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Grounding trait-based root functional ecology

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Abstract

A growing need exists to consider effects of biodiversity dynamics on the functioning of natural and anthropised ecosystems. This requires including the concepts of functional ecology, especially comparative trait-based ecology, in a broad range of theoretical and applied studies. In parallel, the importance of the belowground compartment is increasingly recognised, which has exponentially increased the number of studies that consider root functional traits, despite limited understanding of their meaning. This perspective article i) describes the origins of the trait-based ecology framework, ii) highlights current limitations of root-system studies, and iii) recommends ways to address these limitations.

In recent years, studies claimed that aboveground functional ecology had theoretical foundations without adequate empirical support. Root functional ecology has experienced the same problems and, for several reasons, its foundations seem even more unstable. Firstly, roots are difficult to collect, and it is difficult to precisely define components of the root system that have homogenous functions. Secondly, root systems are complex organs and have a diversity of functions, such as taking up nutrients and water, storing resources, and anchoring plants. Thirdly, the theoretical background used in root functional ecology approaches is based on that of aboveground ecology, specifically leaf functional ecology.

In the past several decades, root ecology benefitted from following in the footsteps of aboveground trait-based functional ecology, which highlighted the existence of a variety of trait spectra that were partially related to species' ecology or their interaction with symbiotic microorganisms. However, root functional ecology is currently at a crossroads and must move beyond this aboveground path and rediscover the origins of root ecology and include new traits based on root architecture and anatomy. Doing so requires developing innovative approaches that are more specific to the belowground compartment to improve understanding of plant roots and include them in large-scale studies.

Keywords: Comparative ecology, Functional ecology, Root ecology, Roots, Functional traits

Introduction

In the past few decades, trait-based approaches have expanded from studies on plant functional ecology to a wide range of disciplines, including theoretical and applied sciences such as agronomy and conservation biology (Auber et al., 2022; Faucon et al., 2017). This phenomenon is due to the ability to integrate and summarise information on plant and animal diversity at a large scale through various trait spectra (Díaz et al., 2015; Toussaint et al., 2021). Species' positions along these spectra are related to their response to environmental changes and their effects on communities and ecosystem functioning (Lavorel et al., 2007). Thus, using the trait-based approach is a way to understand and predict community and ecosystem functioning (Lavorel & Garnier, 2002). Limitations of these approaches, weaknesses of the relations and the limitations of conceptual frameworks remain partially hidden and are often ignored by the readers. As a result, trait-based approaches can be perceived as the best way to explore and predict biodiversity functioning, resulting in excess use and criticisms of their utility (Streit & Bellwood, 2022; Volaire et al., 2020).

Another criticism of plant functional ecology is that it ignored the importance of root system functions or considered them a support or reflection of the aboveground system (Grime, 1977). However, roots function are different than those of the aboveground organs (e.g. water and nutrient uptake, resource storage, and anchorage) and must grow in the soil, which has much more heterogeneous and complex conditions and resource distribution than the aboveground compartment (Hillel, 1998; Jobbágy & Jackson, 2001). This renders the study of roots particularly complex due to the difficulties involved in sampling roots and defining root functions (Freschet, Pagès, et al., 2021). Despite these obstacles, the belowground compartment is increasingly considered, and root traits were included in the recent description of the global plant strategies (Carmona et al., 2021; Weigelt et al., 2021).

Research on root system functions has resulted in the construction of relevant databases (Guerrero-Ramírez et al., 2021; Iversen et al., 2017); however, they do not increase understanding of the belowground compartment to the level of understanding of the aboveground compartment. Moreover, root functional ecology is based on concepts and approaches used in studies that focus on the aboveground compartment. For example, aboveground functional ecology has developed a leaf economic spectrum (LES) related to a species' use of resources, especially carbon (I. J. Wright et al., 2004) and most belowground studies attempt to establish its equivalent for roots (Roumet et al., 2016; Shao et al., 2019). In this theoretical framework, the root economic spectrum should reflect the LES, even though roots and leaves perform different functions. More recently, the databases exploration allows to integrate this root economic spectrum into a more belowground focused root economic space (Bergmann et al., 2020). However, before to consolidate the foundations of the root economic space by assessing the meaning of its different dimensions, it was discussed in relation to the major traits supporting the aboveground economic space (Carmona et al., 2021; Weigelt et al., 2021).

The objective of this perspective article is to review the limitations of current developments in trait-based root functional ecology as well as the opportunities it provides. To this end, it i) describes the origins of the trait-based ecology framework and focus on its initial goals and conceptual and practical limitations; ii) highlights the current limitations of root system studies, and iii) provides new insights on how to address these limitations, especially when multiple traits are considered.

Origin and framework of functional ecology

Functional ecology is concerned with understanding how organisms adapt to the biotic and abiotic characteristics of their habitats (Calow, 1987). Functional ecology differs from autoecology and physiology by adopting a comparative approach that considers a wide range of species. It aims to characterise and compare species'

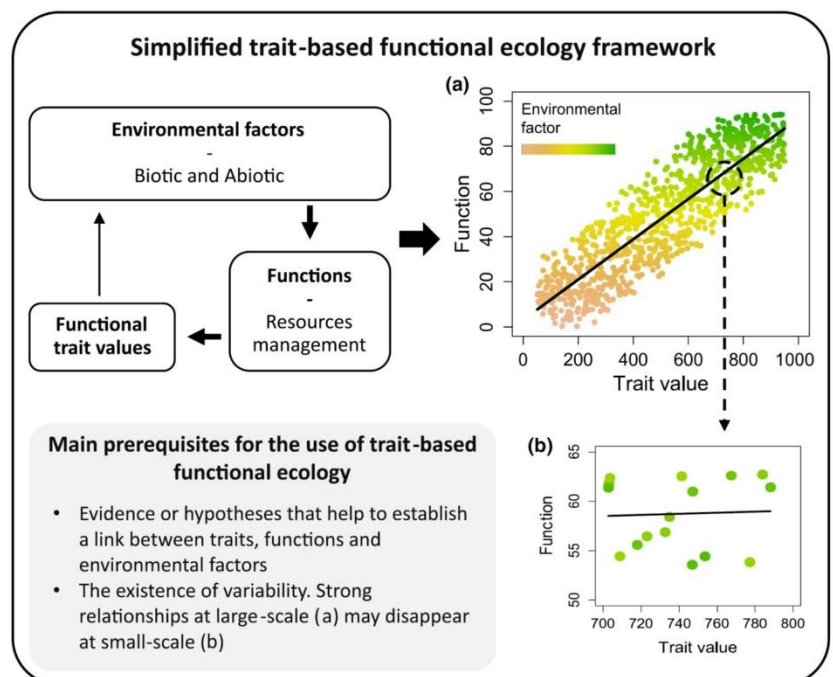
responses to different environments and/or the effects they have on the functioning of their habitats (Figure 1). It also enables classifying species in relation to each other according to their functions, and thus promotes better understanding of biodiversity patterns at different scales (Keddy, 1992).

