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A global Fine-Root Ecology Database to address below-ground challenges in plant ecology

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Viewpoints

A global Fine-Root Ecology Database to address below-ground challenges in plant ecology

Summary

Variation and tradeoffs within and among plant traits are increasingly being harnessed by empiricists and modelers to understand and predict ecosystem processes under changing environmental conditions. While fine roots play an important role in ecosystem functioning, fine-root traits are underrepresented in global trait databases. This has hindered efforts to analyze fine-root trait variation and link it with plant function and environmental conditions at a global scale. This Viewpoint addresses the need for a centralized fine-root trait database, and introduces the Fine-Root Ecology Database (FRED, <http://roots.ornl.gov>) which so far includes >70 000 observations encompassing a broad range of root traits and also includes associated environmental data. FRED represents a critical step toward improving our understanding of below-ground plant ecology. For example, FRED facilitates the quantification of variation in fine-root traits across root orders, species, biomes, and environmental gradients while also providing a platform for assessments of covariation among root, leaf, and wood traits, the role of fine roots in ecosystem functioning, and the representation of fine roots in terrestrial biosphere models. Continued input of observations into FRED to fill gaps in trait coverage will improve our understanding of changes in fine-root traits across space and time.

Introduction

Plant traits serve as proxies for plant functioning and performance, including survival, growth, and resource capture (Grime, 1974; Violle *et al.*, 2007). Suites of plant characteristics are filtered and shaped by evolution and the environment, and affect ecosystem processes ranging from primary production to nutrient and carbon (C) cycling and storage (Lavorel & Garnier, 2002; Reich, 2014; Garnier *et al.*, 2017). Variation and tradeoffs within and among plant traits are increasingly being harnessed by empiricists and modelers to predict plant community composition and ecosystem processes in response to current and future environmental conditions (Lynch, 2007; Soudzilovskaia *et al.*,

2013; van Bodegom *et al.*, 2014; Violle *et al.*, 2014). However, both empirical and modeling efforts focus on above-ground plant traits, with little consideration of below-ground traits and strategies (Wright *et al.*, 2004; Verheijen *et al.*, 2016). The limited availability of root trait data has precluded the consideration of below-ground strategies in the development of plant functional types (PFTs) and in the identification of leading dimensions of plant strategies (Grime, 1974; Westoby *et al.*, 2002), as well as in analyses of the global spectrum of plant form and function (Diaz *et al.*, 2016). This is despite the critical and unique role that fine roots play in plant functioning and ecosystem processes.

Analogous to leaves above ground, fine roots, traditionally defined as <2 mm in diameter, are the most physiologically active component of the below-ground plant system (Kramer, 1969; Fitter, 1982; Jackson *et al.*, 1990; Eissenstat, 1992). Functional traits of fine roots have been linked to variation in root resource acquisition, exudation, respiration, growth, turnover, and decomposition (Kramer, 1969; Poorter *et al.*, 1990; Freschet *et al.*, 2012; McCormack *et al.*, 2012; Kong *et al.*, 2014). In addition, fine roots mediate an array of ecosystem processes, including microbial community dynamics and the cycling and storage of C, nutrients, and water (reviewed in Bardgett *et al.*, 2014).

Recent advances in our definition of fine roots, based on the observation that root orders along the branching hierarchy of roots <2 mm in diameter encompass a diversity of form and function (Wilcox, 1968; Pregitzer *et al.*, 2002), have better positioned root ecologists to understand root trait variation within and among plant species. It has been further suggested that fine-root orders can be grouped into two functional classes, where 'absorptive fine roots' are the most distal, short-lived root orders involved primarily in resource acquisition, and 'transport fine roots' are longer-lived, higher-order roots responsible for resource transport (McCormack *et al.*, 2015b). Comparative analyses that have taken advantage of the linkages between fine-root form and function across the root branching hierarchy have begun to quantify the variation and tradeoffs in fine-root traits along environmental gradients and among plant lineages (Valverde-Barrantes *et al.*, 2013; Kong *et al.*, 2014; Eissenstat *et al.*, 2015; Roumet *et al.*, 2016).

The need for an improved conceptual understanding of root trait covariation, along with an understanding of the responses of root traits to changing environmental conditions and the role of root traits as drivers of ecosystem processes and plant niche partitioning, have been comprehensively reviewed in recent years (Lynch, 2007; Bardgett *et al.*, 2014; Reich, 2014; Laliberté, 2017; Mommer *et al.*, 2016; Weemstra *et al.*, 2016). Here we focus on a foundational aspect of improving our understanding of fine-root traits – the compilation of a centralized fine-root trait database. This represents a critical step towards quantifying variation in fine-root traits across

root orders, species, biomes, and environmental gradients, while also building a platform for future assessments of covariation among root, leaf, and wood traits, and the role of fine roots in ecosystem functioning. We begin this Viewpoint with an introduction of a global fine-root trait database initiative. We continue with an exploration of some of the unanswered questions in below-ground ecology that can be addressed by leveraging a global root trait database, and we conclude by highlighting gaps in our measurement and understanding of fine-root traits that require urgent attention from the root and rhizosphere community.

The need for a global root trait database

Observation of below-ground plant traits is laborious, and the resulting data are precious. However, the accumulation of root trait data in the literature is not easily accessible, as these data are stored in dispersed repositories and in heterogeneous formats. While some root trait data compilations exist, they have been limited to individual root traits related to particular questions or to certain regions of the world (Supporting Information Notes S1), and the widely used global plant trait 'TRY' database (www.try-db.org) reports that <1% of the data deposited describes fine-root functional traits (Kattge *et al.*, 2011). The lack of a centralized root trait database has been identified as 'one of the largest challenges ... facing ecologists working at the interface between root traits and ecosystem processes' (Bardgett *et al.*, 2014). This shortcoming has hindered efforts to analyze intra- and interspecific fine-root trait variation and link it with plant function and environmental conditions at a global scale (Siefert *et al.*, 2015); limited meaningful linkages among above- and below-ground traits (Verheijen *et al.*, 2016); and contributed to the coarse representation of fine-root processes and associated parameters in terrestrial biosphere models (Warren *et al.*, 2015).

