

Frontiers in root ecology: recent advances and future challenges

Amandine Erktan  · M. Luke McCormack · Catherine Roumet

Received: 7 February 2018 / Accepted: 1 March 2018 / Published online: 16 March 2018
© Springer International Publishing AG, part of Springer Nature 2018

Abstract

Background Roots play a pivotal role in defining plant ecological success and mediating terrestrial ecosystem functioning. However, roots are difficult to study as they are hidden in the soil matrix and express a plurality of forms and functions: nutrient acquisition, anchorage, nutrient and water transport.

Scope In this special issue, we gather 20 articles from emerging topics in root ecology. We specifically focus on five frontiers that are essential to better capture plant, soil and ecosystem processes: (1) root structure and soil resource acquisition; (2) root dynamics; (3) root-root interactions; (4) root-microbe interactions and (5) the

effects of roots on soil properties. For each of these sections we provide an overview of our current knowledge, highlight the contributions of this special issue, and pinpoint key remaining challenges for future work. **Conclusions** Root resource acquisition, root dynamics, root-root and root-microbes interaction and the relative importance of root vs. soil properties on soil aggregation were shown to vary among biomes, soil and climate conditions. Such variability gives a complex but realistic picture of root functioning in real ecosystems and lays an important foundation for future work identify broad patterns of root functioning.

Keywords Root ecology · Root traits · Root structure-function relationships · Root dynamics · Root-root interactions · Root-microbes interactions · Plant-soil feedbacks · Soil aggregation

Amandine Erktan, M. Luke McCormack and Catherine Roumet provided equal contributions.

Responsible Editor: Hans Lambers.

A. Erktan
AMAP, INRA, CIRAD, CNRS, IRD, University of Montpellier, Montpellier, France

A. Erktan (✉)
J.F. Blumenbach Institute of Zoology and Anthropology,
University of Goettingen, Untere Karspüle 2, 37073 Goettingen,
Germany
e-mail: amandine.erkтан@gmail.com

M. L. McCormack
Department of Plant and Microbial Biology, University of
Minnesota, St. Paul, MN, USA

C. Roumet
CEFE, CNRS, University Montpellier, University Paul Valéry
Montpellier 3, EPHE, IRD, Montpellier, France

Introduction

Roots play an integral role in defining plant ecological success (Laughlin 2014) and mediating terrestrial ecosystem functioning (Bardgett et al. 2014). At the plant level, roots account for between 16 and 63% of the total plant biomass (Poorter et al. 2012) and conduct essential functions, namely water and nutrient acquisition as well as plant anchorage, resource storage, and in supporting soil microbial communities. At the plant community level, facilitative, complementary and competitive interactions between roots from co-occurring individuals impact community composition. At the ecosystem level, roots

account for between 10 and 60% of net primary productivity in most terrestrial ecosystems (Aerts et al. 1992; McCormack et al. 2015), thus forming a major natural conduit of organic compounds into the soils, with significant consequences on carbon and nutrient cycles. Roots also play an important role in building soil structure by a range of mechanical, biochemical and biological processes (Angers and Caron 1998; Rillig et al. 2015).

Despite the importance of roots in numerous ecological processes, our understanding of functional root ecology remains limited. This is due partly because: (i) roots are hidden in the soil matrix and tracking their growth and biological activity still remains a methodological challenge; and (ii) roots may express a plurality of forms and functions, with nutrient acquisition being performed by the terminal ends while the higher order roots ensure a wider framework for soil exploration, anchorage, nutrient and water transport. Adding further complexity, roots may change form and function through time with both root age and season. Recent efforts have been made to advance our knowledge in root ecology, with several authors advocating for more standardized procedures that allow researchers to compare roots with similar functions across species and environments (McCormack et al. 2015; Freschet and Roumet 2017). Additionally, increasing use of trait-based approaches which rely on comparisons of root traits across a large number of species has also led to a better understanding of individual, community and ecosystem functioning and dynamics (Garnier et al. 2016; Laliberté 2017).

In this special issue, we present emerging topics in plant, root, and soil microbial ecology where new studies are advancing our understanding of belowground ecology. We specifically focus on five frontiers in root ecology that are essential to better capture plant, soil and ecosystem processes: (1) root structure and soil resource acquisition; (2) root dynamics; (3) root-root interactions; (4) root-microbe interactions and (5) the effects of roots on soil properties (Fig. 1). For each of these sections we provide an overview of our current knowledge, highlight the contributions of this special issue, and pinpoint key remaining challenges for future work to address. First, we open this special issue with a Marschner Review by Lambers et al. (2017) synthesizing information across many of these frontiers to develop deeper understanding of the complex and dynamic roles roots play belowground, structuring plant communities, and altering ecosystem processes. Therein, the authors connect root traits and belowground strategies among co-existing plant species to better