Because functional ecology explicitly considers diversity, it works with a large number of entities (e.g., species, populations, genotypes), which has led functional ecologists to develop methods to summarise biodiversity-related information. One of the oldest methods is to use functional types to group plants that have similar morphological characteristics and effects on community functioning. Long before the emergence of modern science, Theophrastus (3rd century BC) classified plant species into four groups (i.e., trees, shrubs, sub-shrubs, and herbs), depending on their life form (Weiher & Keddy, 1999). Although this initial step may seem rudimentary, studies on relations between biodiversity and ecosystem functioning at large scales use similar classifications (Bradford et al., 2014; Duckworth et al., 2000; Poulter et al., 2015). Another way to distinguish species by function is to measure their functional characteristics (i.e., functional traits), which are morphological,

physiological, and phenological characteristics of individuals of a species (Violle et al., 2007). They are simple-to-measure proxies of an organism's function (e.g., carbon fixation, nutrient acquisition, light interception).

Measuring a set of traits of a set of organisms helps estimate the degree to which they perform multiple functions (i.e., their adaptive strategy) in different environments (Figure 1). In the 1970s, John Philip Grime, a pioneer in the field of adaptive strategies, classified grassland species into three main strategies: competitive, stress-tolerant, and ruderal (CSR). This made it possible to distinguish species by their ability to tolerate disturbances or stresses (Grime, 1977; Grime et al., 1997). This classification enables rapid characterisation of plant adaptation to different types of environments, ignoring fine adaptations and specific features. These seminal studies created the framework for trait-based functional ecology and, as a central concept, established the trade-offs involved in fulfilling distinct functions. These trade-offs restrict the range of strategies that organisms can use, as they cannot maximise reproduction, survival, and development at the same time (Bornhofen & Lattaud, 2006; Cox et al., 2010; S. J. Wright et al., 2010).

Figure 1: Simplified trait-based functional ecology framework. Functional ecology is concerned with understanding how organisms adapt to the biotic and abiotic characteristics of their habitats. It enables classifying species in relation to each other according to their functions and ecological requirements by using easy to measure traits. A major prerequisite for the use of this approach is to have evidence or hypothesis that help to establish links between traits, function and environmental factors. This approach is not as effective at finely distinguishing the strategies of a few species with similar ecological requirements or similar degree to which they perform one or various functions.



The LES is the most studied and robust trade-off that structures plant diversity (I. J. Wright et al., 2004). This spectrum distinguishes fast-growing species, which can acquire resources rapidly, from slow-growing species, which cannot, but which can conserve resources over a long period due to a long life span, among other physiological mechanisms (Chapin et al., 1993; Díaz et al., 2004; Grime et al., 1997; I. J. Wright et al., 2004). One trait that defines this spectrum is specific leaf area (SLA) or its inverse, leaf mass area. SLA is positively correlated with photosynthetic efficiency per unit of biomass and relative growth rate but is negatively correlated with leaf life span (I. J. Wright et al., 2004). SLA can explain the position of species along the LES at the global scale and is simple to measure, which renders it a major trait in functional ecology, with more than 430,000 occurrences in the TRY plant trait database (Kattge et al., 2011). An increasing number of studies use SLA (van der Plas et al., 2020), but often ignore its original meaning and limitations (Shipley et al., 2016). These studies also often ignore the comparative and sometimes oversimplified nature of the research that identified large-scale relations between SLA and other traits.

Comparative functional ecology does not consider the specific characteristics of individual species, but focuses more on general patterns, which are explored by comparing traits among species or populations in different environments (Calow, 1987). This approach requires considering many species that have a variety of ecological requirements (Ryser, 2006). Based on these prerequisites, this approach can explain the position of species along environmental gradients (Ordoñez et al., 2009; Reich, 2014; I. J. Wright et al., 2004) or use a few traits to characterise the diversity of plant organisms at the global scale (Carmona et al., 2021; Díaz et al., 2015; Weigelt et al., 2021). However, it is not as effective at finely distinguishing the strategies of a few species with similar ecological requirements (Grime & Hunt, 1975), which challenges its relevance for some studies. Due to its initial success at generalising at the global scale and the use of functional ecology

concepts in multiple disciplines, functional ecology has gradually lost sight of its origins (Shipley et al., 2016), which is exploring the relations between structure and function, as well as function and adaptation based on physiological and ecological knowledge (Calow, 1987).

Is root system ecology functional?

A subject that is difficult to define

One difficulty in describing root systems is understanding what to measure in which component. For most plants, it is simple to identify in which organ to measure photosynthetic activity; it is much less obvious to know which part of the root system to measure to determine nutrient uptake, water uptake, or respiration. Root systems come in a variety of shapes, colours, and organisation, within a root system, some old roots may display absorbing hairs while young one will not, which differs from the images in biology textbooks. The concept of leaves and stems seems universal, and non-specialists can understand that some belowground organs, such as bulbs or rhizomes, are modified leaves and stems, respectively. However, distinct vocabularies are used to describe a given root component, and it is often difficult to make them converge (Freschet, Pagès, et al., 2021). Despite several attempts to standardise sampling based on diameter classes or orders (McCormack et al., 2015; Pérez-Harguindeguy et al., 2013), no clear consensus has emerged, and all options seem mixed depending on the type of plant studied or the question asked (Freschet, Pagès, et al., 2021). Despite the difficulty in estimating the relative proportion of functions performed by a root, studying roots with distinct functions (e.g., absorption, transport, storage) separately seems the most suitable method to describe them in the greatest detail (Freschet, Pagès, et al., 2021; McCormack et al., 2015). However, this approach does make it difficult to compare species whose root systems are organised differently.

