Tansley insight

Below-ground frontiers in trait-based plant ecology

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Summary

Trait-based approaches have led to significant advances in plant ecology, but are currently biased toward above-ground traits. It is becoming clear that a stronger emphasis on below-ground traits is needed to better predict future changes in plant biodiversity and their consequences for ecosystem functioning. Here I propose six 'below-ground frontiers' in trait-based plant ecology, with an emphasis on traits governing soil nutrient acquisition: redefining fine roots; quantifying root trait dimensionality; integrating mycorrhizas; broadening the suite of root traits; determining linkages between root traits and abiotic and biotic factors; and understanding ecosystem-level consequences of root traits. Focusing research efforts along these frontiers should help to fulfil the promise of trait-based ecology: enhanced predictive capacity across ecological scales.

I. The promise of trait-based plant ecology

Trait-based ecology emphasizes functional traits of organisms over their taxonomical relationships to describe and understand ecological patterns. The rapidly growing popularity of this approach lies in its promise of improved predictive capacity across ecological scales (Shipley *et al.*, 2016). To achieve this, trait-based ecology relies on trait data measured across many individuals and species to predict emergent properties of communities and ecosystems. This led to the development of global trait databases collected using standardized protocols, particularly for plants (e.g. Kattge *et al.*, 2011). However, much of trait-based plant ecology focuses on above-ground traits (Fig. 1), while it is becoming clear that a stronger emphasis needs to be placed on below-ground traits (Bardgett *et al.*, 2014). Here, I review recent advances in below-ground trait-based plant ecology and propose six research frontiers (Table 1; Fig. 2), focusing on traits that influence soil nutrient acquisition.

II. Redefining fine roots

Fine roots, like leaves, are primary resource-acquisition organs. However, whereas leaves are narrowly defined, fine roots have traditionally been classified based on an arbitrary diameter cutoff
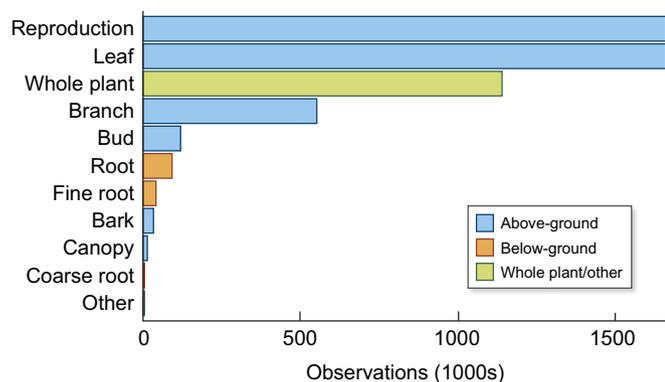
Fig. 1 Number of individual observations (in thousands) for different categories of plant traits available in the TRY database (Kattge *et al.*, 2011). Information was obtained from the TRY website (https://www.try-db.org) on 8 July 2016. All traits were first classified according to which plant parts or organs they are measured from (represented on the x-axis), then put into three broader categories: 'above-ground', 'below-ground' or 'whole plant/other' (represented by bars of different colours). Traits related to reproduction included traits measured on flowers, cones, seeds or spores, or traits related to dispersal and means of vegetative reproduction. 'Branch' included not only traits measured on branches, but also on stems and shoots. 'Whole plant' traits included traits not clearly linked to a particular organ or part (e.g. life form), or traits such as tolerance to certain environmental factors (e.g. frost tolerance). Root traits were classified as 'fine root' or 'coarse root' when this was explicitly specified, or 'root' otherwise.