Harnessing available root trait data

To address the need for a centralized root trait database, we have compiled the Fine-Root Ecology Database (FRED) from published and unpublished data sources (FRED data citation: Iversen *et al.*, 2016; <http://roots.ornl.gov>). This database has been compiled in order to organize fine-root functional trait data into a single common framework, available to empiricists and modelers alike; encourage the community of root and rhizosphere ecologists to provide additional sources of data; allow for the quantification of fine-root trait variation within and among species, across environments, and with regard to other traits; facilitate the improved representation and parameterization of fine-root processes in terrestrial biosphere models; provide an objective tool to highlight gaps and inconsistencies in existing fine-root trait measurements across the globe to spur new measurement campaigns; and create a foundation from which different measures of individual root traits can be meaningfully compared and help to identify appropriate directions for more standardized methods. FRED is focused on fine roots (defined broadly as roots <2 mm in diameter), as coarse roots are studied using different methodology, often at very different scales, and have different traits and trait

interpretations (Stover *et al.*, 2007). However, FRED accepts data collected from roots of all sizes, and already contains observations of coarse roots.

To date, FRED version 1.0 has *c.* 50 000 species-specific root trait observations from 1213 species, and *c.* 20 000 root trait observations collected from mixed plant communities. These data have been compiled from 794 data sources dating from 1925 to the present, and references to the original data sources are included with each observation, along with digital object identifiers (DOIs) for both the data source and dataset (when available). The observations are from ecosystems spanning the globe (Fig. 1), ranging from evergreen and deciduous trees to grasses and forbs in arctic, boreal, temperate, and tropical biomes. In total, the observations encompass > 300 root traits that can be grouped into eight categories: root anatomy, architecture, chemistry, dynamics, morphology, physiology, and the whole-root system, as well as microbial associations (Table 1; <http://roots.ornl.gov/data-inventory>). The traits with the most abundant observations are related to chemistry (fine-root nitrogen (N) concentration), morphology (fine-root diameter and specific root length), microbial associations (fine-root associations with different types of mycorrhizal fungi), and the root system (fine-root standing crop and allocation).

There are many potential pitfalls in the use of data from a large root trait database to infer global patterns, not least because there is substantial evidence to indicate that comparisons of root traits within and among species can be confounded by changes in root form and function across the root branching hierarchy. Also, root trait observations have been collected under different experimental and environmental conditions that might be expected to affect trait observations and responses (Poorter *et al.*, 2016). Therefore, in addition to data on root traits, we also collected ancillary data in categories including climate and soils, plant taxonomy, growth form, growing conditions, and stand and vegetation characteristics, as well as standardized metadata on the study and study location, and the classification and collection of roots. In total, there are *c.* 270 types of ancillary data available (Table S1; <http://roots.ornl.gov/ancillary-data>).

In addition to important root traits such as diameter (or diameter class) and color, ancillary root sampling metadata (Table S1) will facilitate accurate comparisons of root traits within and among species by indicating whether roots were: fine roots, coarse roots, below-ground stems, rhizomes, a mixture of these organs, or the total root or below-ground system; a given age; associated with a specific root functional class (e.g. absorptive or transport fine roots, or a mixture of both) or heterorhizy class (e.g. fibrous or pioneer roots); associated with a specific root order; ordered according to a centripetal or centrifugal numbering scheme; living or dead (or a mixture of both); and collected from a given soil depth. In turn, ancillary data associated with plant growing conditions (Table S1) indicate the conditions under which the root traits were measured, for example, whether roots were collected outdoors from plants growing *in situ* or in pots or collected indoors from pots, chambers, or hydroponic solutions; and collected from across observational gradients, or from experimental treatments that included nutrient, water, temperature, elevated [CO₂], burning, disturbance, girdling, or light manipulations and their associated controls.

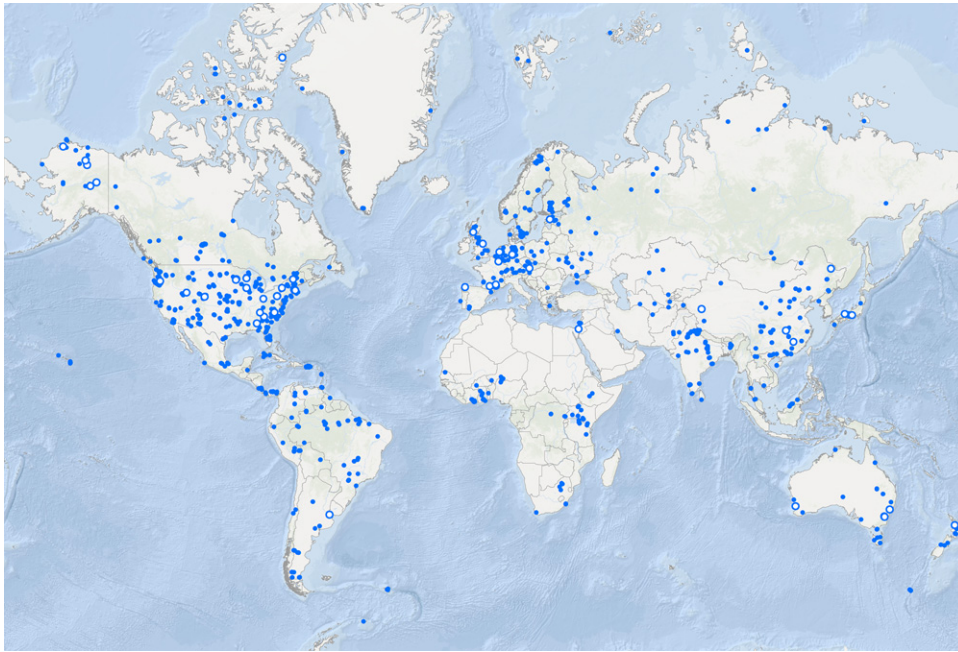


Fig. 1 Map of distinct locations associated with observations in the Fine-Root Ecology Database (FRED). Shown are the locations of studies collecting root trait observations for plants growing outdoors, not in pots (closed blue circles, 979 distinct locations) and the location of studies collecting root trait observations from plants growing in pots, outdoors or indoors, or from plants growing indoors in hydroponic systems or mesocosms (open blue circles, 54 distinct locations). Only c. 60% of the root samples in FRED were associated with georeferenced locations; some locations were estimated from the specified location of the study for the purposes of this figure.

