

Meetings

Fine-root and mycorrhizal traits help explain ecosystem processes and responses to global change

International Symposium on Critical Zone Biochemistry and Belowground Ecological Research, Beijing, China, May 2014

Plant roots and soil biota represent integral, yet poorly understood components of terrestrial ecosystems. Fine roots, and often mycorrhizal fungi, are required for effective water and nutrient uptake to support plant growth and provide sources of labile carbon (C) supporting the broader soil microbial community. Functional differences in root and mycorrhizal traits are partly driven by inherent species differences but may also be impacted by the local soil environment and prevailing climate. However, our current knowledge of fine-root and mycorrhizal diversity merely scratches the surface of their complex functions, interactions with other soil biota, and feedbacks on ecosystem processes and community composition (Wardle *et al.*, 2004). In an effort to address these issues, a recent meeting was convened by the Chinese Ecosystem Research Network, in Beijing, with participants from the USA, New Zealand, and Finland.

'Root systems of perennial plants possess a high degree of complexity and the first step to understanding this complexity is to realize that not all roots and root systems are the same.'

In this report, we discuss two key themes that emerged from the International Symposium on Critical Zone Biochemistry and Belowground Ecological Research. First, we discuss the need to identify broad patterns of root and mycorrhizal trait variation, both across and within species, as an effective means to understand and predict variation in function across species and sites, and through time. Second, we assert that, to fully understand the role roots and mycorrhizal fungi play in ecosystem processes, a broader

perspective that relates their function to both short-term activity (e.g. acquisition of soil resources) and long-term changes in ecosystem function and community composition is required. Finally, we emphasize the need for a global effort in root and mycorrhizal research to synchronize methods of data collection and sharing for more powerful comparisons of belowground activity.

Functional traits below ground

Linking plant traits with function has been a valuable approach for understanding plant systems, particularly above ground, where traits including xylem anatomy, leaf mass per unit area, and leaf nitrogen (N) content often serve as indicators of plant hydraulic conductance, leaf lifespan, and photosynthetic capacity, respectively. Below ground, wide variation in both root and mycorrhizal traits has been observed (Fig. 1) and linking this trait variation to ecosystem processes was a common theme during much of the meeting. More broadly, developing greater appreciation of root and mycorrhizal function across species and environments greatly enhances understanding of whole-ecosystem processes, as roots and soil fungi have been identified as key drivers of C and nutrient cycling in terrestrial systems (Ostonen *et al.*, 2011; Iversen *et al.*, 2012; Clemmensen *et al.*, 2013).

Root systems of perennial plants possess a high degree of complexity and the first step to understanding this complexity is to realize that not all roots and root systems are the same. Even among distal, first-order roots, pioneer and fibrous roots maintain morphological differences at birth that are intrinsically linked to their function (Zadworny & Eissenstat, 2011). These and other differences in root anatomy, morphology, and physiology among and within species often relate to differences in root function (Fig. 2). For example, variations in root diameter, root length density, N concentration, root hair density, and mycorrhizal colonization all have links to total plant uptake capacity and represent tradeoffs among different acquisition strategies. Variation in basic root traits may also provide information on how plastic species of plants may be in response to changing environments. At the meeting, David Eissenstat (Pennsylvania State University, USA) discussed recent work in a common garden where fertilizer application in localized patches increased root survivorship in species with smaller root diameters (more plastic response) but not in those with larger root diameters (less plastic response) (Adams *et al.*, 2013).

Extending beyond roots and further exploring the soil, mycorrhizal fungi form an intimate symbiosis with many plant species and represent the most distal portion of the root–fungal resource acquisition system. Here again, systematic differences in mycorrhizal traits can provide useful clues regarding their activity and persistence in soils (Fig. 2). Recent reviews have highlighted the potential for categorizing mycorrhizal fungi based on observable/measurable traits that then relate to their function and broader

