Viewpoints

Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes

Summary

Trait-based approaches provide a useful framework to investigate plant strategies for resource acquisition, growth, and competition, as well as plant impacts on ecosystem processes. Despite significant progress capturing trait variation within and among stems and leaves, identification of trait syndromes within fine-root systems and between fine roots and other plant organs is limited. Here we discuss three underappreciated areas where focused measurements of fine-root traits can make significant contributions to ecosystem science. These include assessment of spatiotemporal variation in fine-root traits, integration of mycorrhizal fungi into fine-root-trait frameworks, and the need for improved scaling of traits measured on individual roots to ecosystem-level processes. Progress in each of these areas is providing opportunities to revisit how below-ground processes are represented in terrestrial biosphere models. Targeted measurements of fine-root traits with clear linkages to ecosystem processes and plant responses to environmental change are strongly needed to reduce empirical and model uncertainties. Further identifying how and when suites of root and whole-plant traits are coordinated or decoupled will ultimately provide a powerful tool for modeling plant form and function at local and global scales.

Introduction

Understanding the size and form of resource pools stored in plants (e.g. carbon (C), nitrogen (N), water) as well as flux rates into and out of these pools is essential for determining whole-plant- to ecosystem-scale functioning. Knowledge of plant contributions to terrestrial productivity and resource cycling carries additional significance as perturbations of plant-related fluxes can have ecosystem- to global-scale consequences. The high degree of plant diversity and associated variation in how resources are acquired, stored, and turned over among species presents a daunting

challenge to researchers. Among other approaches, advances to our understanding of differential plant impacts on ecosystem processes have come through quantifying variation in plant traits (e.g. anatomical, morphological, chemical, and physiological phenotypes) across species and how that variation influences ecosystem function. To date, however, much of the effort linking plant traits to ecosystem processes has focused above ground. Only recently has the world below our feet begun to garner similar amounts of attention.

As the most dynamic and physiologically active plant component below ground, fine roots have increasingly been the focus of research connecting below-ground ecology to ecosystem processes. They may represent all or most of the herbaceous root system but only a relatively small subset of roots in woody species where there is a strong differentiation between coarse roots, which partly reflect a structural framework for the root system, and fine roots, which play more active roles in the cycling of water, nutrients, and C. Numerous studies have identified tradeoffs between different root traits (Freschet *et al.*, 2010; Reich, 2014) which may parallel tradeoffs between resource conservation and acquisition above ground (e.g. the leaf economics spectrum) (Wright *et al.*, 2004). The most prominent correlations recovered are often between fine-root N concentration and root respiration (positive relationship) or root longevity (negative), and similarly between root diameter and specific root length (negative relationship) or root longevity (positive) (McCormack *et al.*, 2012; Roumet *et al.*, 2016). However, there are many exceptions to these relationships and it remains unclear why only certain species fit the expected patterns. Furthermore, it can be hard to determine if and how root traits array along an axis of conservative to acquisitive strategies, as tradeoffs among fine-root traits may be mitigated or offset by associations with mycorrhizal fungi (Chen *et al.*, 2016). Overall, trait relationships along a resource economics spectrum do not appear to be as consistent in roots as has been observed in leaves (Weemstra *et al.*, 2016).

Where meaningful patterns can be identified, root traits have the potential to improve our understanding of processes operating at larger scales, ranging from whole-plant structure and function to ecosystem C, water, and nutrient cycling (Bardgett *et al.*, 2014). For example, Craine *et al.* (2002) and Roumet *et al.* (2016) each observed strong connections between fine-root traits and ecosystem-scale C and N fluxes, with species possessing long-lived fine roots and low N concentrations contributing to low rates of soil net N mineralization. A wider array of studies has further linked fine-root traits with litter decomposition (Vivanco & Austin, 2006; Hobbie *et al.*, 2010; Roumet *et al.*, 2016). However, progress in drawing these connections has been slow, as the linkages between root traits and ecosystem processes are complex, variable over time and space, and often do not mirror leaf-trait patterns. While a few examples suggest that root trait effects on biogeochemical cycles can

be profound, a paucity of robust empirical connections between root traits and ecosystem processes has subsequently limited their incorporation into ecosystem and terrestrial biosphere models (TBMs) (Warren *et al.*, 2015).

Previous efforts to identify broad patterns in root-trait variation have been highly valuable; however, there is a lack of clarity concerning the mixed, and at times contradictory, results reported among studies. We suggest that this may speak to a larger issue of how and when we measure and compare root-traits across and within species. Specifically, some of the difficulty in determining where patterns of fine-root trait variation do and do not exist may simply be the result of inconsistent and inaccurate measurement of root traits and poor recognition of how and when traits vary with the environment.

In this Viewpoint, we consider functional traits broadly as measurable or determinable aspects of a plant, which impact plant growth, reproduction, or survival (Violle *et al.*, 2007). Focusing on fine-root traits, we discuss key, undervalued or poorly recognized issues that currently limit inferences linking below-ground plant strategies to trait syndromes within whole plants and their impacts on ecosystem processes. We specifically address three topics that were not directly, or were only lightly, considered in previous works. These include issues that can be resolved relatively easily in the short term, such as accounting for spatial and temporal variation in fine-root traits, as well as more difficult issues of how to explicitly incorporate mycorrhizal fungi into assessments of fine-root traits and function, and complex issues of scaling fine-root traits to whole-ecosystem processes. While our discussions are intended to apply generally to all plants, many of the knowledge gaps presented here are especially profound for woody root systems given the additional limitations associated with their study. For example, harvest and measurement of entire root systems and of whole plants is not uncommon for herbaceous plants but extremely rare for mature trees. We also emphasize a need to actively target a greater diversity of fine-root traits to develop a more comprehensive understanding of the relationships among root function, ecosystem processes, and environmental variability. Finally, we discuss the earlier topics in the context of modeling terrestrial processes and consider how improvements in each of these areas can facilitate improved representations of below-ground processes in ecosystem and terrestrial biosphere models.

A better foundation for fine-root trait measurements

Leaves are relatively discrete units and researchers have used a well-defined sampling protocol for leaf-trait studies for decades (Pérez-Harguindeguy *et al.*, 2013). By contrast, a lack of standardized sampling protocols for fine roots still presents a significant hurdle for efforts comparing root traits across species and sites. Indeed, accurate estimation of specific root traits continues to be a serious problem, whether as a result of soil contamination of absorptive roots skewing dry weights, misidentifying absorptive roots from pioneer roots, or assessments of root morphology by scanning approaches that are not carefully checked microscopically. Even the most basic traits, such as fine-root diameter, are measured inconsistently and may variably include all roots less than a

particular diameter cutoff (e.g. ≤ 2 mm), only a single root order within the complex branching hierarchy, or something in between (McCormack *et al.*, 2015). These issues, though still problematic, have received considerable attention elsewhere. Here we focus on three additional issues that are less well-recognized and further obscure our understanding of fine-root traits and their links to plant and ecosystem processes.