These are only a few of the many ways in which the root trait observations in FRED can be organized for comparison. We have compiled this information in a ‘tips for using FRED’ section on the website (<http://roots.ornl.gov/tips>), and we will continue to add to this section with input from the user community.

Data collection is ongoing and will continue for the foreseeable future. We are continuing to make our way through the fine-root trait literature, including classic papers (e.g. Kramer, 1969) and the agronomic literature (e.g. Lynch, 2007), and anticipate annual releases of updated versions of FRED. We recognize that a considerable number of discrete trait datasets still reside with individual researchers, and we encourage the community to notify us of works that have not yet been incorporated. As a first step, we provide a continually updating list of data sources that have been incorporated into FRED at <http://roots.ornl.gov/data-sources>. Researchers can contribute past and future datasets to FRED by contacting the curators at <http://roots.ornl.gov/contact>, or by uploading a data source or data file at <http://roots.ornl.gov/upload>. However, we are only soliciting data that the contributors are willing to make freely available to the broader scientific community with unrestricted access. These data may include more detail on published data (e.g. data from individual replicates rather than the published mean), or data that have never been included in a publication (or are not freely available through a published work).

Version 1 of FRED (FRED 1.0) is available to the broader scientific community with unrestricted access through Oak Ridge National Laboratory at <http://roots.ornl.gov>. This website serves as a point of contact for the community to provide input or additional sources of data, and will also be used for communication, updates, and defining metadata standards.

Engaging the broader community of root and rhizosphere ecologists

FRED seeks to actively expand and engage with other efforts developed in parallel. Several other root trait databases were developed simultaneously to the FRED initiative; these databases targeted a subset of fine-root functional traits to answer questions related to trait–trait tradeoffs, phylogeny, and plant strategies. These include the Rhizopolis database (G. Freschet and C. Roumet), the Kent database (O. Valverde-Barrantes and C. Blackwood), the Alpine Roots Database (V. Onipchenko, N. Soudzilovskaia and J. H. C. Cornelissen), and the Leiden Database (P. van Bodegom and J. E. Jenner) (see Notes S2 for more details on these databases). We envision FRED as a common repository for these and other fine-root trait data and associated ancillary data. Hence, the publicly available data from these databases are available in FRED 1.0.

Interfacing with the TRY plant trait database

The FRED database will be submitted annually to TRY – the global database of plant traits (www.try-db.org/) – under the ‘public (open access)’ data status; each version of FRED will also be archived and available at <http://roots.ornl.gov>. FRED will continue to be curated separately from TRY, as we feel that the definition of root traits and the curation of root trait data by domain experts – root and rhizosphere ecologists – will result in substantially higher data quality compared with trait definition and curation by general trait experts with no specific background in root ecology. For example, several data streams in FRED were flagged and revisited according to methodology, units, or values that were outside the norm of the

Table 1 Root traits and observation counts for species-specific and community-level trait observations in Fine-Root Ecology Database (FRED) 1.0 grouped by trait similarity, where data with 100 or more observations are highlighted in blue

Trait category	Trait type	Trait grouping	No. of traits	Species-specific trait observations	Community-level trait observations	
Anatomy	Aerenchyma	Root aerenchyma presence	1	12	0	
		Root aerenchyma fraction	2	16	0	
	Cortex	Root cortex thickness	1	188	6	
		Hypodermis	Root exodermal wall thickness	1	27	0
	Root passage number		2	54	0	
	Internal mycological structures	Root length fraction that contains arbuscules	1	0	4	
		Root length fraction that contains vesicles	1	0	4	
	Stele	Root stele diameter	1	171	10	
		Root stele ratio	2	187	0	
	Vessels or tracheids	Root cross-sectional fraction of stele area to root area	1	38	0	
		Root vessel or tracheid density	3	158	0	
		Root vessel or tracheid diameter	4	174	0	
		Root vessel or tracheid wall thickness	5	40	0	
		Architecture	Topology	Root branching architecture	1	232
Root branching intensity	3			572	14	
Root external path length	1		4	0		
Root fractal dimension	1		34	0		
Specific root forks density (SRFD)	1		3	9		
Root links	3		46	0		
Root tips	7		219	13		
Root topological index	1		4	0		
Chemistry	Cellulose		Root cellulose and hemicellulose content	5	188	26
			Construction cost	1	27	0
	Macronutrients		Root macronutrients	11	5432	1634
	Micronutrients		Root micronutrients	22	663	323
	Secondary compounds		Root secondary compounds	37	1220	116
Stoichiometry	Root carbon : nitrogen ratio		1	1072	209	
	Other root stoichiometry	10	179	13		
Total nonstructural carbohydrates	Root total nonstructural carbon content	3	390	26		
	Dynamics	Decomposition	Root decomposition rate	6	867	491
Root nitrogen immobilization during decomposition			1	4	0	
Root nitrogen remaining after decomposition			1	480	96	
Lifespan		Root life span	10	925	207	
		Mortality	Root biomass, length, and number mortality rates	10	810	262
Growth			Root biomass, carbon, length, number, and surface area production rates	23	1345	1703
		Relative root growth rate	1	60	0	
Root production amplitude		2	0	52		
Root recovery from pruning		4	81	9		
Proportion of peak root production		1	126	0		
Turnover		Root mass turnover rate	5	491	403	
		Root nutrient turnover rate	2	10	0	
Microbial associations		Mycorrhizal fungi	Mycorrhizal type	1	2426	239
			Mycorrhizal colonization	5	413	78
	Mycorrhizal foraging strategy		4	48	0	
	Arbuscular mycorrhizal colonization		1	50	10	
	Arbuscular mycorrhizal hyphal length per unit soil		1	0	31	
	Arbuscular mycorrhizal spore number per unit soil		1	0	6	
	Ectomycorrhizal colonization		1	0	4	
	Ectomycorrhizal biomass per unit soil	1	12	0		
	Nitrogen fixers	Nodule dry mass per living root mass	1	3	0	
		Nodule dry mass per dead root mass	1	2	0	
	Other rhizosphere microbes	Fungal hyphae percent colonization	1	0	4	
		Bacterial amount in root	2	30	5	
		Fungal amount in root	2	30	5	
		Fungal : bacterial ratio in root	2	39	1	
Microbial carbon and nitrogen in root		2	28	5		
Fungal amount in soil		2	33	6		
Mycoheterotrophy		1	1	2		
Morphology	Diameter	Root diameter	1	2674	234	
		Dry matter content	1	104	0	
	Color	Root color (white or brown)	1	10	0	
	Hairs	Root hair diameter	1	25	0	