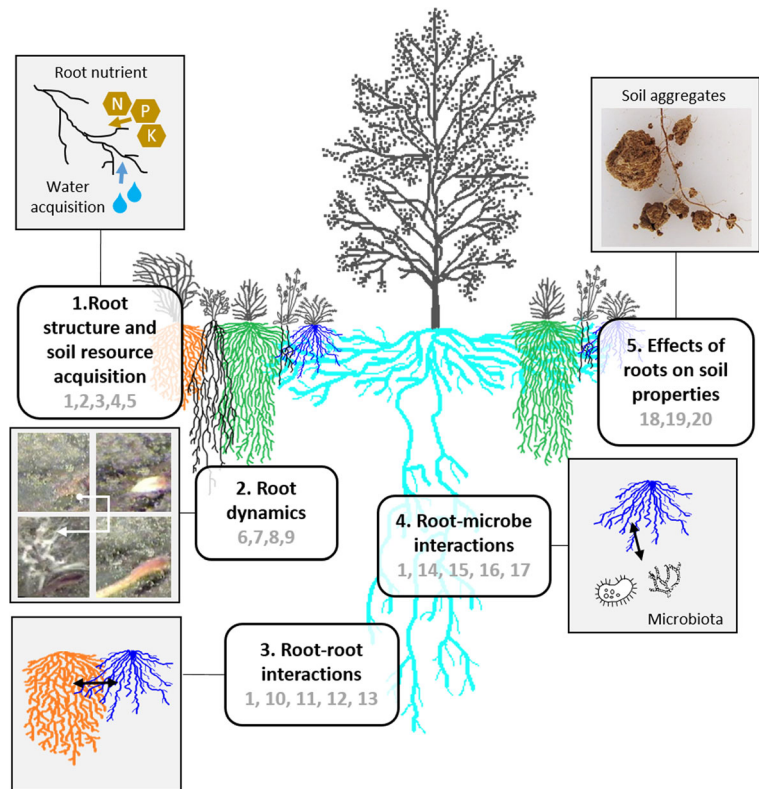
understand the mechanisms structuring plant communities in low fertility environments.

Root structure and soil resource acquisition

In natural and agricultural environments, the ability of plants to efficiently acquire soil resources determines their competitive success and productivity. Plants have developed different rooting strategies to acquire soil resources and cope with high spatio-temporal heterogeneity in soil water and nutrient availability. From an ecological perspective, a major focus of interest is to explore the mechanisms that enable plants to adapt to these heterogeneities and to determine which root traits make the largest contribution to water and nutrient uptake. Due to the lack of experimental data highlighting the link between water and nutrient acquisition and root traits, it is commonly assumed that a suite of correlated root traits (low-density tissues, high surface/mass ratios, thin roots) are associated with greater nutrient uptake, whereas opposite traits are associated with higher resource conservation through long-lived roots. The existence of such an acquisition – conservation trade-off, named the root economics spectrum (RES), is however under debate (Valverde-Barrantes and Blackwood 2016; Kramer-Walter et al. 2016; Weemstra et al. 2016). In this special issue, de la Riva et al. (2017) demonstrate that root morphological traits of 80 woody species covary as expected according to the RES with the notable exception of root diameter, further suggesting the likelihood of multiple dimensions of root trait variation.

The potential multidimensionality of root trait variation highlights the need for in situ experiments determining the physiological basis of root morphological trait variation, which is addressed in three studies in this special issue (Agapit et al. 2017; Dhiman et al. 2017; Hong et al. 2017). Hong et al. (2017) provide insights into the relationships between root traits and nitrogen (N) uptake preferences (NO_3^- , NH_4^+ and glycine). Using an in situ ^{15}N isotope tracer technique they observe that alpine species are able to effectively take up each of the three N forms, which may be an advantage at high altitude where mineralization rate is often low. They also demonstrate that total N uptake is positively related to specific root length, but negatively to total root volume and total root surface area. This suggests a trade-off in which larger root systems help alpine species to adapt to their extreme environment (freeze-thaw cycles

Fig. 1 The five frontiers of research in root ecology addressed in this Special Issue. The grey numbers refer to the articles included in the Special Issue, as numbered according to their order of appearance in the Special Issue. 1: Lambers et al. (2017); 2: de la Riva et al. (2017); 3: Agapit et al. (2017); 4: Hong et al. (2017); 5: Dhiman et al. (2017); 6: Teste et al. (2017); 7: Mohammed et al. (2017); 8: Iversen et al. (2017); 9: Schwieger et al. (2017); 10: Semchencko et al. (2018); 11: Weidlich et al. (2017); 12: Montazeaud et al. (2017); 13: Germon et al. (2017); 14: Rutten and Gómez-Aparicio (2018); 15: Legay et al. (2017); 16: Zemunik et al. (2017); 17: Gang et al. (2018); 18: Poirier et al. (2017); 19: Le Bissonnais et al. (2017); 20: Demenois et al. (2018)