Spatial and temporal variability in fine-root traits

Knowledge concerning the patterns and underlying mechanisms of spatial and temporal variation is less advanced for root traits than for leaf traits. The existence of seasonality in fine-root production is increasingly accepted, though the mechanisms controlling variation in the timing of fine-root production among and within species are not well understood. There is also evidence that seasonality exists for additional fine-root traits and processes that goes beyond patterns of production. For example, fine-root N concentration can vary across seasons in temperate environments (Zadworny *et al.*, 2015), and has been observed to vary with root age and soil depth (Fig. 1). This clearly represents a problem when scaling measurements of root N from a single location and time to represent an entire fine-root system throughout the year, as is often done in empirical and modeling studies alike. Furthermore, root N concentration is frequently used as a proxy or scaler for root uptake capacity and root respiration rates, which then creates further uncertainty in estimates of these and other key fine-root processes. Beyond N concentration, other fine-root traits including additional aspects of root chemistry, uptake capacity, respiration, and morphology have also been observed to vary with season, age, and soil depth (Pregitzer *et al.*, 1998; Volder *et al.*, 2005) (Supporting Information Table S1), indicating that spatiotemporal variation in fine-root traits may actually be common despite being rarely quantified or considered.

The fact that root traits can vary significantly over space and time emphasizes the value of accounting for or constraining these factors when comparing fine-root traits across species and sites. An important first step toward this goal is to identify which traits are likely to be the most variable through space and time and focus efforts to directly account for this variability (Tables 1, S1). Moving forward, it will be important for the community to adopt sampling protocols that account for spatial and temporal variation in root traits and enable comparable linkages to be made between fine-root trait variation and ecosystem processes.

Capturing the role of mycorrhizal fungi in nutrient acquisition

Symbiotic associations between fine roots and a diverse array of soil microorganisms involved in nutrient acquisition are common in terrestrial plants. In particular, a majority of plants form associations with mycorrhizal fungi to increase access to soil resources via enhanced soil exploration and enzymatic activity. Mycorrhizal fungi have the capacity to directly alter root morphology and chemistry, and their symbiotic associations with fine roots can fundamentally alter plant strategies for below-ground resource acquisition (Fig. 2). The added biotic complexity associated with
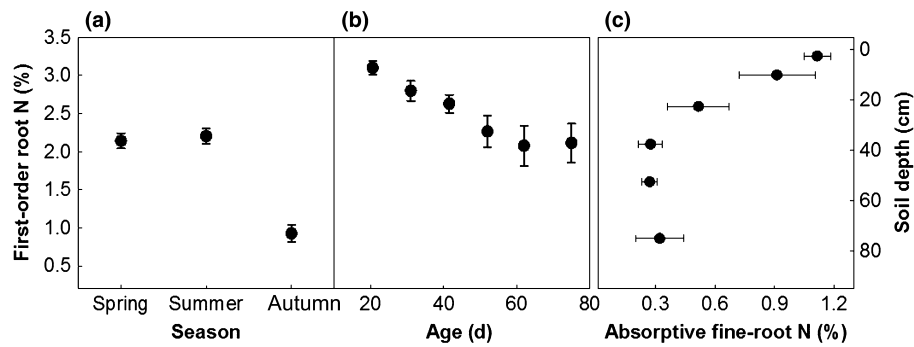
Fig. 1 Variation in nitrogen (N) concentration (%) in first-order fine roots across seasons (a), with age (b), and among absorptive fine roots (first to third orders) with soil depth (c). (a) Patterns of N concentration in *Quercus robur* absorptive roots collected in spring (April), summer (June), and Autumn (October) from a loamy soil in central Poland (Zadworny *et al.*, 2015). (b) Changes in N concentration with root age in *Acer rubrum* from central Pennsylvania, USA (D. Eissenstat & T. Adams, unpublished). (c) Patterns of N concentration in *Liquidambar styraciflua* roots from the Oak Ridge free-air CO_2 enrichment (FACE) site in the southeastern United States from a depth of 0–80 cm (C. Iversen, unpublished). In the middle panel (b), roots from ages 17 and 24 d were combined, as were those from ages 38 and 45 d. This was done to ensure a meaningful number of replicates for a given age class. In all panels, error bars represent ± SE.

these symbioses often challenges our ability to make meaningful root trait comparisons across species. For instance, root nutrient acquisition rates measured on excised roots cannot fully represent the amount and speed of nutrient uptake if connections to mycorrhizal fungi exploring larger soil volumes are broken (Hodge & Fitter, 2010; Chen *et al.*, 2016). The amount of C allocated to mycorrhizal fungi and the environmental context in which the symbiosis occurs (e.g. local fertility and climate) may also determine the overall efficiency of below-ground nutrient acquisition (Yanai *et al.*, 1995; Hasselquist *et al.*, 2016), but comparisons across species and environments are scarce. Still, a mycorrhizal-mediated root trait spectrum has the potential to improve our understanding of plant strategies for resource acquisition among species across environmental gradients.

Directly incorporating mycorrhizal fungi into broader root trait frameworks represents an important long-term goal. In the short term, there is the possibility of using basic root trait data to predict relative mycorrhizal contributions to nutrient acquisition. For example, first-order root diameter has been positively linked to percentage mycorrhizal colonization, suggesting a greater exchange of C and nutrients per unit root length between the symbiotic partners in species with thicker compared with thinner distal roots (Kong *et al.*, 2014). Moreover, there is increasing evidence that mycorrhizal type (e.g. arbuscular mycorrhizal vs ectomycorrhizal) can influence the C cost of nutrient acquisition, the pathway of nutrient acquisition (e.g. root vs fungal hyphae), and whole-ecosystem nutrient economies (e.g. inorganic- vs organic-based nutrient cycling) (Phillips *et al.*, 2013; Chen *et al.*, 2016). It may therefore be possible to use broad divisions in fungal groups, such as mycorrhizal type, to simplify and model key aspects of root–mycorrhizal relationships in the short term (e.g. Orwin *et al.*, 2011; Shi *et al.*, 2015). Still, a richer understanding of mycorrhizal effects on root traits should incorporate more nuanced descriptions of fine-root and fungal-trait variation. Moving forward, steps can now be taken that build on molecular innovations (e.g. high-throughput sequencing), which allow for rapid, affordable characterizations of mycorrhizal fungal communities. Taxonomic information

provided by molecular analysis paired with known functional attributes of different species provides a means to understand functional shifts among communities and infer functional roles of mycorrhizal fungi in different environmental contexts (Peay, 2014). The continued expansion of molecular techniques also enables us to determine the genes possessed and expressed in both plant and fungal partners, which has the potential to significantly advance our understanding of community structure function and species activities in the rhizosphere (Marmeisse *et al.*, 2013).