Many traits or species are called, but few are chosen

Once the difficult sampling stage is completed, the next step is to measure traits. Much of the research on functional root ecology is based on morphological traits that are theoretically or empirically related to functions. Freschet et al. (2021) identified more than 350 publications that address relations among belowground traits, plant functions, and ecosystem functioning. They highlighted the importance of traits in a species' ability to take up nitrogen and phosphorus, such as net uptake capacity, root hair length or density, aerenchyma production, and lateral root extension. However, these traits are not broadly considered in the literature on root functioning, which focuses on four traits: mean root diameter, specific root length (SRL), nitrogen concentration (RN), and root tissue density (RTD).

Their success could be explained by the fact that a large part of the theoretical background on root functional ecology mirrored that of aboveground functional ecology, which resulted in the development of root traits analogous to aboveground traits (*i.e.*, SRL is similar to SLA, RTD to leaf dry matter content, RN to leaf nitrogen content and, to a lesser extent, root diameter to leaf size). This mimicry also leads us to seek to establish the existence of a spectrum of belowground resource economy (RES, root economic spectrum (Roumet et al., 2016)), which distinguishes species in the same way than the LES (I. J. Wright et al., 2004) and supports the idea of a consistent resource economy spectrum at the whole-plant scale (Freschet et al., 2010; Weemstra et al., 2016). However, relations among the traits that support this RES are not consistent among studies. Indeed, the many attempts to highlight the existence of this RES highlighted multi-dimensionality of the relations among traits or non-linearity of the RES, which makes it challenging to describe (Kong et al., 2019; Kramer-Walter et al., 2016; Weemstra et al., 2016). Studies that examine the relation between the LES and RES also reveal strong differences between them. Most notably, Weigelt et al. (2021) observed a strong relation between RTD and leaf mass area, as well as RN and leaf nitrogen concentration, indicating a

correlation between LES and RES. In contrast, Carmona et al. (2021) could not identify any strong relations between traits from these spectrums except between root and leaf nitrogen content. These results challenge the generality of the RES, or at least the ability to define it using knowledge based on aboveground traits. Key features that define root system functioning may be missed when aboveground approaches are used to explain belowground phenomena, and when developing homologous traits for describing organs that perform distinct functions under conditions that differ from those of the leaves.

Another issue is that trait-function relations belowground are not always as generalisable and are not validated at large scales. A recent review showed that only 43 studies published from 1989-2019 considered the relation between root trait values and the ability to acquire nitrogen (one of the relations studied most), and that half of them considered less than nine species, grown in pots or hydroponically (Freschet, Roumet, et al., 2021). Similarly, in a more applied context, only seven studies that focused on the relation between traits and soil stability were published during a similar period, with a mean of 3.6 species considered (Freschet, Roumet, et al., 2021). This indicates that few species and traits are considered due to the difficulty in measuring root traits and the greater number of functions in large samples of plants. Therefore, it is crucial to carefully consider which species are included in studies (Ryser, 2006). To fully understand relations among traits, functions, and plant strategies, it is important to understand species' ecology. This could help select species that ensure these relations to have enough variability in traits and levels of function fulfilment to observe relationships (Figure 1).

Studies on root functional ecology often focus on traits related to resource management and are based on knowledge of aboveground parts and measured for a few easy-to-grow species. This has reduced interest in studying traits that may be more relevant for characterising root systems and their

functions in heterogeneous and changing environments such as soils.

Variations in root trait values along environmental gradients

Despite the limitations mentioned, the construction of databases such as the Fine-Root Ecology Database (FRED) and, more recently, the Global Root traits (GRooT) database (Guerrero-Ramírez et al., 2021; Iversen et al., 2017) have contributed to the understanding of the relation between root traits and characteristics of species' habitats. These studies demonstrate that biomes influence the variation in root traits, particularly diameter. Environments with little seasonality, such as tropical forests, result in higher variation than environments with pronounced seasonality, such as deserts (Ma et al., 2018). Similarly, mean trait values differ among biomes, with a larger mean root diameter observed in tropical environments and boreal forests than in grassland, temperate, or desert areas. Parameters such as annual temperature and precipitation are key factors that explain these variations in traits at large scales (Freschet et al., 2017; Ma et al., 2018; Valverde-Barrantes et al., 2017). Forest species that have low SRL and high RTD are more likely to occur in dry and warm climates, while those that have high SRL and low RTD are more likely to occur in cold climates (Laughlin et al., 2021). However, it seems that this type of trade-off is not the rule, and that unidirectional benefits prevail (Laughlin et al., 2021). For example, species from a dry climate usually have a large root diameter and high RTD, while species with the opposite trait values are not associated with wet climates. In addition to these environmental effects, the traits also carry strong phylogenetic signals (Kong et al., 2019), and relations between a species' traits and adaptation to environmental factors appear to depend on its functional type. For example, the SRL of tree species decreases as values of their ecological indicators for nutrients decreases, while it increases for grasses (Fort & Freschet, 2020). These studies, among others, do not explore in detail the relations between species' trait values and adaptation to their

habitat, but highlight major factors that influence trait values at large scales and enable considering them in finer-scale approaches.