(i.e. ≤ 2 mm diameter). This single-pool, diameter-based classification is problematic because trait data are obtained from roots of different orders, which have different properties and functions. For example, root traits influencing plant performance and biogeochemical processes (e.g. mycorrhizal colonization, root life span) can vary strongly and nonlinearly with increasing root order, reflecting a shift in function from resource absorption to transport (McCormack *et al.*, 2015). One solution is to adopt a functional classification whereby roots ≤ 2 mm in diameter are further separated into absorptive and transport roots on the basis of order, anatomy and morphology (McCormack *et al.*, 2015). This is promising because it speeds up measurement compared with a purely order-based approach (i.e. treating each order separately), while still ensuring meaningful comparisons across plant species (McCormack *et al.*, 2015). Adopting a standardized definition of fine roots is a critical first step for advancing trait-based plant ecology, and applies to all four major root trait categories (Bardgett *et al.*, 2014): morphological (e.g. specific root length), architectural (e.g. branching intensity), physiological (e.g. root exudation) and biotic (e.g. mycorrhizal colonization). Indeed, our ability to derive general principles about root trait variation among species through synthesis of empirical studies depends on standardized measurements being made on roots of comparable function.

III. Quantifying trait dimensionality

One major advance in comparative plant ecology has been the discovery that plant species do not fully occupy multidimensional trait space, because many traits are correlated (e.g. Díaz *et al.*, 2016). A persistent challenge in trait-based ecology is therefore to

measure the minimum number of traits that will maximize the number of independent dimensions represented (Laughlin, 2014). The seemingly low dimensionality in global trait variation (Díaz *et al.*, 2016) offers exciting opportunities for improving dynamic global vegetation models (van Bodegom *et al.*, 2014). However, this apparent simplicity might reflect the relatively low number of traits considered and the absence of root traits. In datasets containing many more traits, including root traits, the number of independent dimensions is often much higher, though it generally does not exceed six (Laughlin, 2014). Therefore, root traits could represent additional independent and ecologically important dimensions of plant functional variation (Bardgett *et al.*, 2014; Laughlin, 2014; Weemstra *et al.*, 2016).

It is still unclear whether variation in fine root traits among plant species is primarily one-dimensional, that is, whether species segregate along a single 'root economics spectrum' (Reich, 2014; de la Riva *et al.*, 2016; Roumet *et al.*, 2016). For example, a recent study proposed two leading dimensions of fine root trait variation: one representing variation in tissue density, and one representing variation in specific root length (SRL) and root diameter (Kramer-Walter *et al.*, 2016). By contrast, Kong *et al.* (2014) found diameter, SRL and tissue density to be correlated along one dimension, with a second orthogonal dimension representing root architecture (e.g. branching intensity). Another outstanding question is whether above- and below-ground traits are coordinated along a whole-plant economics spectrum (Reich, 2014). While some studies have found evidence for such a coordination for some traits (e.g. de la Riva *et al.*, 2016), the emerging perspective is that above-ground trait variation cannot be directly extrapolated to roots (Weemstra *et al.*, 2016). In particular, studies have found that leaf and root life span are uncorrelated (Weemstra *et al.*, 2016). This might reflect the fact that a universal adaptation to nutrient limitation is to reduce nutrient losses by increasing leaf life span, whereas fine root adaptations to increase absorptive area per unit mass (e.g. higher SRL) trade off against root life span (McCormack & Guo, 2014; Laliberté *et al.*, 2015). This illustrates the need for synthetic, global meta-analyses to derive general principles about root trait variation across a wide range of plant species and ecosystems. Because root trait variation among species often shows a phylogenetic signal, particularly for mycorrhizal associations (Brundrett, 2009), these future studies should consider phylogeny when quantifying trait correlations (Kong *et al.*, 2014; Kramer-Walter *et al.*, 2016).

IV. Integrating mycorrhizas

Over 80% of terrestrial plant species associate with mycorrhizal fungi to enhance nutrient acquisition, with arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) symbioses being the two most ecologically important types (Brundrett, 2009). In fact, mycorrhizas probably represent the dominant pathway for the acquisition of major growth-limiting nutrients in many natural ecosystems (Smith *et al.*, 2015). Therefore, an important research challenge is to better integrate mycorrhizas into trait-based plant ecology (Chagnon *et al.*, 2013; Comas *et al.*, 2014; McCormack *et al.*, 2015). While a useful first step is to classify plant species into