Root traits at the level of individual roots, entire root systems and whole plants

Fine-root trait measurements are made at different scales, ranging from nondestructive observations of individual roots to measurements of all of the fine roots in the plant–root system via comprehensive destructive harvests. Subsequent translation of information gathered from individual roots to the whole root system is, however, limited, while analogous scaling between individual leaves and plant canopies has proven quite useful for understanding ecosystem-level implications of functional traits (Reich *et al.*, 1992). For example, relationships among leaf mass fraction (leaf mass/total plant mass), specific leaf area (leaf area per unit mass), and leaf area index (leaf area per unit ground area) provide insights into plant form and functional strategies (Poorter *et al.*, 2015). By comparison, little is known of the relationships among fine-root mass fraction (fine-root mass/total plant mass), specific root length (length per unit mass), and rooting densities (length, area or mass per unit ground area) (Freschet *et al.*, 2015), especially in woody plants.

As we attempt to scale to the whole-plant level, we must understand scaling relationships between total root biomass and that of the whole plant. Previous work has shown that plant size is an important factor (Enquist & Niklas, 2002). We also have a fairly good understanding of how relationships between root biomass and total plant biomass shift with increasing plant size (Poorter *et al.*, 2015), as well as a nascent understanding of how these

Table 1 Hypothesized variations in root traits among species or within species along environmental gradients, with root age, and across seasons for 31 of the most common fine-root traits or trait groups identified from the Fine-Root Ecology Database (FRED, www.roots.ornl.gov)

Trait category	Trait	Across environments (intraspecific)*	Ontogenetic variability (root age)	Seasonal variability	Among species (interspecific)
Anatomy	Cortex thickness	Low to medium	Medium	Low	High
	Passage cell frequency	Medium	Low	Low	High
	Stele diameter	Low to medium	Low	Low	High
Architecture	Branching ratio (no. of roots per higher-order root)	High	Low	Low	High
	Branching intensity (no. of roots per higher-order root length)	High	Low	Low	High
Chemistry	%C	Low	Low	Low	Medium
	%N	Medium	High	High	Medium
	% (other elements)†; e.g. P, K, Ca, Mg, Mn, S, Cu, Fe	Low to medium	Medium	Medium	Medium
	Secondary compounds (e.g. lignin/AIF, phenols)	Medium	Medium	Medium	High
	Nonstructural carbohydrates	Medium	High	Medium	Medium
Dynamics	Decomposition rate (k)	Medium	Medium	Medium	High
	Life span	Medium	na	Medium	High
	Turnover	Medium	na	High	Medium
	Production/mortality (total annual amount)	Medium	na	na	High
	Production/mortality (timing)	Medium	na	na	Medium
Microbial associations	Mycorrhizal type (e.g. arbuscular, ecto-, ericoid)	Low	Low	Low	High
	Mycorrhizal colonization (%)	Medium	Medium to high	Low	High
	N-fixing nodule biomass	Medium	Medium	High	High
Morphology	Average diameter	Low to medium	Medium	Low	High
	Average individual length	Medium	Low	Low	High
	Tissue density	Low	Low	Low	Medium
	Specific root length or specific root area	Medium	Low	Low	High
	Root hair density/length	Medium	High	Medium	High
Physiology	Respiration	Medium	High	High	High
	Specific nutrient uptake rates	Medium	High	High	High
	Specific water uptake rates	Medium	Medium	Medium	Medium
	Exudation	Medium	High	High	High
Root system	Biomass ratios to above ground	Medium	na	Medium	Medium
	Biomass fraction by order or diameter class	Medium	na	Medium	High
	Total biomass	Medium	na	Medium	High
	Depth distribution	Medium	na	Medium	High

AIF, Acid insoluble fraction.
Preliminary hypotheses provided here are based on previous studies of fine-root trait variation (e.g. coefficient of variation). However, these previous studies are often based on limited species or geographic breadth. Here, 'Low' suggests that there is little anticipated variation relevant to the intended comparison while 'High' suggests that there is likely to be significant variation that may reflect adaptations to different environments or contexts. Boxes labeled as 'na' indicate traits or contexts where an estimate of variation is not applicable. More comprehensive tests determining relative levels of variation among and within plant species can help inform empiricists and modelers as to which traits best reflect below-ground plant responses to different environments and competitive contexts. Relevant citations for each trait are provided in Supporting Information Table S1.
*Variability of individual root traits across environmental gradients will probably differ depending on the species and other root traits. For example, species with relatively thick diameter roots may show relatively little variation in mycorrhizal colonization across fertility gradients, while species with relatively thin roots may show large variation in mycorrhizal colonization across fertility gradients.
†Variability will probably differ among elements.

relationships vary with climate (Reich, 2014). Conversely, our knowledge concerning phylogenetic differences in root biomass fractions is less well founded. We may expect some families, such as Poaceae and Cyperaceae, to have particularly high root mass fractions, whereas others, such as Solanaceae, often have very low root mass fractions (Poorter *et al.*, 2015), yet the cause of these differences is unclear. Differences in root mass fractions are also only part of the story and need to be appreciated in the context of maintaining a functional equilibrium within the plant. In principle, relatively small investments in fine-root biomass may be sufficient as long as the plant can compensate by constructing roots with relatively high uptake rates of nutrients and water. Similarly, a relatively small root system could increase its effective soil

exploration and resource acquisition via investments in mycorrhizal fungi, which is not accounted for in standard measures of root biomass.

