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Citation

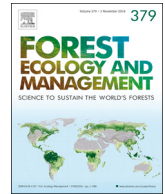
Meier, I. C., Brunner, I., Godbold, D. L., Helmisaari, H. S., Ostonen, I., Soudzilovskaia, N. A., & Prescott, C. E. (2018). Roots and rhizospheres in forest ecosystems: Recent advances and future challenges. *Forest Ecology And Management*, 431, 1-5.
doi:10.1016/j.foreco.2018.08.005

Version: Publisher's Version

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Downloaded from: <https://hdl.handle.net/1887/3203166>

Note: To cite this publication please use the final published version (if applicable).



Editorial

Roots and rhizospheres in forest ecosystems: Recent advances and future challenges[☆]

1. Introduction

Forests and trees play a vital role in sustaining life on earth. Their conservation and sustainable management are closely linked with global challenges such as climate change, food security and environmental protection. For 125 years the International Union of Forest Research Organizations (IUFRO) has been committed to promoting international cooperation in research embracing the full range of topics related to forests and trees. The IUFRO 125th anniversary congress (19–22 September 2017) in Freiburg, Germany, focused on questions related to (1) interactions of trees and soil in forest ecosystems, (2) increases of the forest carbon (C) sink, and (3) resilience of forests to climatic changes. Recognizing the need for improved understanding of the physiology, function and ecology of the belowground biomass of forests, the congress included two sessions devoted to research on roots and rhizospheres. These sessions attracted 37 contributed papers from 14 countries. By exchanging knowledge from the fields of tree physiology, functional ecology, soil biodiversity, and management of individual tree species, communities and forest ecosystems, the participants made a leap forward in our understanding of the importance of the ‘hidden half’ of trees and forests.

2. Roots and ecosystem services

Roots with their associated mycorrhizae are fundamentally important for biomass production, C sequestration, biodiversity, hydrologic function, drought-tolerance, and restoration of forests. Yet our understanding of their functioning has been constrained by the challenges of investigating the belowground ecosystem. During the sessions, recent discoveries about root systems relevant to their capacity to provide each of these ecosystem services were presented.

2.1. Trait spectra of functional root traits

Functional root traits are morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction, and survival (Violle et al., 2007) and offer insights into the ways roots influence ecosystem functioning and provide ecosystem services (Díaz et al., 2007; Prinzing et al., 2008; de Bello et al., 2010). Trait-based concepts that describe the relationships between structure and function (Valverde-Barrantes et al., 2017; Treseder et al., 2018) or emphasize functional relationships among organisms and their role in adaptive root foraging (Ostonen et al., 2017), contribute to the efforts to model

complex belowground ecosystem processes at global scales. Ina C. Meier (University of Goettingen, Germany) presented a study on the translation of the well-established leaf economics spectrum – linking dry mass investments to the return of nutrients in leaves (Wright et al., 2004) – into a root economics spectrum (Liese et al., 2017). Analysis of root traits of 13 dominant and subdominant temperate tree species (representing two phylogenetic groups and two mycorrhizal associations) indicated that the branching of lower-order roots is a leading root trait, as it relates to the mycorrhizal association type and to precision-foraging into nutrient-rich patches. Meier also emphasized the importance of the phylogenetic signal in root morphology that should be considered in root trait analyses across different environments.

A recent trait-based study along an European subarctic boreal to temperate forest gradient highlighted the trilateral relationship between morphological traits of absorptive fine roots, ectomycorrhizal (ECM) exploration types, and the soil bacterial community structure (Ostonen et al., 2017). Along the climate gradient, functional root traits shifted towards a conservative trait spectrum in boreal forests, *i.e.* absorptive fine root biomass increased, root tissue density increased, and specific root length decreased, probably in concert with increased root lifespan (Valverde-Barrantes et al., 2017). In contrast, root traits in temperate forests reflected an acquisitive or intensive strategy of enhanced resource uptake at lower biomass investments, high root cost efficiency and fast growth (Weemstra et al., 2016; Ostonen et al., 2017). Such a root-trait spectrum occurred in climate experiments and along natural climate gradient and seemed to reflect general acclimation patterns to global warming (Parts et al., 2018).