Table 1 Summary table highlighting the main problem, suggestions for future research, outstanding questions and key recent references for each of the six below-ground frontiers in trait-based plant ecology

Below-ground frontier	Problem	Suggestions	Outstanding questions	References
(1) Redefining fine roots	Trait data are collected on different root orders, complicating syntheses and cross-study comparisons	Separating fine roots $\leq 2\,mm$ diameter into two pools (absorptive and transport) before standardized trait measurement	Adopting a standardized definition of fine roots is a prerequisite for answering all the questions below	McCormack *et al.* (2015)
(2) Quantifying trait dimensionality	It is not clear whether a root economics spectrum exists and whether variation in above-ground traits is coordinated with that of root traits	Explore correlations among below- and above-ground traits across a wide range of plant species and ecosystems	What is/are the leading dimension(s) of root functional variation? Is variation in above-ground traits coordinated with that of root traits?	Kong *et al.* (2014); Kramer-Walter *et al.* (2016); Weemstra *et al.* (2016)
(3) Integrating mycorrhizas	Mycorrhizas are ubiquitous and can strongly influence plant performance but are not given enough consideration	Classify plant species into different mycorrhizal types; measure the degree of mycorrhizal root colonization; measure fungal traits directly	Do mycorrhizas represent independent dimensions of plant below-ground functional variation? Do correlations among root traits vary among mycorrhizal types?	Chagnon *et al.* (2013); Comas *et al.* (2014); McCormack *et al.* (2015); Weemstra *et al.* (2016)
(4) Broadening the suite of traits	Too few below-ground traits are typically measured	Consider physiological traits (e.g. root exudation, respiration); evaluate whether certain leaf traits can act as proxies for root functioning; measure root hair length and density	Is root morphology correlated with root physiology?	Hobbie & Högberg (2012); Lambers *et al.* (2015); Roumet *et al.* (2016); Weemstra *et al.* (2016)
(5) Determining trait–environment linkages	We have limited knowledge about below-ground trait variation across environmental gradients	Quantify shifts in below-ground traits (composition, diversity) across environmental gradients (e.g. retrogressive soil chronosequences)	Do trait patterns across gradients indicate different community assembly processes above or below ground? Which root traits explain shifts in plant species abundances across gradients? How do soil abiotic factors interact with soil biota to influence plant species and functional diversity?	Holdaway *et al.* (2011); Laliberté *et al.* (2015); Zemunik *et al.* (2015)
(6) Understanding ecosystem-level consequences	The importance of root and fungal traits for ecosystem functioning, particularly soil carbon (C) storage, is increasingly recognized but still not well understood	Determine which root and mycorrhizal fungal traits drive organic matter decomposition and soil aggregation	Does soil C cycling depend on mycorrhizal type? Can root and fungal traits help to predict soil C storage? How should root traits be incorporated into Earth system models?	Phillips *et al.* (2013); Bardgett *et al.* (2014); Rillig *et al.* (2015); Soudzilovskaia *et al.* (2015)

different mycorrhizal types (Pérez-Harguindeguy *et al.*, 2013; Zemunik *et al.*, 2015), such broad categories do not consider differences in mycorrhizal dependency among plant species, nor do they do justice to the large variation in fungal traits found within mycorrhizal types (Chagnon *et al.*, 2013; Tedersoo & Smith, 2013).

One way forward is to measure the degree of root colonization by mycorrhizal fungi directly using reliable, standardized protocols (Brundrett, 2009) and to treat colonization intensity as a continuous plant trait. While colonization is influenced by external factors such as nutrient availability, a recent study showed that interspecific variation in AM colonization was much higher (53%) than intraspecific variation (26%), supporting the usefulness of root colonization as a plant trait (Soudzilovskaia *et al.*, 2015). Studies on temperate tree species have shown that AM plants with lower root branching intensity, thicker roots and a large cortex support greater rates of AM fungal colonization (Comas *et al.*, 2014; Eissenstat *et al.*, 2015), suggesting stronger mycorrhizal dependency. Conversely, ECM plants maximize branching intensity to promote high fungal colonization of their root tips, showing that correlations between root traits and mycorrhizal colonization actually depend on mycorrhizal type (Comas *et al.*, 2014).

