole duration of the experiment.

Leaf mineral and water content:

The leaf's mineral composition of carbon and nitrogen produces an interesting indicator of a tree's physiological status. Figure 6 shows the C/N ratio for the different treatments. The carbon content is 30 times higher than the nitrogen content and there is no significant difference between the different treatments. The water stress induced by the rainfall exclusion treatment did not induce mineral deficiency in leaves.

The dimensions (length and width) of leaves in the rainfall exclusion sub-plot were found to be significantly smaller than in the two other sub-plots (Welch's two-sample t-test $p < 2.2e^{-16}$; Figure 7). Further, while average leaf length was the same in the control and irrigated sub-plots ($p < 0.6295$, df=345.91) average leaf width was less in the irrigated than the control sub-plot ($p < 2.2e\text{-}16$).

Comparisons of leaf water content showed that water stressed leaves in the rainfall exclusion sub-plot have a lower content (median: 1.61) value than leaves in the control stand (median: 2.18). Moreover, leaves in the control stand have lower water content than that in the irrigated sub-plot (median: 2.55) (Figure 8).

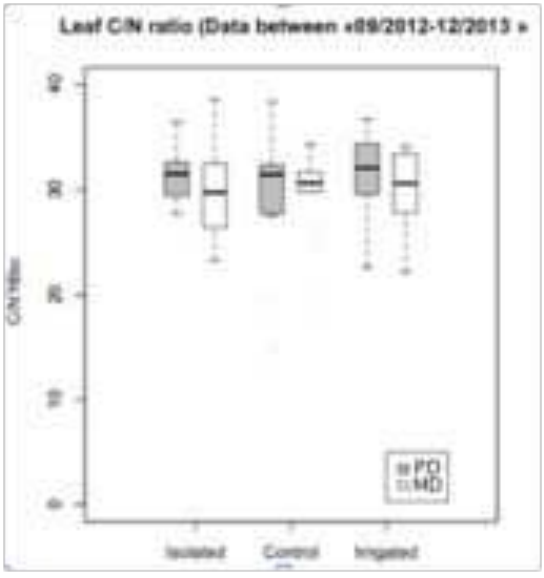


Figure 6: C/N ration in teak leaf collected in predaw (PD) and mid day time (MD).

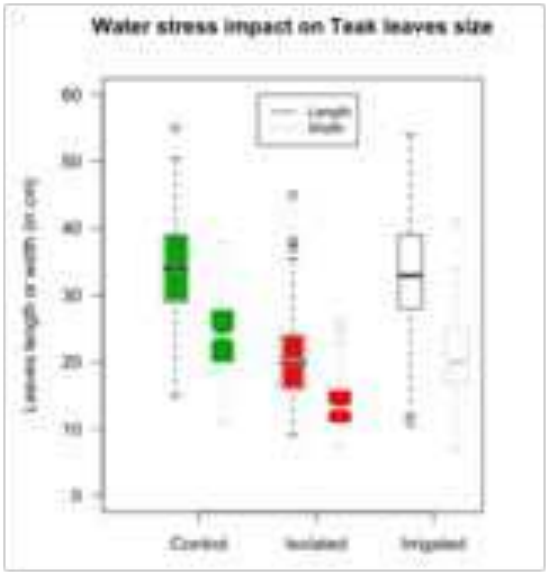


Figure 7: Teak leaf size depending of plot collection.

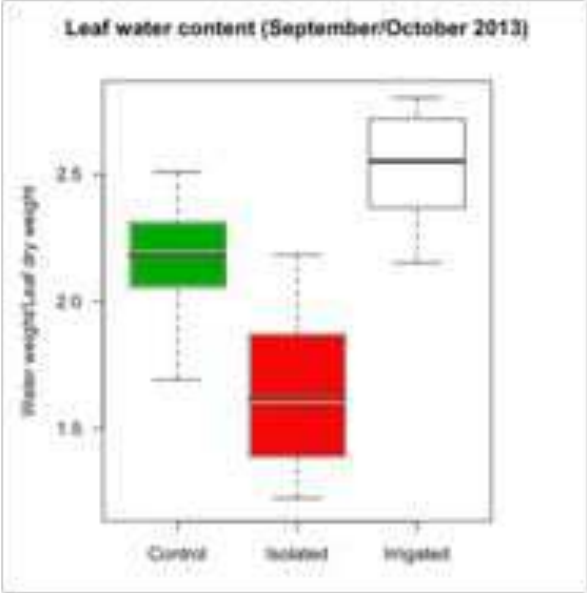


Figure 8: Leaf water content

Measurements of leaf water potential (Figure 9) are indicative of the tree's functioning capacity and physiological status as well. Leaf water potential increases following new leaves' emergence and reaches its maximum value around June as leaves reach maturity and the rainy season sets in.

The lowest leaf water potential values, both pre-dawn and at mid-day were consistently lower in the rainfall exclusion sub-plot. The difference was on average - 5 bar at pre-dawn (+ stat) and - 5 bar at mid-day.

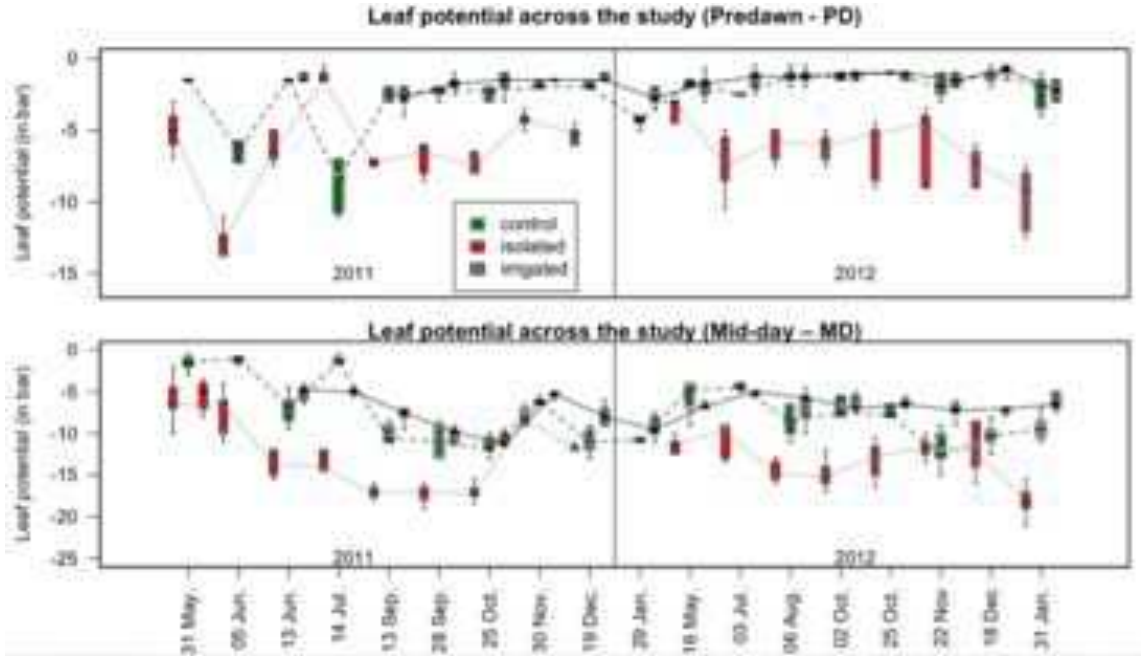


Figure 9: Leaf potential evolution along the studied years

The canopy cover, (Figure 10), was more developed in the control than in the rainfall exclusion sub-plot. The largest differences were observed in 2013, maybe as a result of longer exposure to drought conditions. One can also notice that while refoliation occurred almost simultaneously in both treatments, defoliation started earlier in the rainfall exclusion treatment. This difference is related to the reduced leaf size and number of leaves per tree, which translates into a reduced litter fall in the rainfall exclusion sub-plot compared to that in the control sub-plot (Figure 11). After two years of rainfall exclusion, litter fall was about 25% less in the exclusion sub-plot than in the control sub-plot.

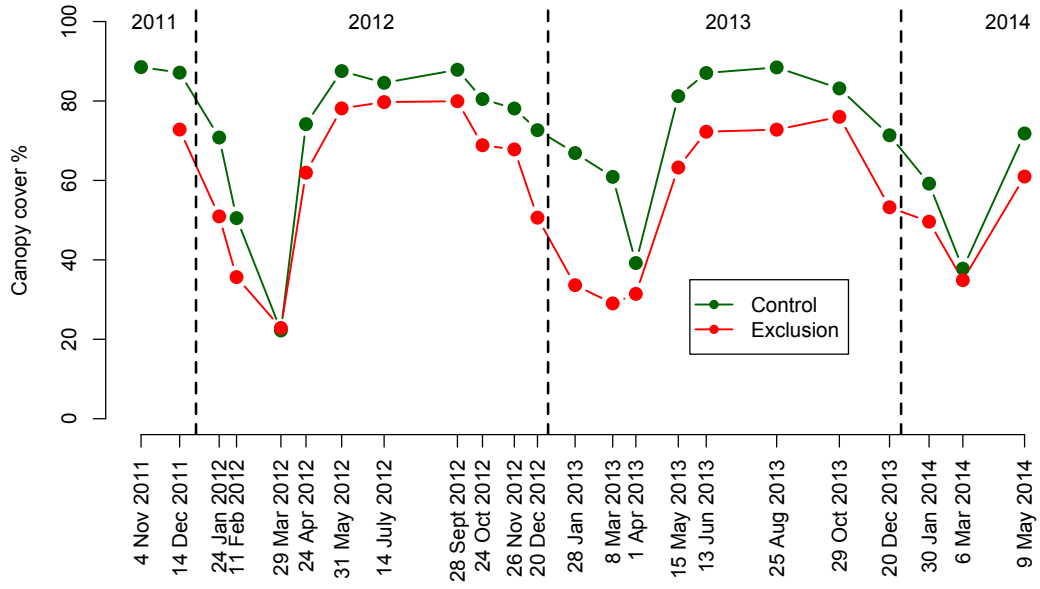


Figure 10: Canopy evolution in isolated and control teak plot.

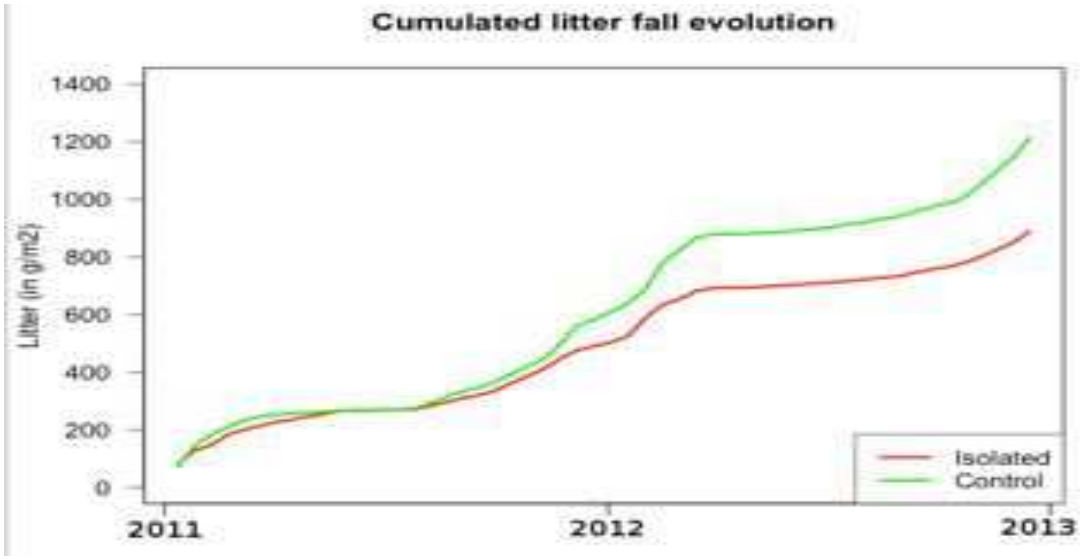


Figure 11: Litter fall cumulated fall biomass along two studied years

The increase of girth in the control stand is higher than in the rainfall exclusion sub-plot, especially when aggregating observations from the two years. Variability in tree girth growth outside the experimental sub-plots was higher than within each sub-plot. Girth increase in the irrigated sub-plot was higher than in the control and rainfall exclusion treatments but not dissimilar to that of trees sampled outside the treatment sub-plots (Figure 12) .

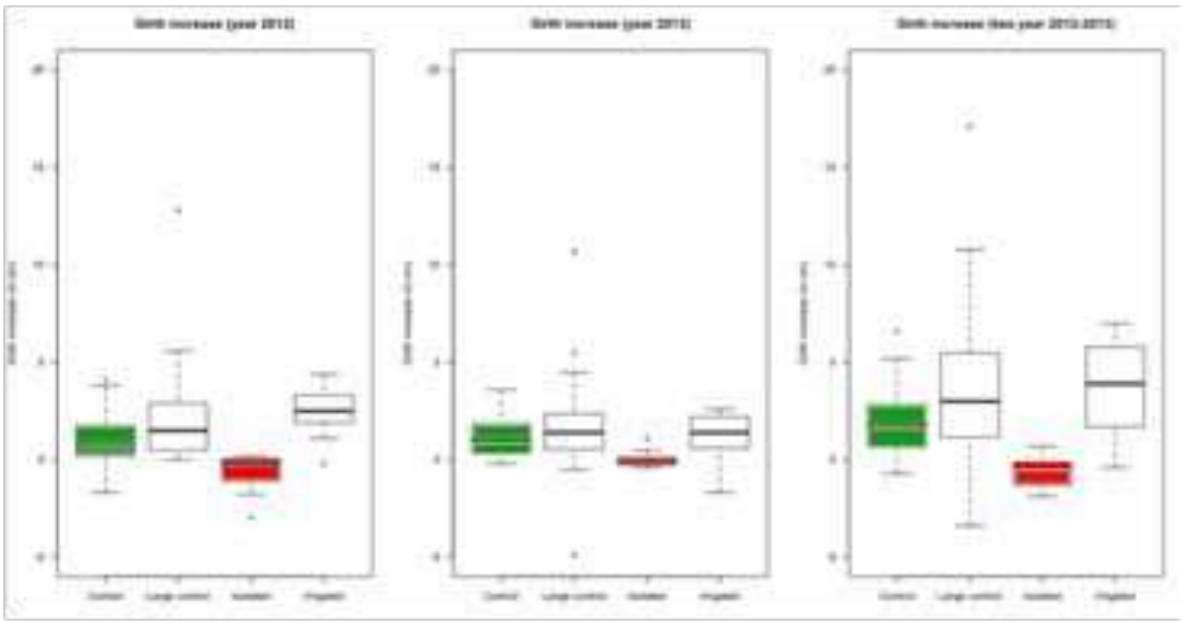


Figure 12: Comparison of trees girth growth in 2012 and 2013

In this 20-year old plantation, teak tree roots were found down to a soil depth of 12 m. At both the control and rainfall exclusion sub-plots, 50% of the total amount of fine root length was found in the first two meters of the soil profile. In the upper layer there is no difference between the isolated and the control site. At deeper depths, a difference is noticeable without being significant (Figure 13).

Monthly root growth monitoring using surface root boxes and access well revealed a clear differentiation between the control and rainfall exclusion sub-plot. In the rainfall exclusion treatment, we observed no root emission for the whole duration of the experiment except at a depth of 4.5 m (Figure 16). On the other hand, in the control sub-plot, roots were emitted at several soil depth increments and fine root growth near the surface appeared to be very responsive to rainfall events occurring at the onset of the rainy season (Figure 16; Figure 17 and Figure 18.).

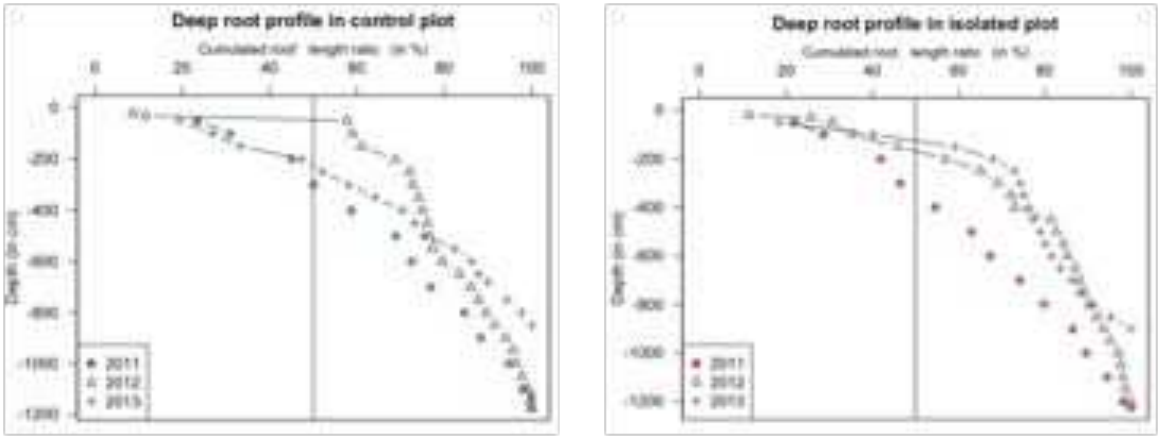


Figure 13: Cumulated root length along a 12 m deep soil profile.

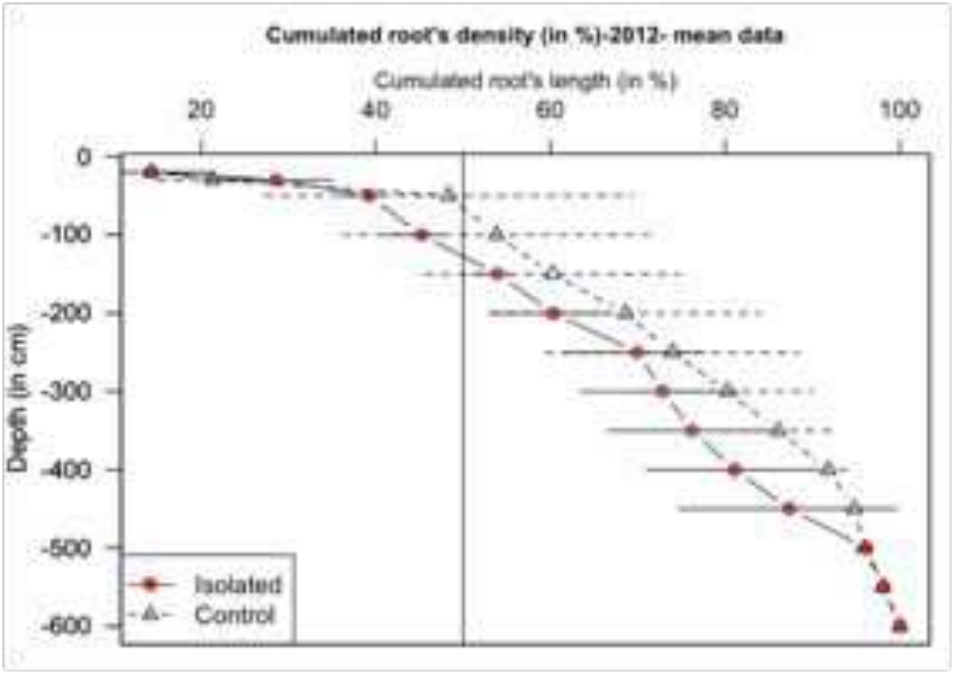


Figure 14: Root length for boxes and windows.

The cumulated root biomass from fine roots down to 12m (Fig. 14) and coarse roots collected down to 2,5m indicate a total of 51,28 (t/ha^{-1}) of root biomass (Table 2).

Roots type	Biomasse (T/Ha)	C (T/Ha)
Anchor roots	18.48	9.24
Coarse roots	11.8	5.9
Medium roots	5.5	2.75
Fines roots	15.5	7.75
Total root	51.28	25.64

Table 2: Root biomasses data collected manually from soil in trenches (85 m3) for anchor, coarse and medium roots. Fine roots come from drill auger sampling at 0.0 to 12.0 m depths. Root density was measured in the lab. (Detailed data available in complementary materials page 134)

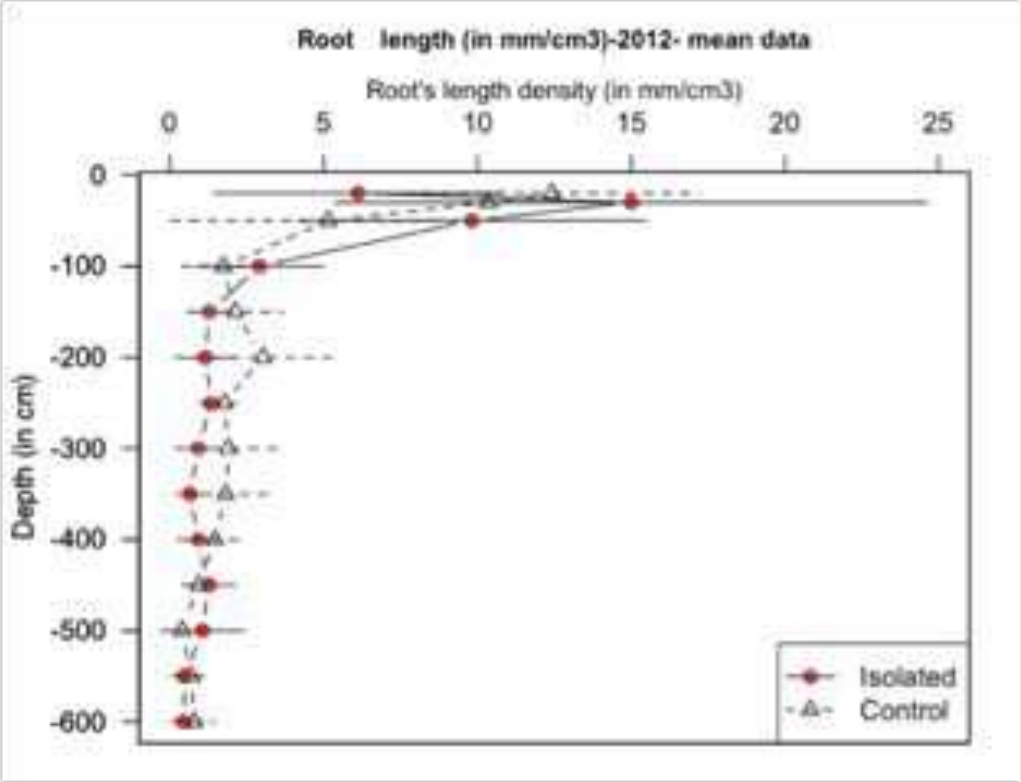


Figure 15: Root's length density down to a 6 m depth in 2012

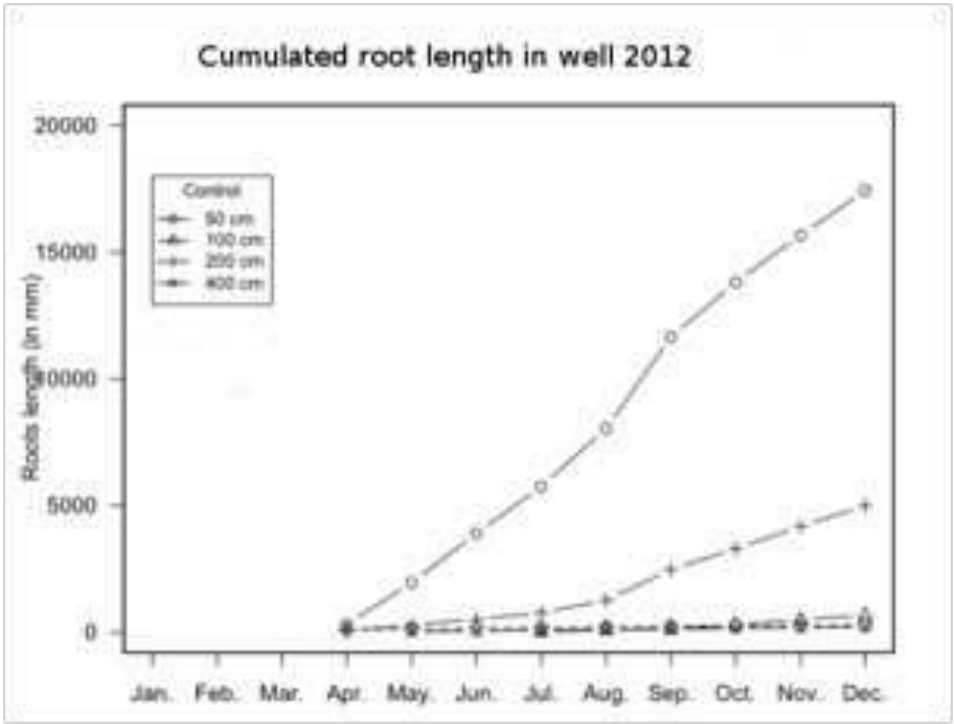


Figure 16: Cumulated root length linked to soil layer with roots (4 windows on Control and 1 window in the isolated well)

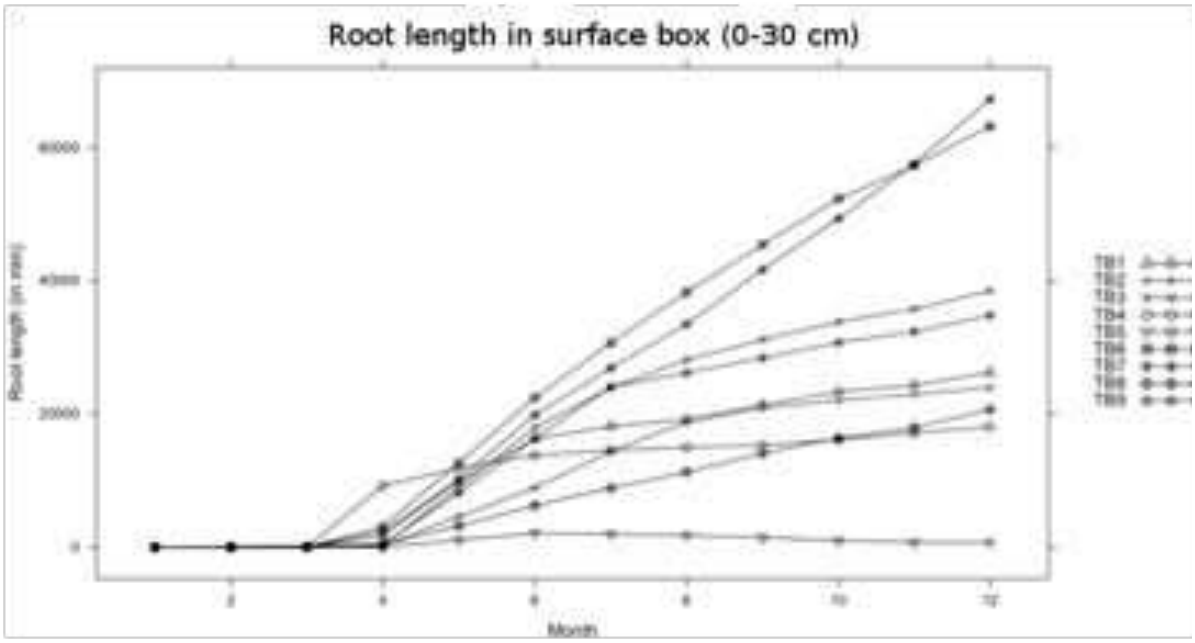


Figure : 17 Root length production in mm in layer 0-30 cm TB= control

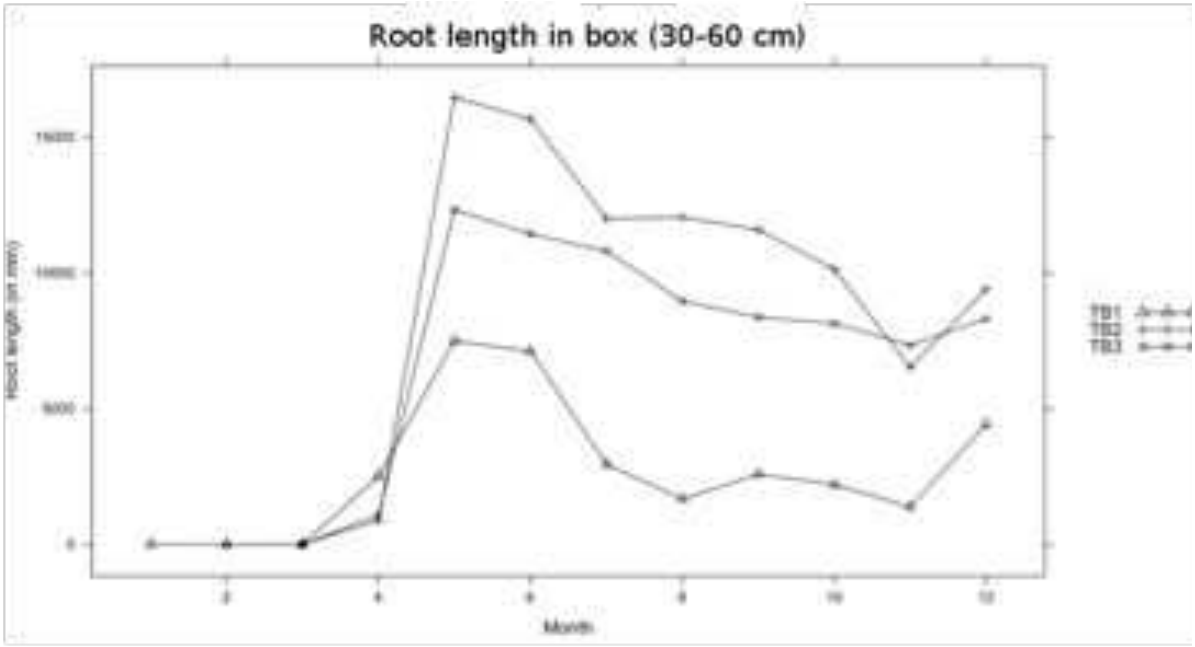


Fig 18: Root length production in mm in layer 30-60 cm; TB= control

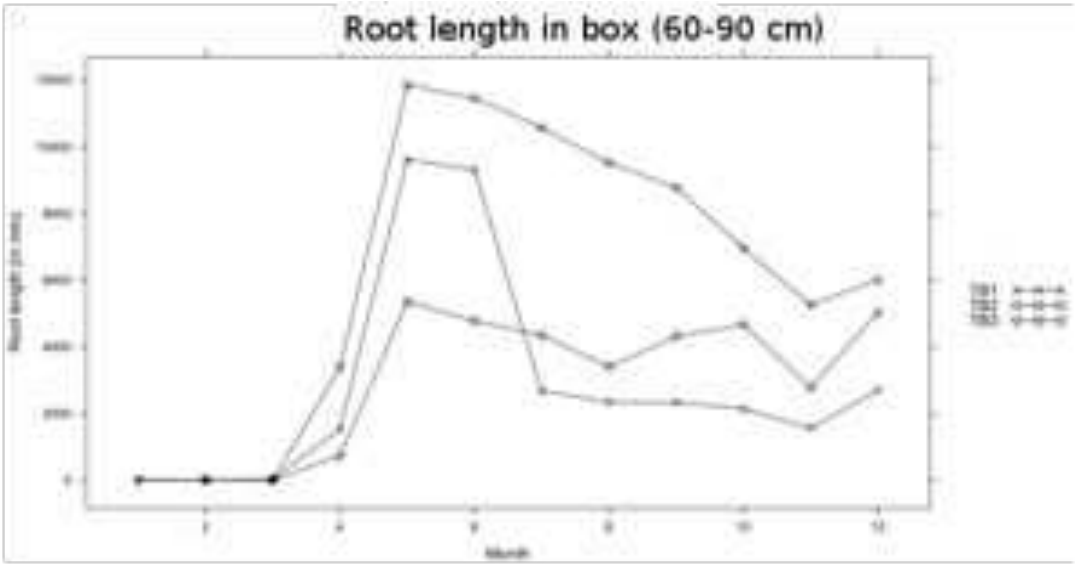


Fig 19: Root length production in mm in layer 60-90 cm TB= control

Discussion

We did not find any horizon devoid of roots down to 12.0 m depth. We can conclude that the maximum rooting depth of teak trees in this context is more than 12.0 m (Fig. 13). This is a high value, even though the maximum rooting depth of trees is known to be highly variable, as the mean maximum value for this parameter is 7.0±1.2 m (Canadell et al. 1996; based on a meta-analysis of nearly 300 hundred references). As showed previously, 50 % of the fine root length was found. On average, in the first 2.30 m of the soil profile which is consistent, qualitatively, with the logistic dose-response curve model of Schenk and Jackson (2002) but implies a D_{50} (the soil depth at which 50% of the total amount of roots is found) much deeper than those presented by these authors.

