



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

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