Another promising but more challenging approach is to compile databases of traits of mycorrhizal fungi measured under standard conditions (Chagnon *et al.*, 2013). For AM fungi, this will be facilitated by the fact that AM fungi are a relatively species-poor group, with many taxa being globally distributed (Davison *et al.*, 2015). Moreover, traits of AM fungi show high phylogenetic trait conservatism, such that assigning traits at the family level could be a reasonable first approximation (Chagnon *et al.*, 2013). For ECM
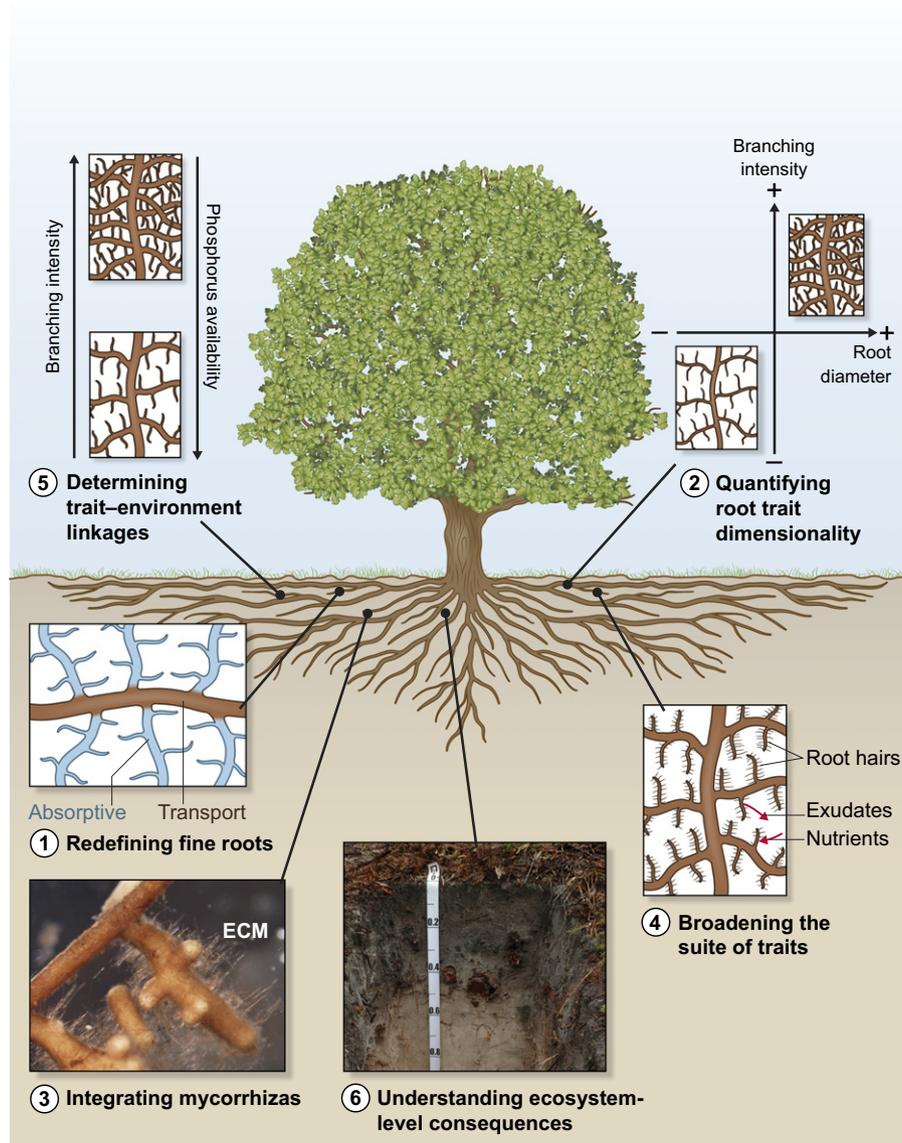
Fig. 2 Six below-ground research frontiers for advancing trait-based plant ecology: (1) redefining fine roots; (2) quantifying root trait dimensionality and determining the degree of coordination between below- and above-ground traits; (3) integrating mycorrhizas; (4) broadening the suite of root traits; (5) determining trait–environmental linkages; and (6) understanding ecosystem-level consequences. The photograph in (3) shows absorptive fine roots of *Fagus grandifolia* (Fagaceae) covered with an ectomycorrhizal (ECM) fungal mantle with emanating hyphae (photograph: Felipe Albornoz). The photo in (6) shows a soil profile from a forested site along a dune chronosequence in southwestern Australia, with a distinct upper horizon enriched with organic matter (photograph: Etienne Laliberté).