From a functional perspective, this study investigated the relative importance of deep rooting for water uptake by teak trees and the potential advantages (such as e.g. improved resilience) that deep rooting can provide to this tree species when exposed to drought conditions.

The rainfall exclusion treatment induced measurable changes in soil water content down to a soil depth of 2.5 m. However, except for soil horizons very near the soil surface, this treatment did not induce a drastic drop in soil water potential, which was only of the order of 2×10^5 Pa at 3 m and well above wilting point at shallower soil depths. Nevertheless, high predawn and midday leaf water potential clearly indicated that trees submitted to rainfall exclusion were struggling to extract water from the soil. The very fact that trees of the rainfall exclusion sub-plot appeared outwardly stressed is a clear indication that, under non-limiting conditions, teak trees mostly relays on water uptake from the shallowest soil horizons (a behaviour consistent with the phenology of the tree which is deciduous

and remains leafless for at least a couple of months during the dry season). Based on rooting profiles derived from destructive sampling, we know that the most densely rooted soil horizon are those above 2.5 m, and for that reason, it is reasonable to propose that, when rainfall is non-limiting, this is the zone in which most water uptake occurs.

Another factor that might have greatly impeded water uptake by the trees in the rainfall exclusion treatment is that, even though soil water potential was not so low throughout the profile, soil water conductivity was only of the order of 1 mm per day. Combined with high evaporative demand during the first weeks of the rainy seasons, this low hydraulic conductivity might have contributed to induce partial dehydration of root tissues, creating poor contact between roots and the soil, and as a consequence, a high resistance to water flow from the soil to the plant, following a scenario similar that proposed by (Stirzaker & Passioura, 1996; Scholz *et al*., 2006). Additionally, drought can modify root endodermis and exodermis and affecting vascular properties of roots tissues (Enstone *et al*., 2003).

On the other hand, we observed that, in the rainfall exclusion treatment, soil water potential was most likely affected by the uptake of water by the trees. Indeed, in strict opposition with what occurred in the control plot, in mid-April 2012, i.e. at the time trees grew new leaves, soil water potential dropped slightly at soil depths of 3 to 5 m, and unlike what occurred in the control treatment, there was no indication of recharge throughout the rainy season. Recharge (as indicated by a slight rise in soil water potential) only started towards the end of December 2012, i.e when trees started to shed their leaves. A similar pattern repeated itself in 2013, but with higher values of soil water potential, probably due to the fact that that year was wetter than the previous year. Furthermore, measurements made at soil depths of 6, 8 and 10 m also showed contrasting dynamics between the rainfall exclusion and control treatments. While soil water potential remained basically constant at those depths in the control treatment, it steadily decreased at all three soil depths in the rainfall exclusion sub-plot, once again consistent with the fact that water taken up below 6 m by the trees without recharge from rainfall as in the control plot, may have induced this slight but steady decrease in soil water potential. The fact that similar trends were consistently captured by all sensors, from 3 to 10 m, allows us to rule out with confidence the possibility that they correspond to an artefact. Soil layers deeper than 6 m appeared only marginally influenced by the rainfall pattern with regard to soil water potential and it can be assumed that, due to their proximity, they were probably submitted to the same hydrological regime dominated by lateral flows. This further reinforces the hypotheses that differences in soil water potential observed at such soil depths were most likely a reflection of a shift towards deeper water uptake in the rainfall exclusion plot.

Several independent measurements confirmed the water stress induced by the rainfall exclusion on teak tree physiology. Leaves were less abundant, smaller and their water content lower than in the

control treatment. More surprisingly, this water stress did not impact the leaf C/N ratio for the leaves collected at the same level in the canopy. While the water stress induced by the rainfall exclusion reduced drastically the tree biomass production, it therefore does not appear to have affected their tissue composition but affect the quantity of tissue. As leaf composition is an indicator of tree healthiness, it can be proposed that even under high water stress teak trees were able to maintain well functioning leaves. Leaf size reduction in the rainfall exclusion treatment illustrates that teak trees under water stress were not able to mobilise enough resources to maintain a full canopy cover. Analyses of girth of trees under rainfall exclusion indicate a negative growth during the first year can indicate that teak trees used a part of stem water storage to supply water demand. The use of this water resource can affect tree phenology (Borchert, 1994). In the second year, 50 % of trees from the rainfall exclusion sup-plot returned to dynamic growth, even if the recorded values were still low compared to the control sub-plot.

Root profiles in both control and rainfall exclusion treatments did not present significant differences. This suggests that teak trees develop a deep root system under normal conditions. The functional importance of such a deep root system might be linked to nutrient uptake such as observed for eucalyptus spp (da Silva *et al*., 2011). It might also represent a so-called safety net, that is a set of organs that are not heavily used under non-limiting conditions, but which can be relied upon when conditions degrade, such as was the case in the rainfall exclusion sub-plot when resisting to stresses. In our case, teak trees might extract water from deep horizon while water is not available on the surface one. This could be extended to mineral uptake or in cases of strained living conditions (salinity for example).

Overall, it can be said that, as a response to the induced water stress, teak trees in the rainfall exclusion treatment entered a state of dormancy with reduced biomass production and reduced canopy cover due to reduced water resources availability. On the one hand, these trees did not display a remarkable adaption strategy involving, for example, a strong allocation of photo-assimilates for the production of new roots at the observed depth. On the other hand, these trees survived despite the rather extreme nature of the treatment applied, most likely due to the fact that they had a deep root system; even though not as efficient as their shallow counterparts, deep roots appear to be a component of foremost importance as a means for this species to buffer the consequences of climate variability.

Perspectives

Beyond the results that we found in this study, we believe that in situ study is essential for understanding the tree growth under the climate variation and the environment evolution. Results on root growth dynamics of teak taking into account an important part of roots profile allow the understanding of their development proprieties in relation with soil and climatic conditions. The

overall development of trees relies essentially on the adaptation capacity of individual roots to their close environment. Stating general rules in that conditions are therefore really challenging. Our efforts to capture a dynamic vision of the root functionalities along a four meter profile over two years are a complementary necessity to static root systems drawings made before 1970 by Lore Kutschera (1960) for example. These drawings recorded from plant observations in the wild are regularly used for model calibration. Our global and dynamic study is bringing a new complementary vision on roots system and provides data to calibrate future models of the global dynamics soil colonization by roots.

Acknowledgements

Jean-Luc Maeght would like to thank Mr. Oloth Sengtaheuanghoung for allowing the access to the field experiment. We are also deeply grateful to the National Agriculture and Forestry Research Institute (NAFRI) of Laos, the French Agence Nationale de la Recherche (project Ecosfix, ANR-2010-STRA- 003) and the French Institute for Research for Development (IRD) for providing the enabling environmental and financial resources.

References

Alcântara BK, Veasey EA. 2013. Genetic diversity of teak (Tectona grandis L.F.) from different provenances using microsatellite markers. *Revista Árvore* **37**: 747–758.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH (Ted), *et al.* 2010. *A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests.*

Anon. 2012. Germplasm Resources Information Network (GRIN). *USDA, ARS, National Genetic Resources Program, National Germplasm Resources Laboratory, Beltsville, Maryland*.

Arcadius Y, Akossou J, Godui A. 2012. Effect of Climatic Factors on the Radial Growth of Teak (Tectona grandis L.F.) in Parakou and Tchaourou districts in northern Benin. *Journal of agricultural science and technology* **2**: 721–730.

Bergeron M, Lacombe S, Bradley RL, Whalen J, Cogliastro A, Jutras M-F, Arp P. 2011. Reduced soil nutrient leaching following the establishment of tree-based intercropping systems in eastern Canada. *Agroforestry Systems* **83**: 321–330.

Bhat KM. 2000. Le bois de teck. *Bois et forets des tropiques* **263**.

Bhat KM, Balasundaran M, Bhat K V, Muralidharan EM, Thulasidas PK. 2007. Processing and Marketing of teak wood products of Planted Forests. Teak regional work shop. Peechi, 1–336.

Bhat K, Hwan MO. 2004. Teak growers unite. *ITTO Trop Forest Update* **14**: 3–5.

Bleby TM, McElrone AJ, Jackson RB. 2010. *Water uptake and hydraulic redistribution across large woody root systems to 20 m depth.*

Bleby TM, McElrone AJ, Jackson RB, Cameron RJ, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED, Djema A, *et al.* 1963. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth A study of the rooting habits of rimu and tawa in pumice soils Maximum rooting depth of vegetation types at the global scale Structure and dynamics of the root system. *Plant Cell and Environment* **33**: 2132–2148.

Böhm W. 1979. *Methods of studying root systems.* Berlin: Springer-Verlag.

Borchert R. **1994**. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology* **75**: 1437–1449.

Chaix G, Monteuuis O, Garcia C, Alloysius D, Gidiman J, Bacilieri R, Goh DKS. **2011**. Genetic variation in major phenotypic traits among diverse genetic origins of teak (Tectona grandis L.f.) planted in Taliwas, Sabah, East Malaysia. *Annals of Forest Science* **68**: 1015–1026.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–5.

Combeau A. **1951**. *Observations sur les sols des Teckeraies dans la region de Sokodé.* Lomé.

Davidson E, Lefebvre P, Brando P. **2011**. *Carbon inputs and water uptake in deep soils of an eastern Amazon forest.*

Dié A, Kitin P, Kouamé FN, Van den Bulcke J, Van Acker J, Beeckman H. **2012**. Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (Tectona grandis) in Ivory Coast. *Annals of botany* **110**: 861–73.

Drechsel P, Schmall S, W. Zech. **1990**. Relationships between growth, mineral nutrition and soil properties in young Teak plantations in Bénin and Liberia. IUFRO-Symposium.651–656.

Enstone DE, Peterson CA, Ma F. **2003**. *Root Endodermis and Exodermis : Structure , Function , and Responses to the Environment.*

FAO. **2011**. *State of the World's Forests*. Rome.

Fofana IJ, Ofori D, Poitel M, Verhaegen D. **2008**. Diversity and genetic structure of teak (Tectona grandis L.f) in its natural range using DNA microsatellite markers. *New Forests* **37**: 175–195.

Goh DKS, Bacilieri R, Chaix G, Monteuuis O. **2013**. Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites. *Tree Genetics & Genomes* **9**: 1329–1341.

Graudal L, Kjær E, Suangtho V. **1999**. *Conservation of genetic resources of teak (Tectona grandis) in Thailand*. Humlebaek.

Guizol P, Roda JM, Muhtaman DR, Laburthe P, Fauveaud S, Antona M. **2005**. LE TECK JAVANAIS, ENTRE SUREXPLOITATION ET EMBARGO. *Bois et Forêts des Tropiques* **284**: 11–21.

Hidalgo E, Moreno V, Morales N. **1986**. Performance of 15 provenances of teak (Tectona grandis) five years after planting in Itabo, Matanzas. *Rev For Baracoa* **16**: 65–75.

Jacoby GC, D'Arrigo RD. **1990**. Teak (Tectona grandis L.F.), a tropical species of large-scale dendroclimatic potential. *Dendrochronologia* **8**: 83–98.

Kaosa-ard A. **1981**. Teak its natural distribution and related factors. *Nat His Bull Siam Soc* **25**: 55–74.

Kashio M, White K. **1998**. Teak for the future. In: Pacific. FRO for A and the, ed. Proceedings of the second regional seminar on teak. Bangkok, .

Lamouroux M. **1957**. *Les sols de teckeraies du Togo.* Lomé.

Liu Y, Zhou Y, Ju W, Wang S, Wu X, He M, Zhu G. **2014**. Impacts of droughts on carbon sequestration by China's terrestrial ecosystems from 2000 to 2011. *Biogeosciences* **11**: 2583–2599.

Madoffe S, Maghembe J. **1988**. Performance of teak (Tectona grandis L.f.) provenances seventeen years after planting at Longuza, Tanzania. *Silvae Genet* **37**: 175–178.

Maeght JL, Henry des Tureaux T, Sengtaheuanghoung O, Stokes A, Ribolzi O, Pierret A. **2012**. Drought effect on teak tree (Tectona grandis) roots on carbon inputs and water uptake in a deep soil of northern Laos. Roots to the Future 8th Symposium of the International Society of Root Research.

Maeght J., Nortourlee L, Reboul-salze F, Bourdon E, Sengtaheuanghoung, O. Soulileuth .B, Hartmann C, Pierret A. **2011**. Environmental impact of understorey management in Teak tree (Tectona grandis L.) plantations: A case study from Luang Prabang, Lao PDR. *Khon Kaen AGR* **39**: 291–294.

Maeght J-L, Pierret A, Sanwangsri M, Hammecker C. **2007**. Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand. International Conference Rhizosphere 2, 26-31 August 2007, Montpellier, France.26–31.

Maeght J-L, Rewald B, Pierret A. **2013**. How to study deep roots—and why it matters. *Frontiers in Plant Science* **4**.

Markewitz D, Devine S, Davidson EA, Brando P, Nepstad DC. **2010**. Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. *The New phytologist* **187**: 592–607.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *The New phytologist* **178**: 719–39.

Nepstad D, Carvalho C de, Davidson E. **1994**. *The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures*.

Nocetti M, Rozenberg P, Chaix G, Macchioni N. **2011**. Provenance effect on the ring structure of teak (Tectona grandis L.f.) wood by X-ray microdensitometry. *Annals of Forest Science* **68**: 1375–1383.

Pandey D, Browna C. **2000**. *Le teck dans le monde*.

Priya PB, Bhat KM. **1998**. *False ring formation in teak (Tectona grandis L . f .) and the in ¯ uence of environmental factors*.

Ram S, Borgaonkar HP, Munot AA, Sikder AB. **2011**. Tree-ring variation in teak (Tectona grandis L.) from Allapalli, Maharashtra in relation to moisture and Palmer Drought Severity Index, India. *Journal of Earth System Science* **120**: 713–721.

Schmall S. **1989**. *Wuchs und Ernährungszustand junger Teak-Bestände auf Vertisolen in Bénin, Westafrika.* (UB Diplomarbeit, Ed.). Unveröff.

Scholz F, Bucci S, Arias N, Meinzer F, Goldstein G, Schulze ED, Mooney HA, Sala OE, Jobbagy E, Buchmann N, *et al.* 2006. Osmotic and elastic adjustments in cold desert shrubs differing in rooting depth: coping with drought and subzero temperatures Biological control of the terrestrial carbon sink Rooting depth, water availability, and vegetation cover along an aridity gradi. *Oecologia*\ **3**\: 1–13\.

Da Silva EV, Bouillet J-P, de Moraes Gonçalves JL, Junior CHA, Trivelin PCO, Hinsinger P, Jourdan C, Nouvellon Y, Stape JL, Laclau J-P. **2011**. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. *Functional Ecology* **25**: 996–1006.

Stirzaker RJ, Passioura JB. **1996**. The water relations of the root-soil interface. *Plant, Cell and Environment* **19**: 201–208.

Streets RJ. **1962**. *Exotic trees of the British Commonwealth.* (U.K:Clarendon Press, Ed.). Oxford.

Tariel J. **1966**. Le Teck en Côte-d'Ivoire. *Bois et Forêts des Tropiques* **107**: 27–47.

Thein HM, Mamoru K, Fukushima M, Minn Y. **2007**. Structure and composition of a teak-bearing forest under the Myanmar selection system: impacts of logging and bamboo flowering. Southeast Asian Studies.303–316.

Thomas TP. **1989**. *Effect of varying soil moisture and bulk density on Teak, Eucalypt and Albizia root growth*. Kerala.

Thomson S, Armstrong C. **1987**. *Calibration of the Watermark model 200 soil moisture sensor*.

Thomson S, Younos T, Wood K. **1996**. Evaluation of calibration equations and application methods for the watermark ® granular matrix soil moisture sensor. *Applied engineering in agriculture* **12**: 99–103.

Troup R. **1921**. *The SilŠiculture of Indian Trees* (P Agricultural Research Institute, Ed.). Oxford University press.

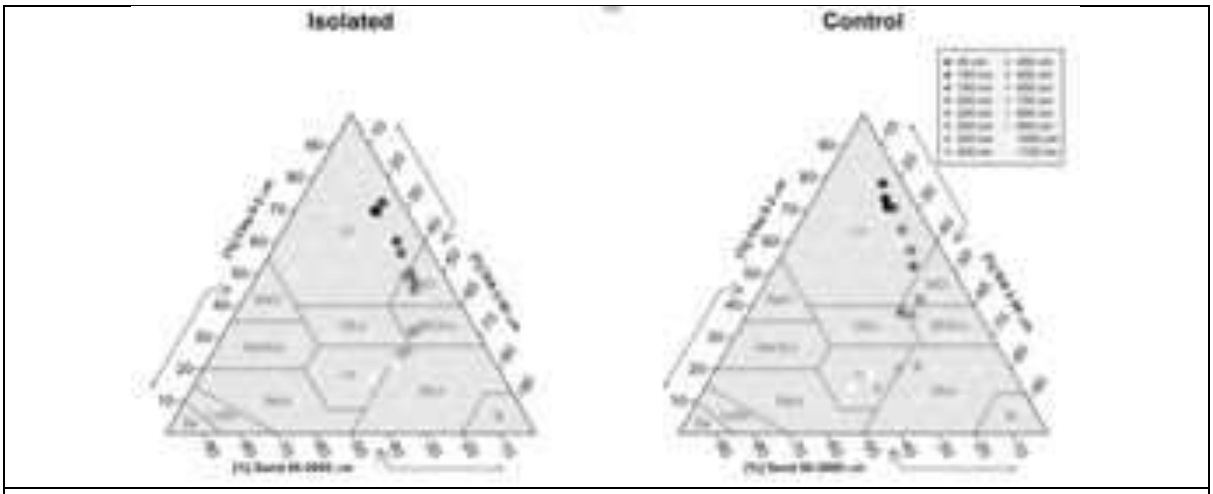
Vanlauwe B, Aihou K, Tossah BK, Diels J, Sanginga N, Merckx R. **2005**. *Senna siamea trees recycle Ca from a Ca-rich subsoil and increase the topsoil pH in agroforestry systems in the West African derived savanna zone*.

Verhaegen D, Fofana IJ, Logossa Z a., Ofori D. **2010**. What is the genetic origin of teak (Tectona grandis L.) introduced in Africa and in Indonesia? *Tree Genetics & Genomes* **6**: 717–733.

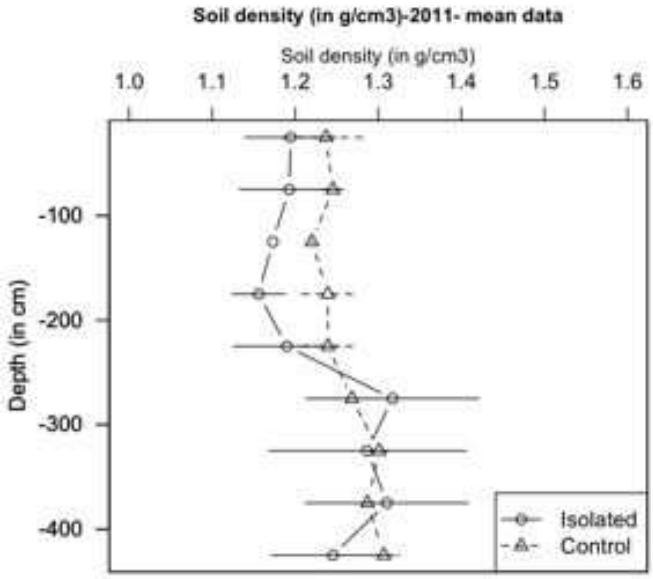
Complementary materials:

Depth	Nitrogen g/kg		Phosphorus g/kg		Potassium (K) cmol+/kg		Carbon total g/kg		CEC Metson cmol+/kg		Soil pH (water)		Soil pH (KCL)	
	Control	Isolated	Control	Isolated	Control	Isolated	Control	Isolated	Control	Isolated	Control	Isolated	Control	Isolated
-50	0.726	0.888	<0.005	<0.005	0.0558	0.0542	8.39	9.87	9.55	9.45	5.07	5.25	4.09	4.38
-100	0.558	0.64	<0.005	<0.005	0.0557	0.042	6.26	7.18	9.26	9.59	5.2	5.24	4.27	4.28
-150	0.521	0.549	<0.005	<0.005	0.0438	0.0481	5.53	5.84	9.07	9.06	5.3	5.24	4.35	4.23
-200	0.516	0.477	<0.005	<0.005	0.0474	0.0463	5.63	5.03	8.42	9.44	5.44	5.62	4.76	5.1
-250	0.366	0.363	<0.005	<0.005	0.0468	0.0408	4.02	4.03	9.67	9.35	5.71	5.5	4.89	4.92
-300	0.257	0.324	<0.005	<0.005	0.0566	0.0477	2.84	3.56	10.1	9.8	5.82	5.7	5.14	5.19
-350	0.135	0.217	<0.005	<0.005	0.0948	0.0395	1.52	2.56	12.6	9.76	6.09	5.58	5.00	4.81
-400	0.257	0.196	<0.005	<0.005	0.0498	0.0513	2.91	2.37	9.91	10.8	5.8	6.01	5.13	5.41
-450	0.38	0.353	<0.005	<0.005	0.0485	0.0562	4.14	4.33	9.58	9.86	5.59	5.63	5.01	4.84
-500	0.092	<0.02	<0.005	<0.005	0.0656	0.0395	1.26	0.921	16.1	8.16	8.24	5.57	7.24	4.16
-600	0.02	<0.02	<0.005	<0.005	0.0979	0.0414	0.85	0.685	11.8	9.15	8.2	5.55	7.04	4.1
-700	0.02	<0.02	<0.005	<0.005	0.0443	0.027	0.39	0.493	12.2	10.4	8.23	5.59	5.52	4.08
-800	0.02	<0.02	<0.005	0.008	0.0918	0.0215	0.509	0.367	16.4	9.59	8.03	5.67	5.28	4.11
-900	0.02	<0.02	<0.005	0.006	0.0697	0.0255	0.321	0.376	16.0	11.7	7.58	5.7	4.6	4.16
-1000	0.066	<0.02	<0.005	<0.005	0.0666	0.0331	0.794	0.223	15.0	12.9	7.28	5.89	4.27	4.17
-1100	0.02	<0.02	<0.005	0.007	0.039	0.088	0.316	0.202	14.1	15.7	6.97	5.96	3.79	4.25

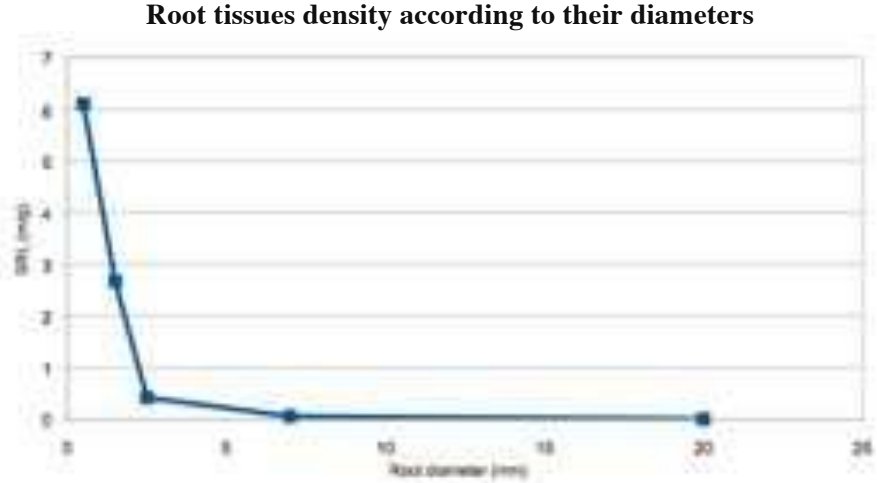
Table 1: Soil chemicals characteristics for isolated and control profile from 0 to 11 m depth



Soil texture triangle in isolated and controlled teak forest down to 11.0 m



Soil density for two profiles on Isolated and control sub-plot collected in wells in 2011.



Root density from 0.5 mm to 20 mm of root diameter.

3.3 Conclusion

Bien qu'encore en cours aujourd'hui, cette deuxième expérimentation visant à étudier l'enracinement profond d'arbres adultes permet d'ores et déjà de tirer certains enseignements. Dans la première partie de la conclusion, je présente et discute les points forts et points faibles de cette expérimentation. Dans la deuxième partie de la conclusion, je présente et discute les principaux éléments de connaissance apportés par cette expérimentation.

3.3.1 Dispositif expérimental :

La mise en place du dispositif d'exclusion totale de pluie avec une toiture jointive, sur une surface supérieure à la surface au sol de la parcelle circonscrite par des tranchées de 2,5 m creusées dans le sol, a permis de limiter les effets des fortes pluies sur les côtés du dispositif. Une des grandes difficultés a été la mise en place de l'étanchéité autour des arbres inclus dans la surface couverte par la toiture. Nous avons opté pour un système de double jupe qui a permis un compromis entre la nécessité d'une bonne étanchéité et le maintien d'une souplesse du dispositif permettant de répondre aux sollicitations du vent (Photo 15). Ce choix n'a pas permis d'éliminer totalement les écoulements le long des troncs. Les mouvements naturels de l'ensemble du dispositif ont entrainé une usure du matériel, qu'il a fallu remplacer régulièrement. La proximité d'autres arbres en partie basse de la toiture ne permettait pas d'installer une zone de captage suffisamment large et profonde pour récolter la totalité de l'eau ruisselant sur le toit lors de pluies à fortes ou très fortes intensités. De plus l'accès pour le nettoyage et la collecte des feuilles de la zone de captage est resté limité et n'a pas permis une élimination facile des débris végétaux qui pouvaient s'y accumuler et ainsi parfois amplifier la perte des pluies collectées.

En raison de ces difficultés techniques, le dispositif de détournement des pluies interceptées par le toit n'a pas donné totale satisfaction. Nos mesures indiquent un taux d'interception des pluies approchant 90 % avec un taux de collecte d'un peu plus de 40%. Les pluies de forte intensités induisent un débordement du dispositif de collecte en avant de la toiture hors zone isolée. Malgré cela, le dispositif a permis d'assécher fortement la surface du sol. En l'absence

d'infiltration latérale possible grâce à l'étanchéité des tranchées, les remontées capillaires ont néanmoins contribué à maintenir le sol à plus 2 m de profondeur à des valeurs de tension de l'eau autour de - 1,5 à – 2 bar.

Une des difficultés à surmonter avec ce dispositif de toiture est d'arriver à continuer à mettre en œuvre des observations des parties aériennes, de collecter les feuilles pour les mesures de potentiel hydrique et permettre les mesures de transpiration. Nous avons donc mis en place un cheminement de passerelles en bambous permettant de circuler au-dessus de la toiture (Photo 16). Cet aménagement a répondu aux attentes mais il est nécessaire de rester prudent lors des déplacements et lors de la collecte des feuilles avec un coupe-feuille de plusieurs mètres de long afin de ne pas perdre l'équilibre. Les passerelles doivent être vérifiées régulièrement et les bambous renouvelés si nécessaire.