Most root trait studies consider fine roots in shallow topsoil layers, even though fine roots in deep soil layers may play an important role in water acquisition of trees (Fan et al., 2017). Bruno Bordron (USP-ESALQ, Brazil) analyzed the change of the functional specialization of eucalypt roots with ontogeny, tree nutrient status and soil depth (Bordron et al., 2018; this issue). He demonstrated that the specific relative uptake potential for K^+ and Ca^{2+} was higher at 3 m soil depth than in the topsoil (especially in fertilized trees), concomitant with an increase in root diameter and a decrease in root tissue density with depth. He concluded that the functional specialization of eucalypt fine roots for cations of low mobility depends on soil depth and increases with fertilizer application.

Two presentations reported on root trait relationships at larger or global scales: Shalom Daniel Addo-Danso (CSIR-Forestry Research Institute of Ghana) showed large variation of fine-root diameter, specific root length, specific root area, and root tissue density within and

[☆] This article is part of the Special Issue “Roots and Rhizospheres in Forest Ecosystems: Recent Advances and Future Challenges” published at the journal Forest Ecology and Management 431, 2018.

among tropical regions (Africa, Asia, and the Neotropics), while climatic variables, including MAP and MAT related differently to morphological traits across the tropics (Addo-Danso, personal communication). Zeqing Ma (CAS, China) studied root anatomical traits of 191 species from tropical forests, temperate forests, grasslands, and deserts (Ma et al., 2017). He demonstrated that tropical woody plants have comparably dense and small vessels and a thicker cortex, which can improve the efficiency of ion exchange and enhance protective functions. These results suggest that plants can acclimate to changing environmental conditions by modifying cortex-ion-absorption and stele-water-transport functions, depending on the primary limiting resource supply and dominant stress factors.

2.2. Fine root dynamics

Fine root dynamics include the production, lifespan, turnover, and decomposition of fine roots, which can consume a large part of the annual C gain of forests (Högberg et al., 2002; Ryan et al., 2010) and influence the fluxes of water and nutrients in forest ecosystems (Volder et al., 2005). Yet despite the assumed key role of fine root dynamics in the C, nutrient and water cycles of forest ecosystems, our understanding of fine root dynamics is still limited due to the notorious difficulty in accessing and observing fine roots directly. Accordingly it was our pleasure to see the increasing number of studies worldwide in this research area.

In a boreal forest stand in northern Finland, fine-root lifespan of birch (1.0 years) was significantly shorter than the root lifespan of the understory vegetation (1.8 years; observed with minirhizotrons) and was positively related to root diameter and soil depth (Ding et al., 2018; this issue). In addition, roots produced later in the growing season had a reduced mortality risk. Total fine-root production in the forest stand was $566 \text{ g m}^{-2} \text{ yr}^{-1}$, where 35% of the annual soil C input was from the understory. The authors emphasized that a stronger focus should be on the quantification of both above- and belowground C cycling of different canopy and understory species in boreal forests. By contrast, fine-root production (estimated with ingrowth cores) did not differ significantly between the investigated hardwood and conifer forest stands in a cool-temperate forest stands in Korea, but varied largely between study years (from 99 to $872 \text{ g m}^{-2} \text{ yr}^{-1}$; An et al., 2017).

The effect of seasonal changes in soil moisture and temperature on fine-root dynamics was also studied in a *Quercus ilex* (evergreen oak) stand in southern Italy (Montagnoli et al., 2018; this issue). Annual fine-root production was comparably low ($135 \text{ g m}^{-2} \text{ yr}^{-1}$) and average fine-root lifespan was only 4 months (estimated from sequential soil coring). Surprisingly, fine root biomass and length peaked in both summer and late autumn. The summer peak was accompanied by reductions in fine-root diameter and was mainly related to soil temperature. This suggests that evergreen oak channeled C preferentially into the production of very fine roots in dry summer soil, which may facilitate nutrient and water uptake in moister soil pores.

The response of trees to summer drought depends on the drought susceptibility of the root systems, which may differ between different tree origins. The International Beech Provenance Trial in Slovenia was used to study the effect tree origin on fine-root growth dynamics and architecture of European beech (Železnik et al., 2018; this issue). Median fine-root longevity varied between 1.7 and 2.6 years among the beech origins (observed with minirhizotrons), and fine-root death most likely occurred during winter. The beech provenance with the slowest aboveground growth rates also had shorter fine-root lifespans. The authors concluded that these differences in fine-root lifespan among beech provenances may contribute to their adaptation to future environmental conditions.