Table 1 (Continued)

Trait category	Trait type	Trait grouping	No. of traits	Species-specific trait observations	Community-level trait observations
		Root hair incidence	2	25	62
		Root hair length	1	65	62
		Root hair cylinder volume	1	28	0
	Length	Root length	1	849	33
	Tissue density	Root tissue density	1	1620	71
	Specific root length	Specific root area	1	471	52
		Specific root length	1	2861	200
Physiology	Exudation	Root exudation	2	12	0
		Root acid phosphatase and phosphatase activity and rate	3	176	3
	Nutrient uptake	Root calcium, magnesium, nitrogen, phosphorus, and potassium turnover	5	22	12
		Root nitrogen uptake	5	228	81
		Root nitrogen uptake preference (NH ₄ -N, NO ₃ -N, organic N)	1	35	2
		Root phosphorus uptake	4	56	0
		Root potassium uptake	1	15	0
		Root rubidium uptake	2	38	0
	Respiration	Root respiration rate	4	556	227
	Water uptake	Root hydraulic conductivity	1	140	0
		Root water uptake	4	388	0
Root system	Allocation within plant	Above-ground : below-ground net primary production ratio	1	95	47
		Fine root : leaf mass and production ratios	2	1803	109
		Root mass fraction	1	5263	116
		Root : shoot biomass ratio	2	588	170
	Allocation within root system	Coarse root : fine root mass ratio	1	1608	37
		Root mass, length, surface area, and tip fraction per root diameter class or root order class	7	835	57
		Root necromass : biomass ratio	1	231	477
		Root species abundance (fraction of root dry mass by species)	1	33	18
	Standing crop	Root length ratio (root length per plant dry mass)	1	56	0
		Root carbon, biomass, necromass, length, surface area, and volume standing crop	19	9201	8890
		Root nutrient standing crop	2	132	335
		Rooting depth	7	190	2871

For the purposes of brevity, we have combined the observations from multiple root traits into groupings based on similarity, where 'No. of traits' refers to the number of root traits grouped for the purposes of this table. For example, the 'root tips' grouping includes the similar traits: root standing crop by tips, root tips per ground area, root tips per root mass, root tips per plant, root tips per soil volume, root tips per root branch, and specific root tip abundance. Each observation in FRED is based on a single trait measurement made by an investigator on fine roots taken from a defined species or plant community at a specific location, date, and time. Many observations are plot or treatment means, and we include measures of variation and sample size where available (though the observation numbers for the measures of variation and sample size are not included in the observation counts presented here). In some cases, multiple trait observations were taken from one collection of roots, but no sample had observations of all root traits (most samples were associated with one or a few traits). The observations have been collected on roots of plants growing in the field, or in hydroponic solution, pots, soil bins, or growth chambers, and collected using methodology ranging from minirhizotrons and rhizotrons to soil excavation and ingrowth cores, to ground penetrating radar, and were taken from experimental treatments as well as along observational gradients. Trait observations made on samples collected from mixed-plant communities (i.e. community-level trait measurements) tended to be made using techniques such as soil coring and minirhizotrons that make it difficult to differentiate individual species. The 317 root trait observations currently housed in FRED 1.0 (and the multitude of ways in which they have been measured) are described in more detail at <http://roots.ornl.gov/data-inventory>.

The individual list of traits in the large 'chemistry' categories are as follows: cellulose traits include root cellulose percentage, root hemicellulose percentage, and root total cellulose and hemicellulose percentages; macronutrient traits include the content per root dry mass, per root carbon, per root fresh mass, per root length, or per the ground area or soil mass of root calcium, carbon, magnesium, nitrogen, phosphorus, potassium, or sulfur; micronutrient traits include the content per root dry mass, per root carbon, per root fresh mass, per root length, or per the ground area or soil mass of root aluminum, arsenic, boron, cadmium, chlorine, chromium, copper, iron, lead, manganese, nickel, silicon, sodium, and zinc; secondary compound traits include the content per root dry mass or per root carbon of root acid hydrolyzable extractives, root nonhydrolyzable in acid extractives, root alkyl carbon, as well as root arabinans, aromatic carbon, ash, root dry mass soluble in ethanol, as well as root galactans, lignin, lignin monophenols, lipids, mannans, root dry mass soluble in neutral solution, root dry mass soluble in nonpolar extractives, as well as root O-alkyl carbon, 12 phenol content, phenols, cinnamyl phenols, free phenols, lignin phenol vegetation index, p-hydroxy phenols, root-bound phenols, root dry mass soluble in polar extractives, as well as root polyphenols, rhamnans, structural carbon, syringyl phenols, vanillyl phenols, water and ethanol-soluble compounds, water-soluble compounds, water-soluble sugars, water-soluble phenols, and xylans; stoichiometry traits include number of acid groups to number of aldehyde groups in syringyl phenols, number of acid groups to number of aldehyde groups in vanillyl phenols, root dihydroxybenzoic acid groups : vanillyl phenols ratio, root nonacid hydrolyzable compounds : mass of nitrogen ratio, root cinnamyl phenol : vanillyl phenol ratio, root lignin : nitrogen ratio, root organic nitrogen : total nitrogen ratio, root polyphenol : nitrogen ratio, root syringyl phenol : vanillyl phenol ratio, and root vanillyl phenol : lignin phenol ratio.

root ecology literature. Also, the association of fine-root trait data with root orders or functional classes was a priority of the FRED curation team.