Un autre défi était de pouvoir accéder de manière sécurisée et permanente aux racines le long du profil de 5 m. La technique des puits d'accès, que nous utilisons depuis plusieurs années et que nous avons décrite dans l'article présenté dans la première partie de cette thèse (Maeght et al. 2013), nous a permis d'accéder aux informations sur la dynamique d'enracinement grâce à un puits aménagé dans la zone isolée et un deuxième dans la zone de contrôle. Comme de nombreuses techniques d'observation, celle du puits a un impact sur son environnement et perturbe le milieu. Cependant, ce dispositif étant pérenne et robuste avec des parois renforcées, ces effets indésirables s'atténuent dans le temps.

Une des limites de notre expérimentation aux champs tient dans l'ampleur des tâches à entreprendre et au budget que nous pouvions y consacrer. Dans ces conditions, il n'était pas possible de travailler sur des surfaces plus grandes, n'y d'aménager plus de puits d'accès. Chaque puits offre néanmoins de bonnes surfaces d'observation et un très bon contact avec le sol sur l'ensemble du profil. En utilisant uniquement le verre pour la construction des fenêtres nous avons résolu les problèmes liés à la corrosion, aux éventuelles rayures, perte de transparence et déformation que subit le plexiglas lorsqu'il est en contact avec le sol. Le dispositif de fenêtres d'accès placées à 45 ° permet la réalisation des prises de vue avec le scanner plat adapté. Nous avons adapté cette méthode de nos premiers travaux (Maeght et al. 2007). Le berceau de mise en place du scanner répond aux exigences de repositionnement du scanner lors de l'acquisition répétée d'images dans les différentes boites de surface. Le nombre de boites de surface (réalisé en inox pour la boite et en verre pour la partie prise

d'image) étant plus facile à mettre en place, nous avons pu d'avantage répéter les observations de surface.

Nous avons tenté d'utiliser les outils les plus adaptés pour l'acquisition des mesures, que ce soit pour les informations recueillies au niveau de la végétation, des données climatiques et édaphiques. Nous avons cependant rencontré des limites, notamment financières, en ce qui concerne la possibilité de mesure de la tension de l'eau du sol. Dans un contexte d'assèchement du sol, tel qu'anticipé sur notre site d'expérimentation, les seuls capteurs en mesure de répondre convenablement à nos besoins auraient été des psychromètres mais, en raison de leur coût particulièrement élevé, nous ne pouvions envisager leur achat. Les Watermark ayant une gamme de mesure une fois et demie plus étendue que les tensiomètres, nous nous sommes tournés vers ces capteurs robustes, fiables et au prix abordable. Les Watermark permettent une gamme de mesure de tension volontairement limitée à -2.5 bar. A ce stade, nous avons capté le signal électrique émis par les Watermark au travers d'un dispositif d'acquisition du signal de type Campbell afin d'assurer la prise des mesures. L'objectif étant d'établir notre propre courbe de calibration afin de pouvoir convertir les mesures de résistances des capteurs en mesure de tension de l'eau du sol au-delà de -2.5 bar. Une solution similaire a été utilisée par Johnston (2000) avec des blocks de gypse. Les travaux étant encore en cours, nous n'avons pas encore pu valider la méthode dans notre contexte.

Concernant les mesures de couverture foliaire, nous avons également dû adapter le protocole classique de mesures hémisphériques avec une approche nous permettant de réaliser des images s'approchant au mieux de ce protocole. A cette fin, nous avons utilisé le logiciel Photosynth (http://photosynth.net/) pour raccorder des prises de vues à faible couverture angulaire et réaliser des mosaïques de la canopé couvrant une surface angulaire de l'ordre de 180 x 50 degrés. Nous avons ensuite utilisé des techniques d'analyse d'images sur la base de programme fonctionnant sous le logiciel ImageJ, un logiciel de traitement d'images du domaine public pour extraire les zones d'interception lumineuse par la couverture foliaire (Photo 17).

Les mesures de potentiel foliaire peuvent se réaliser sans trop de difficultés mais restent sujet à risques au niveau des manipulations des gaz à hautes pressions. Ces opérations doivent donc être réalisées en s'assurant du respect des consignes de sécurité. La collecte des feuilles pour

les mesures de potentiel reste un élément déterminant pour la qualité des mesures. Dans notre cas, avec des hauteurs d'arbres importantes, l'utilisation de matériel adapté permettant de collecter les feuilles correctement et avec un minimum de risques pour l'opérateur n'a pas été très facile à réaliser et reste encore aujourd'hui un point difficile à résoudre. Nous avons pu trouver une solution satisfaisante en prolongeant le coupe feuille au maximum à l'aide de perches de bambous mais ce n'est pas la solution idéale car cela engendre des déséquilibres important lors de la manipulation. Des assemblages en aluminium télescopique faits sur mesure seraient probablement plus performants et moins lourd à manipuler.

En ce qui concerne l'analyse d'images, l'utilisation de notre propre outil Ij _Rhizo pour l'analyse d'images s'est montrée performante. Il n'en demeure pas moins que le temps dévolu au traçage manuel de chaque racine avant leur analyse devient très vite un frein à l'exploitation des données. Tant qu'il n'y aura pas d'évolution majeure pour le traitement automatisé des images, la réalisation des traçages, quel que soit la méthode, est un élément majeur à prendre en compte dans l'élaboration d'une expérimentation. Au fil du traitement des images, il nous est apparu que dans le cas où l'analyse d'images concerne des classes de racines similaires, l'utilisation du format JPEG pourrait s'avérer intéressante si on s'intéresse uniquement aux longueurs racinaires. En effet, ce format de sauvegarde d'image utilise la compression des données pour réduire la taille des fichiers. Comme les pixels des images tracées sont en noir (racines) et blanc (fond de l'image), le poids des fichiers devient proportionnel au nombre de pixels représentés par le traçage des racines (Figure 17). Cette figure traite 1200 fichiers images brute, nous obtenons un R^2 de 0,64 qu'il doit être possible d'améliorer ce résultat par exemple en traitant les fichiers par lot en fonction des espèces étudier et de l'origine des fichiers images. Il serait donc potentiellement possible, dans le cas où les diamètres des racines sont similaires, de créer une courbe de conversion poids des fichiers/longueurs racinaires et de se passer ainsi de la phase de mesure. C'est, de mon point de vue, un élément à explorer pour alléger la part de travail manuel nécessaire aujourd'hui dans l'analyse des images et progresser vers un traitement des images entièrement automatisé qui facilitera la multiplication des analyses d'image à plus grande échelle.



Photo 15: Jupe évitant l'écoulement de l'eau de pluie le long des troncs.



Photo 16: Dispositif de passerelles en bambous permettant d'effectuer les mesures au-dessus de la toiture.

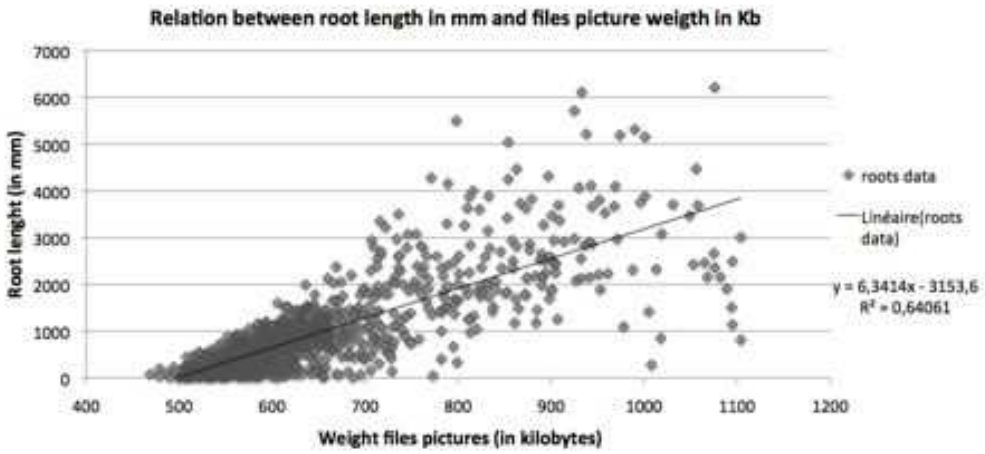


Figure 17: Relation entre la taille des fichiers en format JPEG et la longueur des racines en mm réalisée sur plus de 1200 images

3.3.2 Connaissances apportées :

En complément de la conclusion proposée dans la publication centrale de ce chapitre, nous proposons ci-dessous de revenir sur les conclusions de notre expérimentation.

Malgré leur forte capacité d'adaptation à des régimes hydriques très contrastés en fonction des pays où il est implanté (Kaosa-ard 1981), les tecks que nous avons suivi ont réagi en réduisant fortement leur biomasse aérienne. La LAI a été réduite de plus de 30 % avec une production du nombre de feuilles et une taille des feuilles significativement réduites (Photo 18). La mise à feuille et la chute des feuilles ont été plus précoces et cette tendance s'est poursuivie la deuxième année. Nous avons pu démontrer la forte dépendance des racines fines de surface apparaissant aux premières pluies (Photo 19 et Photo 20) et à l'opposé, l'absence de production de racines en surface en l'absence de pluie. En profondeur, entre 1 et jusqu'à 5 m, cette dynamique de croissance des racines est plus lente pour le témoin et à l'opposé pratiquement inexistante pour le sol isolé de la pluie sauf pour le niveau situé à - 4,5 m de profondeur, qui est le seul où nous avons pu observer une apparition de racines. Nous avons également pu démontrer l'existence de racines fines profondes, au moins jusqu'à 12 m, mais nous n'observons pas de différentiation notable au fil du temps des longueurs racinaires entre le témoin et la zone isolée. Au cours de la deuxième année de mesure, nous avons noté une

reprise de la croissance sur de près de la moitié des arbres du traitement isolé, alors que, après la première année, aucune croissance n'avait pu être mesurée. Nous pouvons émettre l'hypothèse que l'enracinement profond, après un temps d'adaptation, a pu répondre à des demandes de ressources complémentaires. Pour le moment, cette adaptation ne répond cependant pas totalement aux besoins exprimés pour revenir à un développement végétal normal des parties aériennes.

L'eau de pluie interceptée sur la zone d'exclusion de pluie a été mise à profit pour irriguer une troisième zone d'étude. Les apports d'eau complémentaires ont permis d'augmenter artificiellement les apports pluviométriques qui sont passés de 1500 à 2100 mm. La croissance observée démontre la forte sensibilité du teck face à la disponibilité des eaux de surface avec, entre autre, des tailles de feuilles et une croissance des arbres en diamètres significativement supérieures à celles observées dans la zone témoin.

Des hypothèses peuvent être avancées et discutées pour tenter d'apporter des éléments de réponse aux interrogations qui découlent de cette expérimentation d'exclusion de pluie sur teck adulte, que ce soit sur sa forte sensibilité à l'apport d'eau de surface, sur le délai d'adaptation ou le rôle des racines profondes. Ces hypothèses sont présentées dans la dernière partie de cette thèse consacrée à la discussion générale et à la conclusion.



Photo 17: Couverture foliaire dans la zone de contrôle (à gauche) et la zone isolée (à droite) à la même date



Photo 18: Feuilles récoltées en fonction des traitements. De haut en bas: zone irriguée, zone isolée, zone de contôle

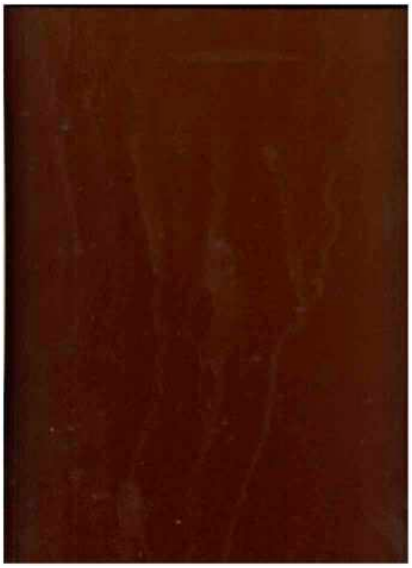


Photo 19: 26-3-12-TB1-30, boite de surface, zone de contrôle, mars 2012

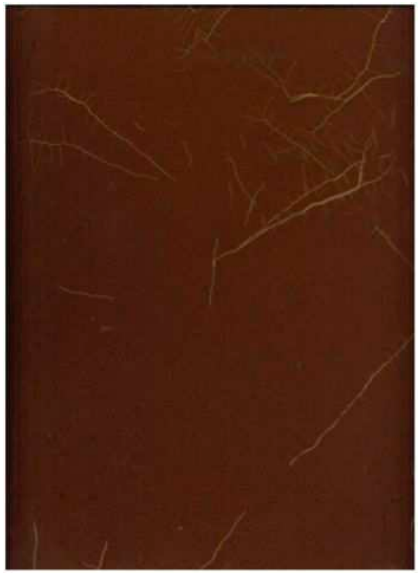


Photo 20: 26-4-12-TB1-30, boite de surface, zone de contrôle, avril 2012

3.3.3 Références

Johnston, W. (2000). Calibration of gypsum blocks and data loggers and their evaluation for monitoring soil water status. *Australian Journal of Experimental Agriculture*, *40*, 1131–1136. Retrieved from http://www.publish.csiro.au/?paper=EA99167

Kaosa-ard, A. (1981). Teak its natural distribution and related factors. *Nat His Bull Siam Soc*, *25*, 55–74.

Maeght, J.-L., Pierret, A., Sanwangsri, M., & Hammecker, C. (2007). Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand. In *International Conference Rhizosphere 2, 26-31 August 2007, Montpellier, France.* (pp. 26–31). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Maeght, J.-L., Rewald, B., & Pierret, A. (2013). How to study deep roots—and why it matters. *Frontiers in Plant Science*, *4*. doi:10.3389/fpls.2013.00299

Chapitre 4:

Discussion, conclusion et perspectives



Photo 21: Effet du brulis sous plantation de tecks adultes dans la région de Luang Prabang

4.1 Discussion générale

L'influence de la variabilité climatique sur l'enracinement superficiel et profond d'arbres adultes en plantation sous contraintes hydriques.

4.1.1 Les contraintes hydriques

Exposés à des contraintes hydriques naturelles ou artificielles, l'hévéa et le teck ont montré leur résilience suite à l'adaptation de leur rythme physiologique aux contraintes imposées. Leurs productions sont toutefois limitées par le déficit hydrique auxquels ils sont soumis. L'eau étant couramment considérée comme un des facteurs les plus importants pouvant affecter la croissance et la distribution des arbres (Hinckley et al. 1991), dans un contexte de changement climatique avec un changement prévu du rythme et de l'intensité des précipitations, nous pouvons nous attendre à des répercussions sur la distribution des espèces et leurs capacités de production. (Zeppel et al. 2014) Ce phénomène peut être amplifier pour les plantations mono-espèces dont les arbres risquent de renforcer leurs compétitions sur les ressources dans les mêmes horizons de sol.

a) Le teck au Laos

Dans le cas du teck au nord Laos, en l'absence de développement de racines superficielles que nous pouvons attribuer à la sècheresse brutalement imposée, l'arbre a du puiser les ressources nécessaires à sa survie au moyen de racines préexistantes, plus ou moins profondes. Ce scénario est en accord avec des études antérieures sur d'autres espèces (*Quercus fusiformis* Small ; *Bumelia lanugi- nosa* Michx ; *Prosopis glandulosa* Torr) au texas (Bleby et al. 2010; Markewitz et al. 2010) et pourrait donc correspondre a un mécanisme générique (« safety net »). Bien que le teck soit capable de se développer sous des régimes hydriques contrastés, il semble pourtant que son rythme de croissance dépende fortement des ressources superficielles dont la teneur eau du sol est un élément essentiel (Arcadius et al. 2012; Dié et al. 2012; Priya and Bhat 1998). Ainsi, bien que les zones montagneuses du nord du Laos soient considérées comme faisant partie de l'aire de répartition naturelle du teck, nous avons pu constater dans le cadre de ce travail que, sous ce climat, une irrigation superficielle avait une influence positive

sur la croissance (augmentation de la circonférence du tronc et de la taille des feuilles) et le statut hydrique (potentiel foliaire) de ces arbres. Il est également clairement apparu que les premières pluies de mousson déterminent l'émission de nouvelles racines superficielles. Des observations réalisées dans les 10 premiers cm de sol d'une forêt de plaine semi-décidue au Panama indiquent une production de racines très saisonnière qui se produit notamment pendant les périodes de transitions de sec à humide, et humide à sec (Cavelier et al. 1999).

L'émission de racines fines superficielles en début de saison des pluies permet très probablement de capter l'infiltration correspondant aux premières averses et ainsi de répondre aux besoins liés a l'émergence et au développement des nouvelles feuilles (Singh and Srivastava 1985; Singh and Srivastava 1986; Srivastava et al. 1986). A l'opposé, dans le cas de sécheresse induite par exclusion de pluie, nous avons pu constater que la foliation et la défoliation se désynchronisent du rythme saisonnier des pluies, très certainement du fait de la disparition du captage des précipitations par l'enracinement superficiel. Dans un tel cas de figure, le teck supplée à ses besoins en eau à partir d'horizons de sol plus profonds, peu ou pas affectés par l'exclusion de pluie. Cette perturbation écophysiologique induit un arrêt quasi-total de la croissance des troncs et des branches, une réduction du nombre et de la taille des feuilles, ainsi qu'une réduction de leur teneur en eau et une baisse du potentiel hydrique foliaire.

Nous avons observé qu'un sous-bois clairsemé a poursuivi sa croissance sous la toiture utilisée pour l'exclusion de pluie dans la plantation de teck au Laos, apparemment insensible à l'absence de pluie pendant les deux années de l'expérimentation. A l'inverse du teck, ces plantes de couvert forestier ne semblent donc pas ou très peu dépendantes des ressources en eau de surface. Se développant dans un contexte de forte compétition, elles ont probablement développé une capacité supérieure à exploiter les ressources en eau disponible de manière hétérogène le long du profil de sol (Casper and Jackson 1997 ; Verweij et al. 2011).

Les observations en puits d'accès dans la plantation de teck de même que les prélèvements destructifs séquentiels à la tarière démontrent qu'aucune racine fine n'a été émise dans les premiers mètres du profil, suite à l'exclusion de pluie. Pourtant, les tensions de l'eau dans le sol en dessous de 1,5 m ne semblent pas limitantes pour l'extraction d'eau (Bengough et al. 2011). Il est ici important de rappeler que la diffusion de l'eau dans le sol est dépendante de nombreux facteurs, dont la texture du sol (Bruckler et al. 2004). Dans le cas de

l'expérimentation avec exclusion de pluie, la texture argileuse du sol jusqu'à 3-4 m induit des valeurs de conductivité hydraulique du sol inférieures à 1 mm par jour, ce qui représente un frein au mouvement de l'eau et à son absorption (Javaux et al. 2013)

Pourquoi le teck n'utilise pas d'avantage l'eau présente plus en profondeur ? Sans création de nouvelles racines, la capacité d'absorption de l'arbre peut se trouver limitée. En effet, nous pouvons émettre l'hypothèse que l'assimilation de l'eau et des nutriments est plus efficace au niveau des tissus racinaires les plus jeunes, dans les zones juste en amont des apex (Zarebanadkouki et al. 2013) qu'au niveau des tissus racinaires plus âgés (Doussan et al. 1998). Le vieillissement et la nécrose des tissus racinaires engendrent par ailleurs une chute des capacités d'absorption du système racinaire (Wells and Eissenstat, 2002)

Nous ne pouvons dissocier cette réflexion des interactions microbiennes en liens avec la rhizosphère et l'humidité du sol. Nous n'avons pas pu développer ce volet dans nos recherches mais nous avons anticipé de futurs travaux en prélevant et conservant à -18 °c des échantillons de sol au contact des racines et à distance de manière régulière et sur différents sites. Nous avons profité de l'aménagement des puits pour effectuer ces prélèvements, nous affranchissant ainsi des risques de contamination des échantillons par des communautés microbiennes de différentes provenances.

Il est en effet certain que les zones rhizosphèriques sont dépendantes des conditions du milieu (Hinsinger et al. 2009), et la rhizosphère est par définition présente autour de toute racine quelle soit de surface ou de profondeur. A ce jour, peu de travaux ont été réalisés pour connaître s'il existe des différences dans la rhizosphère en fonction de la profondeur du sol. De nouveaux travaux indiquent des relations entre l'âge des racines et l'humidité de la rhizosphère (Carminati and Vetterlein 2013).

Concernant l'enracinement de surface, il a été démontré que l'évolution des teneurs en eau du sol influencée par les racines influe fortement sur les communautés présentes dans la rhizosphère (Bengough 2012). On peut donc faire l'hypothèse qu'en ayant pratiquement totalement réduit l'alimentation en eau à la surface du sol, nous avons aussi fortement perturbé les communautés vivantes dans la zone rhizosphérique. Cet impact peut avoir eu un effet sur les actions symbiotiques positives autour des racines (Drew 1975 ; Robinson et al. 1996) et ainsi, amplifier les difficultés d'accès aux ressources pour les arbres. Cependant il est également connu qu'il n'est pas nécessaire de développer de nombreuses racines pour

répondre aux besoins en eau notamment si certaines racines se trouvent en milieux plus favorables à l'absorption (McCully 1999; Passioura and Wetselaar 1972).

Du point de vue nutritionnel, nous n'avons pas noté d'écart significatif entre le rapport C/N des feuilles du traitement isolé et celui du témoin. Malgré le régime hydrique drastique imposé à la surface du sol, l'absence de développement de nouvelles racines dans de nouveaux horizons pose question. Bien que le fait que nous n'en ayons observé que très peu dans les fenêtres ne puisse permettre d'affirmer qu'il n'y ait pas eu d'émission de racines dans d'autres parties non visibles du profile, cette absence de croissance visible étonne, les valeurs de tension de l'eau dans le sol laissant l'eau encore accessible aux plantes (Eissenstat and Yanai 1997; Kramer and Boyer 1995). Un second paramètre limitant la croissance est la résistance à la pénétration. Les travaux de Bengough et al. (2011) indiquent que l'extension racinaire se trouve fortement ralentie, voir totalement annihilée, face à une augmentation de la résistance à la pénétration. Cependant les racines ont la faculté de croitre dans les zones à plus faible densité au sein d'une zone globalement compacte si leur diamètre le permet (Pierret et al. 2004). Nous ne voyons pas de raison à ce que ce constat ne puisse pas s'appliquer aux racines en profondeur. La résistance à la pénétration augmente fortement dès que le niveau de tension de l'eau dans le sol dépasse -2 à -2,5 bar (Bengough et al. 2011;Whalley and Bengough 2013) . Cette courbe générale nous indique que les valeurs mesurées sur notre site se trouvent à des niveaux de tension de sol égals à ceux pouvant limiter l'élongation racinaire. Nous pouvons donc retenir cette hypothèse comme une des explications possible à la très faible production de racines dans les zones que nous avons pu observer

b) L'hévéa en Thailande

Dans le cas de l'hévéa, dans le nord-est de la Thaïlande, nous avons pu observer une dynamique d'enracinement superficiel et profond moins dépendante des eaux de pluie de surface et avec des croissances racinaires significatives en fin de saison sèche. La foliation débute avant les premières pluies et la couverture foliaire est totalement en place lors des premiers pics de pluie. Cet information indique que l'hévéa dans cette zone, en adaptant son cycle, se rapproche du paradoxe des forêts subissant la mousson asiatique formant leurs feuille 1 à 2 mois avant les premières pluies de mousson (Elliott et al. 2006). Les arbres de la forêt de mousson indiennes adaptent cette stratégie phénologique afin d'optimiser l'utilisation des réserves d'eau du sous-sol pour l'activité photosynthétique afin de compenser une saison

de croissance courte pendant la période humide (Kushwaha and Singh 2005). La phénologie de ces forêts semble être contrôlée par l'abondance du stockage d'eau en profondeur et le photopériodisme pour la foliation, paramètre qui détermine aussi la phénologie des arbres dans d'autres espèces forestières tropicales sèches (Borchert 1994; Borchert and Rivera 2001; Rivera et al. 2002).

L'hévéa dans ces conditions climatiques sub-optimales ou difficiles s'adapte à celles-ci (Priyadarshan et al. 2005). L'hévéa dans le Nord-Est de la Thaïlande - le même clone (RRIM600) que celui cultivé dans des zones plus pluvieuses (Carr 2011) - a dans cette région adapté sa phénologie au point d'avoir une période de défoliation totale, ce qui n'est normalement pas le cas pour ce clone. Les stress liés aux manques d'eau sont considérés comme un des facteurs déterminants le rythme de la phénologie (Murphy and Lugo 1986). Nous avons pu observer des croissances racinaires réparties sur l'ensemble du profil de 4,5 m avec des niveaux à plus fortes émergences.

Cet élément peut être justifié par la possibilité qu'en profondeur nous observions des racines de niveau d'ordre différents et donc de diamètre plus faible (Eissenstat and Yanai 1997). La demi-vie des racines fines (< 1 mm) pour l'essentiel du profil reste inférieure à une année et est légèrement supérieure pour les racines observées dans le premier mètre (diamètre > 1 mm). Nous pouvons lier cette information aux études proposées par (Wu et al. 2013) qui confirment l'effet du diamètre et de l'ordre sur la durée de vie de la racine. La durée de vie observée en surface et en profondeur ne semble pas aller dans le sens de nombreuses publications indiquant une durée de vie supérieure pour les racines profondes (Eissenstat and Yanai 1997). Mais comme le rappelait Strand et al. en 2008, il est aussi important de ne pas oublier les problèmes d'observations des diamètres de racines en liens avec leurs durées de vie et les régulières surestimations de leur renouvellement.

Nous pouvons émettre l'hypothèse que, comme pour le cycle végétatif aérien, l'hévéa dans ce contexte ne puisse pas maintenir un réseau de racines actives pendant plusieurs années, et donc assure un renouvellement fréquent de son stock racinaire fin. Ce renouvellement se fait régulièrement avec des pics en fin de saison sèche et en saison des pluies, qui semble être en équilibre entre la réponse aux besoins de la plante et la disponibilité des ressources dans le sol ou dans la plante.

Nous pouvons aussi émettre une seconde hypothèse rejoignant celle proposée pour notre expérimentation sur le teck, mettant en avant que la performance des capacités d'extraction de l'eau et des nutriments par les racines est supérieure pour des tissus et racines jeunes dans les parties apicales (North 2004), et que les zone préférentielles d'absorption évoluent avec la croissance racinaire. Une de mes hypothèses serait qu'une « dormance « longue des racines pourrait induire un vieillissement des tissus et pourrait donc conduire à un renouvellement plus fréquent des racines.

Nous pouvons aussi envisager le fait que pour certaines fonctions des racines, tant que les fonctions sont utilisées, les racines sont maintenues. Si la fonction n'est plus utilisée pour cause de sécheresse par exemple, des mécanismes peuvent permettre à la plante le maintient de son réseau, ou pas, ainsi que la « réactivation » d'une partie de celui-ci lorsque les conditions favorables sont à nouveau présentes (Peek et al. 2006). Dans ce cas de très forte contrainte, il peut être observé que tout ou une partie des tissus racinaires en place puissent dépérir (Peek et al. 2006) comme cela a été démontré pour les parties aériennes comme les branches (Rood et al. 2000) ou les feuilles (Kozlowski and Pallardy 2002). Sur cette même plantation, nous avons pu observer pour l'hévéa le dépérissement de certaines branches qui meurent et se retrouvent au sol. Une partie de celles-ci sont renouvelées l'année suivante en saison favorable (Peek et al. 2006). Dans un contexte aussi difficile pour l'hévéa au point qu'apparaissent des troubles de production de latex, voire un arrêt total (Do et al. 2011; Limpinuntana and Pannengpetch 2012; Priyadarshan et al. 2005), il est possible d'envisager que le renouvellement d'une grande partie de son système racinaire puisse être aussi une forme d'adaptation.

4.1.2 Le stockage de carbone

La biomasse du système racinaire du teck que nous avons pu mesurer dépasse les 45% de la biomasse totale de l'arbre. Si nous n'avons pas trop de difficulté à nous assurer que la totalité de la biomasse aérienne est prise en compte, il est en revanche plus difficile d'évaluer la totalité de la biomasse racinaire. Des racines ont été trouvées dans des échantillons jusqu'à 12 m de profondeur. Pour des raisons techniques, nous n'avons pas pu faire de prélèvements plus profonds, laissant subsister une incertitude sur la profondeur maximum d'enracinement du teck dans ce milieu. La collecte et l'observation des racines les plus fines se heurtent par

ailleurs a diverses limites techniques, qui induisent nécessairement une sous-évaluation des longueurs et biomasses racinaires (Brown and Upchurch 1987; Maeght et al. 2013; Vogt et al. 1995). Le bilan global de la biomasse que nous avons obtenue est donc de fait un minimum, les valeurs réelles de la biomasse souterraine étant probablement encore supérieures.

Comme pour le teck, notre étude de l'enracinement superficiel et profond pour l'hévéa indique des capacités de stockage de la biomasse souterraine supérieure aux données de la littérature (Wauters et al. 2008; Saengruksawong and Khamyong 2012) et ceci même si nous n'avons pas atteint la profondeur maximum d'enracinement et que nous sommes limités aux parties visibles et échantillonnables de cette biomasse.

Cette sous-estimation probable de la masse de carbone stocké dans les racines des arbres étant liée au déficit d'études explorant le profil de sol sur une profondeur significative, on peut considérer qu'il s'agit une tendance générale pour de nombreuses espèces d'arbres.