Given the variation in activity among, and indeed within, root systems, determining the amount of total root biomass may only be a starting point. A second scaling issue, how biomass of absorptive roots relates to that of the total root system, must also be addressed to accurately link individual root function to root system processes (Zadworny *et al.*, 2016). This is especially relevant for woody species, where as much as 50%, or as little as 2% of total roots may be classified as fine (Vogt *et al.*, 1996), and of these only a further subset is likely to be physiologically active in uptake. The crux is, of course, to quantify the physiological activity of these
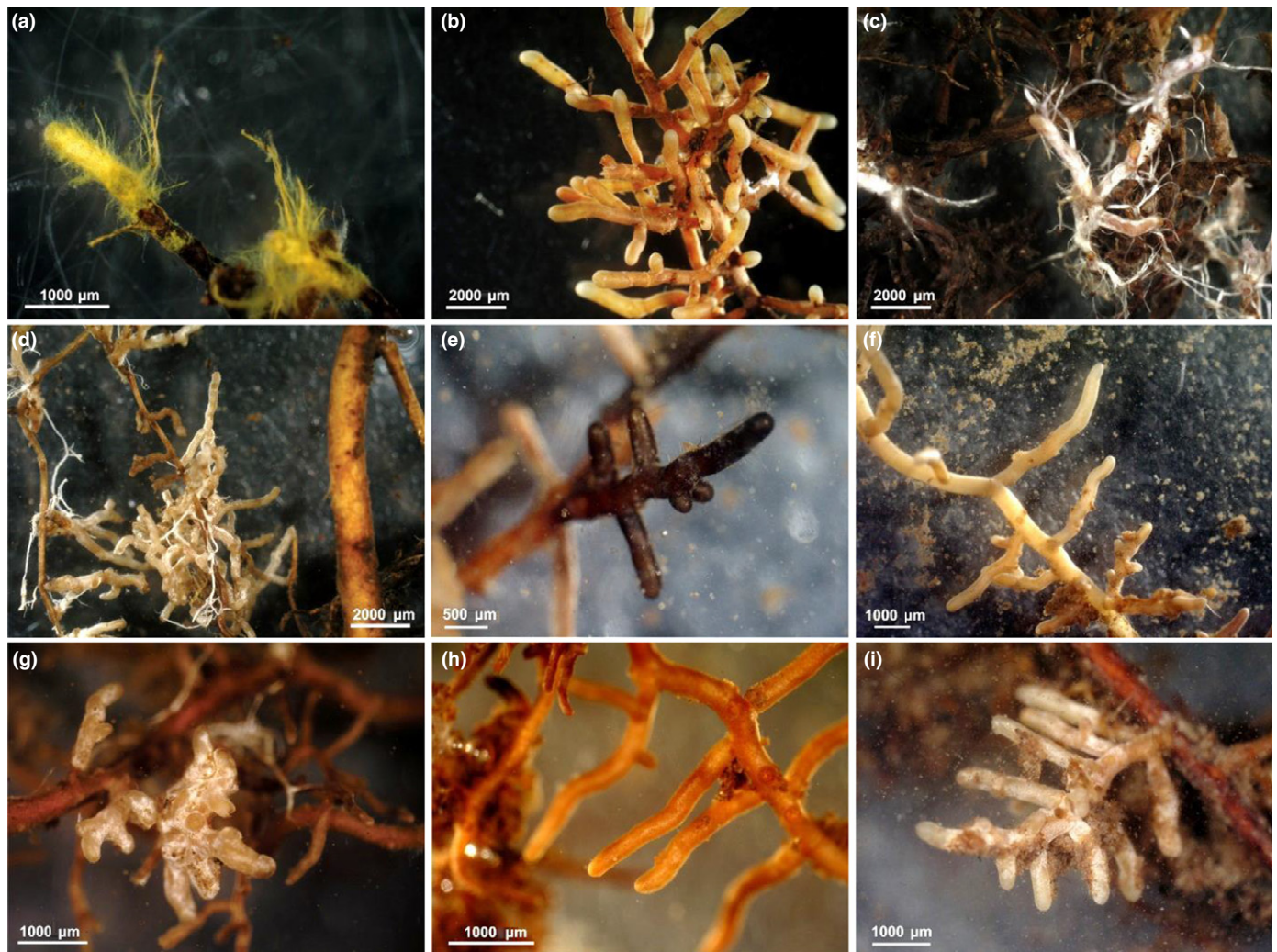
Fig. 2 Dramatic changes in fine-root architecture, morphology, and chemistry elicited by different species of ectomycorrhizal fungi on a single plant host. (a–c) Colonization by the fungal species *Piloderma croceum* (a), *Lactarius uvidus* (b), and *Cortinarius camphoratus* (c) on the host *Tsuga diversifolia*. (d–f) Colonization by the fungal species *Leccinum versipelle* (d), *Tomentella badia* (e), and *Lactarius tabidus* (f) on the host *Betula sp*. (g–i) Colonization by the fungal species *Tylopilus fellus* (g), *Lactarius quietus* (h), and *Russula granulata* (i) on the host *Fagus* sp. Ectomycorrhizas were sampled from Mount Fuji and Mount Ishizuchi, Japan (Miyamoto *et al.*, 2015). Photographs are courtesy of K. Nara and The Ectomycorrhizal Picture Book (http://www.edu.k.u-tokyo.ac.jp/nara_lab/home/ectomycorrhizas).

different roots, and, as discussed earlier, to understand how their activity will be altered by mycorrhizal associations, spatial location, and over time. This knowledge will ensure that measurements made at the individual root level are scaled appropriately to represent whole-plant or ecosystem pools of fine-root biomass and function.

Facilitating better scaling of root traits may require holistic methods that are nondestructive or noninvasive in order to track the dynamics of whole-root systems over large spatial areas and through time. Traditional nutrient and water budgeting approaches at the plant and ecosystem levels can help to constrain estimates, but improved efforts scaling root-level measurements to whole plants and additional whole-ecosystem measurement techniques are also needed. For example, in above-ground systems, rapid determination of leaf area index is commonplace and eddy covariance flux measurements provide a powerful approach to relate leaf-level measures to whole-canopy and ecosystem scales. To our knowledge,

no approach as yet can directly integrate below-ground rooting densities and dynamics in a comparable way. Techniques including ground-penetrating radar resolved at the scale of an individual fine root, scanning technologies (e.g. computed tomography scans, magnetic resonance imaging, as well as neutron imaging) that can visualize roots and water flow through plants (Warren *et al.*, 2013; van Dusschoten *et al.*, 2016) and remote sensing measurements that link canopy properties with below-ground traits of interest (Koteen *et al.*, 2015; Fisher *et al.*, 2016) show significant promise. Still, each of these approaches requires refinement related to the spatial and/or temporal resolution at which each technique can be employed and interpreted, or they require further clarification regarding uncertain empirical linkages between the specific measurement and ecosystem processes of interest. Models can be used to help scaling efforts, but only when the mechanisms underlying particular root processes are sufficiently understood and captured in the model structure (Warren *et al.*, 2015).