Version 0 of FRED (FRED 0.0) has been submitted to TRY and will become available with the release of TRY 4.0. Integration of FRED with TRY trait definitions and explicit naming conventions is ongoing; traits defined by root ecologists in the context of FRED and interfaced with TRY will represent fine-root traits in the context of the Thesaurus of Plant Characteristics (TOP, <http://top-thesaurus.org/>), which provides a consolidated terminological resource for ecology and evolution (Garnier *et al.*, 2017). FRED 0.0 is among the major contributions of trait data to TRY, adding *c.* 250 new root traits to TRY and roughly doubling the number of root records compared with TRY version 3.0 (Fig. S1). However, the number of records for frequently measured and important fine-root traits, for example root N content per dry mass or specific root length (2500 and 2100 records, respectively, in FRED 0.0), are at least an order of magnitude lower than the numbers of records for similar traits of other plant organs, for example leaf N content per dry mass and specific leaf area (65 000 and 137 000 records, respectively, in TRY 3.0), emphasizing the need for continued and targeted efforts to sample fine-root traits across the globe.

Leveraging global root trait data to advance root ecology

In recent decades, the broader community of root and rhizosphere ecologists has pinpointed a number of unanswered questions in below-ground ecology (Bardgett *et al.*, 2014; Reich, 2014; McCormack *et al.*, 2015b; Weemstra *et al.*, 2016). Below we use some of the data compiled in FRED 1.0 to illustrate how a centralized, global fine-root trait database can be used to inform our understanding of four current questions in below-ground ecology: do root traits vary within and among plant functional types; is there a common root- or plant-trait framework describing the variation and covariation in root, leaf, and wood traits; how do root traits vary along environmental gradients; and how should root traits be represented in terrestrial biosphere models?

Do root traits vary within and among plant functional types?

Plant functional types have long been used to aggregate plant species into groups with similar traits (Wullschlegel *et al.*, 2014; Verheijen *et al.*, 2016). However, PFTs have traditionally been grouped according to above-ground traits (e.g. woodiness, differing photosynthetic pathways, leaf type and phenology) and assigned static trait values. These static parameterizations do not represent trait variation within a PFT, or the response of traits to changing environmental conditions, although this understanding is necessary to accurately project the distribution of vegetation and ecosystem processes across the globe (Kattge *et al.*, 2011; van Bodegom *et al.*, 2014).

To illustrate the variation in below-ground traits within- and among traditionally defined PFTs, we examined the variation in one commonly measured fine-root trait – the C : N ratio – for observations of fine roots < 2 mm in diameter (Fig. 2). To

approximate model representations of PFTs (Sargsyan *et al.*, 2014; Verheijen *et al.*, 2015), species in FRED were classified into woody or nonwoody growth forms, broadleaf or needleleaf leaf types, and evergreen or deciduous leaf phenology according to the TRY classification scheme (Kattge *et al.*, 2012). The sampling locations associated with each data point in FRED were overlain on the Köppen–Geiger climate classification map (Kottek *et al.*, 2006) to determine the climate classification, and were then aggregated into tropical, temperate, boreal, and polar biomes according to Poulter *et al.* (2011).

A nonparametric Kruskal–Wallis test indicated that fine-root C : N ratio varied significantly among PFTs (Fig. 2; $P < 0.0001$); woody, broadleaf PFTs (both evergreen and deciduous) from the temperate biome tended to have a lower C : N ratio than the woody, needleleaf PFT from the same biome, as well as nearly all graminoids (Fig. 2; $P < 0.05$ in pairwise comparisons of PFTs with more than two observations; SAS Version 9.2; SAS Institute Inc., Cary, NC, USA). Strikingly, the variation in fine-root C : N ratio within a PFT was greater than the variation among PFTs (Fig. 2). This is consistent with the distribution of variance for several leaf traits (Kattge *et al.*, 2011) and probably reflects species-specific differences and environmental gradients that are not captured by the given aggregations of plant species to PFTs.

The hierarchy of root branching orders, from distal first-order fine roots to more proximal higher-order fine roots, and associated changes in root anatomy, chemistry, morphology, and mycorrhizal association provides another layer of variation that is not often considered in the interpretation of trait patterns for the entire pool of fine roots < 2 mm in diameter. Strikingly, we found that the wide variation in fine-root C : N ratio within a PFT could be spanned by the increase in C : N from first-order roots to fourth-order roots within *one* representative species in a PFT (Fig. 2). Thus the pool of fine roots sampled (e.g. the relative proportion of first- vs fourth order roots) for a given trait can strongly bias the average trait value for a species or a PFT. Furthermore, changes in C : N within a species and root order across environmental gradients or experimental treatments (i.e. multiple symbols for each root order within a PFT in Fig. 2) illustrate the importance of adaptation or phenotypic plasticity in determining fine-root responses to environmental changes (e.g. Larson & Funk, 2016; Zadworny *et al.*, 2016), and it will be important to consider intraspecific trait variation in any future root trait framework.

To facilitate advances in comparative root ecology at a global scale and ensure meaningful comparisons among species and PFTs, we recommend that future research campaigns sample roots based on their position in the root branching hierarchy (i.e. by root order or functional class; Pregitzer *et al.*, 2002; McCormack *et al.*, 2015b), rather than based solely on a standard diameter cutoff. However, we recognize that this is not always feasible, depending on the root trait of interest. Furthermore, root trait research is built on a strong foundation of historical data that have been collected based on diameter classes and cutoffs (e.g. all roots < 2 mm have traditionally been pooled and considered ‘fine’), and root diameter is itself an important root trait associated with nearly every observation in FRED. The field of root ecology will benefit from robust solutions to compare newly collected information on root