La durabilité de ce stock dans le sol dépend de facteurs édaphiques et climatiques mais plusieurs études tendent à montrer que les durées de stockage du carbone d'origine racinaire pourraient être positivement corrélées à la profondeur du sol (Pregitzer 2002 ; Norby et al. 2004). Dans le même temps, certains travaux ont montré que l'injection de carbone en profondeur pourrait stimuler l'activité microbienne du sol et ainsi accélérer la dégradation de la matière organique d'origine racinaire (Fontaine et al. 2007). Par ailleurs, des travaux récents montrent que seule une fraction limitée de la surface des particules argileuses pourrait contribuer à la séquestration effective de matière organique (Vogel et al., 2014). L'estimation la plus précise possible des stocks de carbone en profondeur, en lien avec des études détaillées sur les mécanismes de protection de la matière organique, pourra à terme apporter des informations précieuses quant à la nature du « missing sink » souvent évoqué dans la littérature relative au cycle du carbone à l'échelle globale (Esser et al. 2011; Jackson et al. 1997).

4.1.3 Modélisation et perspectives

D'un point de vue plus général, ces études *in situ* démontrent clairement l'influence de la sècheresse sur la dynamique de l'enracinement qui s'est exprimé de différentes façons selon les cas étudiés et en fonction des profondeurs. Les dynamiques étudiées semblent bien reposer sur la nécessité de la plante à s'alimenter au maximum durant les périodes les plus favorables

jusqu'au limite de ces capacités et de favoriser les périodes de repos lorsque les conditions climatiques deviennent inhabituelles et /ou moins favorable. Les difficultés rencontrées par le teck à répondre à un changement radical et soudain de la quantité et de la localisation des ressources en eau sont un exemple marquant. Malgré la soudaineté du changement imposé, le teck a démontré sa capacité de survie et même à reprendre une croissance dès la deuxième année. Pour un arbre qui semble habituellement tirer l'essentiel de son approvisionnement en eau du premier mètre du sol, son réseau racinaire s'étend pourtant largement en profondeur, facteur probablement essentiel lui ayant permis de s'adapter au changement radical intervenu. Nous rejoignons ici la notion de safety net introduite par certains auteurs ? En ce sens, l'expression utilisée par Schenk en (2008) pour qualifier l'étendue des systèmes racinaires comme étant un réseaux « aussi près que possible de la surface mais également aussi profond que nécessaire » paraît incomplète.

Les données récoltées dans nos études sont autant de valeurs d'entrées potentielles pour les travaux de modélisation visant à simuler le fonctionnement des plantes. La plasticité du système racinaire, l'évolution de ses fonctions en lien avec l'âge des racines, la variabilité du milieu rhizosphérique en fonction des conditions environnementales et de la profondeur démontre à nouveau les difficultés liées à cette tâche.

Simuler l'évolution des plantes entières reste un exercice très complexe même par le biais de simplifications. Très peu de données existent sur la dynamique de croissance d'une plante dans sa globalité, incluant l'ensemble de son système racinaire. Malgré les efforts consentis dans le cadre des deux expérimentations présentées dans cette thèse, les données recueillies ici ne peuvent combler que partiellement les informations manquantes sur la totalité du profil racinaire. Par ailleurs, au regard des interactions entre couvert végétal et conditions environnementales et climatiques, ce sont des informations sur les communautés d'espèces dont une part importante d'arbres adultes, et non seulement des données à l'échelle de la plante entière, qui sont nécessaires.

La réalisation de ce type d'expérimentations visant à étudier l'enracinement de manière la plus étendue possible sur un peuplement établi reste complexe et lourde à réaliser mais elle a été l'occasion de collecter des données originales. Elle ouvre aussi la possibilité de valoriser et d'exploiter d'avantage ces installations en favorisant un travail pluridisciplinaire pour mieux comprendre certains processus encore peu ou pas étudiés à de telles profondeurs,

comme par exemple les interactions entre sol, racines et communautés microbiennes, ou encore les mécanismes régissant la durée de stockage de la biomasse souterraine.

4.1.4 Les recommandations agronomiques

Du point de vue des paysans producteurs, la production de latex dans le nord-est de la Thaïlande semble affectée par les limites dans la capacité d'adaptation de l'hévéa à un environnement défavorable. Le mode d'exploitation du latex calqué sur celui des zones bénéficiant d'une pluviométrie plus abondante, même avec une interruption des saignées durant les périodes de défoliation, devrait être revu afin de permettre aux producteurs de continuer à tirer profit de leurs plantations sur le long terme. Le nombre important d'arbres ayant cessé de produire du latex afin, nous pouvons le supposer, d'assurer leur survie, est là pour les alerter. Des exemples de plantation dans des conditions climatiques encore plus défavorables ont eux dépassé les limites d'adaptation de l'espèce. Ces plantations ne pourront probablement jamais entrer valablement en production tout en ayant mobilisé des terres sur de nombreuses années (Carr 2011; Priyadarshan et al. 2005).

Chercher à produire aux limites de capacités d'adaptations d'une espèce demande avant tout une connaissance parfaite de ses besoins physiologiques et une parfaite adaptation des itinéraires techniques. D'autres approches peuvent être proposées, notamment en réduisant la densité des arbres et en adaptant mieux le rythme d'exploitation. Favoriser les possibilités d'association de production afin de favoriser les synergies entre espèces (Liste and White 2008; Pretzsch et al. 2014) permettrait aux exploitants de tirer profit de leur surface agricole en étant moins dépendant des cours d'un produit unique. Ces associations ne doivent pas entrer en compétition sur des éléments clefs du cycle de production de chaque espèce (Sekiya et al. 2010).

L'influence constatée de la disponibilité en eau de surface sur la capacité de croissance du teck pourrait être mis à profit par les familles laotiennes possédant des petites plantations. Il leur serait par exemple possible de favoriser l'infiltration de l'eau en mettant en œuvre des aménagements simples visant à ralentir le ruissellement des eaux de pluie dont il a été démontré l'importance dans ces zones en liens avec une faible infiltration (Janeau and Bricquet 2003; Valentin et al. 2008). Par exemple l'arrêt du brulis et le maintien du couvert végétale sous plantation permettrait à la fois de ralentir les eaux de ruissellement et d'éviter l'érosion liée à l'impact des gouttes de pluies (Pierret et al. 2011b; Ribolzi et al. 2011).

L'utilisation de techniques de lutte anti-érosive active ou passive pourrait fournir un double bénéfice en limitant les pertes en terre et en favorisant la croissance annuelle du teck en profitant de ses particularités.

4.2 Conclusion générale

Notre travail a permis d'observer l'effet de la sécheresse sur plusieurs mètres d'enracinement pour deux espèces : l'hévéa et le teck. Nous avons pu, par le biais d'un suivi sur le moyen terme (3 ans), observer la diversité de leurs réponses (en termes de croissance et de statut physiologique de leurs parties végétatives aériennes et souterraines) à des conditions climatiques marginales (accès réduit à la ressource en eau), apportant ainsi des données nouvelles pour la modélisation.

Ce travail a notamment permis de montrer que :

- l'enracinement superficiel et profond de l'hévéa demeure actif (émission de nouvelles racines et élongation) même en l'absence de pluie.

- l'hévéa émet des racines fines à toutes les profondeurs > 50 cm en fin de saison sèche, disposant ainsi de racines jeunes dès les premières pluies.

- dans le contexte étudié, l'hévéa atteint les limites de sa capacité de production qui semble conduire à l'arrêt de production de latex mais ne perturbe pas sa croissance.

- le teck semble être très bien adapté à l'exploitation maximale de la pluviométrie dans le premier mètre de sol en favorisant l'émission racinaire dans ce même espace dès les premières pluies. Ce caractère lui permet de tirer profit de conditions édaphiques et climatiques avec un sol à faible conductivité hydraulique et des pluies de fortes intensités limitant la recharge en eau du sol.

- le teck, suite à la suppression pratiquement totale des apports d'eau à la surface du sol pendant deux ans, a réussi à survivre, et après un temps d'adaptation, a modifié ses périodes de feuillaison/défeuillaison. Certains arbres semblent en mesure de reprendre une croissance minimale.

- les limites de l'enracinement de l'hévéa et du teck se situent respectivement au delà de 5 et de 12 mètres de profondeur, c'est- à -dire plus profondément que ce qui est le plus généralement admis.

- l'enracinement mesuré représente une part significative de la biomasse des arbres atteignant pratiquement des valeurs 50% supérieures à celles qui sont communément retenues pour ces espèces.

4.3 Perspectives de recherches

Nos études ouvrent également des champs sur de nouvelles perspectives et sur l'intérêt d'effectuer de nouvelles recherches suite aux questionnements que nous avons pu rencontrer.

Les traits racinaires au-delà d'1 mètre de profondeur mériteraient d'être davantage étudiés en s'attachant également à compléter les connaissances de la dynamique microbienne et des interactions avec la rhizosphère pour ces mêmes horizons profonds. L'âge des racines reste un point clef encore peu renseigné, notamment son effet sur l'évolution des fonctions racinaires, et sur la vitesse de croissance d'une racine en fonction de son ordre. L'âge de la racine et sa profondeur influence-t-elle la vitesse de sénescence et sa dégradation ?

Le fait que certaines racines puissent rester en phase de dormance plus ou moins longtemps reste aussi à étudier. Quels sont les facteurs déclenchant la dormance et ceux déterminants la reprise d'activité ? Dans les cas de reprise d'activités, quelle est l'importance de cette reprise d'activité vis à vis des capacités antérieures de cette même racine ? La dormance prolongée d'une partie du réseau racinaire peut-elle influencer l'émission de nouvelles racines de remplacement plus jeunes? Existe-t-il une différence face à cette dormance en fonction de l'ordre des racines et y a-t-il un effet de la profondeur sur celle-ci ? Quels peuvent être les liens entre durée de dormance et mortalité de la racine ?

Des perspectives existent aussi sur les possibilités de modélisation prenant d'avantage en compte l'enracinement superficiel et profond comme un ensemble interdépendant.

4.4 Références

Arcadius, Y., Akossou, J., & Godui, A. (2012). Effect of Climatic Factors on the Radial Growth of Teak (Tectona grandis L.F.) in Parakou and Tchaourou districts in northern Benin. *Journal of Agricultural Science and Technology*, *2*, 721–730.

Bengough, a G., McKenzie, B. M., Hallett, P. D., & Valentine, T. a. (2011). Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany*, *62*(1), 59–68. doi:10.1093/jxb/erq350

Bengough, a. G. (2012). Water Dynamics of the Root Zone: Rhizosphere Biophysics and Its Control on Soil Hydrology. *Vadose Zone Journal*, *11*(2). doi:10.2136/vzj2011.0111

Bleby, T. M., McElrone, A. J., & Jackson, R. B. (2010). *Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant, cell & environment* (Vol. 33, pp. 2132–48). doi:10.1111/j.1365-3040.2010.02212.x

Borchert, R. (1994). Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology*, *75*(5), 1437–1449. Retrieved from http://www.jstor.org/stable/1937467

Borchert, R., & Rivera, G. (2001). Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiology*, *21*(4), 213–21. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11276415

Brown, D. A., & Upchurch, D. R. (1987). *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics*. (S. S. S. of A. American Society of Agronomy, Crop Science Society of America, Ed.). doi:10.2134/asaspecpub50

Bruckler, L., Lafolie, F., Doussan, C., & Bussières, F. (2004). *Modeling soil-root water transport with non-uniform water supply and heterogeneous root distribution*. *Plant and Soil* (Vol. 260, pp. 205–224). doi:10.1023/B:PLSO.0000030187.33135.b8

Carminati, A., & Vetterlein, D. (2013). Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. *Annals of Botany*, *112*(2), 277–90. doi:10.1093/aob/mcs262

Carr, M. K. V. (2011). THE WATER RELATIONS OF RUBBER (HEVEA BRASILIENSIS): A REVIEW. *Experimental Agriculture*, *48*(02), 176–193. doi:10.1017/S0014479711000901

Casper, B. B., & Jackson, R. B. (1997). Plant Competition Underground. *Annual Review of Ecology and Systematics*, *28*(1), 545–570. doi:10.1146/annurev.ecolsys.28.1.545

Cavelier, J., Wright, S. J., & Santamaría, J. (1999). Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. *Plant and Soil*, *211*(2), 207–213. doi:10.1023/A:1004686204235

Dié, A., Kitin, P., Kouamé, F. N., Van den Bulcke, J., Van Acker, J., & Beeckman, H. (2012). Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (Tectona grandis) in Ivory Coast. *Annals of Botany*, *110*(4), 861–73. doi:10.1093/aob/mcs145

Do, F. C., Pierret, A., Couteron, P., Lesturgez, G., Boithias, L., Isarangkool Na Ayutthaya, S., … Nandris, D. (2011). Spatial distribution of Hevea brasiliensis trunk phloem necrosis within a plot: aggregation but no evidence of constraint on cumulated growth. *Forest Pathology*, *41*(2), 90–100. doi:10.1111/j.1439-0329.2010.00640.x

Doussan, C., Vercambre, G., & Pagés, L. (1998). Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption—Distribution of axial and radial conductances in maize. *Annals of Botany*, *81*, 225–232. Retrieved from http://aob.oxfordjournals.org/content/81/2/225.short

Drew, M. C. (1975). Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. *New Phytologist*. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.1975.tb01409.x/abstract

Eissenstat, D. M., & Yanai, R. D. (1997). The Ecology of Root Lifespan Advances in Ecological Research. In *Advances* (Vol. 27, pp. 1–60). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Elliott, S., Baker, P., & Borchert, R. (2006). Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and …*, 1–10. doi:10.1111/j.1466-822x.2006.00213.x

Esser, G., Kattge, J., & Sakalli, A. (2011). *Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere*. *Global Change Biology* (Vol. 17, pp. 819–842). doi:10.1111/j.1365-2486.2010.02261.x

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). *Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature* (Vol. 450, pp. 277–80). doi:10.1038/nature06275

Hinckley, T. M., Richter, H., & Schulte, P. J. (1991). Water relations. In J. Wiley (Ed.), *Physiology of trees* (A.S. Ragha., pp. 137–162). New York.

Hinsinger, P., Bengough, a. G., Vetterlein, D., & Young, I. M. (2009). *Rhizosphere: biophysics, biogeochemistry and ecological relevance*. *Plant and Soil* (Vol. 321, pp. 117–152). doi:10.1007/s11104-008-9885-9

Jackson, R. B., Mooney, H. a, & Schulze, E. D. (1997). *A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of the National Academy of Sciences of the United States of America* (Vol. 94, pp. 7362–6). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Janeau, J., & Bricquet, J. (2003). Soil crusting and infiltration on steep slopes in northern Thailand. *… Journal of Soil …*, (September), 543–553. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2389.2003.00494.x/full

Javaux, M., Couvreur, V., Vanderborght, J., & Vereecken, H. (2013). Root Water Uptake: From Three-Dimensional Biophysical Processes to Macroscopic Modeling Approaches. *Vadose Zone Journal*, *12*(4). doi:10.2136/vzj2013.02.0042

Kozlowski, T. T., & Pallardy, S. G. (2002). Acclimation and Adaptive Responses of Woody Plants to Environmental Stresses. *The Botanical Review*, *68*(2), 270–334. doi:10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2

Kramer, P. J., & Boyer, J. S. (1995). Roots and root systems. In I. CA: Academic Press (Ed.), *Water Relations of Plant and Soils* (P. J. Kram., pp. 116–166). San Diego.

Kushwaha, C. P., & Singh, K. P. (2005). Diversity of leaf phenology in a tropical deciduous forest in India. *Journal of Tropical Ecologylogy*, *21*, 47–57.

Limpinuntana, V., & Pannengpetch, K. (2012). *Short term effects of latex tapping on micro-changes of trunk girth in Hevea Brasiliensis*. *Australian Journal of* (Vol. 6, pp. 65–72). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Liste, H.-H., & White, J. C. (2008). *Plant hydraulic lift of soil water – implications for crop production and land restoration*. *Plant and Soil* (Vol. 313, pp. 1–17). doi:10.1007/s11104-008-9696-z

Maeght, J.-L., Rewald, B., & Pierret, A. (2013). How to study deep roots—and why it matters. *Frontiers in Plant Science*, *4*. doi:10.3389/fpls.2013.00299

Markewitz, D., Devine, S., Davidson, E. A., Brando, P., & Nepstad, D. C. (2010). Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. *The New Phytologist*, *187*(3), 592–607. doi:10.1111/j.1469-8137.2010.03391.x

Mccully, M. E. (1999). *ROOTS IN SOIL : Unearthing the Complexities of Roots and Their Rhizospheres* (pp. 695–718). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Murphy, P., & Lugo, A. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*, 67–88. Retrieved from http://www.jstor.org/stable/2096989

Norby, R. J., Ledford, J., Reilly, C. D., Miller, N. E., & Neill, E. G. O. (2004). *Fine-root production dominates response of a deciduous forest to atmospheric CO 2 enrichment*. *PNAS* (Vol. 101, pp. 9689–9693). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

North, E. G. (2004). A long drink of water: how xylem changes with depth. *New Phytologist*, *163*(3), 447–449. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.2004.01160.x/full

Passioura, J. B., & Wetselaar, R. (1972). Consequences of banding nitrogen fertilizers in soil. *Plant and Soil*, *36*(1-3), 461–473. doi:10.1007/BF01373498

Peek, M., Leffler, A., & Hipps, L. (2006). Root turnover and relocation in the soil profile in response to seasonal soil water variation in a natural stand of Utah juniper (Juniperus osteosperma). *Tree Physiology*, *26*(11), 1469–76. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16877331

Pierret, A., de Rouw, A., Chaplot, V., Valentin, C., Noble, A., Suhardiman, D., & Drechsel, P. (2011). *Reshaping upland farming policies to support nature and livelihoods: lessons from soil erosion in Southeast Asia with emphasis on Lao PDR. [Management of Soil Erosion Consortium (MSEC) Project report]* (p. 40 p). Marseille, France: Institut de Recherche pour le Développement (IRD); Colombo, Sri Lanka: International Water Management Institute (IWMI). doi:10.5337/2011.213

Pierret, A., Moran, C. J., & Doussan, C. (2004). *Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots*. *New Phytologist* (pp. 967–980). doi:10.1111/j.1469-8137.2005.01389.x

Pregitzer, K. (2002). *Fine roots of trees–a new perspective*. *New Phytologist* (Vol. 154, pp. 267–270). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Pretzsch, H., Rötzer, T., Matyssek, R., Grams, T. E. E., Häberle, K.-H., Pritsch, K., … Munch, J.-C. (2014). Mixed Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica [L.]) stands under drought: from reaction pattern to mechanism. *Trees*. doi:10.1007/s00468-014-1035-9

Priya, P. B., & Bhat, K. M. (1998). *False ring formation in teak (Tectona grandis L . f .) and the in ¯uence of environmental factors*. *Forest Ecology and Management* (Vol. 108, pp. 215–222). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Priyadarshan, P. M., Hoa, T. T. T., Huasun, H., & de Gonçalves, P. S. (2005). Yielding Potential of Rubber (Hevea brasiliensis) in Sub-Optimal Environments. *Journal of Crop Improvement*, *14*(1-2), 221–247. doi:10.1300/J411v14n01_10

Ribolzi, O., Patin, J., Bresson, L. M., Latsachack, K. O., Mouche, E., Sengtaheuanghoung, O., … Valentin, C. (2011). Impact of slope gradient on soil surface features and infiltration on steep slopes in northern Laos. *Geomorphology*, *127*(1-2), 53–63. doi:10.1016/j.geomorph.2010.12.004

Rivera, G., Elliott, S., Caldas, L. S., Nicolossi, G., Coradin, V. T. R., & Borchert, R. (2002). Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees*, *16*(7), 445–456. doi:10.1007/s00468-002-0185-3

Robinson, D., Crop, S., & Dd, D. (1996). Resource Capture by Localized Root Proliferation : Why Do Plants Bother ?, (July 1995), 179–185.

Rood, S. B., Patiño, S., Coombs, K., & Tyree, M. T. (2000). Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees*, *14*(5), 0248–0257. doi:10.1007/s004680050010

Saengruksawong, C., & Khamyong, S. (2012). Growths and Carbon Stocks of Para Rubber Plantations on Phonpisai Soil Series in Northeastern Thailand. *Rubber Thai Journal*, *18*(January), 1–18. Retrieved from http://www.rubberthai.com/book/journal/vol1/vol1-2.pdf

Schenk, H. J. (2008). The Shallowest Possible Water Extraction Profile: A Null Model for Global Root Distributions. *Vadose Zone Journal*, *7*(3), 1119. doi:10.2136/vzj2007.0119

Sekiya, N., Araki, H., & Yano, K. (2010). Applying hydraulic lift in an agroecosystem: forage plants with shoots removed supply water to neighboring vegetable crops. *Plant and Soil*, *341*(1-2), 39–50. doi:10.1007/s11104-010-0581-1

Singh, K. P., & Srivastava, K. (1986). Seasonal variation in the biomass and non-structural carbohydrate content of fine roots of teak (Tectona grandis L. f.) plantations in a dry tropical region. *Tree Physiology*, *1*(1), 31–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14975904

Singh, K., & Srivastava, S. (1985). Seasonal variations in the spatial distribution of root tips in teak (Tectonia grandis Linn. f.) plantations in the Varanasi Forest Division, India. *Plant and Soil*, *84*, 93–104. Retrieved from http://link.springer.com/article/10.1007/BF02197870

Srivastava, S. K., Singh, K. P., & Upadhyay, R. S. (1986). Fine root growth dynamics in teak (Tectona grandis Linn. F.). *Canadian Journal of Forest Research*, *16*(6), 1360–1364. doi:10.1139/x86-240

Strand, A. E., Pritchard, S. G., McCormack, M. L., Davis, M. A., & Oren, R. (2008). Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science (New York, N.Y.)*, *319*(5862), 456–8. doi:10.1126/science.1151382

Valentin, C., Agus, F., Alamban, R., Boosaner, A., Bricquet, J. P., Chaplot, V., … Vadari, T. (2008). *Agriculture , Ecosystems and Environment Runoff and sediment losses from 27 upland catchments in Southeast Asia : Impact of rapid land use changes and conservation practices* (Vol. 128, pp. 225–238). doi:10.1016/j.agee.2008.06.004

Verweij, R. J. T., Higgins, S. I., Bond, W. J., & February, E. C. (2011). *Water sourcing by trees in a mesic savanna: Responses to severing deep and shallow roots*. *Environmental and Experimental Botany* (Vol. 74, pp. 229–236). Elsevier B.V. doi:10.1016/j.envexpbot.2011.06.004

Vogt, K., Vogt, D., Palmiotto, P., Boon, P., & O'Hara, J. (1995). *Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species*. *Plant and soil* (pp. 159–219). Retrieved from http://www.archive.org/details/plantrelationsfi00coul

Wauters, J. B., Coudert, S., Grallien, E., Jonard, M., & Ponette, Q. (2008). Carbon stock in rubber tree plantations in Western Ghana and Mato Grosso (Brazil). *Forest Ecology and Management*, *255*(7), 2347–2361. doi:10.1016/j.foreco.2007.12.038

Whalley, W. R., & Bengough, A. G. (2013). Soil Mechanical Resistance and Root Growth and Function (pp. 1–15).

Wu, Y., Deng, Y., Zhang, J., Wu, J., Tang, Y., Cao, G., … Cui, X. (2013). Root size and soil environments determine root lifespan: evidence from an alpine meadow on the Tibetan Plateau. *Ecological Research*, *28*(3), 493–501. doi:10.1007/s11284-013-1038-9

Zarebanadkouki, M., Kim, Y. X., & Carminati, A. (2013). Where do roots take up water? Neutron radiography of water flow into the roots of transpiring plants growing in soil. *The New Phytologist*, *199*(4), 1034–44. doi:10.1111/nph.12330

Zeppel, M. J. B., Wilks, J. V., & Lewis, J. D. (2014). Impacts of extreme precipitation and seasonal changes in precipitation on plants. *Biogeosciences*, *11*(11), 3083–3093. doi:10.5194/bg-11-3083-2014

5. Références Globales

Abbott ML, Fraley L, Allen MF, et al. (1991) A review: Radiotracer methods to determine root distribution Bidirectional water flows through the soil-fungal-plant mycorrhizal continuum A model for hydraulic redistribution incorporating coupled soil-root moisture transport diversity for osmotic adjust. Environ Exp Bot 31:1–10.

Abiven S, Recous S, Reyes V, Oliver R (2005) Mineralisation of C and N from root, stem and leaf residues in soil and role of their biochemical quality. Biol Fertil Soils 42:119–128. doi: 10.1007/s00374-005-0006-0

ACIAR (1985) Smallholder rubber production and policies. Smallhold. rubber Prod. policies. ACIAR, Adelaide, p 151

Alcântara BK, Veasey EA (2013) Genetic diversity of teak (Tectona grandis L.F.) from different provenances using microsatellite markers. Rev Árvore 37:747–758. doi: 10.1590/S0100-67622013000400018

Allen CD, Macalady AK, Chenchouni H, et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684. doi: 10.1016/j.foreco.2009.09.001

Allen RG, Pereira LS, Raes D, et al. (1998) Crop evapotranspiration - Guidelines for computing crop water requirements - FAO Irrigation and drainage paper 56 By. 1–15.

Allen SC, Jose S, Nair PKR, et al. (2004) Competition for 15 N-labeled fertilizer in a pecan (Carya illinoensis K . Koch) -cotton (Gossypium hirsutum L .) alley cropping system in the southern United States. 151–164.

Angers DA, Caron J (1998) Plant-inducted changes in soil structures: Processes and feedbacks. Biogeochemistry 42:55–72. doi: 10.1023/A:1005944025343

Anon (2012) Germplasm Resources Information Network (GRIN). In: USDA, ARS, Natl. Genet. Resour. Program, Natl. Germplasm Resour. Lab. Beltsville, Maryl.

Arcadius Y, Akossou J, Godui A (2012) Effect of Climatic Factors on the Radial Growth of Teak (Tectona grandis L.F.) in Parakou and Tchaourou districts in northern Benin. J Agric Sci Technol 2:721–730.

De Azevedo MCB, Chopart JL, Medina C de C (2011) Sugarcane root length density and distribution from root intersection counting on a trench-profile, Sci. agric. Sci agric (Piracicaba, Braz) 68:94–101.

Bailey JD, Harjanto NA (2005) Teak (Tectona grandis L.) tree growth, stem quality and health in coppiced plantations in Java, Indonesia. New For 30:55–65. doi: 10.1007/s11056-004-1116-5

Baitulin IO (1979) Kornevaja sistema rastenij aridnoj zony Kazakhstana. [Root systems of plants of the arid zone of Kazakhstan.]. Vestn. sel'skokhoziaistvennoi Nauk. Kazakhstana. In Russian:

Bakker MR (1999) Fine-root parameters as indicators of sustainability of forest ecosystems. For Ecol Manage 122:7–16. doi: 10.1016/S0378-1127(99)00028-6

Bardgett RD (2011) Plant-soil interactions in a changing world. F1000 Biol Rep 3:16. doi: 10.3410/B3-16

Bates GH (1937) A Device for the Observation of Root Growth in the Soil. Nature 139:966–967. doi: 10.1038/139966b0

Bengough a G, McKenzie BM, Hallett PD, Valentine T a (2011) Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. J Exp Bot 62:59–68. doi: 10.1093/jxb/erq350

Bengough a. G (2012) Water Dynamics of the Root Zone: Rhizosphere Biophysics and Its Control on Soil Hydrology. Vadose Zo J. doi: 10.2136/vzj2011.0111

Bengough AG, Castrignano A, Pagès L, Noordwijk M van (2000) Sampling Strategies, Scaling, and Statistics. Root Methods. Springer Berlin Heidelberg, pp 147–173

Bengough AG, Croser C, Pritchard J (1997) A biophysical analysis of root growth under mechanical stress. 155–164.

Bergeron M, Lacombe S, Bradley RL, et al. (2011) Reduced soil nutrient leaching following the establishment of tree-based intercropping systems in eastern Canada. Agrofor Syst 83:321–330. doi: 10.1007/s10457-011-9402-7

Bhat K, Hwan MO (2004) Teak growers unite. ITTO Trop For Updat 14:3–5.

Bhat KM (2000) Le bois de teck. Bois forets des Trop. 263:

Bhat KM, Balasundaran M, Bhat K V, et al. (2007) Processing and Marketing of teak wood products of Planted Forests. Teak Reg. Work shop. Peechi, pp 1–336

Biology GC, Hole W, Isoto E, et al. (2006) Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. 217–229. doi: 10.1111/j.1365-2486.2005.01063.x

Bleby TM, McElrone AJ, Jackson RB, et al. (1963) Water uptake and hydraulic redistribution across large woody root systems to 20 m depth A study of the rooting habits of rimu and tawa in pumice soils Maximum rooting depth of vegetation types at the global scale Structure and dynamics of the root system. Plant Cell Environ 33:2132–2148.

Bleby TM, McElrone AJ, Jackson RB (2010) Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant Cell Environ 33:2132–48. doi: 10.1111/j.1365-3040.2010.02212.x

Blossfeld S, Gansert D, Thiele B, et al. (2011) The dynamics of oxygen concentration, pH value, and organic acids in the rhizosphere of Juncus spp. Soil Biol Biochem 43:1186–1197. doi: 10.1016/j.soilbio.2011.02.007

Böhm W (1979) Methods of studying root systems. 188.

Boithias L, Do FC, Isarangkool Na Ayutthaya S, et al. (2011) Transpiration, growth and latex production of a Hevea brasiliensis stand facing drought in northeast Thailand: The use of the WaNuLCAS model as an exploratory tool. Exp Agric 48:49–63. doi: 10.1017/S001447971100086X

Borchert R (1994) Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. Ecology 75:1437–1449.

Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol 21:213–21.

Bovard BD, Curtis PS, Vogel CS, et al. (2005) Environmental controls on sap flow in a northern hardwood forest. Tree Physiol 25:31–8.

Boyce KC (2005) The evolutionary history of roots and leaves. In: Elsevier C (ed) Vasc. Transp. Plants, NM Holbroo. San Diego, pp 479–500

Breazeale JF (1930) Maintenance of moisture-equilibrium and nutrition of plants at and below the wilting percentage. Agric Exp Stn Tech Bull 137–177.

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–644. doi: 10.1051/forest

Bridhikitti A (2013) Atmospheric aerosol layers over Bangkok Metropolitan Region from CALIPSO observations. Atmos Res 127:1–7. doi: 10.1016/j.atmosres.2013.02.008

Brown DA, Upchurch DR (1987) Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. doi: 10.2134/asaspecpub50

Bruckler L, Lafolie F, Doussan C, Bussières F (2004) Modeling soil-root water transport with non-uniform water supply and heterogeneous root distribution. Plant Soil 260:205–224. doi: 10.1023/B:PLSO.0000030187.33135.b8

Bruijnzeel L a. (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? Agric Ecosyst Environ 104:185–228. doi: 10.1016/j.agee.2004.01.015

Brunner I, Godbold DL (2007) Tree roots in a changing world. J For Res 12:78–82. doi: 10.1007/s10310-006-0261-4

Bryant RL (1997) The Political Ecology of Forestry in Burma: 1824 - 1994. 1–247.

Burgess SSO (2000) Seasonal Water Acquisition and Redistribution in the Australian Woody Phreatophyte, Banksia prionotes. Ann Bot 85:215–224. doi: 10.1006/anbo.1999.1019

Burgess SSO (2010) Can hydraulic redistribution put bread on our table? Plant Soil 341:25–29. doi: 10.1007/s11104-010-0638-1

Burgess SSO, Adams MA, Turner NC, Ong CK (1998) The redistribution of soil water by tree root systems. Oecologia 115:306–311. doi: 10.1007/s004420050521

Buss HL, Bruns MA, Schultz MJ, et al. (2005) The coupling of biological iron cycling and mineral weathering during saprolite formation, Luquillo Mountains, Puerto Rico Hydraulic lift - Water efflux from upper roots improves effectiveness of water-uptake by deep roots Variation in leaf structure and. Geobiology 3:247–260. doi: 10.1007

Cahoon DR, Lynch JC, Knaus RM (1996) Improved cryogenic coring device for sampling wetland soils. J Sediment Res 66:1025–1027.

Calder IR, Rosier PTW, Prasanna KT, Parameswarappa S (1997) Eucalyptus water use greater than rainfall input - possible explanation from southern India. doi: 10:00:41

Caldwell MM, Richards JH (1998) Hydraulic lift : consequences of water ef flux from the roots of plants. Oecologia 151–161.

Cameron R (1963) A study of the rooting habits of rimu and tawa in pumice soils. NZJ 771–785.

Canadell J, Djema A, Lopez B, et al. (1999) Structure and dynamics of the root system. Ecol. Stud.

Canadell J, Jackson RB, Ehleringer JB, et al. (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595. doi: 10.1007/BF00329030

Cannon HL (1960) The development of botanical methods of prospecting for uranium on the Colorado Plateau. 1–50.

Cannon WA (1949) A Tentative Classification of Root Systems. Ecology 30:542. doi: 10.2307/1932458

Carbon BA, Bartle GA, Murray AM, Macpherson DK (1980) The Distribution of Root Length, and the Limits to Flow of Soil Water to Roots in a Dry Sclerophyll Forest. For Sci 26:656–664.

Cardon ZG, Whitbeck JL (2007) The Rhizosphere: An Ecological Perspective. 232.

Carminati A, Vetterlein D (2013) Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. Ann Bot 112:277–90. doi: 10.1093/aob/mcs262

Carr MK V. (2011) The water relations of rubber (Hevea Brasiliensis): a review. Exp Agric 48:176–193. doi: 10.1017/S0014479711000901

Casper BB, Jackson RB (1997) Plant Competition Underground. Annu Rev Ecol Syst 28:545–570. doi: 10.1146/annurev.ecolsys.28.1.545

Cavelier J, Wright SJ, Santamaría J (1999) Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. Plant Soil 211:207–213. doi: 10.1023/A:1004686204235

Cawte HJ, Boyd WE (2010) Laterite nodules: A credible source of iron ore in iron age northeast Thailand? Geoarchaeology 25:626–644. doi: 10.1002/gea.20326

Chaffey N (2013) Secondary Growth of Tree Roots: Cytoskeletal Perspectives. In: Taylor & Francis Group L (ed) Plant roots hidden half. pp 1–19

Chairungsee N, Gay F, Thaler P, et al. (2013) Impact of tapping and soil water status on fine root dynamics in a rubber tree plantation in Thailand. Front Plant Sci 4:1–11. doi: 10.3389/fpls.2013.00538

Chaix G, Monteuuis O, Garcia C, et al. (2011) Genetic variation in major phenotypic traits among diverse genetic origins of teak (Tectona grandis L.f.) planted in Taliwas, Sabah, East Malaysia. Ann For Sci 68:1015–1026. doi: 10.1007/s13595-011-0109-8

Cheng C-M, Wang R-S, Jiang J-S (2007) Variation of soil fertility and carbon sequestration by planting Hevea brasiliensis in Hainan Island, China. J Environ Sci (China) 19:348–52.

Chloupek O, Forster BP, Thomas WTB (2006) The effect of semi-dwarf genes on root system size in field-grown barley. Theor Appl Genet 112:779–86. doi: 10.1007/s00122-005-0147-4

Choat B, Jansen S, Brodribb TJ, et al. (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–5. doi: 10.1038/nature11688

Christina M, Laclau J-P, Gonçalves JLM, et al. (2011) Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. Ecosphere 2:art27. doi: 10.1890/ES10-00158.1

Clemmensen KE, Bahr A, Ovaskainen O, et al. (2013) Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. Science (80-) 339:1615–1618. doi: 10.1126/science.1231923

Clothier BE, Green SR, Deurer M (2007) Preferential flow and transport in soil: progress and prognosis. Eur J Soil Sci 59:2–13. doi: 10.1111/j.1365-2389.2007.00991.x

Collet C, Löf M, Pagès L (2006) Root System Development of Oak Seedlings Analysed using an Architectural Model. Effects of Competition with Grass. Plant Soil 279:367–383. doi: 10.1007/s11104-005-2419-9

Combeau A (1951) Observations sur les sols des Teckeraies dans la region de Sokodé. Lomé

Coulter JM (1899) Plant relation, first book of botany. 1 – 264.

Culver DC, Pipan T (2009) The Biology of Caves and Other Subterranean Habitats. 2009 256.

Dah-Dovonon V (2013) Dynamique des plantations privées de teck (Tectona grandis LF) dans le département de l'Atlantique (sud Bénin): Cas de la Commune de Tori-Bossito. e-Journal … 31–38.

Dalpé Y, Diop T, Plenchette C, Gueye M (2000) Glomales species associated with surface and deep rhizosphere of Faidherbia albida in Senegal. Mycorrhiza 125–129.

Danjon F, Reubens B (2008) Assessing and analyzing 3D architecture of woody root systems , a review of methods and applications in tree and soil stability , resource acquisition and allocation. Topology 1–34. doi: 10.1007/s11104-007-9470-7

Darrah PR, Jones DL, Kirk GJD, Roose T (2006) Modelling the rhizosphere: a review of methods for "upscaling" to the whole-plant scale. Eur J Soil Sci 57:13–25. doi: 10.1111/j.1365-2389.2006.00786.x

Dauer JM, Withington JM, Oleksyn J, et al. (2009) A scanner-based approach to soil profile-wall mapping of root distribution. Dendrobiology 62:35–40.

Davidson E, Lefebvre P, Brando P (2011) Carbon inputs and water uptake in deep soils of an eastern Amazon forest. For … 57:51–58.

Dawson T, Ehleringer J (1991) Streamside trees that do not use stream water. Nature

Dié A, Kitin P, Kouamé FN, et al. (2012) Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (Tectona grandis) in Ivory Coast. Ann Bot 110:861–73. doi: 10.1093/aob/mcs145

Dittmer HJ (1937) A quantitative study of the roots and root hairs of a winter rye plant (Secale cereale). Am J Bot 24:417–420.

Do FC, Pierret A, Couteron P, et al. (2011) Spatial distribution of Hevea brasiliensis trunk phloem necrosis within a plot: aggregation but no evidence of constraint on cumulated growth. For Pathol 41:90–100. doi: 10.1111/j.1439-0329.2010.00640.x

Dodds W, Banks M, Clenan C (1996) Biological properties of soil and subsurface sediments under abandoned pasture and cropland. Soil Biol … 28:837–846. doi: 10.1016/0038-0717(96)00057-0

Doody TM, Benyon RG (2011) Direct measurement of groundwater uptake through tree roots in a cave. Ecohydrology 4:644–649. doi: 10.1002/eco.152

Dougherty MC, Thevathasan N V., Gordon AM, et al. (2009) Nitrate and Escherichia coli NAR analysis in tile drain effluent from a mixed tree intercrop and monocrop system. Agric Ecosyst Environ 131:77–84. doi: 10.1016/j.agee.2008.09.011

Doussan C, Pagès L, Pierret A (2003a) Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. Agronomie 23:419–431. doi: 10.1051/agro:2003027

Doussan C, Pagès L, Pierret A (2003b) Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. Agronomie 23:419–431. doi: 10.1051/agro:2003027

Doussan C, Vercambre G, Pagés L (1998) Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption—Distribution of axial and radial conductances in maize. Ann Bot 81:225–232.

Draye X, Kim Y, Lobet G, Javaux M (2010) Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. J Exp Bot 61:2145–55. doi: 10.1093/jxb/erq077

Drechsel P, Schmall S, W. Zech (1990) Relationships between growth, mineral nutrition and soil properties in young Teak plantations in Bénin and Liberia. IUFRO-Symposium. pp 651–656

Drew MC (1975) Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol.

Dunbabin V, Diggle A, Rengel Z (2003) Is there an optimal root architecture for nitrate capture in leaching environments ?

Dunin F, Smith C, Zegelin S, Leuning R (2001) Water balance changes in a crop sequence with lucerne. Aust J Agric Res 52:247–261.

Dupuy L, Fourcaud T, Stokes A (2005a) A Numerical Investigation into the Influence of Soil Type and Root Architecture on Tree Anchorage. Plant Soil 278:119–134. doi: 10.1007/s11104-005-7577-2

Dupuy L, Fourcaud T, Stokes A, Danjon F (2005b) A density-based approach for the modelling of root architecture: application to Maritime pine (Pinus pinaster Ait.) root systems. J Theor Biol 236:323–34. doi: 10.1016/j.jtbi.2005.03.013

Dupuy LX, Fourcaud T, Lac P, Stokes A (2007) A generic 3D finite element model of tree anchorage integrating soil mechanics and real root system architecture. Am J Bot 94:1506–1514. doi: 10.3732/ajb.94.9.1506

Eamus D, Chen X, Kelley G, Hutley L (2002) Root biomass and root fractal analyses of an open Eucalyptus forest in a savanna of north Australia. Aust J Bot 50:31–41.

Eberbach PL, Hoffmann J, Moroni SJ, et al. (2013) Rhizo-lysimetry: facilities for the simultaneous study of root behaviour and resource use by agricultural crop and pasture systems. Plant Methods 9:3. doi: 10.1186/1746-4811-9-3

Edwards EJ, Benham DG, Marland LA, Fitter AH (2004) Root production is determined by radiation flux in a temperate grassland community. Glob Chang Biol 10:209–227. doi: 10.1111/j.1365-2486.2004.00729.x

Eilers KG, Debenport S, Anderson S, Fierer N (2012) Digging deeper to find unique microbial communities: The strong effect of depth on the structure of bacterial and archaeal communities in soil. Biol Biochem 50:58–65. doi: 10.1016/j.soilbio.2012.03.011

Eissenstat DM, Yanai RD (1997) The Ecology of Root Lifespan Advances in Ecological Research. Advances. pp 1–60

Elliott S, Baker P, Borchert R (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. Glob Ecol … 1–10. doi: 10.1111/j.1466-822x.2006.00213.x

Enstone DE, Peterson CA, Ma F (2003) Root Endodermis and Exodermis : Structure , Function , and Responses to the Environment. J Plant Growth Regul 335–351. doi: 10.1007/s00344-003-0002-2

Esser G, Kattge J, Sakalli A (2011) Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere. Glob Chang Biol 17:819–842. doi: 10.1111/j.1365-2486.2010.02261.x

Fan C, Chen Y (2010) The effect of root architecture on the shearing resistance of root-permeated soils. Ecol Eng 36:813–826. doi: 10.1016/j.ecoleng.2010.03.003

Fang S, Clark R, Liao H (2012) 3D Quantification of Plant Root Architecture In Situ. Meas. roots - An Updat. approach

FAO (2010) Teak resources and market assessment 2010. 1–52.

FAO (2011) State of the World's Forests. 1–179.

Fatahi B, Khabbaz H, Indraratna B (2010) Bioengineering ground improvement considering root water uptake model. Ecol Eng 36:222–229. doi: 10.1016/j.ecoleng.2008.12.027

Fayle DC. (1968) Radial growth of tree roots., Univ Toron. 1–183.

Ferguston JHA (1934) De Dikte van Kern en spinthout van den djati (Tectona grandis L.f.) (Thickness of heartwood and sapwood of teak). 43: 1–19.

Filella I, Peñuelas J (2003) Indications of hydraulic lift by Pinus halepensis and its effects on the water relations of neighbour shrubs. Biol. Plant.

Fitter A, Hodge A, Robinson D (2000) Plant response to patchy soils. In: Hutchings. (ed) A. J. A. Stewart, E. A. John, M. J. Hutchings,. pp 71–90

Fofana IJ, Ofori D, Poitel M, Verhaegen D (2008) Diversity and genetic structure of teak (Tectona grandis L.f) in its natural range using DNA microsatellite markers. New For 37:175–195. doi: 10.1007/s11056-008-9116-5

Fontaine S, Barot S, Barré P, et al. (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–80. doi: 10.1038/nature06275

Ford E, Deans J (1977) Growth of Sitka spruce plantations: spatial distribution and seasonal fluctuations of lengths, weight and carbohydrate concentrations of fine roots. Plant Soil 47:463–485.

Fox J, Castella J-C (2013) Expansion of rubber (Hevea brasiliensis) in Mainland Southeast Asia: what are the prospects for smallholders? J Peasant Stud 40:155–170. doi: 10.1080/03066150.2012.750605

Freckman DW, Virginia RA (1989) Plant-Feeding Nematodes in Deep-Rooting Desert Ecosystems. Ecology 70:1665–1678. doi: 10.2307/1938101

Ghestem M, Sidle RC, Stokes A (2011) The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability. Bioscience 61:869–879. doi: 10.1525/bio.2011.61.11.6

Goh DKS, Bacilieri R, Chaix G, Monteuuis O (2013) Growth variations and heritabilities of teak CSO-derived families and provenances planted in two humid tropical sites. Tree Genet Genomes 9:1329–1341. doi: 10.1007/s11295-013-0642-8

Goldstein G, Meinzer FC, Bucci SJ, et al. (2008) Water economy of Neotropical savanna trees: six paradigms revisited. Tree Physiol 28:395–404.

Gonkhamdee S, Maeght JL, Do F, Pierret A (2009) Growth dynamics of line Heavea brasiliensis roots along a 4.5-m soil profile. Khon kaen Agric J 37:265–276.

Göransson H, Fransson A-M, Jönsson-Belyazid U (2007) Do oaks have different strategies for uptake of N, K and P depending on soil depth? Plant Soil 297:119–125. doi: 10.1007/s11104-007-9325-2

Göransson H, Ingerslev M, Wallander H (2008) The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature Quercus robur, Fagus sylvatica and Picea abies stands. Plant Soil 306:129–137. doi: 10.1007/s11104-007-9524-x

Göransson H, Wallander H, Ingerslev M, Rosengen U (2006) Estimating the relative nutrient uptake from different soil depth of Quercus robur, Fagus sylvatica and Picea abies (L.) Karst. Plant Soil 286:87–97.

GRANIER A, GROSS P (1987) Mesure du flux de sève brute dans le tronc du Douglas par une nouvelle méthode thermique. Ann des Sci For 44:1–14. doi: 10.1051/forest:19870101

Graudal L, Kjær E, Suangtho V (1999) Conservation of genetic resources of teak (Tectona grandis) in Thailand. DFSC Ser Tech notes 38.

Green JJ, Dawson L a., Proctor J, et al. (2005) Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. Plant Soil 276:23–32. doi: 10.1007/s11104-004-0331-3

Großkopf W (1950) Bestimmung der charakteristischen Feinwurzel-Intensitäten in ungünstigen Waldbodenprofilen und ihre ökologische Auswertung., Haller.

Guizol P, Roda JM, Muhtaman DR, et al. (2005) LE TECK JAVANAIS, ENTRE SUREXPLOITATION ET EMBARGO. Bois Forêts des Trop 284:11–21.

Guo D, Li H, Mitchell RJ, et al. (2008) Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. New Phytol 177(2):443–56.

Hacke UG, Jansen S (2009) Embolism resistance of three boreal conifer species varies with pit structure. New Phytol 182:675–86. doi: 10.1111/j.1469-8137.2009.02783.x

Hales S (1727) Vegetable staticks.

Hansson K, Helmisaari H-S, Sah SP, Lange H (2013) Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. For Ecol Manage 309:58–65. doi: 10.1016/j.foreco.2013.01.022

Harper JL, Jones M, Sackville Hamilton NR (1991) The evolution of roots and the problems of analyzing their behaviour. Plant root growth An Ecol. Perspect., D. Atkinso. Blackwell Scientific Publications, Oxford., pp 3–22

Harper RJ, Tibbett M (2013) The hidden organic carbon in deep mineral soils. Plant Soil 368:641–648. doi: 10.1007/s11104-013-1600-9

Harrison R, Footen P, Strahm B (2011) Deep soil horizons: contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. For Sci 57:67–76.

Hartmann C, Lesturgez G, Do FC, et al. (2006) Rubber tree Trunk Phloem Necrosis (TPN) in Northeast Thailand: 1. Investigations on soil heterogeneities linked to disease outbreak. Int. Nat. Rubber Conf. - IRRDB Annu. Meet. Ho Chi Minh City., pp 139–156

He H, Bleby TM, Veneklaas EJ, Lambers H (2012) Arid-zone Acacia species can access poorly soluble iron phosphate but show limited growth response. Plant Soil 358:119–130. doi: 10.1007/s11104-011-1103-5

Herrera J, Verhulst N, Govaerts B (2012) Strategies to identify genetic diversity in root traits. cril.cimmyt.org 97–108.

Hidalgo E, Moreno V, Morales N (1986) Performance of 15 provenances of teak (Tectona grandis) five years after planting in Itabo, Matanzas. Rev Baracoa 16:65–75.

Hiltner P (1904) Über neuere ehrfahrungen und problem auf dem gebiet der bodenbakteriologie unter besonderer berücksichtigung der grundüngung und brache. ArbDtschLandwirt Ges 98:59–78.

Hinckley TM, Richter H, Schulte PJ (1991) Water relations. In: Wiley J (ed) Physiol. trees, A.S. Ragha. New York, pp 137–162

Hinsinger P (1998) How Do Plant Roots Acquire Mineral Nutrients? Chemical Processes Involved in the rhizosphere. adavances Agron 225,265. doi: 10.1016/S0065-2113(08)60506-4

Hinsinger P, Bengough a. G, Vetterlein D, Young IM (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil 321:117–152. doi: 10.1007/s11104-008-9885-9

Hinsinger P, Brauman A, Devau N, et al. (2011) Acquisition of phosphorus and other poorly mobile nutrients by roots. Where do plant nutrition models fail? Plant Soil 348:29–61. doi: 10.1007/s11104-011-0903-y

Hinsinger P, Cloutier-Hurteau B, Jourdan C, Laclau JP (2012) The roots of our soils. Roots to Futur. 8th Symp. Int. Soc. Root Res.

Ho MD, Mccannon BC, Lynch JP (2004) Optimization modeling of plant root architecture for water and phosphorus acquisition. J Theor Biol 226:331–340. doi: 10.1016/j.jtbi.2003.09.011

Hodge a (2006) Plastic plants and patchy soils. J Exp Bot 57:401–11. doi: 10.1093/jxb/eri280

Hodge A, Berta G, Doussan C, et al. (2009) Plant root growth, architecture and function. Plant Soil 321:153–187. doi: 10.1007/s11104-009-9929-9

Horne JEM (1966) Teak in Nigeria. Niger. Inf. Bull. (New Ser. 16:

Horton JL, Hart SC (1998) Hydraulic lift: a potentially irends in Ecomportant ecosystem process. Tree 13:232–235.

Howarth FG (1983) Ecology of cave arthropods. annual Review of entomology. Annu Rev Entomol 365–389.

Howarth FG, James SA, McDowell W, et al. (2007) Identification of roots in lava tube caves using molecular techniques: implications for conservation of cave arthropod faunas. J Insect Conserv 11:251–261. doi: 10.1007/s10841-006-9040-y

Hummel JW, Levan MA, Sudduth KA (1989) Mini-rhizotron installation in heavy soils. Trans. ASAE 32. pp 770–776

Isarangkool Na Ayutthaya S, Do FC, Pannangpetch K, et al. (2011) Water loss regulation in mature Hevea brasiliensis: effects of intermittent drought in the rainy season and hydraulic regulation. Tree Physiol 31:751–62. doi: 10.1093/treephys/tpr058

Isarangkool Na Ayutthaya S, Do FC, Pannengpetch K, et al. (2010) Transient thermal dissipation method of xylem sap flow measurement: multi-species calibration and field evaluation. Tree Physiol 30:139–48. doi: 10.1093/treephys/tpp092

Iversen CM, Murphy MT, Allen MF, et al. (2011) Advancing the use of minirhizotrons in wetlands. Plant Soil 352:23–39. doi: 10.1007/s11104-011-0953-1

Jackson RB (1999) Ecosystem rooting depth determined with caves and DNA. Proc Natl Acad Sci 96:11387–11392. doi: 10.1073/pnas.96.20.11387

Jackson RB, Canadell J, Ehleringer JR, et al. (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411. doi: 10.1007/BF00333714

Jackson RB, Mooney H a, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci U S A 94:7362–6.

Jackson RB, Moore L a, Hoffmann W a, et al. (1999) Ecosystem rooting depth determined with caves and DNA. Proc Natl Acad Sci U S A 96:11387–92.

Jacob J, Krishnakumar R (2006) Tapping Panel Dryness syndrome: what we know and we do not know. In: James, J.; Krishnakumar, R.; Mathew NMK (ed) Tapping Panel Dryness of Rubber Trees. Rubber Research Institute of India, pp 01–27

Jacoby GC, D'Arrigo RD (1990) Teak (Tectona grandis L.F.), a tropical species of large-scale dendroclimatic potential. Dendrochronologia 8:83–98.

Janeau J, Bricquet J (2003) Soil crusting and infiltration on steep slopes in northern Thailand. ... J Soil ... 543–553.

Javaux M, Couvreur V, Vanderborght J, Vereecken H (2013) Root Water Uptake: From Three-Dimensional Biophysical Processes to Macroscopic Modeling Approaches. Vadose Zo J. doi: 10.2136/vzj2013.02.0042

Javaux M, Draye X, Doussan C, et al. (2011) Root Water Uptake: Toward 3-D Functional Approaches. Encycl. Agrophysics, Encycloped. pp 717–722

Javaux M, Schröder T, Vanderborght J, Vereecken H (2008) Use of a Three-Dimensional Detailed Modeling Approach for Predicting Root Water Uptake. Vadose Zo J 7:1079. doi: 10.2136/vzj2007.0115

Jayasankar S, Sudhakara K, Babu L (2003) Provenance variation in growth, physiology, anatomical characteristics and foliar nutrient status of teak (Tectona grandis) seedlings. J Trop Sci 15:37–50.

Jennings CMJ (1974) The hydrogeology of Botswana. 873 p.

Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with minirhizotrons. Environ Exp Bot 45:263–289.

Johnston W (2000) Calibration of gypsum blocks and data loggers and their evaluation for monitoring soil water status. Aust J Exp Agric 40:1131–1136.

Jost G, Schume H, Hager H, et al. (2012) A hillslope scale comparison of tree species influence on soil moisture dynamics and runoff processes during intense rainfall. J Hydrol 420-421:112–124. doi: 10.1016/j.jhydrol.2011.11.057

Junjittakarn J (2012) Short term effects of latex tapping on micro-changes of trunk girth in Hevea Brasiliensis. Aust J Crop Sci 6:65–72.

Justin SHFW, Armstrong W (1987) the Anatomical Characteristics of Roots and Plant Response To Soil Flooding. New Phytol 106:465–495. doi: 10.1111/j.1469-8137.1987.tb00153.x

Kage H, Kochler M, Stutzel H (2000) Root growth of cauliflower (Brassica oleracea L. botrytis) under unstressed conditions: Measurement and modelling. plant Soil 223(1-2):131–145.

Kalliokoski T, Pennanen T (2010) Belowground interspecific competition in mixed boreal forests : fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant Soil 73–89. doi: 10.1007/s11104-009-0177-9

Kaosa-ard A (1981) Teak its natural distribution and related factors. Nat His Bull Siam Soc 25:55–74.

Kaplan EL, Meier P (1958) Nonparametric Estimation from Incomplete Observations. J Am Stat Assoc 53:457–481. doi: 10.1080/01621459.1958.10501452

Kashio M, White K (1998) Teak for the future. Proc. Second Reg. Semin. teak

Kaspar TC, Ewing RP (1997) ROOTEDGE: Software for Measuring Root Length from Desktop Scanner Images. Agron J 89:932. doi: 10.2134/agronj1997.00021962008900060014x

Kavanagh T, Kellman M (1992) Seasonal Pattern of Fine Root Proliferation in a Tropical Dry Forest. Biotropica. The Association for Tropical Biology and Conservation, pp 156–165

Kell DB (2012) Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: why and how. Philos Trans R Soc Lond B Biol Sci 367:1589–97. doi: 10.1098/rstb.2011.0244

Kell DB (2011) Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. Ann Bot 108:407–18. doi: 10.1093/aob/mcr175

Kimura K, Kikuchi S, Yamasaki S (1999) Accurate root length measurement by image analysis. Plant Soil 117–127.

Kleidon A, Heimann M (2000) Assessing the role of deep rooted vegetation in the climate system with model simulations: mechanism, comparison to observations and implications for Amazonian deforestation. Clim Dyn 16:183–199. doi: 10.1007/s003820050012

Kleidon A, Heimann M (1998) A method of determining rooting depth from a terrestrial biosphere model and its impacts on the global water and carbon cycle. Glob Chang Biol 4:275–286. doi: 10.1046/j.1365-2486.1998.00152.x

Kloeppel BD, Gower ST (1995) Construction and installation of acrylic minirhizotron tubes in forest ecosystems. Soil Sci Soc Am J 59:241–243.

Koarashi J, Hockaday WC, Masiello CA, Trumbore SE (2012) Dynamics of decadally cycling carbon in subsurface soils. J Geophys Res 117:G03033. doi: 10.1029/2012JG002034

Kobayashi N, Kumagai T, Miyazawa Y, et al. (2014) Transpiration characteristics of a rubber plantation in central Cambodia. Tree Physiol 34:285–301. doi: 10.1093/treephys/tpu009

Kollert W, Cherubini L (2012) Teak resources and market assessment 2010 (Tectona grandis Linn. F.). Rome

Kornecki TS, Prior SA, Runion GB, et al. (2008) Hydraulic Core Extraction: Cutting Device for Soil–Root Studies. Commun Soil Sci Plant Anal 39:1080–1089. doi: 10.1080/00103620801925588

Körner C (2011) The grand challenges in functional plant ecology. Front Plant Sci 2:1. doi: 10.3389/fpls.2011.00001

Kozlowski TT, Pallardy SG (2002) Acclimation and Adaptive Responses of Woody Plants to Environmental Stresses. Bot Rev 68:270–334. doi: 10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2

Kramer PJ, Boyer JS (1995) Roots and root systems. In: CA: Academic Press I (ed) Water Relations of Plant and Soils, P. J. Kram. San Diego, pp 116–166

Kreutzer K. (1961) Wulzelbildung jungen Waldbaume auf Pseudogleybi. iden Forstwis Cent Bf 80:356–392.

Kristensen HL, Thorup-Kristensen K (2004) Uptake of 15N labeled nitrate by root systems of sweet corn, carrot and white cabbage from 0.2-2.5 meters depth. Plant Soil 265:93–100.

Kristensen HL, Thorup-Kristensen K (2007) Effects of vertical distribution of soil inorganic nitrogen on root growth and subsequent nitrogen uptake by field vegetable crops. Soil Use Manag 23:338–347. doi: 10.1111/j.1475-2743.2007.00105.x

Kushwaha CP, Singh KP (2005) Diversity of leaf phenology in a tropical deciduous forest in India. J Trop Ecol 21:47–57.

Kutschera L (1960) Wurzelatlas mitleleuropaïsher Ackerunkräuter und Kulturpflanzen. Verlag Pub., Franckfurt am Main

Kutschera L, Lichtenegger E (1997) Bewurzelung von Pflanzen in verschiedenen Lebensra¨umen. 5. 1997., Band der W. Landesmuseum, Linz, Austria.