Selecting a diversity of traits to represent fine-root and ecosystem processes

Given the logistical and financial constraints faced by most researchers, it is important to emphasize traits that can be measured consistently, and that can also be meaningfully related to a process with broader significance to root or ecosystem function. For example, individual root diameter and length are relatively easy traits to measure and they are particularly useful because they potentially provide information about root construction costs, root anatomy, mycorrhizal colonization rates, patterns of root life span and strategies for nutrient acquisition (McCormack *et al.*, 2012; Kong *et al.*, 2014; Chen *et al.*, 2016). Substantial effort has been made to synthesize existing information regarding connections among commonly measured root traits or between these traits and ecosystem processes. For further discussion on this topic, we refer readers to several recent publications and references therein (Bardgett *et al.*, 2014; Reich, 2014; Roumet *et al.*, 2016; Weemstra *et al.*, 2016). Here, we instead begin a discussion on which additional traits might warrant greater attention for future studies.

The majority of studies reporting fine-root traits often encompass a relatively small set of basic measurements. These generally include aspects of root morphology and construction such as root diameter (mm), specific root length (m g^{-1}), and root tissue density (g cm^{-3}), as well as basic root chemistry (i.e. root C and N concentrations). However, it can be important to consider a wider diversity of fine-root traits that may be used to understand connections between root form and function. These should include the common measures of morphology, anatomy, and chemistry described earlier, as well as somewhat less common measures of architecture, physiology, root dynamics (e.g. life span, phenology), mechanical traits (e.g. toughness, tensile strength), root system traits (e.g. rooting depth, allocation ratios), and microbial associations (Fig. 3). Obtaining measurements across the wide range of functional trait categories presented in Fig. 3 provides us with a better opportunity to meaningfully capture and understand variation among species and across environmental conditions.

The utility of any single trait ultimately depends on the specific process or function of interest. From an ecosystem perspective, we are generally most interested in aspects of nutrient and water uptake, resource allocation, tissue longevity, respiration, plant anchorage and soil stability, as well as root decomposition and subsequent impacts on microbial populations and soil properties. Some of these traits and processes can be directly measured but often only with great difficulty; the use of simpler traits may provide valuable insight where direct observations are not feasible. For each of the earlier functions or processes, we generally find relevant traits among each of the categories represented in Fig. 3. For example, water uptake is partly controlled by aspects of root anatomy, morphology, architecture and root-system structure while root longevity is often related to aspects of anatomy, morphology, physiology, chemistry, and rooting depth. Perhaps unsurprisingly, understanding of each process is substantially improved by incorporating multiple traits from different categories.

Given the wide range of questions to which trait measures can be applied, identifying which individual traits are the most important

is challenging, and perhaps not meaningful. However, considering a series of questions or principles may help to determine the relative value of one particular trait over another:

• Which traits can be measured relatively easily, or at least consistently, and accurately?

• Which traits can be most confidently linked to root function or processes of interest across species and environments?

• Which traits express consistent, quantifiable variation, either among species or within species but across environmental gradients, such that comparisons of means and variances have the capacity to reflect meaningful shifts in root function?

• Which traits are related to whole-plant trait syndromes (e.g. trait economics or hydraulic networks) such that incorporation of those root traits provides a better understanding of the functional strategy of a whole plant? Can we quantify functional tradeoffs that impact plant and ecosystem performance?

• Which traits are likely to affect broader ecosystem processes (e.g. root exudation constitutes a relatively small proportion of total plant C but can prime microbial processes and accelerate decomposition of organic matter)?

Similar to above-ground stem and leaf traits, different frameworks can be used to aggregate variation among multiple fine-root traits and their subsequent impacts on function and process. For example, a trait economics approach would predict that 'fast' plants have highly acquisitive root tissues, potentially with relatively thin root diameters, high specific root lengths, short root life spans, and fast decomposition rates, while 'slow' plants should express the opposite (Reich, 2014; Roumet *et al.*, 2016). However, other frameworks may also be useful for describing fine-root trait variation, particularly in cases where single frameworks fail to meaningfully capture variation at both the fine-root and whole-plant levels (Weemstra *et al.*, 2016). For instance, comparing relatively thick-rooted species with thin-rooted species may be useful for interpreting foraging and acquisition strategies together with potential tradeoffs with mycorrhizal fungi (Eissenstat, 1992; Chen *et al.*, 2016). Rooting depth patterns (i.e. deep vs shallow), stress tolerance, microbial associations, and patterns of primary vs secondary tissue development within the branched root system of woody plants can all give insights into how plant species adapt to different climates, soil fertilities, and compete for below-ground resources (Bardgett *et al.*, 2014; Zadworny *et al.*, 2016). As consistent patterns of fine-root trait variation emerge, these and other frameworks will provide an empirical foundation to model fine-root processes at ecosystem to global scales.