Relations are more difficult to observe at fine scales due to cross-effects of abiotic micro-environmental and biotic factors (Thakur & Wright, 2017; Weemstra et al., 2021). One trend indicates that SRL and root tissue density increase and diameter decreases as nutrient availability in the environment decreases, whether along a chronosequence or along a land-use gradient (Holdaway et al., 2011; Prieto et al., 2015). This shift from conservative strategies in fertile environments to acquisitive strategies in resource-poor environments could indicate that an acquisitive strategy provides good return on investment in resource-poor environments, whereas plants can afford to invest strongly in their tissues under optimal growth conditions. The most recent studies on relations among root diameter, SRL, and investment in mycorrhizal symbioses (Bergmann et al., 2020) indicate that these results can be interpreted as a shift from “collaborative” plants (low SRL) under fertile conditions to “autonomous” plants (high SRL “do it yourself” strategies) under resource-poor conditions, in which symbiosis has higher costs than benefits (Lambers et al., 2008). However, these relations are rarely strong; in the case of the chronosequence study, the shift from large-scale to community-level measurements erases any relation, and at the latter level, only RTD is strongly related to resource availability (Holdaway et al., 2011). Other studies have observed positive relations between soil resource availability and SRL or its homolog, specific root area (de la Riva et al., 2018; Fort et al., 2016). These results support the hypothesis that acquisitive strategies are advantageous in fertile environments because they allow plants to acquire resources more efficiently and thus help species to compete for these resources by acquiring the most nutrients at low cost (Carvajal et al., 2019; I. J. Wright & Westoby, 1999). This agrees with an experiment on the relation between traits and competitive ability (Fort et al., 2014; Mommer et al., 2011). These results, which are only a sample

of those on variations in traits along small-scale environmental gradients, clearly show the diversity and fragility of fine-scale knowledge.

A recent study investigated intraspecific variation in root traits along an elevational gradient (Weemstra et al., 2021). One objective was to assess whether intraspecific variation along this and other gradients (e.g. temperature, precipitation, soil and vegetation properties) was similar to interspecific variation across a range of species. One main result was the diversity of relations obtained for a given factor (e.g. linear or unimodal, positive or negative) depending on the species. This study clearly shows the difficulty in identifying generalisable relations between trait values and gradients. It also demonstrates that species, or even populations and individuals, respond differently to changes in resources, especially due to their evolutionary history (Weemstra et al., 2021). This indicates the need to better consider the populations included in approaches and to better characterise i) the environmental context that plants experience during their life cycle (e.g. by using more than annual means) and ii) the micro-environment in studies at fine scales.

These often-conflicting results indicate the need to explore relations between trait values and species' ability to respond to small-scale environmental conditions, including abiotic and biotic factors. This would improve understanding of the mechanisms that structure plant communities and influence their functioning.

Following in the footsteps or exploring a new path?

Root functional ecology is currently at a crossroads, and must choose between i) following the aboveground path by filling databases with a few morphological traits that are easily measured for new sets of species or ii) returning to the origins of root ecology by including new traits identified in studies of root architecture and anatomy. Both options could improve understanding of root system ecology. The latter seems more likely to generate significant advances, however, especially

at a fine scale. Here, we present traits that could be integrated or reintegrated into root functional ecology to improve the description of plant strategies.

Root system organisation and soil exploration

Soil resources are unevenly distributed; for example, topsoil is less likely to be oxygen deficient (Hillel, 1998) and contains higher nutrient concentrations than the subsoil (Jobbágy & Jackson, 2001). As a result, a root system's shape and location within the soil, as well as a root's location within the root system, are strongly related to the resources they can take up and the conditions they experience.

Traits that define root system architecture provide information on interactions between plants and their environment, especially resource acquisition. The depth and lateral spread of root systems of natural vegetation seem related to climate conditions and the type of biome; for example, rooting depth is positively correlated with mean annual precipitation, which results in deeper root systems in tropical biomes (Schenk & Jackson, 2002a, 2005). At the biome level, the size of root systems should be considered as a function of soil properties. For example, for a root system of a given size in a given climate, a plant growing in coarse soil should take up less water than one growing in a fine soil due to the soil's lower water-holding capacity and deeper infiltration (Jackson et al., 2000; Sperry et al., 1998). Absolute rooting depth is often difficult to determine, but it has been estimated as 95% or 99% of root biomass, which can be predicted using root distribution throughout a soil profile (Pérez-Harguindeguy et al., 2013; Schenk & Jackson, 2002b). At a finer scale, the crown root angle appears to be a good indicator of a plant's ability to take up nutrients, especially phosphorus, when in a nutrient deficit (Lynch, 2011). Genotypes with a larger crown root angle can grow more roots in the topsoil than other plants can; consequently; they export more phosphorus, and their growth is influenced less by a phosphorous deficit than genotypes with a smaller

crown root angle (Liao et al., 2001). Several parameters can be used to describe root system architecture in detail, such as the position of secondary and tertiary roots relative to the primary root, the angle between mother and daughter roots at the latter's base, and their gravitropism (Fitter, 1987; Fitter et al., 1991). These parameters can accurately describe root system organisation, which can be used to estimate the overlap of root depletion zones within a root system and thus the effectiveness of resource acquisition (Fitter, 1987; Fitter et al., 1991). Because this method is time-consuming, it cannot describe a large number of individuals, which is a prerequisite of comparative ecology. This is why root length density per unit of soil volume, which is easier to measure, was widely adopted to determine the intensity of soil foraging (Freschet, Pagès, et al., 2021). This trait is related

to the amount of resources, especially water and nitrogen, exported by species from the soil layer in which the root length density was measured (Fort et al., 2017; Mommer et al., 2011). These results show the relevance of describing the spatial organisation of the root system at different scales to better understand relations between plants and their environment (Figure 2).