fungi, trait measurements will be more difficult given the higher diversity and polyphyletic origin of the group (Tedersoo & Smith, 2013). Nevertheless, data on ECM hyphal exploration types (Tedersoo & Smith, 2013) offer a useful first step given the functional importance of the external mycelium for soil resource acquisition. For example, in boreal forests, higher soil nitrogen availability favours ECM fungal species with short-range or contact exploration types (Sterkenburg *et al.*, 2015). Combining fungal trait measurements with next-generation sequencing, which allows description of entire mycorrhizal communities on plant roots, should allow us to evaluate the degree of covariation between root and mycorrhizal fungal traits (Chagnon *et al.*, 2013).

V. Broadening the suite of below-ground traits

The revised handbook for standardized plant trait measurement comprises over 20 leaf and stem traits but only three below-ground traits (Pérez-Harguindeguy *et al.*, 2013), highlighting the need for broadening the suite of below-ground traits. While in practice the number of root traits considered in empirical studies is generally larger (e.g. Kramer-Walter *et al.*, 2016; de la Riva *et al.*, 2016), morphological and chemical traits of fine roots are favoured, while physiological traits are rarely considered (Ushio *et al.*, 2015; Roumet *et al.*, 2016). This contrasts with leaf traits, for which analyses of trait variation have included physiological traits such as

photosynthetic capacity and dark respiration, thus allowing relationships between form and function to be directly evaluated (Weemstra *et al.*, 2016).

Recently, Roumet *et al.* (2016) showed that fine root respiration correlated positively with root nitrogen (N) concentration and SRL and negatively with root dry matter content, suggesting that chemical or morphological traits could be useful proxies for overall metabolic activity. Still, considering physiological traits that directly influence nutrient acquisition would be useful, given that nutrient limitation is a major driver of plant community assembly and ecosystem functioning. For example, Maire *et al.* (2009) found evidence for a tradeoff between uptake of different N forms (i.e. NO_3^- and NH_4^+) among co-occurring grass species that was unrelated to root morphology. Conversely, root phosphatase activity, an important trait governing phosphorus (P) acquisition, was positively correlated with root specific surface area and negatively correlated with root diameter in tropical tree species (Ushio *et al.*, 2015). The extent to which root morphological traits can reflect variation in root physiology, particularly with regard to nutrient uptake, requires further study.

Given the difficulties associated with measuring root physiological traits, it would be worth exploring the potential of some easily measurable leaf traits that could be used as a time-integrated proxy for nutrient acquisition. For example, leaf manganese (Mn) concentration has recently been suggested as a way to screen for plant species deploying a P-mobilizing strategy via carboxylate release (Lambers *et al.*, 2015). Similarly, foliar $\delta^{15}N$ could provide a glimpse into different N-acquisition strategies used by co-occurring plant species, such as the degree of reliance on mycorrhizas for N acquisition (Hobbie & Högberg, 2012). Still, even though a stronger focus on physiological root traits will be important, it must be pointed out that certain understudied morphological traits, such as root hair density and length, also deserve further attention as they can strongly influence resource acquisition (Bates & Lynch, 2001).