An alternative approach to estimate fine-root lifespan is from its radiocarbon (^{14}C) signature (Gaudinski et al., 2001; Sah et al., 2013). Solly et al. (2018) recorded the annual growth rings of fine roots from Norway spruce, Scots pine, European beech, and dwarf birch trees

grown in temperate, boreal, and sub-arctic forests, and compared the result with the ^{14}C ages of fine roots. In temperate and boreal forests, the chronological age of fine roots was 1–3 years, while at the sub-arctic site, fine roots were significantly older (4–12 years). The chronological age of spruce fine roots in the boreal forest was about 10 years younger than their ^{14}C age, especially in the largest diameter fraction. This difference indicates that there is a time lag between the assimilation of C and the production of fine roots, most likely due to internal C storage. It also indicates that a dendrochronological approach is better suited to estimating the true age of fine roots.

2.3. Management of C sequestration

The forests of the world contain about 860 Pg of C, half of which is in the soil and litter (Pan et al., 2011). The manner in which forests are managed can influence SOC stocks (Jandl et al., 2007), and considerations of the influences of forest management activities benefit from considering interrelationships with roots systems. Colin Bergeron (University of Alberta, Canada) used destructive sampling to develop allometric equations for above- and below-ground biomass for three tree species (*Populus tremuloides*, *Populus balsamifera* and *Picea glauca*) and seven shrub species in a Canadian boreal mixedwood forest (Bergeron et al., 2017). The below-ground tree biomass represented about 15% of the total C before harvest and > 20% of the total plant C following variable retention harvesting, which is similar to recent estimates that stump-root systems account for around 15–20% of the total stand biomass of boreal Norway spruce forests (Merilä et al., 2014; Kaarakka et al., 2018). Retention of root and stump systems during conventional harvesting can therefore mitigate C losses associated with forest harvesting. Adrian Gallo and Jeff Hatten (Oregon State University, USA) reported that soil C pools remained stable or even increased with extreme C removal of aboveground residuals, and that the increase in soil C appeared to originate from root C (Gallo and Hatten, personal communication). This response of forest soil to harvesting appears to be widespread, as indicated by a meta-analysis of soil C:N across many biomass-harvesting experiments (e.g. LTSP studies; Boca and Hatten, personal communication) and is supported by other studies that have raised concerns about the harvesting of root systems for bioenergy stock in Nordic countries (Walmsley and Godbold, 2010; Kaarakka et al., 2018).

Forest management generally aims to increase the aboveground biomass production for greater harvests while belowground responses have received less attention. Heljä-Sisko Helmisaari (University of Helsinki, Finland) reviewed studies on the response of aboveground-belowground interactions to forest management. She showed that N fertilization shifts biomass and C partitioning from fine roots and mycorrhizas to aboveground biomass among different forest ecosystems, which may affect the amount of belowground litter and decrease long-term soil C sequestration in fertilized stands. In addition, decreased fine root and mycorrhizal biomass in N-fertilized stands may deteriorate the responsiveness of managed forest trees to summer droughts. By contrast, irrigation of dry soil may increase both fine root biomass and C stocks in the mineral soil, as illustrated by Ivano Brunner (Swiss Federal Research Institute WSL, Switzerland) (Brunner, personal communication). Forest-floor C stocks declined despite the increased leaf litter inputs, indicating that litter decomposition was faster or more complete in this irrigation experiment in the Swiss Alps. Forest C sequestration and the vertical distribution of soil C stocks may also be managed by including specific tree species and increasing tree species diversity (Vesterdal et al., 2013; Dawud et al., 2016). Lars Vesterdal (University of Copenhagen, Denmark) reported on an empirical study across six European regions in which near-infrared reflectance spectroscopy was used to determine the tree species share in fine root biomass in over 200 monoculture and mixed species forest stands (Vesterdal, personal communication). Tree species diversity had a positive influence on topsoil C stores (Dawud et al., 2017); while fine root biomass was

mainly explained by the proportion of conifer trees (Finér et al., 2017). Tree species identity influenced the vertical distribution of fine root biomass and soil C. The authors concluded that selecting specific tree species combinations rather than increasing diversity *per se* may be more relevant in mixed-species forest management for affecting soil C stores (Finér et al., 2017).

2.4. Future challenges: tsunamis, heavy forest equipment, and seedling regeneration

Coarse roots are fundamentally important for trees as they provide soil anchorage and act as transport channels for nutrients and water. Yet our understanding of coarse-root functions is poor. Todo et al. (2018; this issue) investigated coarse-root anchorage in a Japanese coastal pine forest. The authors showed that the relationship between tree size and anchorage did not differ between land-side and sea-side plots, suggesting that the plate root systems of sea-side trees are acclimated to strong winds and the shallower ground water table: the lower critical turning moment of the plate-root system of sea-side pine trees is compensated for by enhanced horizontal root development. This knowledge of tree anchorage will be especially important for the management of coastal pine forests in the face of the expected increases in external forces such as tsunamis, storms, and typhoons.