Fine-root traits for ecosystem and terrestrial biosphere models

Ecosystem models and TBMs generally encompass processes related to resource uptake, plant growth, and plant mortality, often by quantifying fluxes of energy, water, and nutrients. These are represented through a series of mechanistic or statistical relationships using estimates of different plant functional traits aggregated at either the level of species or the plant functional type, depending on the model and the spatial extent being considered. Above ground, crucial aspects of leaf physiology are incorporated into
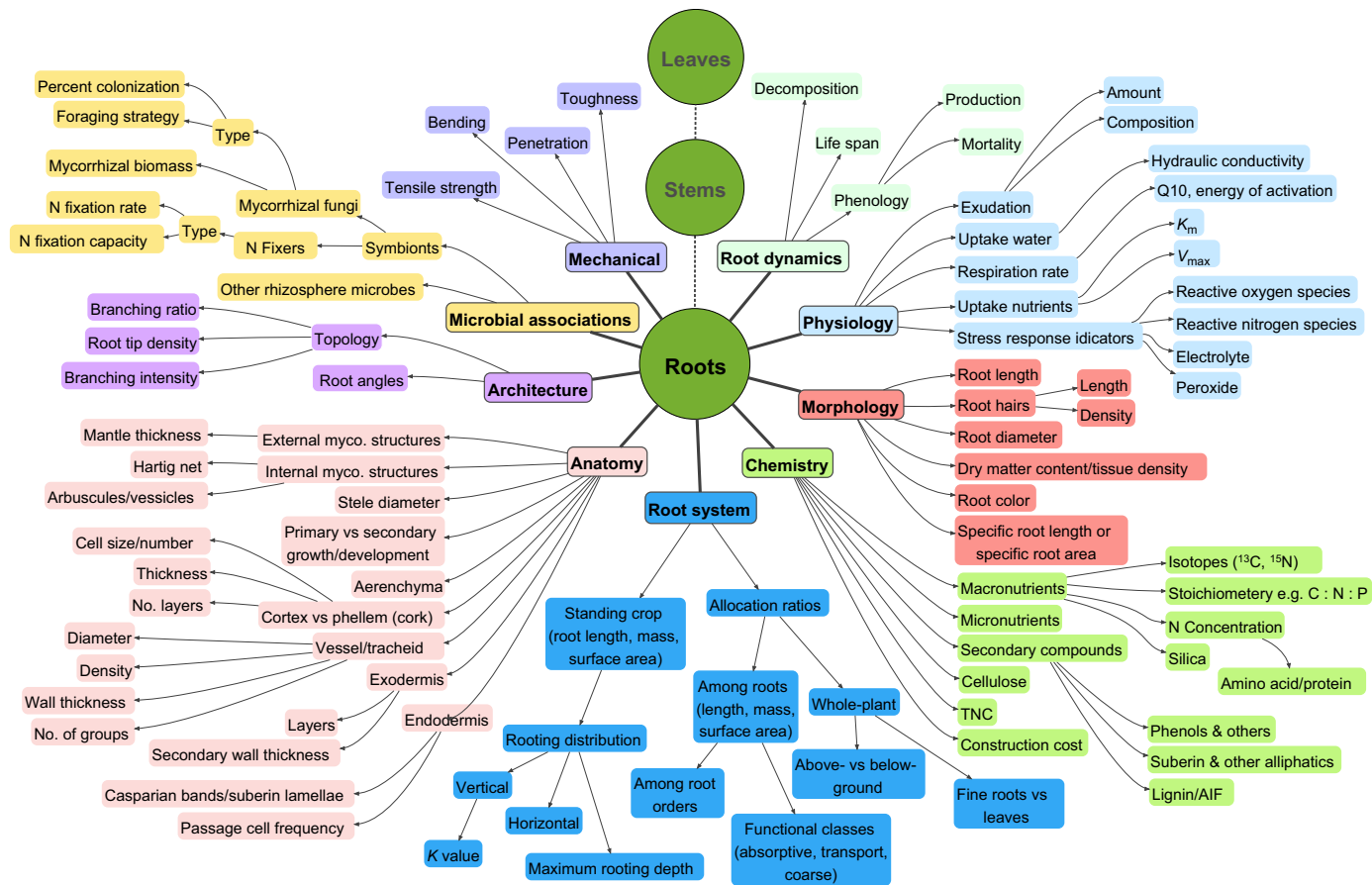
Fig. 3 Map of common traits relevant to the functioning of fine roots. Traits are grouped into differet categories of anatomy, architecture, chemistry, mechanical, morphology, physiology, root dynamics, microbial associations, and root system. Supporting Information Fig. S1 presents a similar trait map with the most immediately model-relevant traits highlighted. AIF, acid-insoluble fraction; K value under Rooting depth, scaling constant associated with a vertical depth distribution; K_m, half-saturation constant (associated Michaelis-Menten type kinetics); myco, mycorrhizal; TNC, total nonstructural carbohydrates; V_{max}, maximum reaction rate.

most models using well established, mechanistic relationships with the environment (e.g. Farquhar–von Caemmerer model, Ball–Berry model, Penman–Monteith equation). However, functional analogs in fine roots are much less well understood and poorly incorporated into models. For example, only over the last decade has soil N availability and acquisition become a relatively common feature of TBMs capable of limiting plant growth, and still essentially none of these models control potential rates of N uptake based directly on root-level physiology.

In spite of, or perhaps because of, these limitations, the role of fine-root traits in terrestrial models has received considerable attention recently. There is increasing recognition that the simplistic representations of root processes contained in many of the models we rely on to understand plant and terrestrial ecosystem productivity must be improved to capture their dynamic responses to environmental change (Iversen, 2010; Smithwick *et al.*, 2014; Warren *et al.*, 2015). In an effort to focus future measurements of fine-root traits for use in models, it is important to identify which root traits are currently most used and which traits are likely to be of high value in modeling applications moving forward. In a comparison of 11 models, Warren *et al.* (2015) identified annual root production, maximum rooting depth, and root mortality/

turnover as being the most commonly represented root traits, while root respiration, root distribution and aspects of root chemistry were also relatively common (Fig. S1). Importantly, empirical estimates for many of these traits are quite variable and contribute to a high degree of uncertainty in models (Dybzinski *et al.*, 2011).

Depending on the modeling approach, appropriate trait values may be needed to prescribe parameter estimates *a priori* (e.g. maximum rooting depth, root distribution, and root chemistry) while others may emerge as model outputs following model simulations (e.g. annual root production), or, in some cases, are allowed to vary with environmental conditions (e.g. root respiration often set to vary with temperature). Therefore, some trait measurements are specifically needed to parameterize model inputs, while others are needed to benchmark or validate model outputs. However, in essentially all cases there is a need to reduce current degrees of uncertainty for fine-root variables to improve confidence in model predictions of terrestrial productivity. Some advances can be accomplished quickly thanks to improved coverage in plant trait databases and by updating prescribed relationships between traits and fluxes. For example, many TBMs scale tissue-specific root respiration directly to the whole ecosystem via its relationship with root N concentration. Yet, current model

relationships often do not reflect the expansion of available data and empirical relationships identified over the past decade (e.g. Reich *et al.*, 2008). Still, rich data sources are increasingly being used to constrain modeled relationships and this trend will likely continue. Yet, as efforts to scale individual root traits to understand the function of an entire root system continue, it becomes increasingly important to recognize and quantify separate functional pools of root biomass. This will help to ensure that empirical relationships, like those between N concentration and respiration, are modeled appropriately within a functional pool of roots and can then be scaled more accurately to the ecosystem level.

Although there is potential for changes in root-related parameters to significantly alter outcomes in many ecosystem models and TBMs, it is important to recognize that few of these models directly incorporate root function, particularly in relation to nutrient uptake (Warren *et al.*, 2015). Not surprisingly, few models therefore currently require parameterization of root traits that are directly associated with root acquisition of soil resources. However, many ecosystem-scale models have built-in relationships between fine-root biomass and potential uptake of soil resources such that more root biomass equates to more nutrient uptake. A growing number of TBMs have now begun to incorporate similar relationships and potential roles of mycorrhizal fungi as well (Ghimire *et al.*, 2016). These changes mean that accurate quantification of functionally absorptive fine-root surface area and biomass (i.e. not just all biomass < 2 mm diameter) is needed to allow models to more directly tie root function to active fine-root biomass (McCormack *et al.*, 2015). Once separate measures of functionally distinct fine-root pools are more widely available it will be possible to incorporate dynamic allocation regimes to mediate patterns of annual fine-root production in response to environmental gradients (Iversen, 2010; Warren *et al.*, 2015). These allocation regimes could be based on optimization approaches where allocation to roots is predicted to maximize resource acquisition in different environments (Yanai *et al.*, 1995; McMurtrie & Dewar, 2013), or, more specifically, game theoretic approaches that predict growth and traits of successful competitors (Gersani *et al.*, 2001; Dybzinski *et al.*, 2011). Importantly, these and other approaches that underpin model assumptions are built on a basic appreciation of fine-root traits and their linkages, or scaling, to ecosystem-level processes.