Root length is only one parameter that can determine a plant's soil exploration strategy. Root hairs increase the exchange surface between roots and the soil, which serves a major function in resource acquisition (Fitter et al., 1991; Lynch, 2011). For example, root hairs increased root-soil contact and phosphorus uptake for a barley genotype, but their effectiveness depended on soil properties (Haling et al., 2013). Their length appears to be positively related to a plant's ability

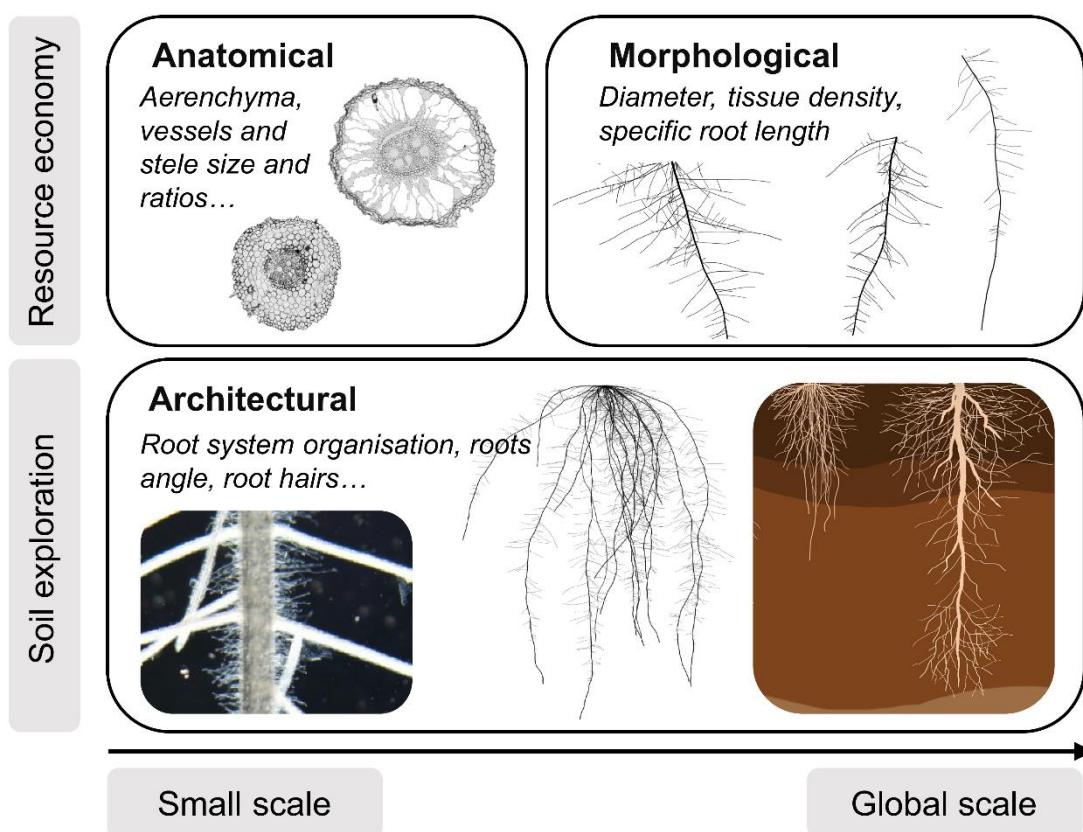


Figure 2: Hypothetical relation between the type of traits, i.e. anatomical, architectural and morphological, and the level of organisation and functions about which they can provide information. The global scale patterns represent the biodiversity responses to climatic and edaphic conditions at the biome scale, the small scale represents the soil aggregate level. Soil exploration encompasses both the position of the roots along the soil profile and the exploitation of soil resources within the root system through the proliferation of absorbent hairs or fine roots. Resources economy represents the different ways in which plants can manage their resources to explore the soil and acquire water and nutrients. Root system representation done with ArchiSimple model (Pagès et al., 2014).

to adequately respond to a water deficit (Marin et al., 2021) or to the amount of phosphorus they can take up under a phosphorus deficit (Gahoonia & Nielsen, 2004). Root hairs also influence soil functioning and extend a plant's influence on soil parameters by forming rhizosheaths (Burak et al., 2021). Using root hair length could improve the description of root strategies, as it can be easily measured from high-resolution images manually (Fort et al., 2015) or semi-automatically (Vincent et al., 2017). Root hairs density was also measured in a comparative ecology study, which demonstrated its relevance for defining plant strategies (Freschet et al., 2018). However, measuring root hairs density for a large number of plants remains difficult and time consuming (Vincent et al., 2022).

Although mycorrhizal fungi are not plant organs and deserve their own functional description, it is difficult to discuss soil exploration without considering mycorrhizal associations. Unlike the traits already mentioned, the mycorrhizal status of species is considered in global-scale analyses (Bergmann et al., 2020; Weigelt et al., 2021). Despite this strong interest, mycorrhizal type is often considered a qualitative variable that provides information on whether a species is able to establish mycorrhizal symbiosis and, if so, the type of symbiosis (i.e. ericoid, arbuscular, and/or ectomycorrhizal). It might be more complex but useful to identify traits that are related to the efficiency with which the root-fungi association exchanges resources or the degree to which a species or genotype depends on its mycorrhizal network to explore the soil.

Root tissue organisation

The internal organisation of root tissue is strongly related to a species' or genotype's adaptation to grow and acquire resources within a variety of soils and climates (Wahl & Ryser, 2000; Yamauchi et al., 2021). Root tissues consist of the epidermis, which produces the root hairs; the cortex, which is composed of parenchymal tissues; and the central part (i.e. the stele), which is bounded by the endodermis and contains the vessels. The epidermis and cortex absorb resources

and interact with the biotic and abiotic environment, while the stele transports resources and exchanges them with the rest of the plant. Study their organisation and proportions within the root is a promising tool for understanding the variety of root functions.

Among anatomical features, the aerenchyma (i.e. large gas space in the cortex) is studied the most in ecology due to its ability to allow root respiration under anoxic conditions (Armstrong, 1980; Pedersen et al., 2021). Producing aerenchyma decreases the cost of root functioning (Zhu et al., 2010), which explains why genotypes that produce large aerenchyma are able to grow more roots and acquire more resources than others under stressful conditions (Postma & Lynch, 2011a, 2011b). This decrease in the maintenance and functioning cost could be adaptive under limiting growth conditions and indicate the benefit of aerenchyma production for grass species adapted to flooded or dry environments, which have limited resource availability (Yamauchi et al., 2021). Despite this non-linear relation between the root cross-section occupied by aerenchyma and a species' adaptation to water availability, determining plant aerenchyma production could help to understand a plant's resource-acquisition strategy and ability to respond to stress.