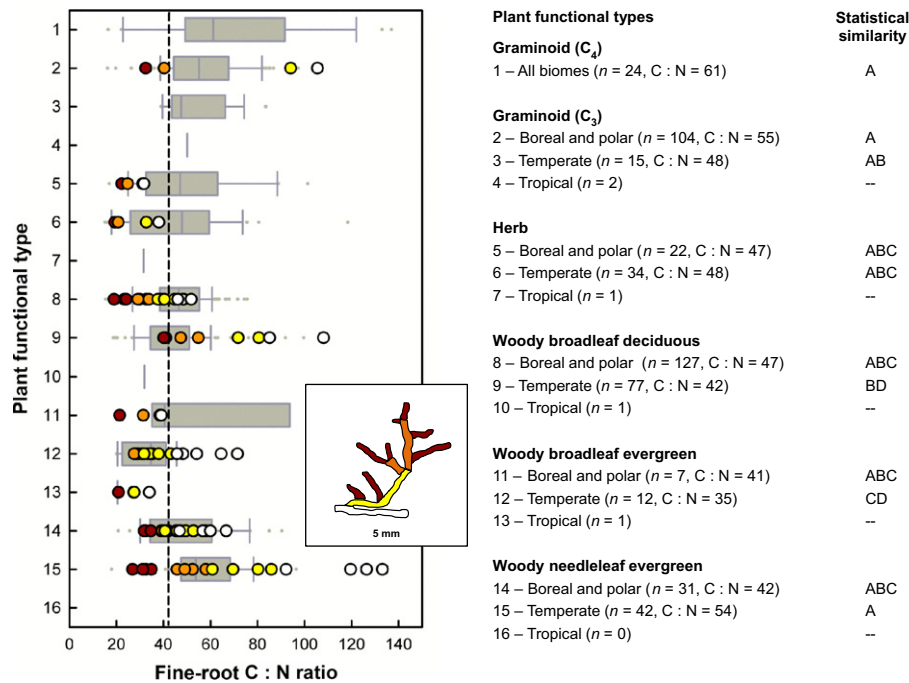


Fig. 2 The carbon to nitrogen ratio (C : N in $g\ g^{-1}$) of fine roots < 2 mm in diameter (gray box plots) and of individual root orders (circles) varied within and among 16 plant functional types (PFTs). The box plots (gray bars) include observations of fine-root populations (all roots < 2 mm) from plants growing *in situ* (i.e. not in pots), outside. We excluded fine roots specified as dead in the original data source (see Supporting Information Notes S3 for data sources). The lines shown on the box plots are the median, 25th and 75th percentiles, with whiskers at the 10th and 90th percentiles, and outliers as closed symbols; the reported values associated with each PFT are the median of the C : N ratio for all fine roots within a PFT, where *n* = the number of records. There were manifold more fine-root N records than C records, and where fine-root C and N were not both reported by a data source, but root N concentration was reported, we used the average C concentration within a PFT to determine the fine-root C : N ratio for these records. To approximate terrestrial biosphere model representation of PFTs, observations were classified into woody or nonwoody life forms, broadleaf or needleleaf leaf types (we included scale-shaped with needleleaf), and evergreen or deciduous leaf phenology according to the TRY classification scheme (Kattge *et al.*, 2012). Sampling locations were overlain on the Köppen–Geiger climate classification map (Kottek *et al.*, 2006) to determine the climate classification, and were then aggregated into tropical (Af, Am, Aw, and BSh), temperate (BWk, BSk, Csa, Csb, Csc, Cwa, Cwb, Cwc, Cfa, Cfb, Cfc), boreal (Dsa, Dsb, Dsc, Dsd, Dwa, Dwb, Dwc, Dwd, Dfa, Dfb, Dfc, Dfd), and polar (ET, EF, ETH, EFH) biomes according to Poulter *et al.* (2011). There were few observations from polar biomes that fitted our criteria, so plant growth forms from the polar biome were combined with similar growth forms in the boreal biome for the purposes of this figure. PFTs with similar uppercase letters indicate that the fine-root C : N ratio was statistically similar at $P < 0.05$. A dashed line is shown at 42; this is the single parameter for fine-root C : N ratio across all PFTs in the commonly used Community Land Model (Sargsyan *et al.*, 2014). Overlain on top of the box plots are measurements of fine roots sampled across individual root orders for one representative species within a PFT (red, orange, yellow, and white circles signify the C : N ratio of individual fine-root orders one through four, respectively, ordered hierarchically as in the inset diagram; used with permission from Pregitzer *et al.* (2002) and recolored to indicate root orders one through four). The one species used as a representative of the individual PFTs were: *Elymus hordae* (Kitag.) S.L.Chen (PFT 2), *Geum alleppicum* Jacq. (PFT 5), *Apocynum venetum* L. (PFT 6), *Quercus robur* L. (PFT 8), *Alnus formosana* (Burkill) Makino (PFT 9), *Vaccinium corymbosum* L. (PFT 11), *Ardisia quinquegona* Blume (PFT 12), *Elaeocarpus sylvestris* (Lour.) Poir. (PFT 13), *Pinus sylvestris* L. (PFT 14), and *Pinus palustris* Mill. (PFT 15). Multiple observations within a root order class were made in some cases (see Notes S4 for data sources).

orders with the treasure trove of historical and ongoing data collection based on diameter cutoffs (McCormack *et al.*, 2015b).

Is there a common root- or plant-trait framework describing the variation and covariation in root, leaf, and wood traits?

Theory predicts that root traits and trait tradeoffs, in a manner analogous to leaves, fall along a gradient from acquisitive to conservative strategies (i.e. the root economics spectrum (RES); Weemstra *et al.*, 2016). However, evidence for an RES is weak, perhaps in part because the RES has only been tested for < 100 species (Roumet *et al.*, 2016), while the leaf economics spectrum (LES) has been tested against > 10 000 species (Wright *et al.*, 2004). Also, comparison of the RES and LES is complicated by the difficulty of understanding the relevant unit for comparison – for

example, first-order roots may be most analogous to leaves as a resource-acquiring organ, while higher-order roots may have a function similar to that of twigs (McCormack *et al.*, 2015b). Furthermore, the RES may be multidimensional, requiring a more diverse sampling of root traits and environmental conditions (Weemstra *et al.*, 2016). The identification of central dimensions of an RES and other independent axes of variation would represent a substantial advance to the field of below-ground ecology.

The evaluation of an RES can take advantage of FRED's capacity to differentiate among root orders and to examine multiple root traits and trait tradeoffs simultaneously. For example, a decline in fine-root N concentration with increasing root order (and root diameter) may indicate an important dimension within an RES, reflecting tradeoffs in root construction cost, life span, and maintenance respiration (Pregitzer *et al.*, 1997), the balance of

which determines the below-ground strategy of a given plant species. As an illustration, we examined the relationship among observations of root N concentration, root order, and root diameter compiled in FRED 1.0. For the purposes of this illustration, we chose observations from woody plants growing *in situ* outside, across all treatments, biomes and leaf types, where roots were ordered according to the morphometric (centripetal) classification scheme (Fig. 3). On average (indicated by the box plots on the x - and y -axes), fine-root diameter increased and fine-root N concentration declined as root order increased. However, there was substantial unexplained variation in fine-root N concentration within fine-root orders and across fine-root diameter classes (Fig. 3) that merits further investigation.