VI. Determining trait–environment linkages

Determining how plant trait distributions vary across environmental gradients is required to advance predictive models of plant community assembly (Laughlin & Laughlin, 2013). However, our knowledge on root trait variation along gradients considerably lags behind that of above-ground traits. Recent progress has been made by studying long-term retrogressive soil chronosequences, which provide strong natural fertility gradients while minimizing variation in climate and geology. For example, declining soil fertility along the Franz Josef chronosequence in New Zealand favoured plant species with high SRL, high root tissue density and low nutrient concentrations (Holdaway *et al.*, 2011), while mycorrhizal plants declined in abundance at the expense of nonmycorrhizal plants along the Jurien Bay chronosequence in Australia (Zemunik *et al.*, 2015). Furthermore, declining P availability along the Jurien Bay chronosequence led to a high diversity in plant nutrient-acquisition strategies despite strong functional convergence in leaf nutrient-use traits, suggesting that fundamentally different community assembly mechanisms may operate below and above

ground (Zemunik *et al.*, 2015). Given that predictions of plant species abundances in trait-based models improve when root traits are considered (Laughlin, 2014), more studies on root trait variation along edaphic gradients are needed. Consideration of root traits can also help us to predict the effects of global environmental changes. For example, a recent meta-analysis shows that mycorrhizal type strongly determines how plants respond to elevated atmospheric CO_2 (Terrer *et al.*, 2016).

Besides abiotic factors, there is also increasing interest in determining how soil biotic factors shape plant species and functional diversity. In particular, soilborne pathogens are increasingly recognized as drivers of plant species coexistence and diversity within communities (Bever *et al.*, 2015). However, because root traits that influence nutrient acquisition, including associations with mycorrhizal fungi, can also influence susceptibility to soilborne pathogens (Laliberté *et al.*, 2015), one emerging question is how root traits determine the strength and direction of feedback between plants and their associated soil biota (Kardol *et al.*, 2013). Answering this question could help us understand how high plant diversity is maintained in species-rich ecosystems (Laliberté *et al.*, 2015).

VII. Understanding ecosystem-level consequences

Trait-based approaches offer potential not only for predicting how plant communities respond to environmental changes (Shipley *et al.*, 2016), but also for understanding how these community changes in turn drive ecosystem processes (Bardgett *et al.*, 2014). In particular, roots and their associated mycorrhizal fungi drive long-term soil carbon (C) storage by influencing organic matter decomposition (Clemmensen *et al.*, 2013; Phillips *et al.*, 2013) and by promoting soil aggregation (Rillig *et al.*, 2015). Recent studies show that root morphological (e.g. SRL, dry matter content) and chemical (e.g. lignin concentration) traits predict root decomposability at both the individual (Roumet *et al.*, 2016) and ecosystem levels (Prieto *et al.*, 2016). Moreover, mycorrhizal types (e.g. AM vs ECM) have contrasting effects on soil C dynamics (Phillips *et al.*, 2013), and measuring the proportion or roots colonized by AM vs ECM fungi at the community level could help to predict soil C stocks (Soudzilovskaia *et al.*, 2015). However, fungal traits within mycorrhizal types are also important: for example, high melanin concentrations in fungal hyphae promote soil C accumulation (Clemmensen *et al.*, 2015). We are just beginning to unravel links between root and mycorrhizal fungal traits and soil C cycling and other important ecosystem processes (Bardgett *et al.*, 2014), but this knowledge is critically needed to improve global terrestrial C models (Warren *et al.*, 2015).

VIII. Conclusions

While trait-based approaches have allowed significant recent advances in plant ecology, it is now clear that a stronger emphasis on below-ground traits is required (Bardgett *et al.*, 2014). In this review, I proposed six below-ground research frontiers to further advance trait-based plant ecology (Fig. 2). Focusing research efforts along these below-ground frontiers should help us to answer some

outstanding questions in trait-based plant ecology (Table 1) and thus bring us one step closer to fulfilling its promise: an improved capacity to predict how plant communities and ecosystems will respond to environmental changes.

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