and droughts) at the cost of a reduced efficiency in the uptake of soil N. Also using ^{15}N to study uptake, but in a lab setting, Agapit et al. (2017) demonstrate that plants could adjust their biomass allocation to forage for N contained in earthworm casts. Furthermore, they show that root length production also responds to the age of the earthworm casts, suggesting that changes in the availability and mobility of N in the casts over time impacts root foraging behavior. Regarding water uptake, Dhiman et al. (2017) use high-resolution, in situ neutron radiography to follow the dynamics of soil water uptake in the bulk soil and in the rhizosphere at a mm scale. Despite smaller diameter roots having greater water uptake rates per unit of root surface area than thicker and older roots, they represent less total root area and are thus less important for total plant water uptake. These studies linking root morphology and physiology improve our understanding of root structure-function relationships; indicating that total water and nutrient uptake relies not only on the morphology and uptake rate per unit root mass or length of a given root, but also on the allocation of biomass across the entire root system.

Many fundamental questions concerning which root traits drive water and nutrient acquisition remain to be answered but face significant challenges. First, roots are more complex than leaves in that they acquire water but also numerous macro- and micro-nutrients differing in their mobility in soil. In addition, one particular resource can be taken up by different mechanisms. Therefore, the root traits of interest for predicting resource uptake might vary widely according to the resource and the context considered. Second, all roots, except the oldest, possess some uptake capacity, but there is increasing evidence that uptake capacity decreases with increasing root orders and with root age in relation to changes in root anatomy (Rewald et al. 2012; Gambetta et al. 2013; Dhiman et al. 2017). The relative contribution of first-order roots, which are the most active but often make up a relatively low proportion of total biomass in a mature root system, vs higher order roots requires further studies. Third, as mentioned recently by Laliberté (2017) further research on root structure-function relationship needs further consideration of understudied traits such as mycorrhizal colonization, root hair length and density, root foraging capacity, and root anatomy.

Root dynamics

Root phenology, or the timing of root production and mortality, mediates the ability of a plant to efficiently acquire temporally variable resources in the soil. Additionally, the lifespan and turnover of root systems ultimately controls the standing root biomass of the root system. Together, these critical aspects of root dynamics help determine plant success in terrestrial ecosystems. Previous studies have highlighted that variation in root dynamics across species may be predictable based on other measurable root traits (Tjoelker et al. 2005; McCormack et al. 2012), and shown that within species patterns of root dynamics may be plastic and vary with multiple environmental factors (Pregitzer et al. 1993; Adams et al. 2013; McCormack et al. 2014). At the same time, these studies also highlighted the tremendous amount of unexplained variation and a pressing need for observations to enhance our understanding of variation in root dynamics across species and environments.

This special issue showcases studies observing root dynamics across a wide range of ecosystems and biomes including dry Mediterranean woodland (Teste et al. 2017), relatively cold temperate to warm temperate agroforestry systems (Mohammed et al. 2017), a boreal forested bog (Iversen et al. 2017), and subarctic tundra (Schwieger et al. 2017). Perhaps not surprisingly, the paucity of data available in each system makes these studies unique, often with few other studies against which comparisons can be made. As a result, each brings up important questions regarding the role of root dynamics in belowground plant strategies. For example, Teste et al. (2017) observe that cluster roots have very short lifespans which may help maximize uptake of limiting and immobile resources (e.g. phosphorus, P). At the same time, these species risk losing some of these resources to other plant species with longer-lived roots that may benefit from nutrients mobilized by cluster roots and after cluster roots die. The relative advantages of each strategy for resource uptake mediated by root dynamics requires further testing to assess its overall importance determining facilitative or competitive outcomes among species. Schwieger et al. (2017) observe a late season pulse of root production after leaf senescence, yet, it remains unclear if these roots serve an immediate purpose for resource uptake, facilitate overwintering and resource storage, or simply represent an advance deployment of roots needed to capture nutrients mobilized early the following spring.

Exciting opportunities remain for future work to expand our understanding of root dynamics across a range of species adapted to diverse environments.

Our next frontier is to better predict variation in root dynamics, not just across species, but also within species in response to different environmental conditions. Natural heterogeneity within the soil environment has led many investigators to ask how root dynamics respond to patchy availability of nutrients and water (e.g. Pregitzer et al. 1993; Adams et al. 2013). More recently, human-induced changes in nutrient availability (e.g. atmospheric N deposition), levels of atmospheric CO₂, and climate have left many wondering how these local- to global-scale changes will impact fine-root dynamics within plant species in the coming decades (Eissenstat et al. 2000; McCormack and Guo 2014). Given the context dependency of many belowground responses to environmental change, this area of research has remained challenging and more observational and manipulative studies are sorely needed. Here again, studies in this special issue provide important insights into the responses of root phenology and lifespan to multiple environmental changes. Within species responses to water availability and temperature were key factors investigated in three studies (Mohammed et al. 2017; Schwieger et al. 2017; Teste et al. 2017), while the study by Iversen et al. (2017) establishes an important baseline for future manipulations of temperature and atmospheric CO₂ as part of an established long-term experiment. By combining observations across species with manipulative experiments within species, future work may be able to discern broader generalities in belowground plant responses to shifts in the abiotic environment that will likely be experienced by plants around the globe in the coming years.