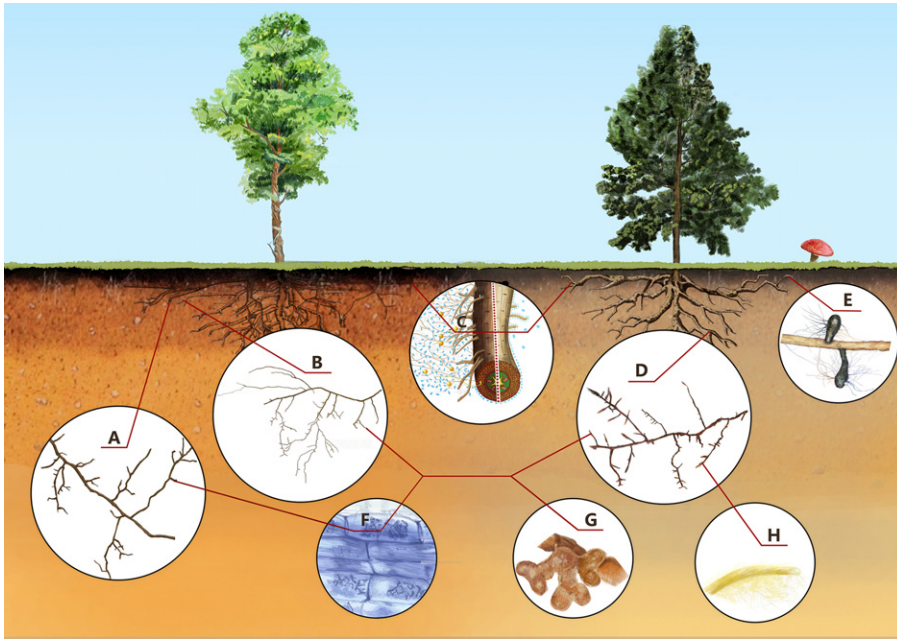


Fig. 1 Trait diversity expressed by fine roots and mycorrhizal fungi. Plant species vary widely in their root architecture and root diameter, with some species expressing relatively coarse (A), medium (D), and relatively fine (B) root morphology. Different species of both angiosperms and gymnosperms may be colonized by arbuscular mycorrhizal fungi (F) and/or ectomycorrhizal fungi, which may express a range of morphologies on colonized roots (E, G, H). In addition to or, in some cases, instead of relying on mycorrhizal fungi, exudates from plant roots and high densities of root hairs can help improve uptake of soil resources (C). Approximate magnifications for panel drawings are $\times 2$ (A, B, and D), $\times 8\text{--}10$ (E, G, and H), $\times 15$ (C), and $\times 40$ (F). Background and panels were drawn by Ying Wang.

ecosystem impacts (Van Der Heijden & Scheublin, 2007; Chagnon *et al.*, 2013; Phillips *et al.*, 2013; Koide *et al.*, 2014). For example, at the meeting Erik Hobbie (University of New Hampshire, USA) presented recent work showing that C and N isotopes can be used to infer activity and exploration strategies of ectomycorrhizal fungi (Hobbie & Agerer, 2009), while others have reported that the degree of fungal tissue melanization may relate to stress tolerance and persistence (Fernandez & Koide, 2013). Indeed, the high diversity and often cryptic nature of mycorrhizal fungi may necessitate the use of functional traits to better understand mycorrhizal form, functional relationships, and ecosystem effects.

Looking through a broader lens

Ecosystem responses to climate change, altered land use, and species invasions are often the result of complex interactions among

multiple ecosystem components. As such, observing below- and aboveground processes independently may result in limited and potentially erroneous conclusions. Based on a series of experiments conducted using species common in grasslands of Inner Mongolia, China, Wen-Hao Zhang (Institute of Botany, Chinese Academy of Sciences, China) presented evidence that shifts in species abundance with N deposition, long thought to be the result of increasing light competition, may result from multiple factors including a decrease in soil pH which increases the availability of manganese (Mn), leading to Mn toxicity in forbs (W-H. Zhang, unpublished). As a result of fundamental differences between dicots and monocots in their biochemical pathways for uptake of Mn and iron, grasses were favored over forbs and overall ecosystem diversity declined. Interestingly, similar declines in sugar maple (*Acer saccharum*) have been observed with chronic N deposition in parts of the northeast USA. Here again, declines resulted from altered plant nutrition that first began with an increased availability of Mn in acidified soils and