The distribution of the root cross-section between the stele and the cortex (i.e. cortex:steele ratio) is also a key factor in a plant's adaptation to limiting conditions. This includes the response of grassland *Fabaceae* species to water and phosphorus deficits (Fort et al., 2015); the soil water requirements of wheat, rice, and maize genotypes (Yamauchi et al., 2019); and the hydrological niche of grass species (Yamauchi et al., 2021). Genotype or species adapted to dry conditions had lower cortex:steele ratios than those adapted to waterlogging (Yamauchi et al., 2019, 2021). A large cortex is associated with plants with fast growing strategies (Wahl & Ryser, 2000) that are able to grow in resources rich environment (Yamauchi et al., 2021). Moreover, a large root with a thick cortex allows mycorrhizal symbiosis to

be established, as it requires space to develop the exchange (Eissenstat et al., 2015). At a finer scale, the size of xylem vessels and the proportion of their root cross-sectional area are positively correlated with plant size (Wahl & Ryser, 2000). The deep roots and large xylem vessels of some wheat genotypes can efficiently take up water from deep soil but are not the most efficient to respond to long droughts as they deplete water resources (Blum, 2011). More generally, xylem vessel size and organisation are related to a plant's growth strategy (Wahl & Ryser, 2000; Yamauchi et al., 2021) and can be used to determine the water and resource transport capacity of a root section (Jackson et al., 2000). However, it is difficult to extrapolate water flux in a root section to the total uptake capacity of an entire root system due to the influence of plant size (Hernández et al., 2010). Using root anatomical features to improve functional studies seems promising to better understand root trait values and functions especially the one related to species response to small-scale resources availability (Figure 2). However, these properties, observed at fine scales, are influenced by a plant's size, investment in its organs, and the shape of its root system.

Conclusion

Growing interest in the ecology of root systems has resulted in advances, including the construction of databases that allow the identification of large-scale patterns in trait variations. However, little is known about the mechanisms and constraints that support these relations and the morphological traits broadly used to not allow to deal with a large part of the root system functions (Figure 2). As a result, contradictory hypotheses exist about the relations among trait values, functions, and adaptation of individuals to the environment, without the ability to confirm their validity over a wide range of conditions, species, or genotypes.

Existing studies are often difficult to compare and integrate into broader approaches due to the complexity of measuring the traits underlying the approaches, as well as the difficulty

in selecting the components in which these traits are measured and their associated functions. Therefore, the standardisation efforts in recent years are essential to produce more generalisable results. However, this standardisation must not hinder including new traits or using architectural and anatomical traits in approaches, because these improvements are needed to identify functions and better understand the relations between plants and their environment.

Reinforcing the foundations of this approach is especially necessary in a context in which trait-based functional ecology, including root ecology, is expanding to include other approaches and in which its concepts are used in other disciplines and in applied fields in need of predictive power. Exploring the datasets from experiments with a variety of objectives and methods is only one way to reinforce these foundations. Innovative studies are required to improve understanding of relations between trait values and plant functions to render root ecology more functional.

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References

- Armstrong, W. (1980). *Aeration in Higher Plants* (pp. 225–332). [https://doi.org/10.1016/S0065-2296\(08\)60089-0](https://doi.org/10.1016/S0065-2296(08)60089-0)
- Auber, A., Waldock, C., Maire, A., Goberville, E., Albouy, C., Algar, A. C., McLean, M., Brind'Amour, A., Green, A. L., Tupper, M., Vigliola, L., Kaschner, K., Kesner-Reyes, K., Beger, M., Tjiputra, J., Toussaint, A., Violle, C., Mouquet, N., Thuiller, W., & Mouillot, D. (2022). A functional vulnerability framework for biodiversity conservation. *Nature Communications*, *13*(1), 4774. <https://doi.org/10.1038/s41467-022-32331-y>
- Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, *6*(27), 1–10. <https://doi.org/10.1126/sciadv.aba3756>
- Blum, A. (2011). Plant water relations, plant stress and plant production. In *Plant Breeding for Water-Limited Environments*. Springer New York. <https://doi.org/10.1007/978-1-4419-7491-4>
- Bornhofen, S., & Lattaud, C. (2006). Life History Evolution of Virtual Plants: Trading Off Between Growth and Reproduction. In *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics): Vol. 4193 LNCS* (pp. 808–817). https://doi.org/10.1007/11844297_82
- Bradford, J. B., Schlaepfer, D. R., Lauenroth, W. K., & Burke, I. C. (2014). Shifts in plant functional types have time-dependent and regionally variable impacts on dryland ecosystem water balance. *Journal of Ecology*, *102*, 1408–1418. <https://doi.org/10.1111/1365-2745.12289>
- Burak, E., Quinton, J. N., & Dodd, I. C. (2021). Root hairs are the most important root trait for rhizosheath formation of barley (*Hordeum vulgare*), maize (*Zea mays*) and *Lotus japonicus* (Gifu). *Annals of Botany*, *128*(1), 45–57. <https://doi.org/10.1093/aob/mcab029>
- Calow, P. (1987). Towards a Definition of Functional Ecology. *Functional Ecology*, *1*(1), 57. <https://doi.org/10.2307/2389358>
- Carmona, C. P., Bueno, C. G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A. D., Pärtel, M., Zobel, M., & Tamme, R. (2021). Fine-root traits in the global spectrum of plant form and function. *Nature*, *597*(7878), 683–687. <https://doi.org/10.1038/s41586-021-03871-y>
- Carvajal, D. E., Loayza, A. P., Rios, R. S., Delpiano, C. A., & Squeo, F. A. (2019). A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. *Journal of Ecology*, *107*(3), 1079–1092. <https://doi.org/10.1111/1365-2745.13092>
- Chapin, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *American Naturalist*, *142*(1), 78–92.
- Cox, R. M., Parker, E. U., Cheney, D. M., Liebl, A. L., Martin, L. B., & Calsbeek, R. (2010). Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Functional Ecology*, *24*(6), 1262–1269. <https://doi.org/10.1111/j.1365-2435.2010.01756.x>
- de la Riva, E. G., Marañón, T., Pérez-Ramos, I. M., Navarro-Fernández, C. M., Olmo, M., & Villar, R. (2018). Root traits across environmental gradients in Mediterranean woody communities: are they aligned along