Capturing root-trait variation to improve ecosystem and terrestrial biosphere models

In the previous sections, we discussed three targeted areas for improving understanding of fine-root traits and their linkages to ecosystem processes, including developing better appreciation of spatial and temporal variation in trait values; explicitly considering the role of mycorrhizal fungi in determining fine-root function and below-ground processes; and improving approaches for scaling traits measured at the root level to understand processes at the root system or ecosystem level. Gains in each of these areas can then be directly applied towards improving both the current

parameterizations and future model descriptions of below-ground processes. We provide brief examples for each of these in the following paragraphs which highlight the substantial capacity for making tractable and meaningful improvements to ecosystem- and global-scale models by capturing and understanding species and global variation in root traits.

Fine-root trait variation There has been considerable discussion concerning the spatial deployment of fine roots in models, particularly in regard to potential water and nutrient uptake and soil C storage at different soil depths (Iversen, 2010). Temporal variation, though less often considered, may also have significant impacts on model behavior even within current model frameworks. In most TBMs, fine roots represent a significant sink for C at the time when roots are 'constructed' and they continue to lose C thereafter as standing root biomass incurs an ongoing respiratory cost. However, few models facilitate realistic patterns of root phenology as the timing of root construction (birth) is generally inflexible and often forced to coincide with leaf production. This approach may lead to overestimations or underestimations of C loss via root respiration when, in reality, a substantial portion of the root population may be produced much earlier or much later than leaf out, depending on the species and climate. Improving rooting depth distributions and defining patterns of fine-root phenology that are independent of leaf phenology represent two tractable ways in which models can more accurately represent spatiotemporal variation in fine roots. Both changes improve realism of model structures and facilitate a more mechanistic relationship between fine roots and model estimates of water acquisition and root respiration.

Mycorrhizal impacts on root traits Incorporating aspects of mycorrhizal ecology into TBMs is, in many ways, more challenging than allowing for spatial and temporal variability in fine-root processes that already exist within most models. Directly incorporating mycorrhizal fungi could require incorporation of multiple new root and mycorrhizal biomass pools, each with their associated fluxes of C, water, and nutrients for which there are few reliable data for model parameterization. The added complexity and scant data probably ensure that detailed, root- and/or species-level descriptions of mycorrhizal activity are not possible and are unwarranted in the near term. However, simpler divisions among plants that predominately associate with arbuscular mycorrhizal fungi or ectomycorrhizal fungi may provide a tractable means to begin incorporating this crucial aspect of below-ground ecology into terrestrial models (Orwin *et al.*, 2011; Shi *et al.*, 2015). This work builds on the idea that patterns of nutrient cycling should differ predictably with different mycorrhizal associations (Phillips *et al.*, 2013). While more data are needed to assess the generality of these differences to diverse ecosystem types around the globe, they may represent a useful lens with which to interpret and potentially model ecosystem processes.

Scaling root traits for models Mechanistic models are often dependent on accurate scaling relationships between processes occurring at the individual-tissue level (e.g. leaf or root) and

those that are quantified at the ecosystem level (e.g. canopy photosynthesis and productivity or below-ground resource uptake). Unfortunately, scaling relationships between individual roots to the function of entire root systems are not as well established as those determined above ground. As a starting point, it is critical that we first improve our estimates of fine-root biomass and appreciation of how biomass patterns shift among species and environmental conditions, given the sensitivity of most models to changes in biomass allocation ratios. Moreover, future prospects of linking root biomass more directly to root function will require explicit consideration of both total biomass and, specifically, functionally active biomass across full rooting depth profiles. Finally, while probably not possible at the global scale, ecosystem-scale models should begin to include estimates of how fine-root traits and processes shift through time (e.g. declining uptake capacity and respiration as roots age) and with depth (e.g. declining metabolic activity and nutrient concentrations decline with increasing depth), which would allow for more accurate scaling of individual root functions to ecosystem-scale processes. Only when the empirical evidence allows us to draw clear linkages across scales, from roots to whole ecosystems, can we be confident in our ability to model plant strategies for resource acquisition, growth, and competition in dynamic environments both above and below ground.

Conclusions

Cohesive and predictable patterns of fine-root trait variation are needed to improve representations of below-ground processes in models and thus overall model performance, yet these broad patterns have been difficult to achieve. The limited availability of comprehensive and comparable empirical datasets represents a major limitation to model parameterization. While efforts are under way to bring wide-ranging root trait datasets together, along with associated climate and edaphic information (www.roots.ornl.gov), continued work measuring relatively simple root traits and processes at the level of individual roots and whole-root systems is still sorely needed. Identification of broad trait associations may be possible within established trait economics or competition-optimization frameworks but may also require approaches that group suites of traits into separate modules to better reflect the diversity of below-ground strategies (e.g. morphology – thick vs thin roots; anatomy – primary vs secondary tissue development; different mycorrhizal types and variable intensity of associations). Given the unique set of drivers and constraints faced by fine roots independent of constraints above ground, it is likely that many fine-root traits and plant species will not align well with traditional trait frameworks used in leaves. Even so, recognizing where and how these and other frameworks can be used will help inform better functional trait relationships in models. Subsequent iterations of model function and parameter improvements can then help to identify the largest gaps in empirical understanding and guide the next generation of ecological studies and root trait measurements.