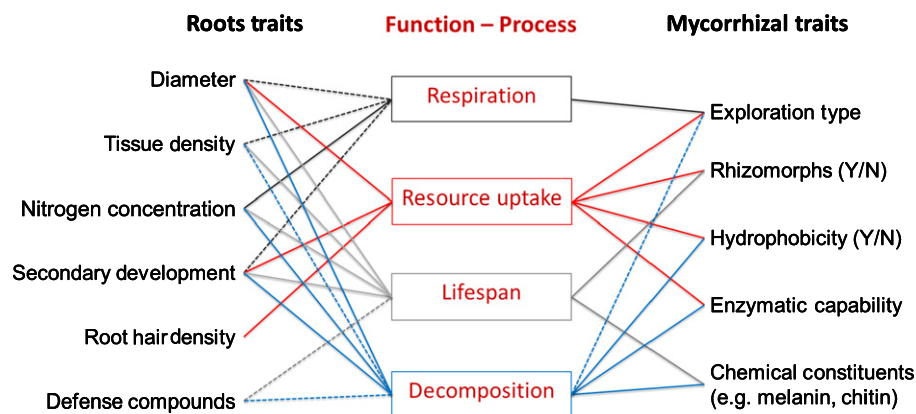


Fig. 2 Links between relatively easy-to-measure root and mycorrhizal traits and relatively difficult-to-measure root and fungal processes of greatest interest to terrestrial biosphere models. Direct relationships that have been previously reported are shown as solid lines while additional, hypothesized relationships that require further testing are shown as dashed lines. The simplified list of traits and processes shown is not comprehensive and could be expanded to include other aspects of root and mycorrhizal ecology (e.g. root branching intensity, root exudation, root endophyte communities, and specific root and mycorrhizal uptake rates).

reduced availability of primary nutrients (St Clair & Lynch, 2005). In both ecosystems, only by observing aboveground portions of ecosystems in the context of belowground processes could changes in ecosystem function be understood.

Species invasions offer some of the most compelling examples demonstrating the need to integrate belowground processes into a whole-ecosystem perspective. Indeed, many studies now link interactions among roots and soil biota as important factors determining the success of an invading plant species. For example, the success of the invasive garlic mustard (*Alliaria petiolata*) is attributed, at least in part, to its ability to inhibit mycorrhizal fungi, thereby reducing the ability of many competing plant species to obtain soil resources (Stinson *et al.*, 2006). Recent work presented by Ian Dickie (Lincoln University, New Zealand) provides evidence for facilitation of invasive *Pinus contorta* in New Zealand by co-invasion of ectomycorrhizal symbionts which may be further mediated by invasions of nonnative mammals (Dickie *et al.*, 2010; J. R. Wood *et al.*, unpublished). This is a fascinating example of how multi-stage and multi-component interactions dictate the composition and function of many terrestrial ecosystems, including novel ecosystems created through concurrent invasions of multiple species from multiple continents.

United efforts to understand root, soil, and global terrestrial ecosystem processes

Currently, many ecosystem- and global-scale models express highly simplified descriptions of root processes with little to no mechanistic function tied to spatial and temporal patterns of root growth (Smithwick *et al.*, 2014). Furthermore, few models explicitly incorporate mycorrhizal fungi requiring C and nutrient fluxes through mycorrhizal biomass to be captured indirectly if at all (but see Orwin *et al.*, 2011; Phillips *et al.*, 2013; Deckmyn *et al.*, 2014). However, accurately modeling ecosystem processes along environmental gradients or responses to global change factors requires greater empirical understanding of root and mycorrhizal processes in conjunction with their impacts on ecosystem functioning (Ostonen *et al.*, 2011; Iversen *et al.*, 2012). To that end, some of the most important discussions in Beijing were centered on the development of a functional database of root traits and a network linking rhizosphere–ecosystem research across the globe.