Root-root interactions

When multiple plants co-occur in a given soil volume, overlapping root systems compete for limiting soil resources. Species co-existence has long been assumed to be related to niche differentiation due to differences in rooting depth (Parrish and Bazzaz 1976; Berendse 1982). However, this idea has found only little support in recent empirical studies (Mommer et al. 2010; Hoekstra et al. 2015; Kraft et al. 2015), which instead highlight direct competitive interactions among species belowground. The belowground mechanisms involved in species co-existence thus remain a major knowledge gap in plant

ecology. This special issue adds an essential milestone to this research frontier by gathering several empirical studies (Germon et al. 2017; Montazeaud et al. 2017; Semchenko et al. 2017; Weidlich et al. 2017), showing that both competitive and facilitative interactions are important mechanisms acting between roots of co-occurring species. Semchenko et al. (2017) demonstrate that vertical root distribution is not related to niche complementarity but more to competitive interactions. In particular, they showed that species with large root systems and extensive horizontal spread are strong competitors and suppress their neighbors while species with deeper, less branched root systems were more able to tolerate direct competition. Using genetically transformed plants, Weidlich et al. (2017) show that roots from a non-legume species can forage toward the roots of a legume species and provide empirical evidence of the importance of facilitative interactions belowground. Stepping from interactions between species to interactions between genotypes, Montazeaud et al. (2017) show that productivity of rice plants (*Oryza sativa*) grown in pairs was inversely related to the distance (i.e. difference) in root morphological traits between genotypes. Digging down to 17 m depth, Germon et al. (2017) demonstrate that fine-root exploration of the soil significantly increased when mixing two tree species, *Acacia mangium* and *Eucalyptus grandis*, compared to trees grown in monocultures. Altogether, these results further support the importance of direct competition over the niche complementarity hypothesis.

We identify two next steps in the field of root-root interactions. First, evidence for greater importance of competition over niche complementarity demonstrated in this special issue is based on morphological root traits and biomass distributions related to soil exploration. Nevertheless, roots with similar morphologies and depth distributions can display different mechanisms of acquiring nutrient resources. For example, plant species have developed different ways to acquire P, including special root types releasing organic acids. Niche complementarity may thus exist between co-existing root systems, but more on a physiological basis rather than based on morphological aspects. Second, roots are not only interacting with other roots for resource acquisition, but they interact with a variety of soil organisms as well. Notably, associations with mycorrhizal fungi can strongly modify root structure and function and may alter competitive interactions (Lin et al. 2015). Similarly, the host of fungi and bacteria living within the rhizosphere is also of key importance for most root functions, including resource acquisition (Brink

2016). Widening root-root interactions toward a more integrated framework including roots and soil organisms is surely the next step to explore (Mommer et al. 2016). This special issue contributes to this as introduced in the following section.

Root-microbe interactions

The diversity of organisms living in soils and especially those living in close vicinity to plant roots is largely influenced by plant species identity (Kowalchuk et al. 2002). In turn, these soil organisms can influence plant growth and performance (Van der Putten et al. 1993). These interactions referred to as plant-soil feedbacks (Ehrenfeld et al. 2005), have been increasingly studied in the last decade (Van der Putten et al. 2013), although key aspects remain unanswered. Studies in this special issue focus on two questions: (i) how do plant-soil feedbacks vary with abiotic conditions, especially climatic change and soil P impoverishment and (ii) what are the molecular mechanisms by which soil microbes influence plant growth and performance, especially for non-agronomic species.

Using a precipitation gradient to investigate how climatic conditions influence plant-soil feedbacks, Rutten and Gómez-Aparicio (2018) demonstrate that plant-soil feedbacks depend on species and on their associated soil microbial communities. Plant-soil feedbacks were generally negative (i.e. less shoot biomass when grown on home microbial inocula) for *Quercus ilex* across the gradient, but ranged from positive to negative for *Q. suber* moving from drier to wetter sites. Such variability in plant-soil feedbacks is expected to have important consequences on plant community composition in response to climate change, and the work of Rutten and Gómez-Aparicio (2018) is, to our knowledge, the first to provide experimental evidence for this along a precipitation gradient. Also focusing on how climatic conditions influence plant-soil feedbacks, Legay et al. (2017) show that the legacy effect of a previous drought favored the resistance of *Lolium perenne* to a new drought event. This positive effect was then attributed to the selection of microorganisms during the first drought event. Focusing on severely P-depleted soils, Zemunik et al. (2017) show that the proportion of non-mycorrhizal plant species increased linearly with P-impoverishment in soils. The authors suggest that in severely P-depleted soils, acquisition of P through the release of carboxylates is favored over the widely spread symbiosis between