Laclau J-P, Ranger J, de Moraes Gonçalves JL, et al. (2010) Biogeochemical cycles of nutrients in tropical Eucalyptus plantations. For Ecol Manage 259:1771–1785. doi: 10.1016/j.foreco.2009.06.010

Laio F, Tamea S, Ridolfi L, et al. (2009) Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics. Water Resour Res. doi: 10.1029/2008WR007292

Lambers H, Shane MW, Cramer MD, et al. (2006) Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits. Ann Bot 98:693–713. doi: 10.1093/aob/mcl114

Lamouroux M (1957) Les sols de teckeraies du Togo. Lomé

Lee J-E, Oliveira RS, Dawson TE, Fung I (2005) Root functioning modifies seasonal climate. Proc Natl Acad Sci U S A 102:17576–81. doi: 10.1073/pnas.0508785102

Lewis DC, Burgy RH (1964) The Relationship between oak tree roots and groundwater in fractured rock as determined by tritium tracing. J Geophys Res 69:2579. doi: 10.1029/JZ069i012p02579

Limpinuntana V, Pannengpetch K (2012) Short term effects of latex tapping on micro-changes of trunk girth in Hevea Brasiliensis. Aust J 6:65–72.

Liste H-H, White JC (2008) Plant hydraulic lift of soil water – implications for crop production and land restoration. Plant Soil 313:1–17. doi: 10.1007/s11104-008-9696-z

Liu Y, Zhou Y, Ju W, et al. (2014) Impacts of droughts on carbon sequestration by China's terrestrial ecosystems from 2000 to 2011. Biogeosciences 11:2583–2599. doi: 10.5194/bg-11-2583-2014

Lobet G, Couvreur V, Meunier F, et al. (2014) Plant Water Uptake in Drying Soils. Plant Physiol. doi: 10.1104/pp.113.233486

Lobet G, Hachez C, Draye X (2013) Root Water Uptake and Water Flow in the Soil–Root Domain. Plant Roots Hidden Half. Inc, CRC Press, pp 24–1, 24–18

Lorenz K, Lal R (2005) The Depth Distribution of Soil Organic Carbon in Relation to Land Use and Management and the Potential of Carbon Sequestration in Subsoil Horizons. Adv Agron 88:35–66. doi: 10.1016/S0065-2113(05)88002-2

Madoffe S, Maghembe J (1988) Performance of teak (Tectona grandis L.f.) provenances seventeen years after planting at Longuza, Tanzania. Silvae Genet 37:175–178.

Maeght J-L, Pierret A, Sanwangsri M, Hammecker C (2007) Field monitoring of rice rhizosphere dynamics in saline soils of NE Thailand. Int. Conf. Rhizosph. 2, 26-31 August 2007, Montpellier, Fr. pp 26–31

Maeght J-L, Rewald B, Pierret A (2013) How to study deep roots—and why it matters. Front Plant Sci. doi: 10.3389/fpls.2013.00299

Maeght J., Nortourlee L, Reboul-salze F, et al. (2011) Environmental impact of understorey management in Teak tree (Tectona grandis L.) plantations: A case study from Luang Prabang, Lao PDR. Khon Kaen AGR 39:291–294.

Maeght JL, Henry des Tureaux T, Sengtaheuanghoung O, et al. (2012) Drought effect on teak tree (Tectona grandis) roots on carbon inputs and water uptake in a deep soil of northern Laos. Roots to Futur. 8th Symp. Int. Soc. Root Res.

Majdi H, Pregitzer K, Morén A-S, et al. (2005) Measuring Fine Root Turnover in Forest Ecosystems. Plant Soil 276:1–8. doi: 10.1007/s11104-005-3104-8

Malézieux E, Crozat Y, Dupraz C, et al. (2009) Mixing plant species in cropping systems: concepts, tools and models. A review. Agron Sustain Dev 29:43–62. doi: 10.1051/agro:2007057

Manlay RJ, Kairé M, Masse D, et al. (2002) Carbon , nitrogen and phosphorus allocation in agro-ecosystems of a West African savanna I . The plant component under semi-permanent cultivation. 88:215–232.

Mao Z, Bonis M, Rey H (2013) Which processes drive fine root elongation in a natural mountain forest ecosystem? Plant Ecol. …

Marciszewska K, Tulik M (2013) Hydraulic Efficiency and Safety of Xylem Sap Flow in Relation to Water Stress in Woody Plants. 1–32. doi: 10.5772/56656

Markewitz D, Devine S, Davidson EA, et al. (2010) Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. New Phytol 187:592–607. doi: 10.1111/j.1469-8137.2010.03391.x

Matamala R, Gonza MA (2003) Impacts of Fine Root Turnover on Forest NPP and Soil C. Science (80-) 302:1385–1387.

Materechera S a., Dexter a. R, Alston a. M (1991) Penetration of very strong soils by seedling roots of different plant species. Plant Soil 135:31–41. doi: 10.1007/BF00014776

McCormack ML, Eissenstat D, Prasad A, Smithwick E (2013) Regional scale patterns of fine root lifespan and turnover under current and future climate. Glob. Chang. Biol.

McCormack ML, Guo D (2014) Impacts of environmental factors on fine root lifespan. Front Plant Sci 5:1–11. doi: 10.3389/fpls.2014.00205

McCulley RL, Jobbágy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia 141:620–8. doi: 10.1007252Fs00442-004-1687-z

Mccully ME (1999) ROOTS IN SOIL : Unearthing the Complexities of Roots and Their Rhizospheres. 695–718.

McDougall WB (1916) The Growth of Forest Tree Roots. Am J Bot 3:384–392.

McDowell N, Pockman WT, Allen CD, et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178:719–39. doi: 10.1111/j.1469-8137.2008.02436.x

McElrone AJ, Bichler J, Pockman WT, et al. (2007) Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. Plant cell Environ 30:1411–1421.

McElrone AJ, Pockman WT, Martinez-Vilalta J, Jackson RB (2004) Variation in xylem structure and function in stems and roots of trees to 20 m depth. New Phytol 163:507–517. doi: 10.1111/j.1469-8137.2004.01127.x

McMurtrie RE, Iversen CM, Dewar RC, et al. (2012a) Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging. Ecol Evol 2:1235–50. doi: 10.1002/ece3.266

McMurtrie RE, Iversen CM, Dewar RC, et al. (2012b) Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging. Ecol Evol 2:1235–50. doi: 10.1002/ece3.266

Meyer BS, Anderson DB (1939) Plant Physiology. Braunworth and Co,, Bridgebort

Michot D (2003) Spatial and temporal monitoring of soil water content with an irrigated corn crop cover using surface electrical resistivity tomography. Water Resour Res 39:1138. doi: 10.1029/2002WR001581

Misra RK, Dexter AR, Alston AM (1986) M a x i m u m axial and radial growth pressures o f plant roots Introduction Plant roots are capable of exerting pressure both in the axial and radial directions . The hydrostatic pressure (P) in the root cells is balanced against the wall pressure (. Plant Soil 326:315–326.

Mitchell P, Black J (1968) Distribution of peach roots under pasture and cultivation. Aust J Exp Agr 8(30):106–111.

Moran CJ, Pierret A, Stevenson AW (2000) X-ray absorption and phase contrast imaging to study the interplay between plant roots and soil structure. Plant Soil 223:99–115.

Moreira MZ, Scholz FG, Goldstein G, Franco AC (2003) Hydraulic lift in a neotropical savanna. 573– 581.

Mulia R, Dupraz C (2006) Unusual Fine Root Distributions of Two Deciduous Tree Species in Southern France: What Consequences for Modelling of Tree Root Dynamics? Plant Soil 281:71–85. doi: 10.1007/s11104-005-3770-6

Murphy P, Lugo A (1986) Ecology of tropical dry forest. Annu Rev Ecol Syst 17:67–88.

Nadelhoffer K, Raich J (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147.

Nakaji T, Noguchi K, Oguma H (2007) Classification of rhizosphere components using visible–near infrared spectral images. Plant Soil 310:245–261. doi: 10.1007/s11104-007-9478-z

Nepstad D, Carvalho C de, Davidson E (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 669:372666–372666. doi: 10.1038/372666a0

Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol 194:337–52. doi: 10.1111/j.1469-8137.2012.04088.x

Newton M, Zedaker SM (1981) Excavating roots with explosives. 5.

Nicoullaud B, Darthout R, Duval O, et al. (1995) Étude de l ' enracinement du blé tendre d ' hiver et du maïs dans les sols argilo-limoneux de Petite Beauce. 183–200.

Nielsen N, Thorup-Kristensen K (1998) Modelling and measuring the effect of nitrogen catch crops on the nitrogen supply for succeeding crops. Plant Soil 203:79–89.

Nobel PS, Cui M (2010) Hydraulic Conductances of the Soil , the Root-Soil Air Gap , and the Root : Changes for Desert Succulents in Drying Soil. Changes 43:319–326.

Nocetti M, Rozenberg P, Chaix G, Macchioni N (2011) Provenance effect on the ring structure of teak (Tectona grandis L.f.) wood by X-ray microdensitometry. Ann For Sci 68:1375–1383. doi: 10.1007/s13595-011-0145-4

Van Noordwijk M, Brouwer G, Meijboom F, et al. (2000) Trench profile techniques and core break methods. In: Springer-Verlag. BH (ed) Smit AL, Bengough AG, Engels C, van Noordwijk M, Pellerin S Van der Geijn ,eds. Root methods. pp 212–233

Norby RJ, Ledford J, Reilly CD, et al. (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO 2 enrichment. PNAS 101:9689–9693.

Normaniza O, Faisal HA, Barakbah SS (2007) Engineering properties of Leucaena leucocephala for prevention of slope failure. 2:215–221. doi: 10.1016/j.ecoleng.2007.11.004

North EG (2004) A long drink of water: how xylem changes with depth. New Phytol 163:447–449.

Novak T, Perc M (2012) Duality of terrestrial subterranean fauna. ... J Speleol 41:181–188.

Oliveira RS, Dawson TE, Burgess SSO, Nepstad DC (2005) Hydraulic redistribution in three Amazonian trees. Oecologia 145:354–63. doi: 10.1007/s00442-005-0108-2

Pagès L, Bruchou C, Garré S (2012) Links Between Root Length Density Profiles and Models of the Root System Architecture. Vadose Zo J. doi: 10.2136/vzj2011.0152

Pandey D, Browna C (2000) Le teck dans le monde. 51:3–13.

Pankhurst CE, Pierret A, Hawke BG, et al. (2002) Microbiological and chemical properties of soil associated with macropores at different depths in a red-duplex soil in NSW Australia. Plant Soil 238:11–20.

Passioura JB, Wetselaar R (1972) Consequences of banding nitrogen fertilizers in soil. Plant Soil 36:461–473. doi: 10.1007/BF01373498

Peek M, Leffler A, Hipps L (2006) Root turnover and relocation in the soil profile in response to seasonal soil water variation in a natural stand of Utah juniper (Juniperus osteosperma). Tree Physiol 26:1469–76.

Peñuelas J, Filella I (2003) Deuterium labelling of roots provides evidence of deep water access and hydraulic lift by Pinus nigra in a Mediterranean forest of NE Spain. Environ Exp Bot 49:201–208. doi: 10.1016/S0098-8472(02)00070-9

Phillips DL, Johnson MG, Tingey DT, et al. (2000) Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. Soil Sci Soc Am J 64:761. doi: 10.2136/sssaj2000.642761x

Phillips WS (1963) Depth of Roots in Soil. Ecology 44:424. doi: 10.2307/1932198

Pierret A, Doussan C, Capowiez Y, et al. (2007a) Root Functional Architecture: A Framework for Modeling the Interplay between Roots and Soil. Vadose Zo J 6:269. doi: 10.2136/vzj2006.0067

Pierret A, Doussan C, Pages L, et al. (2007b) Is impeded root growth related to the occurrence of rubber tree Trunk Phloem Necrosis (TPN)? Preliminary results from NE Thailand. IRRDB Annu. Meet. pp 489–498

Pierret A, Doussan C, Pagès L (2006) Spatio-temporal Variations in Axial Conductance of Primary and First-order Lateral Roots of a Maize Crop as Predicted by a Model of the Hydraulic Architecture of Root Systems. Plant Soil 282:117–126. doi: 10.1007/s11104-005-5373-7

Pierret A, Gonkhamdee S, Jourdan C, Maeght J-L (2013) IJ_Rhizo: an open-source software to measure scanned images of root samples. Plant Soil. doi: 10.1007/s11104-013-1795-9

Pierret A, Hartmann C, Maeght J., et al. (2011a) Biotic Regulation : Plants. In: Ritz K (ed) Archit. Biol. soild life Inn. Sp., Cabi. Cabi, Armidale, pp 87–103

Pierret A, Latchackak K, Sengtaheuanghoung O, Valentin C (2007c) Interactions between root growth , slope and soil detachment depending on land use : a case study in a small mountain catchment of Northern Laos. Plant Soil 51–64. doi: 10.1007/s11104-007-9413-3

Pierret A, Moran CJ, Doussan C (2004) Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. New Phytol 967–980. doi: 10.1111/j.1469-8137.2005.01389.x

Pierret A, Moran CJ, Pankhurst CE (1999) Differentiation of soil properties related to the spatial association of wheat roots and soil macropores. 200660:51–58.

Pierret A, de Rouw A, Chaplot V, et al. (2011b) Reshaping upland farming policies to support nature and livelihoods: lessons from soil erosion in Southeast Asia with emphasis on Lao PDR. [Management of Soil Erosion Consortium (MSEC) Project report]. 40 p. doi: 10.5337/2011.213

Poelman G, Koppel J van de, Brouwer G (1996) A telescopic method for photographing within 8× 8 cm minirhizotrons. Plant Soil 163–167.

Poot P, Lambers H (2008) Shallow soil endemics: adaptive advantages and constraints of a specialized rootâ€ system morphology. New Phytol 371–381. doi: 10.1111/j.1469-8137.2007.02370.x

Pregitzer K (2002) Fine roots of trees–a new perspective. New Phytol 154:267–270.

Pregitzer K, Hendrick R, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. New Phytol 575–580.

Pregitzer KKS, Laskowski MJM, Burton AJ, et al. (1998) Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol 18:665–670.

Pretzsch H, Rötzer T, Matyssek R, et al. (2014) Mixed Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica [L.]) stands under drought: from reaction pattern to mechanism. Trees. doi: 10.1007/s00468-014-1035-9

Priya PB, Bhat KM (1998) False ring formation in teak (Tectona grandis L . f .) and the in ¯ uence of environmental factors. For Ecol Manage 108:215–222.

Priyadarshan PM, Hoa TTT, Huasun H, de Gonçalves PS (2005) Yielding Potential of Rubber (Hevea brasiliensis) in Sub-Optimal Environments. J Crop Improv 14:221–247. doi: 10.1300/J411v14n01_10

Pumijumnong N (2012) Teak Tree Ring Widths: Ecology and Climatology Research in Northwest Thailand. Sci, Tech Dev 31:165–174.

Ram S, Borgaonkar HP, Munot AA, Sikder AB (2011) Tree-ring variation in teak (Tectona grandis L.) from Allapalli, Maharashtra in relation to moisture and Palmer Drought Severity Index, India. J Earth Syst Sci 120:713–721. doi: 10.1007/s12040-011-0090-5

Rao GG, Rao PS, Rajagopal R, et al. (1990) Influence of soil, plant and meteorological factors on water relations and yield in. 175–180.

Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269:341–356. doi: 10.1007/s11104-004-0907-y

Rawitscher F (1948) The water economy of the vegetation of the Campos cerrados in southern Brazil. Brazil J Ecol 36:237–268.

Reboleira AS, Borges P, Gonçalves F, et al. (2011) The subterranean fauna of a biodiversity hotspot region - Portugal: an overview and its conservation. Int J Speleol 40:23–37. doi: 10.5038/1827-806X.40.1.4

Reubens B, Poesen J, Danjon F, et al. (2007) The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. Trees - Struct Funct 21:385–402. doi: 10.1007/s00468-007-0132-4

Rewald B, Ephrath JE (2013) Minirhizotron techniques. Plant roots hidden half

Rewald B, Ephrath JE, Rachmilevitch S (2011) A root is a root is a root? Water uptake rates of Citrus root orders. Plant Cell Environ 34:33–42. doi: 10.1111/j.1365-3040.2010.02223.x

Rewald B, Leuschner C (2009) Does root competition asymmetry increase with water availability? Plant Ecol Divers 2:255–264.

Rewald B, Meinen C, Trockenbrodt M, et al. (2012) Root taxa identification in plant mixtures – current techniques and future challenges. Plant Soil 359:165–182. doi: 10.1007/s11104-012-1164-0

Ribolzi O, Patin J, Bresson LM, et al. (2011) Impact of slope gradient on soil surface features and infiltration on steep slopes in northern Laos. Geomorphology 127:53–63. doi: 10.1016/j.geomorph.2010.12.004

Richards J, Caldwell M (1987) Hydraulic lift: Substantial nocturnal water transport between soil layers by Artemisia tridentata roots. Oecologia 486–489.

Richter AK, Walthert L (2007) Does low soil base saturation affect fine root properties of European beech (Fagus sylvatica L .)? Plant Soil 69–79. doi: 10.1007/s11104-007-9338-x

Richter DD, Markewitz D (1995) How Deep Is Soil? Bioscience 45:600–609. doi: 10.2307/1312764

Ridolfi L, D'Odorico P, Laio F (2006) Effect of vegetation–water table feedbacks on the stability and resilience of plant ecosystems. Water Resour Res 42:W01201. doi: 10.1029/2005WR004444

Ritson P, Sochacki S (2003) Measurement and prediction of biomass and carbon content of Pinus pinaster trees in farm forestry plantations, south-western Australia. For Ecol Manage 175:103–117. doi: 10.1016/S0378-1127(02)00121-4

Rivera G, Elliott S, Caldas LS, et al. (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. Trees 16:445–456. doi: 10.1007/s00468-002-0185-3

Rizzo D, Gross R (2000) Distribution of Armillaria melea on pear root systems and comparison of excavation techniques. Stokes A, ed. Support. roots trees woody plants form, Funct. Physiol. Dev. plant soil Sci., Kluwer Aca. pp 305–307

Robinson D (1991) Roots and resource fluxes in plants and communities. In: D. Atkinson (ed.) (ed) Plant root growth An Ecol. Perspect., Special pu. Blackwell Scientific, Oxford., pp 103–130

Robinson D, Crop S, Dd D (1996) Resource Capture by Localized Root Proliferation : Why Do Plants Bother ? 179–185.

Rodrigo V (2007) Ecophysiological factors underpinning productivity of Hevea brasiliensis. Brazilian J Plant Physiol 19:245–255.

Rood SB, Patiño S, Coombs K, Tyree MT (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees 14:0248–0257. doi: 10.1007/s004680050010

Rosling A, Landeweert R, Lindahl BD, et al. (2003) Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. New Phytol 159:775–783. doi: 10.1046/j.1469-8137.2003.00829.x

Ross P (1961) The plant ecology of the teak plantations in Trinidad. Ecology 42:387–398.

Rumpel C, Kögel-Knabner I (2011) Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. Plant Soil 338:143–158. doi: 10.1007/s11104-010-0391-5

Rumpel C, Kögel-knabner I (2011) Deep soil organic matter — a key but poorly understood component of terrestrial C cycle. 143–158. doi: 10.1007/s11104-010-0391-5

Saengruksawong C, Khamyong S (2012) Growths and Carbon Stocks of Para Rubber Plantations on Phonpisai Soil Series in Northeastern Thailand. Rubber Thai J 18:1–18.

Sangsing K, Kasemsap P, Thanisawanyangkura S, et al. (2004) Xylem embolism and stomatal regulation in two rubber clones (Hevea brasiliensis Muell. Arg.). Trees - Struct Funct 18:109–114. doi: 10.1007/s00468-003-0286-7

Santner A, Calderon-Villalobos LIA, Estelle M (2009) Plant hormones are versatile chemical regulators of plant growth. Nat Chem Biol 5:301–7. doi: 10.1038/nchembio.165

Sarojam N (2005) An annotated bibliography on teak: (Tectona grandis Linn. f). 1–461.

Schenk H (2002) The global biogeography of roots. Ecol Monogr 72:311–328.

Schenk HJ (2008a) Soil depth, plant rooting strategies and species' niches. New Phytol 178:223–5. doi: 10.1111/j.1469-8137.2008.02427.x

Schenk HJ (2008b) The Shallowest Possible Water Extraction Profile: A Null Model for Global Root Distributions. Vadose Zo J 7:1119. doi: 10.2136/vzj2007.0119

Schenk HJ, Jackson RB (2002) Rooting depths , lateral root spreads and below-ground / above-ground allometries of plants in water-limited. J Ecol 480 – 494.

Schmall S (1989) Wuchs und Ernährungszustand junger Teak-Bestände auf Vertisolen in Bénin, Westafrika. Unveröff

Schmidt MWI, Torn MS, Abiven S, et al. (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56. doi: 10.1038/nature10386

Scholz F, Bucci S, Arias N, et al. (2006) Osmotic and elastic adjustments in cold desert shrubs differing in rooting depth: coping with drought and subzero temperatures Biological control of the terrestrial carbon sink Rooting depth, water availability, and vegetation cover along an aridity gradi. Oecologia\ 3\:1–13\. doi: 10.1007/s00442-012-2368-y

Schulte P (2006) Water flow through junctions in Douglas-fir roots. Plant, Cell & Environ 29:70–6.

Schwinning S (2010) Ecohydrology Bearings - Invited Commentary The ecohydrology of roots in rocks. 245:238–245. doi: 10.1002/eco

Sekiya N, Araki H, Yano K (2010) Applying hydraulic lift in an agroecosystem: forage plants with shoots removed supply water to neighboring vegetable crops. Plant Soil 341:39–50. doi: 10.1007/s11104-010-0581-1

Shalyt MS (1952) Podzemnaja cast' nekotorykh lugovykh, stepnykh i pustynnykh rastenyi i fitocenozov. Tra- vjanistye, polukustarnigkovye i kustarnigkovye rastenija i fitocenozy pustynnoj Zo. [belowgr. parts some meadow, steppe, desert plants plant communities., [In Russia. Akademii nauk SSSR., pp 71–139

Shimamura S, Yoshida S, Mochizuki T (2007) Cortical Aerenchyma formation in hypocotyl and adventitious roots of Luffa cylindrica subjected to soil flooding. Ann Bot 100:1431–9. doi: 10.1093/aob/mcm239

Da Silva EV, Bouillet J-P, de Moraes Gonçalves JL, et al. (2011) Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. Funct Ecol 25:996–1006. doi: 10.1111/j.1365-2435.2011.01867.x

Silva JS, Rego FC (2003) Root distribution of a Mediterranean shrubland in Portugal. Plant Soil 255:529–540.

Silva MS, Martins RP, Ferreira RL (2011) Cave lithology determining the structure of the invertebrate communities in the Brazilian Atlantic Rain Forest. Biodivers Conserv 20:1713–1729. doi: 10.1007/s10531-011-0057-5

Silva S, Whitford WG, Jarrell WM, Virginia RA (1989) The microarthropod fauna associated with a deep rooted legume, Prosopis glandulosa, in the Chihuahuan Desert. Biol. Fertil. Soils 7:

Singh K, Srivastava S (1985) Seasonal variations in the spatial distribution of root tips in teak (Tectonia grandis Linn. f.) plantations in the Varanasi Forest Division, India. Plant Soil 84:93–104.

Singh KP, R.P. Singh (1981) Seasonal variations in biomass and energy of small roots in a tropical dry deciduous forest. OIKOS 37:88–92.

Singh KP, Srivastava K (1986) Seasonal variation in the biomass and non-structural carbohydrate content of fine roots of teak (Tectona grandis L. f.) plantations in a dry tropical region. Tree Physiol 1:31–6.

De Smet I, J. White P, Bengough a. G, et al. (2012) Analyzing Lateral Root Development: How to Move Forward. Plant Cell Online 1–7. doi: 10.1105/tpc.111.094292

Smit DAL (2000) Root Methods. 587.

Snider J, Moya M, Garcia MG, et al. (2009) Identification of the microbial communities associated with roots in lava tubes in new mexico an Hawai. Proc. the15th Int. Congr. Speleol. Kerrville, Texas United States of America, p vol. 2 718–723

Snyder K a., James JJ, Richards JH, Donovan L a. (2008) Does hydraulic lift or nighttime transpiration facilitate nitrogen acquisition? Plant Soil 306:159–166. doi: 10.1007/s11104-008-9567-7

Sodarak H (2000) Shifting Cultivation Practices By Hmong , Khamu and Lao ethnic categories In The Nam Nane Watershed , Nane District , Luang Phrabang province. 1–82.

Sookmark U, Pujade-Renaud V, Chrestin H, et al. (2002) Characterization of polypeptides accumulated in the latex cytosol of rubber trees affected by the tapping panel dryness syndrome. Plant Cell Physiol 43:1323–33.

Souvanthong BP (1995) Shifting Cultivation in Lao PDR : An overview of land use and policy initiatives. 1–40.

Srivastava SK, Singh KP, Upadhyay RS (1986) Fine root growth dynamics in teak (Tectona grandis Linn. F.). Can J For Res 16:1360–1364. doi: 10.1139/x86-240

Stirzaker RJ, Passioura JB (1996) The water relations of the root-soil interface. Plant, Cell Environ 19:201–208. doi: 10.1111/j.1365-3040.1996.tb00241.x

Stoeckeler JH, Kluender WA (1938) The hydraulic method of excavating the root systems of plants. Ecology 19:355–369.

Stokes A, Bakker MR (2013) Root Systems of Woody Plants. Plant Roots Hidden Half. Inc, CRC Press, pp 29–1, 29–18

Stone EL, Comerford NB (1994) Plant and Animal Activity Below the Solum. Proc. Symp. Whole Regolith Pedol., Minneapolis, Minnesota, 3 Novemb. 1992. pp 57–74

Stone EL, Kalisz PJ (1991) On the maximum extent of tree roots. For Ecol Manage 46:59–102. doi: 10.1016/0378-1127(91)90245-Q

Stone FD (2010) Bayliss lava tube and the discovery of a rich cave fauna in tropical Australia. 14th Int. Symp. Vulcanospeleology. pp 47–58

Strand AE, Pritchard SG, McCormack ML, et al. (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–8. doi: 10.1126/science.1151382

Strebel O, Duynisveld WHM, Böttcher J (1989) Nitrate pollution of groundwater in Western Europe. Agric Ecosyst Environ 26:189–214.

Streets RJ (1962) Exotic trees of the British Commonwealth. 712–725.

Strong D, Sale P, Helyar K (1999) The influence of the soil matrix on nitrogen mineralisation and nitrification III. Predictive utility of traditional variables and process location within the pore. Aust J Soil Res 37:137–149.

Sverdrup H, Hagen-Thorn A, Holmqvist J, et al. (2002) Biogeochemical processes and mechanisms. Developing principles and models for sustainable forestry in Sweden. In: I.Stjernquist ed. by HS and (ed)Kluwer Academic Publishers, Dodrecht, the Netherlands., pp 91–196

Tariel J (1966) Le Teck en Côte-d'Ivoire. Bois Forêts des Trop 107:27–47.

Thein HM, Mamoru K, Fukushima M, Minn Y (2007) Structure and composition of a teak-bearing forest under the Myanmar selection system: impacts of logging and bamboo flowering. Southeast Asian Stud. pp 303–316

Thomas TP (1989) Effect of varying soil moisture and bulk density on Teak, Eucalypt and Albizia root growth. 7 PP.

Thomson S, Armstrong C (1987) Calibration of the Watermark model 200 soil moisture sensor.

Thomson S, Younos T, Wood K (1996) Evaluation of calibration equations and application methods for the watermark ® granular matrix soil moisture sensor. Appl Eng Agric 12:99–103.

Thorup-Kristensen K, Dresbøll DB (2010) Incorporation time of nitrogen catch crops influences the N effect for the succeeding crop. Soil Use Manag 26:27–35. doi: 10.1111/j.1475-2743.2009.00255.x

Tittonell P, Vanlauwe B, Leffelaar PA, Giller KE (2005) Estimating yields of tropical maize genotypes from non-destructive , on-farm plant morphological measurements. Response 105:213–220. doi: 10.1016/j.agee.2004.04.002

Tobin B, Čermák J, Chiatante D, et al. (2007) Towards developmental modelling of tree root systems. Plant Biosyst - An Int J Deal with all Asp Plant Biol 141:481–501. doi: 10.1080/11263500701626283

Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2010) Shovelomics: high throughput phenotyping of maize (Zea mays L.) root architecture in the field. Plant Soil 341:75–87. doi: 10.1007/s11104-010-0623-8

Troup R (1921) The SilŠiculture of Indian Trees. 697–768.

Troxler J, Svercel M, Natsch A, et al. (2012) Persistence of a biocontrol Pseudomonas inoculant as high populations of culturable and non-culturable cells in 200-cm-deep soil profiles. Soil Biol Biochem 44:122–129. doi: 10.1016/j.soilbio.2011.09.020

Trumbore SE, Gaudinski JB (2003) The secret lives of roots. Science (80-) 302:1344.