An important potential side effect of forest harvesting is compaction of soil due to the use of heavy equipment. Soil compaction is particularly problematic for root systems of trees, as it interferes with both water flow and gas exchange. Flores Fernández et al. (2018; this issue) investigated mulching and liming as means of rehabilitating compacted soils of skid trails in Germany and found reduced bulk density, increased diffusion and increased macropore volume in the mulched soils. These factors significantly correlated with fine-root density of planted alder in the upper 20 cm of soil.

Specific consideration of roots also contributes to successful forest restoration, as the condition of the root system determines the quality of the seedlings used in regeneration, and their success following out-planting (Grossnickle and MacDonald, 2018). Cold acclimatization of both shoots and roots is essential to the overwinter survival of seedlings in boreal forests, and the processes do not occur simultaneously in the two tissue types. Di et al. (2018; this issue) demonstrate the utility of measurements of electrical impedance for monitoring the frost hardening of the root system in order to assess a safe time for moving Scots pine seedlings to freezer storage.

3. Forest rhizosphere ecology and biogeochemistry

Although forest soils constitute a primary important control mechanism for the functioning of forest ecosystems, little is known about the rhizosphere processes that underpin these controls. In particular the importance of soil and rhizosphere biodiversity and associated biogeochemical cycles is poorly understood. These relationships may be strongly dependent on changing climatic and nutrient conditions along environmental gradients and, thus, be affected by global change and biological invasions.

Roots interact with rhizosphere microbes to stimulate the metabolism of recalcitrant soil organic matter (SOM). This change in native C mineralization and N-cycling in response to the enhanced release of C-rich substrates from roots to soil – that is in response to enhanced root exudation – is defined as the ‘microbial priming effect’ (Kuzyakov, 2010). While studies on root-induced N-cycling provide strong evidence of links between root-derived C and N-cycling, the mechanisms that drive these dynamics are still poorly understood (Meier et al., 2017). One important source of uncertainty regarding priming effects is which components of SOM are primed. Jussi Heinonsalo (University of Helsinki, Finland) analyzed the influence of pine roots on the decomposition of SOM originating from the organic horizon of a boreal forest (Pumpanen et al., 2017). They showed that roots changed C and N

pools in the soluble SOM fraction. As a consequence, this SOM fraction had the largest abundance of ^{14}C and ^{15}N , suggesting that the soluble SOM fraction (partly) originates from scavenging or mining of nutrients from the oldest part of SOM and has probably already gone through several stages of microbial decomposition.

Elevated atmospheric N deposition can both increase soil N availability and alter litter chemistry; and each of these changes may affect litter decomposition and forest C sequestration across broad parts of the Northern Hemisphere (Xia et al., 2018). Kurt Pregitzer (College of Natural Resources, Idaho, USA) investigated the effects of chronic simulated N deposition on decomposition of leaf litter and fine-root litter in sugar maple-dominated hardwood forests and found that N additions had minor effects on leaf litter decomposition, but significantly inhibited the later stages of fine-root decomposition. This inhibition was likely caused by decreases in lignin-degrading enzyme activities, as most of the lignin is contained in fine roots. Slowed fine root decomposition and greater retention of root residues explained the greater part of the c. 26% increase in surface soil C under N deposition (Pregitzer et al., 2008; Xia et al., 2018). The authors concluded that fine roots are an important driver of the additional soil organic C accumulation under nitrogen (N) deposition (Xia et al., 2018).

N deposition and increasing summer droughts under global change have also raised concerns of widespread nutrient imbalances and a large-scale undersupply of essential plant nutrients such as phosphorus (P) for important temperate tree species in the near future (Talkner et al., 2015; Köhler et al., 2018). Jörg Luster (Swiss Federal Research Institute WSL, Switzerland) analyzed the ability of beech saplings to mobilize rhizosphere P from soil as a function of the plant P status and the genetic memory (Luster, personal communication). Their results indicated an active contribution of the trees in mobilizing mineral-bound P, but a strong dependence on the microbial community for active release of P from the major organic P pool – which may potentially be stimulated by microbial priming effects.