- the root economics spectrum? *Plant and Soil*, 424(1–2), 35–48. <https://doi.org/10.1007/s11104-017-3433-4>
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, a., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, a., ... Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, 15(3), 295. [https://doi.org/10.1658/1100-9233\(2004\)015\[0295:TPTTDE\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2004)015[0295:TPTTDE]2.0.CO;2)
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2015). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171. <https://doi.org/10.1038/nature16489>
- Duckworth, J. C., Kent, M., & Ramsay, P. M. (2000). Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography: Earth and Environment*, 24(4), 515–542. <https://doi.org/10.1177/030913330002400403>
- Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., & Koide, R. T. (2015). Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist*, 208(1), 114–124. <https://doi.org/10.1111/nph.13451>
- Faucon, M. P., Houben, D., & Lambers, H. (2017). Plant Functional Traits: Soil and Ecosystem Services. *Trends in Plant Science*, 22(5), 385–394. <https://doi.org/10.1016/j.tplants.2017.01.005>
- Fitter, A. H. (1987). An architectural approach to the comparative ecology of plant root systems. *New Phytologist*, 106, 61–77.
- Fitter, A. H., Stickland, T. R., Harvey, M. L., & Wilson, G. W. (1991). Architectural analysis of plant root systems 1. Architectural correlates of exploitation efficiency. *New Phytologist*, 118(3), 375–382. <https://doi.org/10.1111/j.1469-8137.1991.tb00018.x>
- Fort, F., Cruz, P., Catrice, O., Delbrut, A., Luzarreta, M., Stroia, C., & Jouany, C. (2015). Root functional trait syndromes and plasticity drive the ability of grassland Fabaceae to tolerate water and phosphorus shortage. *Environmental and Experimental Botany*, 110, 62–72. <https://doi.org/10.1016/j.envexpbot.2014.09.007>
- Fort, F., Cruz, P., & Jouany, C. (2014). Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. *Functional Ecology*, 28(4), 1030–1040. <https://doi.org/10.1111/1365-2435.12217>
- Fort, F., Cruz, P., Lecloux, E., Bittencourt de Oliveira, L., Stroia, C., Theau, J.-P. P., & Jouany, C. (2016). Grassland root functional parameters vary according to a community-level resource acquisition-conservation trade-off. *Journal of Vegetation Science*, 27(4), 749–758. <https://doi.org/10.1111/jvs.12405>
- Fort, F., & Freschet, G. T. (2020). Plant ecological indicator values as predictors of fine-root trait variations. *Journal of Ecology*, January, 1–13. <https://doi.org/10.1111/1365-2745.13368>
- Fort, F., Volaire, F., Guillioni, L., Barkaoui, K., Navas, M.-L., & Roumet, C. (2017). Root traits are related to plant water-use among rangeland Mediterranean species. *Functional Ecology*, 31(9), 1700–1709. <https://doi.org/10.1111/1365-2435.12888>

- Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., & Aerts, R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, *98*(2), 362–373. <https://doi.org/10.1111/j.1365-2745.2009.01615.x>
- Freschet, G. T., Pagès, L., Iversen, C. M., Comas, L. H., Rewald, B., Roumet, C., Klimešová, J., Zadworny, M., Poorter, H., Postma, J. A., Adams, T. S., Bagniewska-Zadworna, A., Bengough, A. G., Blancaflor, E. B., Brunner, I., Cornelissen, J. H. C., Garnier, E., Gessler, A., Hobbie, S. E., ... McCormack, M. L. (2021). A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist*, *232*(3), 973–1122. <https://doi.org/10.1111/nph.17572>
- Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., Bardgett, R. D., de Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M. L., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M., Bagniewska-Zadworna, A., ... Stokes, A. (2021). Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*, 0–2. <https://doi.org/10.1111/nph.17072>
- Freschet, G. T., Valverde-Barrantes, O. J., Tucker, C. M., Craine, J. M., McCormack, L. M., Violle, C., Fort, F., Blackwood, C. B., Urban-Mead, K. R., Iversen, C. M., Bonis, A., Comas, L. H., Cornelissen, J. H. C., Dong, M., Guo, D., Hobbie, S. E., Holdaway, R. J., Kembel, S. W., Makita, N., ... Roumet, C. (2017). Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology*, *38*(1), 42–49. <https://doi.org/10.1111/1365-2745.12769>
- Freschet, G. T., Violle, C., Bourget, M. Y., Scherer-Lorenzen, M., & Fort, F. (2018). Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. *New Phytologist*, *219*(4), 1338–1352. <https://doi.org/10.1111/nph.15225>
- Gahoonia, T. S., & Nielsen, N. E. (2004). Barley genotypes with long root hairs sustain high grain yields in low-P field. *Plant and Soil*, *262*(1), 55–62.
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, *111*(982), 1169–1194. <https://doi.org/10.1086/283244>
- Grime, J. P., & Hunt, R. (1975). Relative Growth-Rate: Its Range and Adaptive Significance in a Local Flora. *The Journal of Ecology*, *63*(2), 393. <https://doi.org/10.2307/2258728>
- Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, H. I., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., ... Whitehouse, J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos*, *79*(2), 259–281. <http://www.jstor.org/stable/10.2307/3546011>
- Guerrero-Ramírez, N. R., Mommer, L., Freschet, G. T., Iversen, C. M., McCormack, M. L., Kattge, J., Poorter, H., van der Plas, F., Bergmann, J., Kuyper, T. W., York, L. M., Bruelheide, H., Laughlin, D. C., Meier, I. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., Valverde-Barrantes, O. J., ... Weigelt, A. (2021). Global root traits (GRooT) database. *Global Ecology and Biogeography*, *30*(1), 25–37. <https://doi.org/10.1111/geb.13179>
- Haling, R. E., Brown, L. K., Bengough, A. G., Young, I. M., Hallett, P. D., White, P. J., & George, T. S. (2013). Root hairs improve root penetration, root-soil contact, and phosphorus