arbuscular mycorrhizal fungi and plant roots. Together, these studies provide experimental evidence that plant-soil feedbacks partly determine plant success but that they are also context dependent with climatic conditions and the soil (a)biotic environment both playing important roles. While these studies focus on feedbacks at the level of the entire rhizosphere community, another study in this issue by Gang et al. (2018), provides insights into the positive effects of the rhizobacterium *Klebsiella* SGM 81 on the growth and development of root hairs by *Dianthus caryophyllus*. A mutualistic relationship between *Klebsiella* SGM 81, living and producing indole acetic acid (IAA) in close vicinity to the roots of *D. caryophyllus* was identified as the main mechanism explaining the enhanced root hair production and plant growth.

These studies each work to decipher the complex, and often context dependent interactions between plant roots and soil organisms. While they collectively shed light on novel mechanisms mediating these interactions, a big picture perspective of how root-microbiome interactions are modulated by environmental conditions still requires (i) widening the range of organisms considered, and (ii) consideration of a broader panel of environmental conditions, including a variety of climate and soil properties.

Effects of roots on soil properties: The case of soil aggregation

While the contributions of roots to soil biogeochemical processes such as C and nutrient cycling has received substantial attention (Silver and Miya 2001; Jones et al. 2004; Rasse et al. 2005; Orwin et al. 2010; Bengtson et al. 2012), fewer studies emphasize the effect of roots on soil structural properties (Hallett et al. 2013). Soil structure, defined by the arrangement of soil aggregates and the resulting pore space, partly determines water and nutrient movement as well as gas fluxes in soils (Peng et al. 2015). Roots may influence soil structure through a range of biophysical, biochemical, and biological mechanisms (Angers and Caron 1998; Six et al. 2004; Rillig et al. 2015). Despite some progress, two considerable knowledge gaps remain regarding the effects of roots on soil aggregation: (i) a lack of mechanistic understanding based on empirical and quantitative evidence to predict how root traits drive soil aggregation (Rillig et al. 2015), and (ii) uncertainty concerning the relative importance of roots compared to other biotic

and abiotic factors in determining soil aggregation in natural ecosystems.

Previous pioneering studies provided empirical evidence that root traits influence soil aggregation (Miller and Jastrow 1990; Carter et al. 1994; Graf and Frei 2013; Erktan et al. 2016; Gould et al. 2016). This special issue contributes to the development of a trait-based approach linking roots to soil structure with the innovative study of Poirier et al. (2017), investigating how morphological and chemical root traits of 13 Mediterranean species influence soil aggregation in a common garden experiment, and the studies of Le Bissonnais et al. (2017) and Demenois et al. (2018), who assess connections between root traits and other soil properties together with aggregate stabilities across land-use and vegetation gradients. While high root length densities have long been associated with greater soil aggregation (Miller and Jastrow 1990; Angers and Caron 1998; Jastrow et al. 1998), these studies move our knowledge further by pinpointing the positive role of chemical traits, namely root soluble compounds, in promoting soil macroaggregate formation and stabilization (Le Bissonnais et al. 2017; Poirier et al. 2017)

Various abiotic and biotic factors influencing soil aggregation (including soil properties, climate, vegetation characteristics, soil fauna, etc.) have been previously reviewed independently (Six et al. 2004; Bronick and Lal 2005), yet very few studies have investigated the relative importance of these multiple factors in natural ecosystems (Degens et al. 1994; Pohl et al. 2009; Erktan et al. 2016). Such information is crucial to reach a realistic understanding of what drives soil aggregation and requires a multidisciplinary approach merging soil physics and ecology. Le Bissonnais et al. (2017) and Demenois et al. (2018), each assess the relative importance of soil vs. root characteristics on soil aggregation across Mediterranean and tropical soils, respectively. Both studies demonstrate that soil aggregate stability is jointly driven by aspects of soil biochemistry (soil organic carbon, sesquioxides, etc.) and root characteristics (root mass and length density, root soluble compounds, etc.), depending on the soil type and the regional scale considered. Demenois et al. (2018) also incorporate measures of fungal biomass and its contribution to soil aggregate stability, taking an important step towards linking roots together with their associated soil microbial communities on soil properties in “real” conditions.