4. Mycorrhizal symbiosis

The great majority of forest plants, and nearly all tree species, live in close association with soil fungi, forming mycorrhizal symbiotic associations. Mycorrhizal fungi build extensive mycelial networks in soil (Leake et al., 2004; Soudzilovskaia et al., 2015), together with roots creating in boreal ecosystems the largest soil C pool (Clemmensen et al., 2013) that mediates soil C sequestration processes (Soudzilovskaia et al., 2015; Averill and Hawkes, 2016) as well as soil formation and structure (Rillig and Mummey, 2006; Leifheit et al., 2014). Among the mycorrhizal associations types arbuscular mycorrhiza, ectomycorrhizal and ericoid mycorrhiza are by far the most wide-spread in terms of plant biomass (Read, 1991; Soudzilovskaia et al., 2018). The majority of forests plants are associated with one of these mycorrhizal types (Smith and Read, 2008): trees typically feature ecto- and/or arbuscular mycorrhizas, shrubs any of the three mycorrhizal types and herbaceous plants are mostly arbuscular or non-mycorrhizal.

The mode and extent of mycorrhizal impacts on ecosystem functioning differs between the mycorrhizal associations types (Soudzilovskaia et al., 2015; Terrer et al., 2016). Johnson et al. (2013) proposed a framework to explore how the three most wide-spread mycorrhizal types relate to ecosystem functioning and how these relations respond to global change. The authors proposed to delineate three interacting principles governing the mechanisms of mycorrhizal impacts on ecosystem functioning: (1) optimal resource allocation, *i.e.* both plants and fungi direct their biomass and energy towards acquiring the most limiting resources; (2) biotic context, which stresses the importance of plant-to-plant, fungi-to-fungi, and plant-fungal interactions in resource competition; (3) fungal adaptability, which plays an important role in mycorrhizal responses to global change drivers (Johnson et al., 2013). All three mechanism are important for functioning of mycorrhizas in forest ecosystems and for understanding mycorrhizal

impacts on forests within the context of (human-induced) vegetation shifts – through alterations in relative dominance of distinct mycorrhizal types these shifts are likely to alter biogeochemical cycles related to mycorrhizal C and nutrient pathways (Soudzilovskaia et al., 2015).

Liese et al. (2018) demonstrated that the mycorrhizal type governs root exudation of temperate tree species. They demonstrated that soil drought increased root exudation by twofold and the photosynthetic C cost thereof by tenfold in ECM trees, whereas the increase of root exudation in arbuscular mycorrhizal (AM) trees was much less pronounced. By contrast, AM trees had higher absolute and relative inorganic N acquisition rates than ECM trees. The authors concluded that these systematic differences in key biogeochemical processes support hints on the key role of the mycorrhizal types in coupling C and N cycles in temperate forests.

While we are gaining understanding of the role of mycorrhizal fungi in the processes in forest soils, the processes taking place in the so-called ‘canopy soils’, epiphytic organic mats formed in tree canopies, are poorly understood. Old-growth temperate rainforests of the Pacific Northwest, U.S.A., have canopy soils up to 40 cm depth. Korena Mafune (University of Washington, USA) found distinct communities of soil microorganisms including mycorrhizal fungi, in canopy soils relative to forest-floor soils (Mafune et al., 2017).

Progress during the last two decades in molecular high-throughput sequencing methods now allow for rapid and detailed characterization of soil and rhizosphere microbial communities. These powerful techniques have enabled the elucidation of impacts of biotic and abiotic drivers on community composition of mycorrhizal fungi in forest soils. Van der Linde et al. (2018) found that both environmental and plant host type were the main predictors of the variation in ectomycorrhizal fungal diversity in European forests. In *Picea abies* forests in the north-eastern Italian Alps, Nicola La Porta (Fondazione Edmund Mach, Italy) demonstrated influences of forest management practices, bedrock material, slope and stand age on soil fungal diversity (La Porta, personal communication).

Together, the papers presented in this special issue and the other talks presented at the IUFRO Congress demonstrate that improved understanding of tree roots systems and root-associated organisms can enhance our ability to predict responses of forests to global change and intensified forest management. Further research is needed on the linkages between soil communities and soil functions, and on how interactions between microbial – and in particular fungal – diversity and plants affect the functioning of forest ecosystems.

Acknowledgements

This work was supported by the German Research Foundation (Deutsche Forschungsgemeinschaft DFG) [grant number ME 4156/2-1] and the European Regional Fund (Centre of Excellence: EcolChange).

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