There is growing evidence that the spectrum of fine-root strategies is only partly correlated with that of leaves (Freschet *et al.*, 2010; Reich, 2014; Valverde-Barrantes *et al.*, 2015). FRED 0.0 has been integrated with the TRY plant trait database, allowing for better quantification of relationships or tradeoffs between and among above- and below-ground traits (Liu *et al.*, 2010; McCormack *et al.*, 2012; Kong *et al.*, 2014). This integration could help to identify either linkages or explicit decoupling of root and leaf responses in the context of a whole-plant economics spectrum (Reich, 2014; Weemstra *et al.*, 2016).

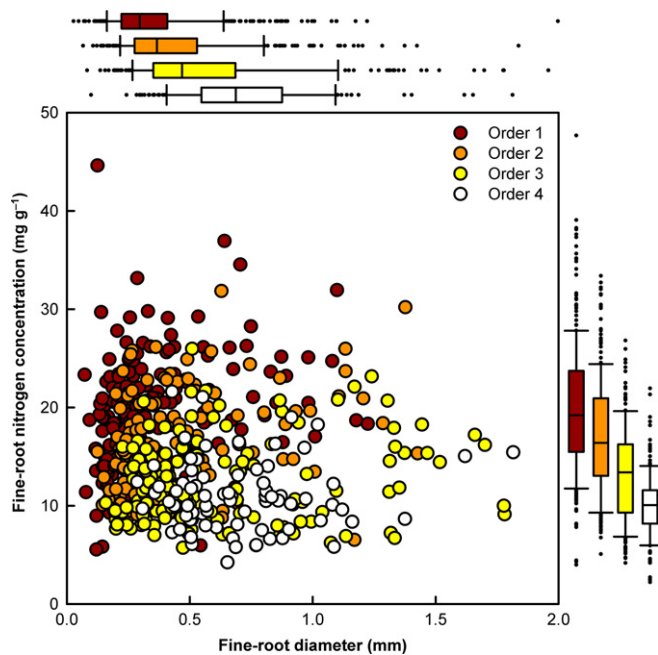


Fig. 3 Within a species, fine-root nitrogen (N) concentration tends to decline with increasing root diameter and root order, but was highly variable within an order and diameter class among species and across environmental conditions for the data compiled in the Fine-Root Ecology Database (FRED). For the purposes of this figure, we included fine roots < 2 mm that were sampled from woody plants growing *in situ* outside, across all treatments, biomes and leaf types, and that had been sampled by order using the morphometric (centripetal) classification scheme. We excluded fine roots specified as dead (see Supporting Information Notes S5 for data sources). The box plots shown for the x - and y -axis indicate the increase in fine-root diameter and decline in fine-root N concentration as order increases; shown are the median, 25th and 75th percentiles, with whiskers at the 10th and 90th percentiles, and outliers are closed symbols for each root order class.

How do root traits vary along environmental gradients?

Relatively few hypotheses have been formulated to explain patterns in fine-root trait variation along large climatic, environmental, and biogeographical gradients. Some of the mechanisms proposed include phylogenetically constrained evolution of fine-root traits (Chen *et al.*, 2013), phenotypic plasticity or adaptation in fine-root responses to environmental change (Larson & Funk, 2016; Zadworny *et al.*, 2016), global patterns in mycorrhizal affiliations and colonization (Soudzilovskaia *et al.*, 2015), and coevolution of above- and below-ground traits to reflect broad ecological strategies at the whole-plant level (the plant economics spectrum; Freschet *et al.*, 2010). These hypotheses can be tested against the data compiled in FRED 1.0, which holds root trait information from > 1200 species spanning environmental gradients across the globe. Furthermore, the site-specific edaphic and climatic data compiled in FRED (e.g. soil texture and biogeochemistry, mean annual temperature and precipitation) can facilitate the development or benchmarking of trait–environment relationships and global trait maps (van Bodegom *et al.*, 2014). In turn, the above-ground biomass and community composition data compiled in FRED allow for the scaling from root traits of individual species to community traits that strongly determine different ecosystem properties and services (Lavorel & Grigulis, 2012). Lastly, the joint use of fine-root and mycorrhizal databases may provide unique opportunities for global quantitative estimations of mycorrhizal abundance in soils and fine roots, as well as the opportunity to develop model and empirical linkages among fine-root and mycorrhizal traits (Soudzilovskaia *et al.*, 2015).

How should root traits be represented in terrestrial biosphere models?

The lack of resolution in our conceptual understanding and parameterization of fine-root processes in large-scale models has implications for projections of ecosystem C, water, and nutrient fluxes under changing environmental conditions (Matamala & Stover, 2013; Warren *et al.*, 2015). For example, model sensitivity or uncertainty analyses indicate that processes ranging from gross primary production to leaf area index, vegetation N content, and soil C storage are sensitive to variation in fine-root traits, including the relative allocation of biomass to fine roots, fine-root life span and turnover, fine-root C:N ratio, and the maximum rate of fine-root N uptake per unit root mass (Zaehle & Friend, 2010; Sargsyan *et al.*, 2014; McCormack *et al.*, 2015a). However, a lack of comprehensive root trait data has made it difficult to accurately parameterize these processes in models. Moreover, other critical processes related to fine-root function and ecosystem feedbacks, including mycorrhizal association and plant–microbe interactions in the rhizosphere, are rarely explicitly represented in models (Warren *et al.*, 2015; Treseder, 2016), in part because data are scarce.

Coarse representation or parameterization of fine-root processes in current terrestrial biosphere models can be improved by harnessing the information contained in FRED. For example, the order-specific fine-root C:N data incorporated thus far into

FRED 1.0 (closed circles in Fig. 2) provide compelling evidence that an explicit representation of two distinct fine-root pools in terrestrial biosphere models could better capture differences in the chemistry and function of distal ‘absorptive’ fine roots compared with more proximal fine roots, whose function is mainly transport (McCormack *et al.*, 2015b). Also, while the median fine-root C : N ratio for most PFTs in FRED 1.0 falls near 42 (dashed line in Fig. 2), a parameter used to represent the fine-root C : N ratio for all PFTs in a commonly used terrestrial biosphere model (Sargsyan *et al.*, 2014), one fixed parameter value cannot capture the wide variation in fine-root C : N ratio within and among PFTs across the globe. Rather, this variation may be better captured by the next generation of global modeling efforts, which are moving beyond fixed parameter estimates for plant traits to embrace trait tradeoffs and relationships between traits and the environment (van Bodegom *et al.*, 2014; Koven *et al.*, 2016).