Building on these and previous studies, future work should target two main areas to decipher how roots

broadly influence soil aggregation. First, root physiological traits have received relatively little attention compared to morphology, length, and biomass, yet, aspects of root physiology, notably root exudation, are likely to change the soil biochemistry with direct and indirect consequences on soil aggregation (Rillig et al. 2015). Second, as stated in previous sections, roots interact with a variety of soil organisms, with potentially important effects on soil aggregation. Up to now, research linking root-associated organisms to soil aggregation has largely centered on the symbiosis between roots and arbuscular mycorrhizal fungi (Rillig and Mummey 2006). However, the broader microbial community within the rhizosphere likely plays an important role in soil aggregation. Larger soil organisms, such as collembolan feeding on root-associated fungi are also thought to have a significant influence on soil aggregation (Siddiky et al. 2012). Therefore, to reach a more realistic understanding of root contributions to soil aggregation, further research is needed that links roots together with their associated soil organisms in field systems to capture their cohesive effects on soil aggregation.

Conclusions

In the field of root ecology, a central challenge is to understand root functioning in soil with all its physical, chemical and biological complexity (Ryan et al. 2016). In this Special Issue root nutrient acquisition, root dynamics, root-root and root-microbe interactions and the relative importance of root vs. soil properties on soil aggregation were shown to greatly vary among biomes, soil and climate conditions. Such variability gives a complex but realistic picture of root functioning in real ecosystems. In the near term, studies run under controlled conditions, are highly useful and may more easily achieve a mechanistic understanding of root functioning. This is the case of the dominance of competitive and facilitative interactions over the niche complementarity hypothesis, observed several times among independent studies of the Special Issue. Future long-term research should further push our frontiers capturing and quantifying root functions in real soils and the relative importance of different factors allowing plant coexistence, such as competitive and facilitative interactions through soil microbiota, and their implications for plant diversity and ecosystem functioning.

Acknowledgements This special issue was born following a very stimulating session on root ecology at the EcoSummit conference held in Montpellier, France in 2016. We acknowledge the LabEx CeMEB, Mediterranean Centre for Environment and Biodiversity, for providing financial support for the organization of the session and Alexia Stokes and Sebastien Barot for accommodating the conference. We are grateful to Monique Weemstra for her helpful comments and review. A. Erktan was financed by the TAFER project supported by Agropolis Fondation and SYSTRA under the reference ID 1200-014 and ID 1200-013 through the “Investissements d’avenir” program (Labex Agro: ANR-10-LABX-001-01).

References

- Adams TS, McCormack ML, Eissenstat DM (2013) Foraging strategies in trees of different root morphology: the role of root lifespan. *Tree Physiol* 33:940–948
- Aerts R, Bakker C, Decaluwe H (1992) Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. *Biogeochem* 15:175–190
- Agapit C, Gigon A, Puga-Freitas R, Zeller B, Blouin M (2017) Plant-earthworm interactions: influence of age and proportion of casts in the soil on plant growth, morphology and nitrogen uptake. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3544-y>
- Angers DA, Caron J (1998) Plant-induced changes in soil structure: processes and feedbacks. *Biogeochem* 42(1–2):55–72
- Bardgett RD, Mommer L, de Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends Ecol and Evol* 29:692–699
- Bengtson P, Barker J, Grayston SJ (2012) Evidence of a strong coupling between root exudation, C and N availability, and stimulated SOM decomposition caused by rhizosphere priming effects. *Ecol Evol* 2:1843–1852
- Berendse F (1982) Competition between plant populations with different rooting depths. 3. Field experiments. *Oecologia* 53: 50–55
- Brink SC (2016) Unlocking the secrets of the rhizosphere. *Trends Plant Sci* 21(3):169–170
- Bronick CJ, Lal R (2005) Soil structure and management: a review. *Geoderma* 124:3–22
- Carter MR, Angers DA, Kunelius HT (1994) Soil structural form and stability, and organic matter under cool-season perennial grasses. *Soil Sci Soc Am J* 58:1194–1199
- De la Riva EG, Marañón T, Pérez-Ramos IM, Navarro-Fernández CM, Olmo M, Villar R (2017) Root traits across environmental gradients in Mediterranean woody communities: are they aligned along the root economics spectrum? *Plant Soil*. <https://doi.org/10.1007/s11104-017-3433-4>
- Degens BP, Sparling GP, Abbott LK (1994) The contribution from hyphae, roots and organic carbon constituents to the aggregation of a sandy loam under long-term clover-based and grass pastures. *Eur J Soil Sci* 45:459–468
- Demenois J, Rey F, Ibanez T, Stokes A, Carriconde F (2018) Linkages between root traits, soil fungi and aggregate stability in tropical plant communities along a successional