M. Luke McCormack[1]*, Dali Guo[2], Colleen M. Iversen[3], Weile Chen[4], David M. Eissenstat[4,5], Christopher W. Fernandez[1], Le Li[2,6], Chengen Ma[2,6], Zeqing Ma[2], Hendrik Poorter[7], Peter B. Reich[8,9], Marcin Zadworny[10] and Amy Zanne[11]

[1]Department of Plant and Microbial Biology, University of Minnesota, St Paul, MN 55108, USA;
[2]Center of Forest Ecosystem Studies and Qianyanzhou Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;
[3]Climate Change Science Institute and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA;
[4]Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA 16802, USA;
[5]Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802, USA;
[6]University of the Chinese Academy of Sciences, Beijing 100101, China;
[7]Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, Jülich D-52425, Germany;
[8]Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA;
[9]Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, NSW 2751, Australia;
[10]Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, Kórnik 62-035, Poland;
[11]Department of Biological Sciences, George Washington University, Washington, DC 20052, USA
(*Author for correspondence: tel +1 612 625 1234; email mltmcc@gmail.com)

References

Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29: 692–699.
Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging

strategies of temperate trees. *Proceedings of the National Academy of Sciences, USA* **113**: 8741–8746.

Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, Knops J. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* **16**: 563–574.

van Dusschoten D, Metzner R, Kochs J, Postma JA, Pflugfelder D, Bühler J, Schurr U, Jahnke S. 2016. Quantitative 3D analysis of plant roots growing in soil using magnetic resonance imaging. *Plant Physiology* **170**: 1176–1188.

Dybzinski R, Farrior C, Wolf A, Reich PB, Pacala SW. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *American Naturalist* **177**: 153–166.

Eissenstat DM. 1992. Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* **15**: 763–782.

Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* **295**: 1517–1520.

Fisher JB, Sweeney S, Brzostek ER, Evans TP, Johnson DJ, Myers JA, Bourg NA, Wolf AT, Howe RW, Phillips RP. 2016. Tree-mycorrhizal associations detected remotely from canopy spectral properties. *Global Change Biology* **22**: 2596–2607.

Freschet GT, Cornelissen JH, van Logtestijn RS, Aerts R. 2010. Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist* **186**: 879–889.

Freschet GT, Swart EM, Cornelissen JH. 2015. Integrated plant phenotypic responses to contrasting above-and below-ground resources: key roles of specific leaf area and root mass fraction. *New Phytologist* **206**: 1247–1260.

Gersani M, O'Brien EE, Maina GM, Abramsky Z. 2001. Tragedy of the commons as a result of root competition. *Journal of Ecology* **89**: 660–669.

Ghimire B, Riley WJ, Koven CD, Mu M, Randerson JT. 2016. Representing leaf and root physiological traits in CLM improves global carbon and nitrogen cycling predictions. *Journal of Advances in Modeling Earth Systems* **8**: 598–613.

Hasselquist NJ, Metcalfe DB, Inselsbacher E, Stangl Z, Oren R, Näsholm T, Högberg P. 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. *Ecology* **97**: 1012–1022.

Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia* **162**: 505–513.

Hodge A, Fitter AH. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences, USA* **107**: 13754–13759.

Iversen CM. 2010. Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist* **186**: 346–357.

Kong D, Li L, Ma C, Zeng H, Guo D. 2014. Leading dimensions of root trait variation in subtropical forests. *New Phytologist* **203**: 863–872.

Koteen LE, Raz-Yaseef N, Baldocchi DD. 2015. Spatial heterogeneity of fine root biomass and soil carbon in a California oak savanna illuminates plant functional strategy across periods of high and low resource supply. *Ecohydrology* **8**: 294–308.

Marmeisse R, Nehls U, Öpik M, Selosse MA, Pringle A. 2013. Bridging mycorrhizal genomics, metagenomics and forest ecology. *New Phytologist* **198**: 343–346.

McCormack ML, Adams TS, Smithwick EA, Eissenstat DM. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist* **195**: 823–831.

McCormack ML, Dickie IA, Eissensat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of belowground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505–518.

McMurtrie RE, Dewar RC. 2013. New insights into carbon allocation by trees from the hypothesis that annual wood production is maximized. *New Phytologist* **199**: 981–990.

Miyamoto Y, Sakai A, Hattori M, Nara K. 2015. Strong effect of climate on ectomycorrhizal fungal composition: evidence from range overlap between two mountains. *ISME Journal* **9**: 1870–1879.

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.

Peay KG. 2014. Back to the future: natural history and the way forward in modern fungal ecology. *Fungal Ecology* **12**: 4–9.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte M, Cornwell W, Craine J, Gurvich D. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.

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.

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**: 736–749.

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**: 665–670.

Reich PB. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Reich PB, Tjoelker MG, Pregitzer KS, Wright IJ, Oleksyn J, Machado JL. 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters* **11**: 793–801.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.

Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N, Vrignon-Brenas S, Cao KF, Stokes A. 2016. Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist* **210**: 815–826.

Shi M, Fisher JB, Brzostek ER, Phillips RP. 2015. Carbon cost of plant nitrogen acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the community land model. *Global Change Biology* **22**: 1299–1314.

Smithwick EAH, Lucash MS, McCormack ML, Sivandran G. 2014. Improving the representation of roots in terrestrial models. *Ecological Modelling* **291**: 193–204.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116**: 882–892.

Vivanco L, Austin AT. 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America. *Oecologia* **150**: 97–107.

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant and Soil* **187**: 159–219.

Volder A, Smart DR, Bloom AJ, Eissenstat DM. 2005. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytologist* **165**: 493–501.

Warren JM, Bilheux H, Kang M, Voisin S, Cheng C-L, Horita J, Perfect E. 2013. Neutron imaging reveals internal plant water dynamics. *Plant and Soil* **366**: 683–693.

Warren JM, Hanson PJ, Iversen CM, Kumar J, Walker AP, Wullschleger SD. 2015. Root structural and functional dynamics in terrestrial biosphere models–evaluation and recommendations. *New Phytologist* **205**: 59–78.

Weemstra M, Mommer L, Visser EJ, Ruijven J, Kuyper TW, Mohren GM, Sterck FJ. 2016. Towards a multidimensional root trait framework: a tree root review. *New Phytologist* **211**: 1159–1169.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Yanai RD, Fahey TJ, Miller SL. 1995. Efficiency of nutrient acquisition by fine roots and mycorrhizae. In: Smith WK, Hinckley TM, eds. *Resource physiology of conifers: acquisition, allocation, and utilization*. San Diego, CA, USA: Academic Press, 75–103.

Zadworny M, McCormack ML, Mucha J, Reich PB, Oleksyn J. 2016. Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. *New Phytologist* **212**: 389–399.

Zadworny M, McCormack ML, Rawlik K, Jagodziński AM. 2015. Seasonal variation in chemistry, but not morphology, in roots of *Quercus robur* growing in different soil types. *Tree Physiology* **35**: 644–652.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Map of common traits relevant to the functioning of fine roots with emphasis placed on traits with increased importance in modeling contexts.

Table S1 Hypothesized levels of variation in root traits together with relevant citations listed for each trait

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