Filling gaps in our measurements and understanding of root traits

The collection of root trait data into a centralized framework, FRED, allows for an objective characterization of gaps in our understanding of root traits and associated ecosystem processes. A common characteristic for all databases is that not all traits, plant functional types, and biomes are equally represented. Indeed, the distribution of observations across the traits in FRED is uneven, showing a long tail with a low number of observations per trait, typical of biodiversity data (see the example from FRED 0.0 in Fig. S1); 96% of the root traits in FRED 1.0 have <1000 observations, and 71% have <100 observations (e.g. Table 1). Furthermore, certain regions of the world are underrepresented, including South America, Africa, Asia, and Australia (Fig. 1). Specifically, data are lacking from tropical and polar biomes, where even commonly measured fine-root traits – such as the root C : N ratio – are underrepresented in FRED (Fig. 2). This is particularly unsettling given the enormous biodiversity in the tropics, and presents significant challenges to root and whole-plant trait research, where data scarcity precludes accurate determination of trait–trait relationships across two or more traits, identification of meaningful linkages between root traits and root and plant function, and the quantification of intra- and interspecific trait variation among species and across environmental conditions (Violle *et al.*, 2014; Siefert *et al.*, 2015).

In order to fill the gaps in FRED trait observations, more species-specific measurements are needed, especially observations from underrepresented regions that span root traits in multiple categories on a single plant or species, including anatomy, morphology, physiology, and microbial associations (Weemstra *et al.*, 2016). Much of the root trait data in FRED have been measured on mixed plant communities, and on root system traits such as fine-root standing crop rather than traits that are likely to be closely related to root function. While root system traits are critical for scaling to the ecosystem level, we are lacking fundamental data on root resource acquisition, respiration, and life span needed to robustly link root form with function and introduce better representations of root function in terrestrial biosphere models (Warren *et al.*, 2015).

Furthermore, we have limited data on the root traits that influence the formation and stabilization of soil aggregates and the cycling of nutrients in the soil (e.g. root hair incidence and morphology, root exudation rates, and root dependence on mycorrhizal fungi associations; Bardgett *et al.*, 2014). Lastly, the field of molecular biology is continuing to advance our understanding of the links among the expression of root traits and their molecular underpinnings (Lynch, 2007; Ghosh & Xu, 2014), and molecular-based root traits should be included in global root trait analyses as frameworks are developed to incorporate them more directly (Rivas-Ubach *et al.*, 2012).

FRED also highlights gaps in the standardization of root trait measurements across datasets. For example, even the relatively standard fine-root traits compiled by FRED have been measured in a number of different ways; this is particularly striking for root production and mortality, which have been measured using root screens, soil cores and ingrowth cores, minirhizotrons and rhizotrons, and variably quantified as fine-root biomass, length, number, or surface area changes over time periods ranging from days to years. A systematic update of the terminology and measurements used for fine-root traits, including what defines a ‘unique’ trait (Bohm, 1979; Sutton & Tinus, 1983; Perez-Harguindeguy *et al.*, 2013; Garnier *et al.*, 2017), can improve comparisons across root orders, species, and biomes and also reduce common problems with how the data are interpreted and used by modelers.

Targeted field campaigns that allow for a more complete coverage of root functional traits, especially in currently underrepresented regions of the globe, as well as more standardized measurements and trait definitions, will facilitate ongoing research efforts aiming to capture changes in fine-root traits across broad environmental gradients and over time, and how these patterns may affect ecosystem processes (Chen *et al.*, 2013; Li *et al.*, 2015). For example, Kong *et al.* (2014) examined the interspecific variation in 14 root traits across 96 tree species in understudied subtropical China, focusing solely on first-order roots to facilitate meaningful trait comparisons. In turn, Zadworny *et al.* (2016) examined the intraspecific variation in seven root traits across multiple root orders within a single tree species along an environmental gradient in Europe. Similar campaigns focusing on other important PFTs have been undertaken in other regions of the globe (Roumet *et al.*, 2016) and more should be considered. In addition, these extensive field campaigns should be combined with intensive, mechanistic measurements of the linkages between these commonly measured root traits and their function (Jackson *et al.*, 1990).

Conclusions

We have compiled a centralized fine-root trait database to provide a tool with which researchers can better access, understand, and interpret the variation in root traits observed worldwide. FRED represents a critical step towards quantifying variation in fine-root traits within the root branching hierarchy, as well as across species, biomes, and environmental gradients, while also building a platform for future assessments of tradeoffs among root, leaf, and wood traits, and their role in ecosystem functioning. Continued

engagement of the broader root and rhizosphere community with terrestrial biosphere models, as well as targeted campaigns that focus on a broader sampling of root functional traits across underrepresented species, functional types, or biomes, will facilitate rapid advances in our understanding and prediction of fine-root trait variation across the globe.

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Author contributions

C.M.I., M.L.M., A.S.P., and D.B.S. conceptualized FRED. A.S.P. harvested data for FRED. C.M.I., M.L.M., A.S.P., C.B.B., G.T.F., J.K., C.R., D.B.S., N.A.S., O.J.V.-B., P.M.v.B., and C.V. discussed and wrote the manuscript.

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Supporting Information

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

Fig. S1 Comparison of root trait observations in FRED 0.0 with TRY 3.0.

Table S1 Ancillary data observations in FRED

Notes S1 Previously compiled databases that include root traits related to particular questions or certain regions of the world.

Notes S2 Other recently compiled root trait databases that have targeted a subset of fine-root functional traits.

Notes S3 Data sources for Fig. 2: variation in the C : N ratio of fine roots within and among plant functional types.

Notes S4 Data sources for Fig. 2: root order-specific C : N ratios.

Notes S5 Data sources for Fig. 3: variation in fine-root N concentration with root diameter and root order.

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Key words: database, fine roots, Fine-Root Ecology Database (FRED), functional traits, terrestrial biosphere models.



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