- vegetation gradient. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3529-x>
- Dhiman I, Bilheux H, DeCarlo K, Painter SL, Santodonato L, Warren JM (2017) Quantifying root water extraction after drought recovery using sub-mm in situ empirical data. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3408-5>
- Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. *Annu Rev Environ Resour* 30:75–115
- Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. *New Phytol* 147:33–42
- Erktan A, Cécillon L, Graf F, Roumet C, Legout C, Rey F (2016) Increase in soil aggregate stability along a Mediterranean successional gradient in severely eroded gully bed ecosystems: combined effects of soil, root traits and plant community characteristics. *Plant Soil* 398:121–137
- Freschet G, Roumet C (2017) Sampling roots to capture plant and soil functions. *Funct Ecol* 31(8):1506–1518
- Gambetta GA, Fei J, Rost TL, Knipfer T, Matthews MA, Shackel KA, Walker MA, McElrone AJ (2013) Water uptake along the length of grapevine fine roots: developmental anatomy, tissue-specific aquaporin expression, and pathways of water transport. *Plant Physiol* 163(3):1254–1265
- Gang S, Saraf M, Waite CJ, Buck M, Schumacher J (2018) Mutualism between *Klebsiella* SGM 81 and *Dianthus caryophyllus* in modulating root plasticity and rhizospheric bacterial density. *Plant Soil*:1–16
- Garnier E, Navas M-L, Grigulis K (2016) Plant functional diversity – organism traits, community structure, and ecosystem properties. Oxford University Press, Oxford. ISBN: 978-0-19-875736-8
- Germon A, Guerrini IA, Bordron B, Bouillet JP, Nouvellon Y, de Moraes Gonçalves JL, Jourdan C, Ranieri Ribeiro P, Laclau JP (2017) Consequences of mixing *Acacia mangium* and *Eucalyptus grandis* trees on soil exploration by fine-roots down to a depth of 17 m. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3428-1>
- Gould IJ, Quinton JN, Weigelt A, De Deyn GB, Bardgett RD, Seabloom E (2016) Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecol Lett* 19:1140–1149
- Graf F, Frei M (2013) Soil aggregate stability related to soil density, root length, and mycorrhiza using site-specific *Alnus incana* and *melanogaster variegatus* s.L. *Ecol Eng* 57:314–323
- Hallett P, Mooney S, Whalley R (2013) Soil physics: new approaches and emerging challenges. *Eur J Soil Sci* 64:277–278
- Hoekstra NJ, Suter M, Finn JA, Husse S, Luscher A (2015) Do belowground vertical niche differences between deep- and shallow-rooted species enhance resource uptake and drought resistance in grassland mixtures? *Plant Soil* 394:21–34
- Hong J, Ma X, Yan Y, Zhang X, Wang X (2017) Which root traits determine nitrogen uptake by alpine plant species on the Tibetan plateau? *Plant Soil*. <https://doi.org/10.1007/s11104-017-3434-3>
- Iversen CM, Childs J, Norby RJ, Ontl TA, Kolka RK, Brice DJ, McFarlane KJ, Hanson PJ (2017) Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3231-z>
- Jastrow JD, Miller RM, Lussenhop J (1998) Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biol Biochem* 30:905–916
- Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. *New Phytol* 163:459–480
- Kowalchuk GA, Buma DS, de Boer W, Klinkhamer PG, van Veen JA (2002) Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. *Antonie Van Leeuwenhoek* 81(1–4):509–520
- Kraft NJB, Godoy O, Levine JM (2015) Plant functional traits and the multidimensional nature of species coexistence. *P Natl Acad Sci USA* 112:797–802
- Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ Laughlin DC (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *J Ecol* 104:1299–1310
- Laliberté E (2017) Below-ground frontiers in trait-based plant ecology. *New Phytol* 213(4):1597–1603
- Lambers H, Albornoz F, Kotula L, Laliberté E, Ranathunge K, Teste FP, Zemunik G (2017) How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impoverished hyperdiverse ecosystems. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3427-2>
- Laughlin DC (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. *J Ecol* 102:186–193
- Le Bissonnais Y, Prieto I, Roumet C, Nespoulous J, Metayer J, Huon S, Villatoro M, Stokes A (2017) Soil aggregate stability in Mediterranean and tropical agro-ecosystems: effect of plant roots and soil characteristics. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3423-6>
- Legay N, Piton G, Arnoldi C, Bernard L, Binet MN, Mouhamadou B, Pommier T, Lavorel S, Foulquier A, Clément JC (2017) Soil legacy effects of climatic stress, management and plant functional composition on microbial communities influence the response of *Lolium perenne* to a new drought event. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3403-x>
- Lin G, McCormack ML, Guo D (2015) Arbuscular mycorrhizal fungal effects on plant competition and community structure. *J Ecol* 103(5):1224–1232
- McCormack ML, Guo D (2014) Impacts of environmental factors on fine root lifespan. *Front Plant Sci* 5(205)
- McCormack ML, Adams TS, Smithwick EA, Eissenstat DM (2012) Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol* 195:823–831
- McCormack ML, Adams TS, Smithwick EA, Eissenstat DM (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95:2224–2235
- McCormack ML, Dickie IA, Eissenstat DM et al (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol* 207:505–518
- Miller RM, Jastrow JD (1990) Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biol Biochem* 22(5):579–584
- Mohammed A, Stokes A, Mao Z, Jourdan C, Sabatier S, Pailler F, Fournier S, Dufour L, Monnier Y (2017) Linking above-and belowground phenology of hybrid walnut growing along a climatic gradient in temperate agroforestry systems. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3417-4>