Development of an improved, publicly available database coupled with an organized network of sites investigating links between above- and belowground ecology could provide an efficient way to gain and supply data needed by modelers. Led by Colleen Iversen (Oak Ridge National Laboratory, USA), efforts are underway to develop a comprehensive root trait database through expansions of the existing TRY plant trait database (www.try-db.org) and additional service through Oak Ridge National Laboratory (ORNL) data centers. Importantly, this database will (1) accommodate submission of root traits by individual root order, which enables more meaningful comparisons across species, and (2) emphasize traits and processes with specific relevance to terrestrial biosphere models. Furthermore, recent efforts in China have also seen the development of a domestic network of sites focused on linking belowground and whole-ecosystem processes, RhizoNet. Though in

its infancy, this and other networks may be developed into coordinated global networks where open exchange of ideas and research methodologies will greatly improve cross-site data comparisons and enhance overall appreciation of terrestrial processes.

Together, these and other efforts to identify global patterns of root and mycorrhizal traits across diverse phylogenies will pay dividends in the future as we seek to understand root and fungal responses to environmental perturbations. As consistent patterns emerge, these basic trait data can then be used to inform novel hypotheses testing the mechanisms that determine variation in rhizosphere function. Ultimately, understanding rhizosphere processes may be the key to accurately describing and anticipating global patterns of ecosystem functioning today and into the future.

M. Luke McCormack^{1*}, Emily Lavelly² and Zeqing Ma¹

¹Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China;

²Department of Plant Science, The Pennsylvania State University, University Park, PA 16802, USA

(*Author for correspondence: tel + 13261534030; email mltmcc@gmail.com)

References

- Adams TS, McCormack ML, Eissenstat DM. 2013. Foraging strategies in trees of different root morphology: the role of root lifespan. *Tree Physiology* 33: 940–948.
- Chagnon P-L, Bradley RL, Maherali H, Klironomos JN. 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science* 18: 484–491.
- Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339: 1615–1618.
- Deckmyn G, Meyer A, Smits MM, Ekblad A, Grebenc T, Komarov A, Kraigher H. 2014. Simulating ectomycorrhizal fungi and their role in carbon and nitrogen cycling in forest ecosystems. *Canadian Journal of Forest Research* 44: 535–553.
- Dickie IA, Bolstridge N, Cooper JA, Peltzer DA. 2010. Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist* 187: 475–484.
- Fernandez CW, Koide RT. 2013. The function of melanin in the ectomycorrhizal fungus *Cenococcum geophilum* under water stress. *Fungal Ecology* 6: 479–486.
- Hobbie EA, Agerer R. 2009. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. *Plant and Soil* 327: 71–83.
- Iversen CM, Keller JK, Garten CT, Norby RJ. 2012. Soil carbon and nitrogen cycling and storage throughout the soil profile in a sweetgum plantation after 11 years of CO₂-enrichment. *Global Change Biology* 18: 1684–1697.
- Koide RT, Fernandez C, Malcolm G. 2014. Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist* 201: 433–439.
- Orwin KH, Kirschbaum MU, St John MG, Dickie IA. 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecology Letters* 14: 493–502.
- Ostonen I, Helmissaari HS, Borken W, Tedersoo L, Kukumägi M, Bahram M, Lindroos AJ, Nöjd P, Uri V, Merilä P. 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Global Change Biology* 17: 3620–3632.

- Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199: 41–51.
- Smithwick EAH, Lucash MS, McCormack ML, Sivandran G. 2014. Improving the representation of roots in terrestrial models. *Ecological Modelling* 291: 193–204.
- St Clair SB, Lynch JP. 2005. Base cation stimulation of mycorrhization and photosynthesis of sugar maple on acid soils are coupled by foliar nutrient dynamics. *New Phytologist* 165: 581–590.
- Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* 4: e140.
- Van Der Heijden MGA, Scheublin TR. 2007. Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* 174: 244–250.
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van Der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629–1633.
- Zadworny M, Eissenstat DM. 2011. Contrasting the morphology, anatomy and fungal colonization of new pioneer and fibrous roots. *New Phytologist* 190: 213–221.

Key words: belowground, ecosystem ecology, hyphae, mycorrhiza, net primary productivity, rhizomorphs, root morphology, root production.



About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <25 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**