Valentin C, Agus F, Alamban R, et al. (2008) Agriculture , Ecosystems and Environment Runoff and sediment losses from 27 upland catchments in Southeast Asia : Impact of rapid land use changes and conservation practices. 128:225–238. doi: 10.1016/j.agee.2008.06.004

Vanapalli SK, Oh WT (2012) Stability Analysis of Unsupported Vertical Trenches in Unsaturated Soils. GeoCongress 2012. American Society of Civil Engineers, Reston, VA, pp 2502–2511

Vanlauwe B, Aihou K, Tossah BK, et al. (2005) Senna siamea trees recycle Ca from a Ca-rich subsoil and increase the topsoil pH in agroforestry systems in the West African derived savanna zone. Plant Soil 269:285–296. doi: 10.1007/s11104-004-0599-3

Verhaegen D, Fofana IJ, Logossa Z a., Ofori D (2010a) What is the genetic origin of teak (Tectona grandis L.) introduced in Africa and in Indonesia? Tree Genet Genomes 6:717–733. doi: 10.1007/s11295-010-0286-x

Verhaegen D, Fofana IJ, Logossa Z a., Ofori D (2010b) What is the genetic origin of teak (Tectona grandis L.) introduced in Africa and in Indonesia? Tree Genet Genomes 6:717–733. doi: 10.1007/s11295-010-0286-x

Verweij RJT, Higgins SI, Bond WJ, February EC (2011) Water sourcing by trees in a mesic savanna: Responses to severing deep and shallow roots. Environ Exp Bot 74:229–236. doi: 10.1016/j.envexpbot.2011.06.004

Virginia RA, Jarrell WM (1987) Approaches for studying the function of deep root systems. Plant response to …

Virginia RA, Jenkins MB, Jarrell WM (1986) Depth of root symbiont occurrence in soil. Biol Fertil Soils. doi: 10.1007/BF00257591

Vogel J, Bronson D, Gower ST, Schuur EAG (2014) The response of root and microbial respiration to the experimental warming of a boreal black spruce forest. Can J For Res 140505143419008. doi: 10.1139/cjfr-2014-0056

Vogel JG, Valentine DW, Ruess RW (2005) Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. Can J For Res 35:161–174. doi: 10.1139/x04-159

Vogt K, Vogt D, Palmiotto P, et al. (1995) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 159–219.

Vogt KA, Vogt DJ, Palmiotto PA, et al. (1996) Review of root dynamics in forest ecosystems grouped by climate , climatic forest type and species. Plant Soil 159–219.

Vos J, Groenwold J (1983) Estimation of root densities by observation tubes and endoscope. Plant Soil 300:295–300.

Waddington J (1971) Observation of plant roots in situ. Can J Bot 49:1850–1852. doi: 10.1139/b71-261

Wagner B, Gärtner H, Ingensand H, Santini S (2010) Incorporating 2D tree-ring data in 3D laser scans of coarse-root systems. Plant Soil 334:175–187. doi: 10.1007/s11104-010-0370-x

Wang Y, Zhang B, Lin L, Zepp H (2011) Agroforestry system reduces subsurface lateral flow and nitrate loss in Jiangxi Province, China. Agric Ecosyst Environ 140:441–453. doi: 10.1016/j.agee.2011.01.007

Wardle DA, Bardgett RD, Klironomos JN, Seta H (2004) Ecological Linkages Between Aboveground and Belowground Biota. Society 304:1629–1633.

Watt M, Magee L, McCully M (2008) Types, structure and potential for axial water flow in the deepest roots of fieldâ€ grown cereals. New Phytol 178:135–46. doi: 10.1111/j.1469-8137.2007.02358.x

Wauters JB, Coudert S, Grallien E, et al. (2008) Carbon stock in rubber tree plantations in Western Ghana and Mato Grosso (Brazil). For Ecol Manage 255:2347–2361. doi: 10.1016/j.foreco.2007.12.038

Wearver JE (1915) A study of the root-systems of prairie plants of southeastern Washington. Plant World. pp 18:227–248; 273–292.

Weaver JE (1919) The Ecological Relations of Roots. Caregie Institution of Washincton

Weaver JE, Bruner WE (1927) Root development of vegetable crops. Development 1–7.

Whalley WR, Bengough AG (2013) Soil Mechanical Resistance and Root Growth and Function. pp 1–15

White RG, Kirkegaard JA (2010) The distribution and abundance of wheat roots in a dense, structured subsoil--implications for water uptake. Plant Cell Environ 33:133–48. doi: 10.1111/j.1365-3040.2009.02059.x

Woodward FI, Osborne CP (2000) The representation of root processes in models addressing the responses of vegetation to global change. New Phytol 147:223–232.

Wu Y, Deng Y, Zhang J, et al. (2013) Root size and soil environments determine root lifespan: evidence from an alpine meadow on the Tibetan Plateau. Ecol Res 28:493–501. doi: 10.1007/s11284-013-1038-9

Xiong Y, Fan P, Fu S, et al. (2012) Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees. Plant Soil 363:19–31. doi: 10.1007/s11104-012-1290-8

Yao S, Merwin I, Brown M (2009) Apple root growth, turnover, and distribution under different orchard groundcover management systems. HortScience 44:168–175.

Yuan ZY, Chen HYH (2012) Indirect methods produce higher estimates of fine root production and turnover rates than direct methods. PLoS One 7:e48989. doi: 10.1371/journal.pone.0048989

Yuen JQ, Ziegler AD, Webb EL, Ryan CM (2013) Uncertainty in below-ground carbon biomass for major land covers in Southeast Asia. For Ecol Manage 310:915–926. doi: 10.1016/j.foreco.2013.09.042

Zamora DS, Jose S, Napolitano K (2009) Competition for 15N labeled nitrogen in a loblolly pine–cotton alley cropping system in the southeastern United States. Agric Ecosyst Environ 131:40–50. doi: 10.1016/j.agee.2008.08.012

Zapater M, Hossann C, Bréda N, et al. (2011) Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. Trees 25:885–894. doi: 10.1007/s00468-011-0563-9

Zarebanadkouki M, Kim YX, Carminati A (2013) Where do roots take up water? Neutron radiography of water flow into the roots of transpiring plants growing in soil. New Phytol 199:1034–44. doi: 10.1111/nph.12330

Zeppel MJB, Wilks J V., Lewis JD (2014) Impacts of extreme precipitation and seasonal changes in precipitation on plants. Biogeosciences 11:3083–3093. doi: 10.5194/bg-11-3083-2014

Zobel BJ, , Van Buijtenen JP (1989) Wood variation. Its causes and control, T. E. Time.

Zobel R (2005) Primary and secondary root systems. Roots Soil Manag Interact between roots soil 2005.

Zoon FC, Tienderen PH (1990) A rapid quantitative measurement of root length and root branching by microcomputer image analysis. Plant Soil 126:301–308. doi: 10.1007/BF00012833

Annexes

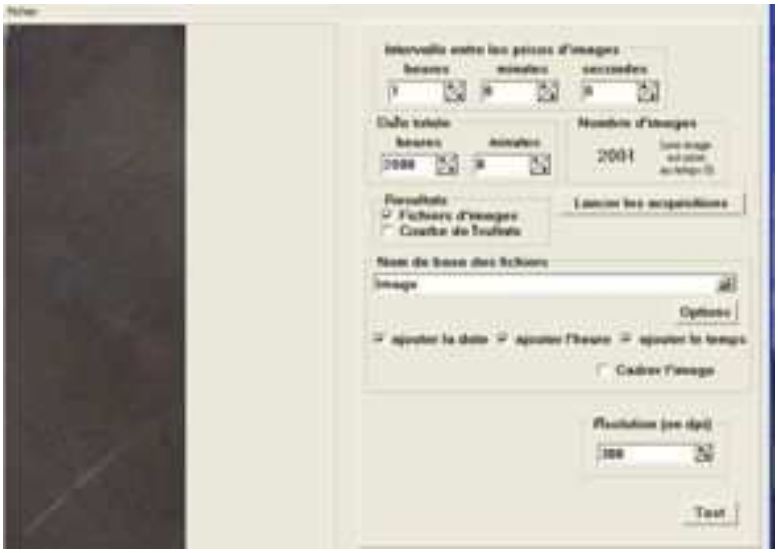
Annexe I: Logiciel personnalisé pour acquisition automatisée

Logiciel personnalisé *(Delphi)* **pour acquisition automatisée:**

Choix :
- source
- intervalle de prise d'images
- durée de la période de prise de vue
- définition en dpi
- possibilité de recadrage

Ci-dessous, extrait d'écran des fenêtres à renseigner avant de débuter l'acquisition automatisé d'image provenant de n scanners.







Annexe II a: IJ_Rhizo : an open-source software to measure scanned images of root samles ; Article publié dans Plant & Soil, 2013

Plant Soil
DOI 10.1007/s11104-013-1795-9

REGULAR ARTICLE

IJ_Rhizo: an open-source software to measure scanned images of root samples

Alain Pierret · Santimaitree Gonkhamdee · Christophe Jourdan · Jean-Luc Maeght

Received: 18 February 2013 / Accepted: 29 May 2013
© Springer Science+Business Media Dordrecht 2013

Abstract
Background and aims This paper provides an overview of the measuring capabilities of IJ_Rhizo, an ImageJ macro that measures scanned images of washed root samples. IJ_Rhizo is open-source, platform-independent and offers a simple graphic user interface (GUI) for a main audience of non-programmer scientists. Being open-source based, it is also fully modifiable to accommodate the specific needs of the more computer-literate users. A comparison of IJ_Rhizo's performance with that of the widely used commercial package WinRHIZO™ is discussed.
Methods We compared IJ_Rhizo's performance with that of the commercial package WinRHIZO™ using two sets of images, one comprising test-line images, the second consisting of images of root samples collected in the field. IJ_Rhizo and WinRHIZO™ estimates were compared by means of correlation and regression analysis.
Results IJ_Rhizo "Kimura" and WinRHIZO™ "Tennant" were the length estimates that were best linearly correlated with each other. Correlation between average root diameter estimates was weaker, due to the sensitivity of this parameter to thresholding and filtering of image background noise.
Conclusions Overall, IJ_Rhizo offers new opportunities for researchers who cannot afford the cost of commercial software packages to carry out automated measurement of scanned images of root samples, without sacrificing accuracy.

Keywords Root length · Root washing · Image analysis · Open-source · Winrhizo

Responsible Editor: Timothy Cavagnaro.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-013-1795-9) contains supplementary material, which is available to authorized users.

A. Pierret (✉)
UMR Bioemco, Institut de Recherche pour le Développement (IRD) c/o National Agriculture and Forestry Research Institute (NAFRI), P.O. Box 4199, Ban Nongviengkham, Xaythany District, Vientiane, Lao P.D.R.
e-mail: apierret@gmail.com

S. Gonkhamdee
Department of Plant Science & Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Khon Kaen 40002, Thailand

C. Jourdan
UMR Eco&Sols, CIRAD, 2 place Viala, 34060 Montpellier, France

J.-L. Maeght
UMR Bioemco, Institut de Recherche pour le Développement (IRD) c/o UMR AMAP, CIRAD TA A51/PS2, 34398 Montpellier cedex 5, France

Published online: 04 July 2013

Introduction

Plant roots influence many biogeochemical cycles, most notably, those of carbon, nitrogen and water (Nepstad et al. 1994; Esser et al. 2011). Quantification of plant root geometry, in particular parameters such as root length, root length density or root diameters, is pivotal to understand many plant physiological functions and associated eco-services (e.g. Gyssels et al. 2006; Roumet et al.

2006; Stokes et al. 2009; Zobel et al. 2006). In this context, plant root measurements form an essential component of a vast array of scientific disciplines, including agronomy (Christina et al. 2011), plant physiology and breeding (Kell 2011) but also civil engineering (Mickovski et al. 2010), hydrology and climatology (Zeng et al. 1998; Kleidon and Heimann 1998; Feddes et al. 2001) as well as biogeochemistry (Rasse et al. 2005; Schmidt et al. 2011). Root length is arguably one of the most commonly measured parameters, largely because of its value as a general, integrative indicator of plant response to environmental factors (Edwards et al. 2004), and also because of its role in the control of water and nutrient fluxes (Clothier and Green 1997; Ryser 2006). Indeed, as per December 2012, a search with the key expression "root length" covering the 20-year period spanning from 1993 to 2012 on the Thomson-Reuters "Web of Science" (WoS) database yielded over 4,850 references (or a yearly average of more than 240 papers, rising from about 150/year in the early 1990s to more than 350/year in 2010, with a H-index of 82), distributed across 6 main WoS subject areas, namely: agriculture (46.4 %), plant sciences (34.4 %), environmental sciences- ecology (11.9 %), forestry (5.2 %), water resources (1.6 %) and meteorology-atmospheric sciences (0.43 %).

From a methodological standpoint, although there is significant evidence in the literature that soil structure and plant roots can barely be considered as separate entities (Pierret and Moran 2011) and despite inherent limitations, most notably with respect to labour requirements and accuracy (Pierret et al. 2005), root washing, i.e. the physical separation of roots from the soil into which it is embedded, combined with image analysis, has become the most widely used method to quantify root length and other parameters such as root diameter. Roots physically separated from soil following core washing can be measured using a wide range of methods, ranging from manual line-intersection counting methods (Newman 1966; Tennant 1975) to automated, image analysis methods using a flat bed scanner and dedicated software. Being incomparably more convenient, faster and replicable than manual techniques (e.g. Zoon and van Tienderen 1990; Kaspar and Ewing 1997; Dowdy et al 1998), image analysis has rapidly become the preferred approach to measuring root samples from core washing. Building upon these advantages, WinRHIZO™ (Regent Instruments Inc., Canada) has now presumably become the most widely used commercial package specifically designed for the analysis of scanned images of root samples physically separated from soil by washing (Bouma et al. 2000; Himmelbauer et al. 2004; Magalhaes et al. 2011; Nelson and Phan 2006; Vegapareddy et al. 2010). As a general rule, image analysis packages used for root analysis allow the measurement of a variety of geometrical and architectural root parameters (Lobet et al. 2011) and an increasing number of them is readily available as freeware and open-source software (Le Bot et al. 2010). Currently available software for root measurements can be found at the "*Root Image Analysis*" website (http://www.root-image-analysis.org/).

About two decades ago, Ewing and Kaspar (1995) were probably the first to extensively review algorithms usable for measuring root length and then developed (Kaspar and Ewing 1997) a so-called edge chord algorithm dedicated to root measurements (available as RootEdge from http://www.ars.usda.gov/Services/docs.htm?docid=10784). More recently, Kimura et al. (1999) proposed a simple to implement, fast, yet accurate neighbourhood averaging procedure that is largely independent of sample orientation and that has been independently reported to be one of the least biased length estimators currently available (Zeng et al. 2006; 2008). Similarly, Zobel (2008) recently reviewed the main image analysis routines available to measure root diameters and root diameter distributions.

This paper provides an overview of the measuring capabilities of IJ_Rhizo, an open-source solution for measuring scanned images of washed root samples, written as a macro for ImageJ (http://rsbweb.nih.gov/ij/), which is a public domain Java image processing program developed at the National Institutes of Health of the USA. The main purposes of the paper are to: explain how to run IJ_Rhizo via its simple graphical user interface (GUI); describe its outputs; compare, based on two sets of images, IJ_Rhizo's performance with that of the commercial package WinRHIZO™, the root measurement software most widely used worldwide.

Materials and methods

Computing environment

IJ_Rhizo, is a macro for ImageJ, which is a public domain Java image processing program developed at the National Institutes of Health. It is a powerful image

analysis package that runs, either as an online applet or as a downloadable application, on any computer with a Java 1.4 (or later) virtual machine. Downloadable distributions of ImageJ are available for Windows, Mac OS and Linux from http://rsbweb.nih.gov/ij/. A macro is a simple program that automates a series of ImageJ commands. A macro is saved as a text file and executed by selecting a menu command, by pressing a key or by clicking on an icon in the ImageJ toolbar. IJ_Rhizo results from incremental developments in response to our needs for specific measuring tools and/or functionalities as we were conducting our own research; it is freely available from (www.plant-image-analysis.org/software/IJ_Rhizo)

Image pre-processing, computations and handling of the macro

Compared to the prototype version of the macro previously presented by Pierret et al. (2007), IJ_Rhizo offers a simple GUI so that it can be used by end-users with limited computer literacy, as well as options to customize: image resolution; the size of image border to be excluded from processing; background particle cleaning; root length correction including the Kimura et al. (1999) estimator; and the choice of automatic versus user-defined thresholding. The two root length estimates that proved to be best correlated (see Results and discussion section) were the Tennant method of WinRHIZO™ and the Kimura method of IJ_Rhizo. The line-intersect method (Tennant 1975) is derived from counting the number of intercepts between roots and the perpendicular lines of a grid superimposed to a root sample or its image. The Kimura (Kimura et al. 1999) approach is based on discriminating each pixel of the medial axis transform image of a root sample (or *skeleton*) according to its number of orthogonal and diagonal (vertical or horizontal) neighbours. Detail about the image pre-processing and computations currently offered by IJ_Rhizo and how to use the software is given in the Supplementary section.

Comparison of IJ_Rhizo with WinRHIZO™ - Root image collection and acquisition

Our comparison of IJ_Rhizo and WinRHIZO™ performance was based on two sets of images. The first set of images consisted of real root samples extracted from soil cores that were collected in vineyards at Pech Rouge INRA research station, Gruissan, France (N 43°08′35.18″ - E 03°07′57.44″). 44 cubic soil monoliths (10×10×10 cm) were collected down to a depth of 1 m in two plots where two grape varieties (Merlot and Viognier) are grown. Roots were washed from soil manually and sorted based on their appearance as dead or live roots. After removing debris, a greyscale image was acquired using a digital scanner equipped with a positive film transparency unit (Epson Expression 10000XL). It was not found necessary to use a dye such methylene blue or toluidine blue to stain washed roots, as contrast between roots and background was naturally sufficient for subsequent image segmentation. The second set of images included 10 scans of A4 transparency sheets on which test lines were drawn with two black pens (point sizes 0.5 and 1 mm) and one additional blank transparency. It was assumed that, compared to images of root samples, these test images should include no or very few "parasite" objects in the background.

The two sets of images were processed with both IJ_Rhizo and WinRHIZO™ (v. Pro 2005; Regent Instruments, Montreal, QC, Canada). WinRHIZO™ settings used were as follows: image mode: 8-bit Gray (Std); resolution: 400 dpi; scale: 100 %; calibration: intrinsic for scanner; Root/background and colour analysis: based on grey levels (threshold)—Manual—Dark on white background; particle cleaning: on. Output images of scanned root samples were saved in TIF format. Processing parameters used with IJ_Rhizo were: Image Resolution: 400 dpi; Width of excluded border 50; Perform particle cleaning—on (1 mm^2 / 0.75); Perform root length correction: on; Perform Kimura root length correction: on; Type of threshold: Automatic; Output file extension: .xls. IJ_Rhizo can indifferently handle TIF or JPEG images as input images but exclusively saves files as JPEG.

While the comparison between IJ_Rhizo and WinRhizo was not carried out using the latest version of WinRhizo, but a version purchased in 2005, the list of updates and changes that the software went through since 2005 (as listed under http://www.regentinstruments.com/products/rhizo/WinRHIZOMostRecent.html) does not reveal any changes in the procedures used to compute root length and diameter since the 2005 version.

IJ_Rhizo and WinRHIZO™ estimated root parameters were compared using linear regression analysis and coefficient of correlation. All statistics were computed using the R project for statistical computing, version 2.15.1 (2012-06-22; R Development Core Team 2012).

Results and discussion

Performance of IJ_Rhizo compared to the commercial package WinRHIZO™

Root length estimates

Overall, the root length estimates obtained with IJ_Rhizo and WinRHIZO™ on the set of test line images were found to be strongly linearly correlated with multiple r^2 coefficients at least equal to 0.997 (Table 1). Correlation coefficients between different IJ_Rhizo and WinRHIZO™ length estimates were comparable to that between the two WinRHIZO™ length estimates "length" and "Tennant". The comparison based on root sample images confirmed that root length estimates computed using IJ_Rhizo and WinRHIZO™ were well correlated (Table 2). The smallest absolute differences in length were found between IJ_Rhizo "corrected" estimates and the WinRHIZO™ "Tennant" values, with an average error of 10 % and 25 % of samples differing by more than 10 % from each other. The best linear fit was found between IJ_Rhizo "Kimura" and WinRHIZO™ "Tennant" estimates, with an average error of 8.7 % (assuming an average length overestimation of 24.5 % with IJ "Kimura" as compared to WinRHIZO™ "Tennant"). The linear regression between IJ_Rhizo "Kimura" and WinRHIZO™ "Tennant" (r^2=0.991, $p<2.2\times10^{-16}$; Fig. 1) was actually better than that between the two WinRHIZO™ estimates "Length" and "Tennant" (r^2=0.985, $p<2.2\times10^{-16}$), which is consistent with previous results obtained by Tajimaa and Kato (2011) with ImageJ and WinRHIZO™.

Root diameter estimates

Average diameter estimates obtained with the two pieces of software on the set of test line images were also strongly linearly correlated, although to a lesser extent than length estimates (r^2=0.991). However, average root diameter estimates generated by IJ_Rhizo and WinRHIZO™ using root images compared relatively poorly, with an average error of 18 %, the linear fit between the two estimates (IJ_Dia=0.859 WR_Dia+0.0268, r^2=0.893, $p<2.2e-16$; Fig. 2), indicating that average diameters derived from IJ_Rhizo were about 86 % on average that derived from WinRHIZO™ (it must be noted that, in the absence of any calibration, this is not indicative of one estimate being more accurate than the other).

Recent studies demonstrated that subtle shifts in root diameter distributions were observed in response to environmental stresses such as nutrient deficiency (Zobel et al. 2006). Hence, the actual relevance of the average root diameter as an informative parameter for root analysis is highly questionable: as pointed out by Ryser (2006), when the root diameter distribution is skewed or bimodal, as is frequently the case, the very notion of average diameter becomes relatively meaningless. As an effort to address this need for informative root functional descriptors, IJ_Rhizo generates, in addition to the main "ResultAll.txt" output file and for each image analysed, a root radius distribution file, stored as a text file and named using the input image name exclusive of the original extension. Figure 3 shows an example of such a file and the corresponding root radius distribution histogram. A similar feature is

Table 1 Linear regressions between different length computations methods implemented in IJ_Rhizo and WinRHIZO™, applied to test line images (n=15)

IJ_Rhizo (x)	WinRHIZO™ (y)	Linear regression	r^2	p-value
Raw length	*Length*	y=1.697x−13.692	0.997	$<2.2\times10^{-16}$
Raw length	*Tennant length*	y=1.237x+8.955	0.997	$<2.2\times10^{-16}$
Corrected length	*Length*	y=1.198x−20.417	0.997	2.34×10^{-16}
Corrected length	*Tennant length*	y=1.239x+1.172	0.997	$<2.2\times10^{-16}$
Kimura length	*Length*	y=0.934x−15.955	0.997	$<2.2\times10^{-16}$
Kimura length	*Tennant length*	y=0.966x+6.276	0.998	$<2.2\times10^{-16}$
	Tennant = f(length)	y=1.033x+24.019	0.998	$<2.2\times10^{-16}$
Average diameter	*Average diameter*	y=0.981x−0.036	0.991	1.3×10^{-12}

Table 2 Linear regressions between different length computations methods implemented in IJ_Rhizo and WinRHIZO™, applied to real root sample images (n=44)

IJ_Rhizo (x)	WinRHIZO™ (y)	Linear regression	r^2	p-value
Raw length	*Length*	y=0.995x+23.267	0.987	$<2.2\times10^{-16}$
Raw length	*Tennant length*	y=1.113x−65.618	0.990	$<2.2\times10^{-16}$
Corrected length	*Length*	y=0.988x+22.170	0.988	$<2.2\times10^{-16}$
Corrected length	*Tennant length*	y=1.106x−66.927	0.990	$<2.2\times10^{-16}$
Kimura length	*Length*	y=0.791x+25.399	0.987	$<2.2\times10^{-16}$
Kimura length	*Tennant length*	y=0.886x−63.853	0.991	$<2.2\times10^{-16}$
	Tennant f(length)	y=1.109x−82.166	0.985	$<2.2\times10^{-16}$
Average diameter	*Average diameter*	y=1.040x+0.050	0.893	$<2.2\times10^{-16}$

also available in WinRHIZO™ but we did not compare it to results from IJ_Rhizo here. A further improvement of root diameter determination provided by IJ_Rhizo would be to include the kernel multiplication approach proposed by Kimura and Yamasaki (2003).

Possible causes for differences in root parameter measurements

It is virtually impossible to attribute differences in length estimation to a single cause. The fact that IJ_Rhizo with the "Kimura" length calculation yielded estimates 13 % greater on average than the WinRHIZO™ "Tennant" estimates is not unexpected as Zeng et al. (2006) reported that Kimura's method, while yielding the most accurate length estimates in most situations, had a slight tendency towards overestimation. The influence of thresholding algorithms should not be overlooked as they are known to significantly affect length measurements (Tajimaa and Kato 2011); this is particularly the case when the contrast between roots and background is weak or when the background includes objects that can interfere with the analysis (such as scratches on the container used to lay out the roots over the scanner window, or scratches on the scanner window itself). This is further confirmed by the fact that values yielded by the two software on test line images, relatively free of such background noise, compared better than that obtained on root sample images. This issue is one of the reasons why, by default, IJ_Rhizo saves the pre-processed image resulting from background particle removal and segmentation procedures, thus allowing post-processing inspection and straightforward interpretation of unexpected results on individual images (such as incorrect exclusion margins selection, inappropriate thresholding, excessive/insufficient background objects filtering, etc.). WinRHIZO™ includes a similar filtering procedure, the result of which can easily be assessed visually using an overlay function, but, being proprietary software, no detail on the actual algorithms applied is available (to the best of our knowledge, only a short abstract which does not provide any insight into algorithmic procedures has been published on WinRHIZO™ by Arsenault et al. (1995)).

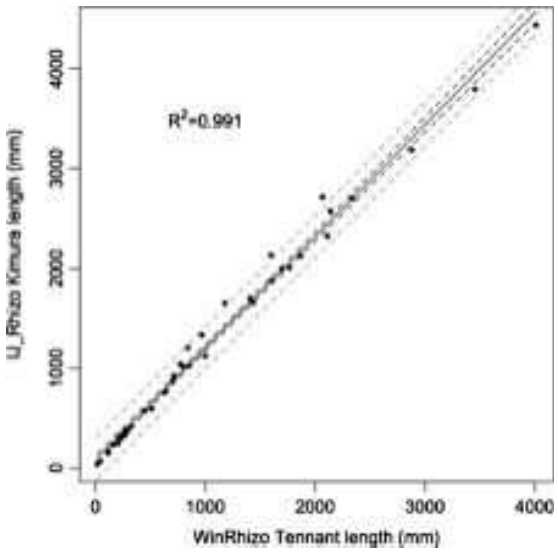


Fig. 1 Comparison between IJ_Rhizo "Kimura" and WinRHIZO™ "Tennant" length measurements made on a dataset of 44 samples. Linear regression (*solid line*), 95 % confidence and prediction intervals (thick and thin dashed lines, respectively)

Another potential source of discrepancies between software could stem from the fact that, while

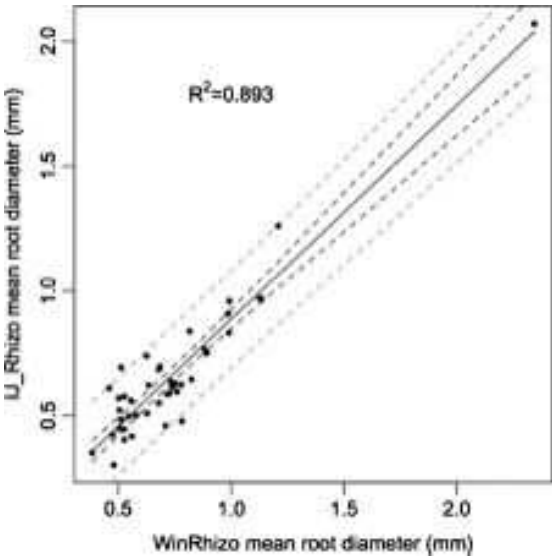


Fig. 2 Comparison between IJ_Rhizo and WinRHIZO™ average root diameter measurements made on a dataset of 44 samples. Linear regression (*solid line*), 95 % confidence and prediction intervals (thick and thin dashed lines, respectively)

WinRHIZO™ uses TIF images, IJ_Rhizo uses Jpeg compressed images with a quality factor of 75 (default value in ImageJ but can be adjusted). However, this hypothesis seems week, given the rather good agreement between length and diameter measurements obtained using the two pieces of software on test-line images. Further, the fact that the two pieces of software yielded very similar projected surfaces areas of root objects in the segmented versions of our test line images (data not shown) indicates that jpeg compression was not a major source of error, as long as images had a good enough spatial resolution and were well-contrasted.

Finally, but most importantly, untangling and spreading root samples evenly, without crossovers also remains one of the major challenges that hampers the accuracy of root length measurements. Although WinRHIZO™ includes algorithms aimed at limiting the impact of root overlaps on length estimates, it must be remembered that the key to accuracy is, regardless of the software used, to ensure as much as practically achievable that roots that make up a root sample are not in contact with each other during scanning (Zobel 2003). Further, Meng-Ben and Qiang (2009) recently found experimentally that WinRHIZO's overlap correction efficacy was often not sufficient and could lead to substantial root length underestimation.