- Mommer L, van Ruijven J, de Caluwe H, Smit-Tiekstra AE, Wagemaker CAM, Ouborg NJ, Bogemann GM, van der Weerden GM, Berendse F, de Kroon H (2010) Unveiling belowground species abundance in a biodiversity experiment: a test of vertical niche differentiation among grassland species. *J Ecol* 98:1117–1127
- Mommer L, Kirkegaard J, van Ruijven J (2016) Root–root interactions: towards a rhizosphere framework. *Trends Plant Sci* 21(3):209–217
- Montazeaud G, Violle C, Fréville H, Luquet D, Ahmadi N, Courtois B, Bouhaba I, Fort F (2017) Crop mixtures: does niche complementarity hold for belowground resources? An experimental test using rice genotypic pairs. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3496-2>
- Orwin KH, Buckland SM, Johnson D, Turner BL, Smart S, Oakley S, Bardgett RD (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *J Ecol* 98:1074–1083
- Parrish JAD, Bazzaz FA (1976) Underground niche separation in successional plants. *Ecology* 57:1281–1288
- Peng X, Horn R, Hallett P (2015) Soil structure and its functions in ecosystems: Phase matter & scale matter. *Soil Till Res* 146:1–3
- Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. *Plant Soil* 324(1–2):91–102
- Poirier V, Roumet C, Angers DA, Munson AD (2017) Species and root traits impact macroaggregation in the rhizospheric soil of a Mediterranean common garden experiment. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3407-6>
- Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. *New Phytol* 125:575–580
- Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. *Plant Soil* 269(1–2):341–356
- Rewald B, Raveh E, Gendler T, Ephrath JE, Rachmilevitch S (2012) Phenotypic plasticity and water flux rates of citrus root orders under salinity. *J Exp Bot* 63(7):2717–2727
- Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. *New Phytol* 171:41–53
- Rillig MC, Aguilar-Trigueros CA, Bergmann J, Verbruggen E, Veresoglou SD, Lehmann A (2015) Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytol* 205:1385–1388
- Rutten G, Gómez-Aparicio L (2018) Plant-soil feedbacks and root responses of two Mediterranean oaks along a precipitation gradient. *Plant Soil*. <https://doi.org/10.1007/s11104-018-3567-z>
- Ryan PR, Delhaize E, Watt M, Richardson AE (2016) Plant roots: understanding structure and function in an ocean of complexity. *Ann Bot* 118:555–559
- Schwieger S, Kreyling J, Milbau A, Blume-Werry G (2017) Autumnal warming does not change root phenology in two contrasting vegetation types of subarctic tundra. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3343-5>
- Semchenko M, Lepik A, Abakumova M, Zobel K (2017) Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3282-1>
- Siddiky RK, Schaller J, Caruso T, Rillig M (2012) Arbuscular mycorrhizal fungi and collembola non-additively increase soil aggregation. *Soil Biol Biochem* 47:93–99
- Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419
- Six J, Bossuyt H, Degryze S, Denef K (2004) A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil Tillage Res* 79(1):7–31
- Teste FP, Marchesini VA, Veneklaas EJ, Dixon KW, Lambers H (2017) Root dynamics and survival in a nutrient-poor and species-rich woodland under a drying climate. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3323-9>
- Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol* 167:493–508
- Valverde-Barrantes OJ, Blackwood CB (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum: commentary on Kramer-Walter et al. (2016). *J Ecol* 104:1311–1313
- Van der Putten WH, Van Dijk C, Peters BAM (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362(6415):53–56
- Van der Putten WH, Bardgett RD, Bever JD et al (2013) Plant-soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276
- Weemstra M, Mommer L, Visser EJW, van Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ (2016) Towards a multidimensional root trait framework: a tree root review. *New Phytol* 211(4): 1159–1169
- Weidlich EW, Temperton VM, Faget M (2017) Neighbourhood stories: role of neighbour identity, spatial location and order of arrival in legume and non-legume initial interactions. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3398-3>
- Zemunik G, Lambers H, Turner BL, Laliberté E, Oliveira RS (2017) High abundance of non-mycorrhizal plant species in severely phosphorus-impooverished Brazilian campos rupestres. *Plant Soil*. <https://doi.org/10.1007/s11104-017-3503-7>