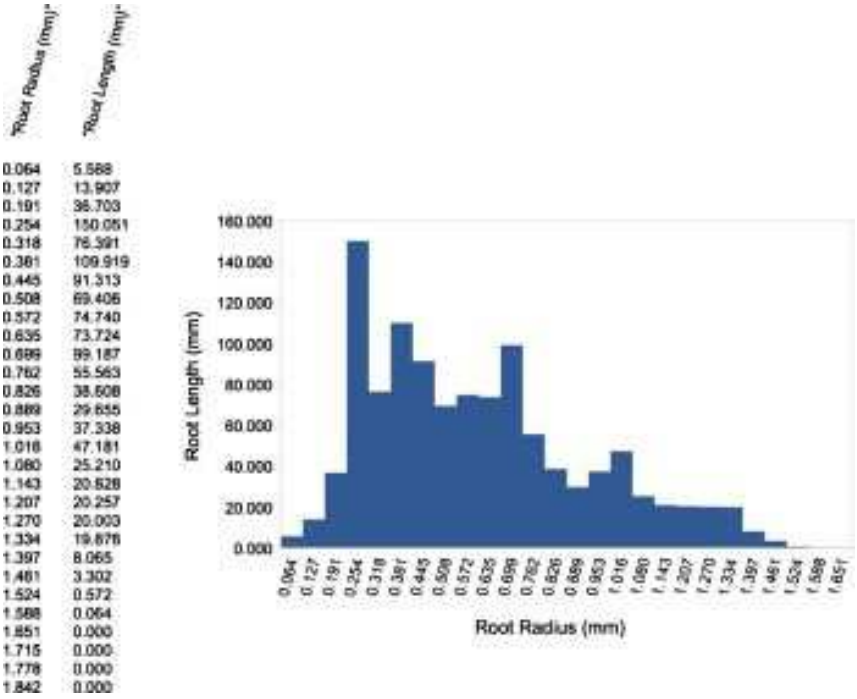


Fig. 3 Typical example of a root radius distribution and corresponding histogram

Software execution

Processing speed appeared to be related to the hardware used and to several image parameters, among which were image size, root length, root diameter distribution and processing options. It is therefore only possible to provide rough estimates of processing times here. As an indication, it took on average 6–7 min to process each of the root sample files used in this work (3607×2188 pixels), using a computer equipped with a 1.86 GHz Intel Core 2 Duo processor and 2 min with a more recent 1.7 GHz dual-core Intel Core i5. With the latter hardware, processing took between 50 and 120 s when root length was about 0.5 m at most while it exceeded 250 s for some images with more than 1 m of root length. Because of this loose linear relationship with image size, the processing of A4 frames with a resolution of 600 dpi will take, for example, 7 and 25 min on the 1.7 GHz dual-core Intel Core i5 and 1.86 GHz Intel Core 2 Duo configurations, respectively.

General computational features

IJ_Rhizo is offered as an exchange platform for researchers who need to compute root length measurements and who, beyond the final results, also want to understand precisely what they did, how they did it and IJ_Rhizo being open-source, it is up to individual users to run it as is or modify it to accommodate their specific needs. Indeed, all the operations applied to input data when running IJ_Rhizo, are by essence available; one could therefore decide to save more and different output images or compute additional measurements, etc. Nevertheless, it must be noted that, in contrast with commercial software, IJ_Rhizo was not developed within the framework of product design and development specifications and did not undergo formal quality assurance testing. However, its performance against that of RootEdge (Kaspar and Ewing 1997), which is known to perform consistently with WinRHIZO™ (Himmelbauer et al. 2004) was previously tested and published (Pierret et al. 2007). In addition, over the years, IJ_Rhizo has been successfully run on a wide range of hardware and operating systems, including Microsoft Windows, Mac OS and Linux, and it has been used for research purposes to measure over 2800 scanned images of root samples of a variety of annual and perennial plant species such as rice, maize, job's tear, teak and rubber tree (e.g. Gonkhamdee 2010).

Conclusion

In this paper, we presented the main features of IJ_Rhizo, an ImageJ macro that automatically measures root length and radius from scanned images of washed root samples. Being based on a public domain, Java image processing package, IJ_Rhizo has the advantage of being free of charge: all that is needed to carry out root measurements with IJ_Rhizo is a professional-grade A4 flatbed scanner with transparency mode, that can be purchase for under USD 1,000. By comparison, the price tag for a basic WinRHIZO™ License together with a flatbed scanner retailed by Regent Instruments is about USD 4,000. While the main target audience for IJ_Rhizo is non-programmers having no or limited experience in image processing, being open-source based, it is fully modifiable to accommodate the specific needs of users interested in understanding and controlling all the steps relevant to measuring plant roots. Comparison of IJ_Rhizo's performance with that of the widely used commercial package WinRHIZO™ indicated that IJ_Rhizo "Kimura" and WinRHIZO™ "Tennant" root length estimates were well-correlated, although the former were on average 13 % greater than the latter. Correlation between average root diameter estimates produced by the two packages was weaker, which relates to the sensitivity of this parameter to thresholding and filtering of image background noise. However, like WinRHIZO™, IJ_Rhizo automatically generates root radius distributions for each sample analysed, an approach that provides much more detailed insight into root morphology than the average diameter. Overall, IJ_Rhizo offers new opportunities for researchers who cannot afford the cost of commercial software packages to carry out automated measurement of scanned images of root samples, without sacrificing accuracy.

Acknowledgements The authors would like to thank the French Institute for Rubber (IFC), and Michelin/Socfinco/SIPH Rubber Tree Plantations Companies and the French Agence Nationale de la Recherche (project Ecosfix, ANR-2010-STRA-003), the French Institute for Research for Development (IRD) and International Centre for Agricultural Research for Development (CIRAD) for providing the enabling environment and financial resources that, over the years, allowed us to develop IJ_Rhizo. We

also are deeply grateful to the National Agriculture and Forestry Research Institute (NAFRI) of Laos, and Khon Kaen University (KKU), Thailand for their continued logistical support, and to all the owners/farmers who kindly granted us access to their fields for sampling purposes. We are also grateful to Dr. Boris Rewald, BOKU, Austria, for making constructive comments about this manuscript.

References

Arsenault J-L, Pouleur S, Messier C, Guay R (1995) WinRHIZO™, a root-measuring system with a unique overlap correction method. HortSci 30:906

Bouma TJ, Nielsen KL, Koutstaal B (2000) Sample preparation and scanning protocol for computerised analysis of root length and diameter. Plant Soil 218:185–196

Christina M, Laclau J-P, Gonçalves JLM, Jourdan C, Nouvellon Y, Bouillet J-P (2011) Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. Ecosphere 2:art27

Clothier BE, Green SR (1997) Roots: the big movers of water and chemical in soil. Soil Sci 162:534–543

Dowdy RH, Smucker AMJ, Dolan MS, Fergusson JC (1998) Automated image analyses for separating plant roots from soil debris elutrated from soil cores. Plant Soil 200:91–94

Edwards EJ, Benham DG, Marland LA, Fitter AH (2004) Root production is determined by radiation flux in a temperate grassland community. Global Change Biol 10:209–227

Esser G, Kattge J, Sakalli A (2011) Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere. Global Change Biol 17:819–842

Ewing RP, Kaspar TC (1995) Accurate perimeter and length measurement using an edge chord algorithm. J Computer-assisted Microsc 7:91–100

Feddes RA, Hoff H, Bruen M, Dawson TE, de Rosnay P, Dirmeyer P, Jackson RB, Kabat P, Kleidon A, Lilly A, Pitman AJ (2001) Modeling root water uptake in hydrological and climate models. Bull Am Meteorol Soc 82:2797–2809

Gonkhamdee S (2010) Analysis of the interplay between crop and inter-crop roots in young rubber tree plantations of NE Thailand. PhD of the "Université d'Avignon et des pays de Vaucluse" (UAPV). France and Khon Kaen University, Thailand

Gyssels G, Poesen J, Liu G, van Dessel W, Knapen A, de Baets S (2006) Effects of cereal roots on detachment rates of single- and double-drilled topsoils during concentrated flow. Eur J Soil Soc 57:381–391

Himmelbauer ML, Loiskandl W, Kastanek F (2004) Estimating length, average diameter and surface area of roots using two different image analysis systems. Plant Soil 260:111–120

Kaspar TC, Ewing RP (1997) ROOTEDGE: software for measuring root length from desktop scanner images. Agron J 89:932–940

Kell DB (2011) Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. Ann Bot 108:407–418

Kimura K, Kikuchi S, Yamasaki S (1999) Accurate root length measurement by image analysis. Plant Soil 216:117–127

Kimura K, Yamasaki S (2003) Accurate root length and diameter measurement using NIH Image: use of Pythagorean distance for diameter estimation. Plant Soil 254:305–315

Kleidon A, Heimann M (1998) Optimised rooting depth and its impacts on the simulated climate of an atmospheric general circulation model. Geophys Res Lett 25(3):345–348

Le Bot J, Serra V, Fabre J, Draye X, Adamowicz S, Pagès L (2010) DART: a software to analyze root system architecture and development from captured images. Plant Soil 326:261–273

Lobet G, Pagès L, Draye X (2011) A novel image-analysis toolbox enabling quantitative analysis of root system architecture. Plant Physiol 157:29–39

Magalhaes PC, de Souza TC, Cantao FRO (2011) Early evaluation of root morphology of maize genotypes under phosphorus deficiency. Plant Soil and Environment 57:135–138

Meng-Ben W, Qiang Z (2009) Issues in using the WinRHIZO system to determine physical characteristics of plant fine roots. Acta Ecologica Sinica 29:136–138

Mickovski SB, Bransby M, Bengough AG, Davies MCR, Hallett PD (2010) Resistance of simple plant root systems to uplift loads. Revue canadienne de géotechnique 47:78–95

Nelson BD, Phan N (2006) Evaluation of partial resistance in soybean to Phytophthora sojae using WinRhizo root analysis software. Phytopathology 96:S83

Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, da Silva ED, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666–669

Newman EI (1966) A method of estimating the total length of root in a sample. J Appl Ecol 3:139–145

Pierret A, Moran CJ, Doussan C (2005) Conventional detection methodology is limiting our ability to better under- stand the roles and functions of fine roots. New Phytol 66:967–980

Pierret A, Latchackak K, Chathanvongsa P, Sengtaheuanghoung O, Valentin C (2007) Interactions between root growth, slope and soil detachment depending on land use: a case study in a small mountain catchment of Northern Laos. Plant Soil 301:51–64

Pierret A, Moran CJ (2011) Plant roots and soil structure. In: Glinski J, Horabik J, Lipiec J (eds) Encyclopedia of agrophysics. Springer, Dordrecht, pp 628–632

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269:341–356

Roumet C, Urcelay C, Díaz S (2006) Suites of root traits differ between annual and perennial species growing in the field. New Phytol 170:357–368

Ryser (2006) The mysterious root length. Plant Soil 286:1–6

Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DA, Nannipieri P, Rasse DP, Weiner S, Trumbore

SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56
Stokes A, Atger C, Bengough AG, Fourcaud T, Sidle RC (2009) Desirable plant root traits for protecting natural and engineered slopes against landslides. Plant Soil 324:1–30
Tajimaa R, Kato Y (2011) Comparison of threshold algorithms for automatic image processing of rice roots using freeware image. J Field Crops Res 121:460–463
Tennant D (1975) A test of a modified line intersect method of estimating root length. J Ecology 63:995–1001
Vegapareddy M, Richter GM, Goulding KWT (2010) Using digital image analysis to quantify the architectural parameters of roots grown in thin rhizotrons. Plant Biosystems 144:499–506
Zeng G, Birchfield ST, Wells CE (2006) Detecting and measuring fine roots in minirhizotron images using matched filtering and local entropy thresholding. Mach Vis Appl 17:265–278
Zeng G, Birchfield ST, Wells CE (2008) Automatic discrimination of fine roots in minirhizotron images. New Phytol 177:549–557
Zeng X, Dai Y-J, Dickinson RE, Shaikh M (1998) The role of root distribution for climate simulation over land. Geophys Res Letters 25:4533–4536
Zobel RW (2003) Sensitivity analysis of computer-based diameter measurement from digital images. Crop Sci 43:583–591
Zobel RW, Alloush GA, Belesky DP (2006) Differential root morphology response to no versus high phosphorus, in three hydroponically grown forage chicory cultivars. Environ Experimental Botany 57:201–208
Zobel RW (2008) Hardware and software efficacy in assessment of fine root diameter distributions. Comput Electron Agric 60:178–189
Zoon FC, van Tienderen PH (1990) A rapid quantitative measurement of root length and root branching by microcomputer image analysis. Plant Soil 126:301–308

Annexe II b: IJ Rhizo: Supplementary section

Image pre-processing

The purpose of the first part of the IJ_Rhizo macro is to remove pixels at the image periphery when these pixels are known to include values that could mistakenly be considered as "root related objects". The size of the image margin to be excluded from analysis is set to a default value but can also be adjusted by the user. Once this operation is completed, the image is subsequently segmented, i.e. transformed into a binary image in which objects and background are coded with a unique value. The threshold value applied for the segmentation is either defined automatically by the function "*FindThres*" which analyses the local slope of the image histogram, or entered manually by the user. The principle of "*FindThres*" is inspired from the procedure first described by Vogel and Kretzschmar (1996). Starting from the lowest grey level value (0), a positive change in the slope of the histogram is sought and recorded as *ThInf*. Then, starting from *ThInf + 1* a slope > 1000 at a "distance" of more than 100 grey levels from *ThInf* is recorded as *ThSup*. Finally the threshold value *Thres* is defined as:

$$Thres = ((95 * ThSup) + (5 * ThInf)) / 100 \qquad \text{Eq (1)}$$

Note that this approach only works for sufficiently contrasted images with dark objects on a light background, so that two separate and well-defined peaks exist in the histogram. In the case of insufficiently contrasted images, the user-defined threshold approach will be preferred.

Next, IJ_Rhizo calls an optional routine "*CleanParticles*" which removes undesirable objects by comparing their size and shape to two reference values. These two values are either user-defined or pre-set, with a default value of 1 mm^2 for size, and a default "circularity" value of 0.75 for shape - a circularity value of 1.0 indicating a perfect circle. This particle cleaning routine is most useful to remove small debris and

grains of sand that often get mixed with roots from soil washing samples, but it is a rather computer-intensive operation, particularly on large images. This optional routine is run by default but can be unselected by the user when using it is deemed unnecessary. Subsequently, the thresholded / cleaned image is saved as a jpeg file as it often proves useful to check these images once the processing is complete to evaluate the output results.

Skeletonization, Euclidean Distance Map and Root Radius Distributions

Further into IJ_Rhizo's execution, the thresholded image is re-opened and skeletonized, i.e. that objects are thinned iteratively until they are represented by a one-pixel-wide line (Russ, 1994). The number of pixels making up this skeleton image is then computed. Multiplied by the image resolution, it is used to produce a first, but rather crude, estimate of root length.

IJ_Rhizo then generates the root radius distribution, which indicates how much length there is in every root radius class. To this end, the thresholded image is used to derive the so-called Euclidean Distance Map (EDM; Russ, 1994) in which pixels corresponding to objects are labelled according to their distance to the edge of the object in which they are included (Kimura and Yamasaki, 2003). By combining the EDM and the skeleton images, it is therefore possible to produce a skeleton labelled with discrete root radius values. A table is then created in which, for each radius values, the corresponding number of pixels is reported. By multiplying both root radius and pixel numbers by a factor corresponding to the image spatial resolution, this results in a root radius distribution histogram with values scaled to an approximation of their actual sizes (for a critical discussion of the limitations of this method, see Kimura and Yamasaki, 2003). By convention, the root radius distribution of each image is saved in the output file directory as a text file named “XXX.txt” where XXX is the input image name exclusive of the original extension. Note that the last bin of these root radius distribution histograms corresponds to background pixels and should therefore be disregarded.

A fourth part is used to implement an optional length correction; a property of the skeleton-based technique is that the assessed length of objects is underestimated in

a proportion directly related to their thickness (or radius). This is because more pixels must be removed from around a thick object than from a thinner one to produce a skeleton (Figure 1). Consequently, using the EDM labelled skeleton produced previously, this part of the macro estimates, for each individual object, the number of pixels to be added to the overall skeleton length.

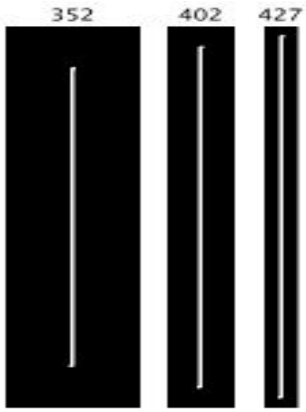


Fig. 1 Test image with three objects of identical maximum length (450 pixels) but of different thicknesses (100, 50 and 25 pixels from left to right); the skeletons (in white) are represented within the shapes of the original objects (in black), and their length (in pixels) is reported above each object, clearly illustrating the effect of object thickness on skeleton length.

Computations

Finally, the fourth part of IJ_Rhizo is dedicated to calculations of values to be written in the main output file. By convention, the main output file is named "*ResultAll.txt*" and is saved in the output file directory. In its current version, IJ_Rhizo computes 11 parameters. Four of these are expressed as a number of pixels, namely, the size of the uncorrected skeleton (*Raw_Skel*), the size of the corrected skeleton (*Skel_Corr*), the size of the Kimura skeleton (*Kimura*), i.e. a skeleton whose pixels were discriminated and their size weighed according to their number of orthogonal and diagonal neighbours (according to the procedure of Kimura et al., 1999) and the projected surface area (*Surf_Area*), which corresponds to the number of object pixels in the thresholded image. The six other parameters are the uncorrected, corrected and

Kimura root lengths, the average root diameter, the equivalent root surface area and the equivalent root volume. All these parameters (Table 1) are scaled according to the spatial resolution of input images and computed as follows:

The uncorrected root length *Raw_RL* (in mm):

$$Raw_RL = Raw_Skel * (25.4/ImRes) \quad \text{Eq (2)}$$

Where *Raw_Skel* is the number of pixels that make up the skeleton and *ImRes*, the image spatial resolution in dots per inch (dpi);

The corrected root length *Rlc* (in mm):

$$RLc = Raw_RL + (XtraPix * (25.4/ImRes)) \quad \text{Eq (3)}$$

Where *XtraPix* is the number of extra pixels found through the EDM-based length correction computation, *Raw_Skel* the number of pixels that make up the uncorrected skeleton and *ImRes*, the image spatial resolution in dots per inch (dpi);

The *Kimura_length* (in mm):

$$Kimura_length = Kimura * (25.4/ImRes) \quad \text{Eq (4)}$$

Where *Kimura* is the size of the skeleton computed according to the procedure of Kimura et al., (1999) and *ImRes* is the image spatial resolution in dots per inch (dpi);

The average root diameter *Mean_Dia* (in mm):

$$Mean_Dia = Surf_Area/RLc \qquad \text{Eq (5)}$$

Here *RLc* is the corrected root length and *Surf_Area* is the projected surface area of all the root objects within the image – i.e. the number of object pixel multiplied by the surface area of one pixel which is $(25.4/ImRes)^2$ where *ImRes* is the image spatial resolution in dots per inch (dpi); note that if the user does not choose to compute the *RLc*, *Raw_RL* is used by default (which in turn yields a higher and less accurate value of *Mean_Dia);*

The average root diameter derived from the root radius distribution histogram *Mean_Dia_C* (in mm)*:*

$$Mean_Dia_C = \frac{\sum_{i=1}^{n}(lr_i * r_i)}{\sum_{i=1}^{n} lr_i} \qquad \text{Eq (6)}$$

Where r_i is a root radius bin of the root radius distribution histogram, n is the number of root radius bins and lr_i is the scaled length corresponding to each root radius bin.

The equivalent root surface area assuming perfectly cylindrical geometry of all roots, *Eq_Surf* (in mm^2):

$$Eq_Surf = Surf_Area * \pi \quad \text{Eq (7)}$$

Where *Surf_Area* is the projected surface area of all the root objects. The equivalent root volume assuming perfectly cylindrical geometry of all roots, *Eq_Vol* (in mm^3):

$$EqVol = (Mean_Dia/2)^2 * RLc * \pi \quad \text{Eq (8)}$$

Name	**Corresponding parameter**	**unit**
File_Name	Name of input image file	N/A
Raw_Skel	Size of uncorrected skeleton	pixels
Skel_Corr	Size of corrected skeleton	pixels
Kimura	Size of Kimura skeleton	pixels
Raw_RL	Root length derived from uncorrected skeleton	mm
Rlc	Root length derived from corrected skeleton	mm
Kimura_length	Root length derived from Kimura skeleton	mm
Mean_Dia	Average root diameter Mean_Dia derived from *Surf_Area* and *Rlc*	mm
Mean_Dia_C	Average root diameter derived from the root radius distribution histogram	mm
Eq_Surf	Equivalent root surface area assuming perfectly cylindrical geometry of all roots	mm^2
Eq_Vol	Equivalent root volume assuming perfectly cylindrical geometry of all roots	mm^3
Surf_Area	Projected surface area of root objects multiplied by the actual surface area of one pixel	mm^2

Table 1. List and description of IJ_Rhizo parameters as saved in the "*ResultAll.txt*" main output file.

Running IJ_Rhizo

To use IJ_Rhizo, it is necessary to first run the ImageJ program. The macro itself can thence be launched from the Plugins menu, in ImageJ main window's menu bar. This is done by selecting Plugins>Macros>Run... from the ImageJ toolbar (Figure 2)

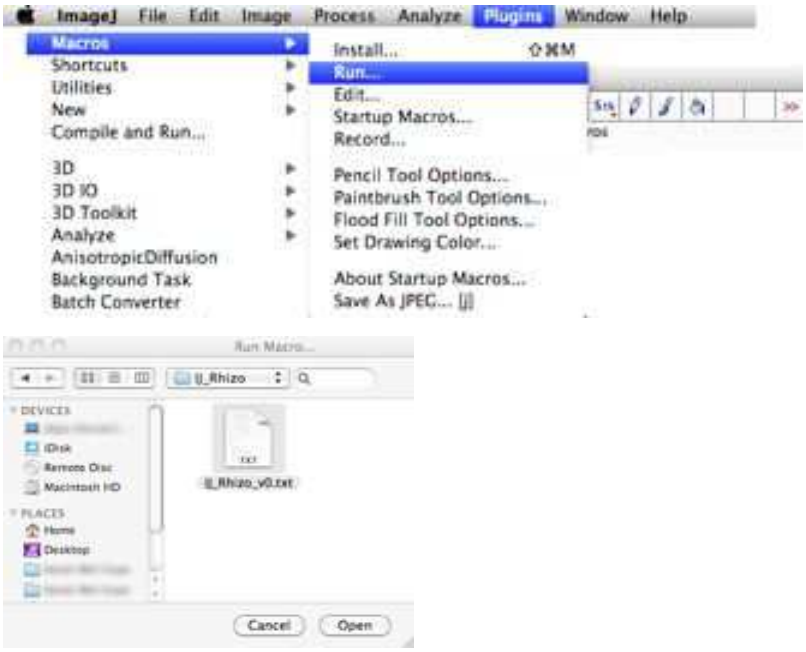


Fig. 2 Launching the root processing macro from the ImageJ toolbar and selecting the macro from the “Run Macro...” window

This triggers the opening of a “Run Macro...” window (Figure 2), from which the user needs to select the text file in which the macro has been previously saved. Navigation to this file is possible by selecting appropriate folders in the left hand side part of the “Run Macro...” window. Once in the right directory, select the macro by clicking on its name. As soon as the macro is started, the user is prompted to select a source directory, by selecting it in the “Choose Source Directory” window. The source directory is a directory in which all the image files that need to be processed must be stored prior to launching the macro. Once the source directory is selected, the user is prompted to select a destination directory, by selecting it in the “Choose Destination Directory” window. The destination directory is an empty directory which must be

created by the user prior to launching the macro and in which all the macro's output files will be recorded.

Finally, it is necessary to set a number of parameters, prior to running the macro. To this end, the user is prompted with an “Input Data” window (Figure 3). In the first box, at the top of this dialog window, the user must enter the spatial resolution of the images to be processed, in “dots per inch” (dpi). Note that all the images contained in the source directory must have the same spatial resolution. If not, the output measurements produced by the macro will only be valid for those images that have a resolution equal to that entered in the box. The default value for this parameter is 600 dpi.

The next box (Width of excluded border) requires input for the width of the image margin that may need to be excluded from the analysis (typically because it contains non root-related information such as the edge of the tray used during the root scanning process).

Below is a “Perform particle cleaning” tick box. This box should be ticked to exclude undesirable objects from the analysis, such as small debris or grains of sand. The size of the smallest particle included in the analysis can be adjusted here, as well as a shape parameter (a value of 1 and 0 corresponding to a circle and line, respectively). By default, objects down to 1 mm^2 and up to 0.75 in circularity are included in the analysis.

Finally, a “perform root length correction” tick box can be selected if loss of length related to the skeleton approached used by the macro for estimating root length needs to be accounted for. This applies chiefly when thick roots, with diameters of several tens of pixels are included in the images to be analysed. Note that this correction is rather computing intensive and will substantially slow down the overall processing.

If the “type of threshold” is set to “User defined”, a new dialog will automatically open so that lower and upper threshold values are entered (Figure 3).

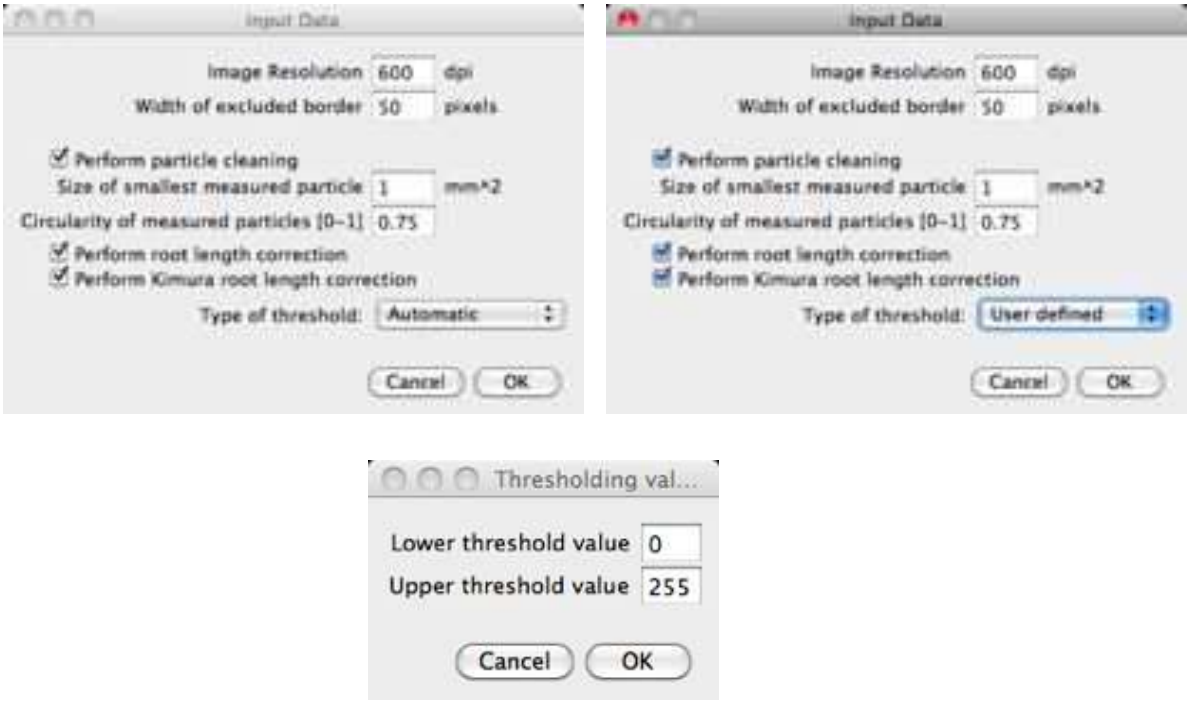


Fig. 3 The input data and thresholding dialog boxes, used to set input data and processing options

Note: to be able to run the macro, the user must previously install the Morphological Operators for ImageJ (download as a single zip file from: http://www.dentistry.bham.ac.uk/landinig/). Figure 4 shows an example "ResultAll.txt" output file produced by IJ_Rhizo, edited as a spreadsheet.

	A	B	C	D	E	F	G	H	I	J	K	L
1	File_Name	Raw_Skel	Skel_Corr	Kimura	Raw_RL	Ric	Kimura_length	Mean_Dia	Mean_Dia_C	Eq_Surf	Eq_Vol	Surf_Area
2	sampA	9489.00	9503.00	12217.72	601.28	603.44	775.83	1.40	1.34	2657.35	931.22	845.88
3	sampB	18642.00	18676.00	23900.86	1177.42	1179.58	1511.35	0.48	0.43	1761.96	209.44	592.85
4	sampC	22989.00	23093.00	29585.29	1459.80	1480.08	1865.97	0.82	0.72	3768.14	773.88	1199.44
5	sampD	8300.00	8368.00	10792.57	527.05	532.64	685.33	1.47	1.29	2456.47	901.53	781.92
6	sampE	8575.00	8751.00	11274.61	550.86	555.69	715.94	0.53	0.48	926.11	122.82	294.79
7	sampF	6863.00	6207.00	7682.66	378.65	384.14	488.48	1.30	1.10	1610.37	523.58	512.60
8	sampG	6211.00	6413.00	7898.41	394.40	407.25	501.55	0.49	0.45	832.92	78.28	201.46
9	sampH	546.00	584.00	709.51	34.67	37.72	45.05	1.33	1.12	157.95	62.64	60.28
10	sampI	988.00	1014.00	1234.87	62.74	64.39	78.41	0.83	0.58	127.88	20.21	40.71
11	sampJ	14206.00	14472.00	18697.43	902.08	918.97	1184.76	1.05	0.94	3131.82	849.34	999.89
12	sampK	16.00	16.00	17.66	1.02	1.14	1.12	0.14	0.12	0.49	0.02	0.16

Fig. 4 Typical example of an output file produced by IJ_Rhizo, edited as a spreadsheet

References

Kimura K, Kikuchi S, Yamasaki S (1999) Accurate root length measurement by image analysis. Plant Soil 216:117–127

Kimura K, Yamasaki S (2003) Accurate root length and diam- eter measurement using NIH Image: use of Pythagorean distance for diameter estimation. Plant Soil 254:305–315

Russ JC (1994) The image processing handbook, 2nd edn. CRC Press, Boca Raton, 155 p.

Vogel HJ, Kretzschmar A (1996) Topological characterisation of pore space in soil-sample preparation and digital image processing. Geoderma 73:23–38