- acquisition in soils of different strength. *Journal of Experimental Botany*, 64(12), 3711–3721. <https://doi.org/10.1093/jxb/ert200>
- Hernández, E. I., Vilagrosa, A., Pausas, J. G., & Bellot, J. (2010). Morphological traits and water use strategies in seedlings of Mediterranean coexisting species. *Plant Ecology*, 207(2), 233–244. <https://doi.org/10.1007/s11258-009-9668-2>
- Hillel, D. (1998). *Environmental Soil Physics* (Academic Press).
- Holdaway, R. J., Richardson, S. J., Dickie, I. A., Peltzer, D. A., & Coomes, D. A. (2011). Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology*, 99(4), 954–963. <https://doi.org/10.1111/j.1365-2745.2011.01821.x>
- Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M., & Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*. <https://doi.org/10.1111/nph.14486>
- Jackson, R. B., Sperry, J. S., & Dawson, T. E. (2000). Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Sciences*, 5(11), 482–488.
- Jobbágy, E. G., & Jackson, R. B. (2001). The distribution of soil nutrients with depth: Global patterns and the imprint of plants. In *Biogeochemistry* (Vol. 53).
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van BODEGOM, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. a., Ackerly, D. D., Anand, M., ... Wirth, C. (2011). TRY - a global database of plant traits. *Global Change Biology*, 17(9), 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Keddy, P. A. (1992). A pragmatic approach to functional ecology. *Functional Ecology*, 6, 621–626.
- Kong, D., Wang, J., Wu, H., Valverde-Barrantes, O. J., Wang, R., Zeng, H., Kardol, P., Zhang, H., & Feng, Y. (2019). Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communications*, 10, 2203.
- Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, 104(5), 1299–1310. <https://doi.org/10.1111/1365-2745.12562>
- Lambers, H., Raven, J. a, Shaver, G. R., & Smith, S. E. (2008). Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution*, 23(2), 95–103. <https://doi.org/10.1016/j.tree.2007.10.008>
- Laughlin, D. C., Mommer, L., Sabatini, F. M., Bruelheide, H., Kuyper, T. W., McCormack, M. L., Bergmann, J., Freschet, G. T., Guerrero-Ramírez, N. R., Iversen, C. M., Kattge, J., Meier, I. C., Poorter, H., Roumet, C., Semchenko, M., Sweeney, C. J., Valverde-Barrantes, O. J., van der Plas, F., van Ruijven, J., ... Weigelt, A. (2021). Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology and Evolution*, 5(8), 1123–1134. <https://doi.org/10.1038/s41559-021-01471-7>
- Lavorel, S., Díaz, S., & Cornelissen, J. (2007). Plant functional types: are we getting any closer to the Holy Grail? In J. G. Canadell, D. Pataki, & L. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (Springer-Verlag, Issue i).

<http://www.springerlink.com/index/L307V6V230W43036.pdf>

- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: *Functional Ecology*, *16*, 545–556.
- Liao, H., Rubio, G., Yan, X., Cao, A., Brown, K. M., & Lynch, J. P. (2001). Effect of phosphorus availability on basal root shallowness in common bean. *Plant and Soil*, *232*, 69–79.
- Lynch, J. P. (2011). Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. *Plant Physiology*, *156*(3), 1041–1049.
<https://doi.org/10.1104/pp.111.175414>
- Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R. D., Eissenstat, D. M., McCormack, M. L., & Hedin, L. O. (2018). Evolutionary history resolves global organization of root functional traits. *Nature*, *555*(7694), 94–97.
<https://doi.org/10.1038/nature25783>
- Marin, M., Feeney, D. S., Brown, L. K., Naveed, M., Ruiz, S., Koebernick, N., Bengough, A. G., Hallett, P. D., Roose, T., Puértolas, J., Dodd, I. C., & George, T. S. (2021). Significance of root hairs for plant performance under contrasting field conditions and water deficit. *Annals of Botany*, *128*(1), 1–16. <https://doi.org/10.1093/aob/mcaa181>
- McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., Helmisaari, H.-S., Hobbie, E. A., Iversen, C. M., Jackson, R. B., Leppälammil-Kujansuu, J., Norby, R. J., Phillips, R. P., Pregitzer, K. S., Pritchard, S. G., Rewald, B., & Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist*, *207*(3), 505–518.
<https://doi.org/10.1111/nph.13363>
- Mommer, L., Visser, E. J. W., Ruijven, J., Caluwe, H., Pierik, R., & Kroon, H. (2011). Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. *Plant and Soil*, *344*(1–2), 347–360.
<https://doi.org/10.1007/s11104-011-0752-8>
- Ordoñez, J. C., van Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, *18*(2), 137–149.
<https://doi.org/10.1111/j.1466-8238.2008.00441.x>
- Pagès, L., Bécel, C., Boukcim, H., Moreau, D., Nguyen, C., & Voisin, A. S. (2014). Calibration and evaluation of ArchiSimple, a simple model of root system architecture. *Ecological Modelling*, *290*(C), 76–84.
<https://doi.org/10.1016/j.ecolmodel.2013.11.014>
- Pedersen, O., Sauter, M., Colmer, T. D., & Nakazono, M. (2021). Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytologist*, *229*(1), 42–49.
<https://doi.org/10.1111/nph.16375>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234.
- Postma, J. A., & Lynch, J. P. (2011a). Theoretical evidence for the functional benefit of root cortical aerenchyma in soils with low phosphorus availability. *Annals of Botany*, *107*(5), 829–841.
<https://doi.org/10.1093/aob/mcq199>

- Postma, J. A., & Lynch, J. P. (2011b). Root cortical aerenchyma enhances the growth of maize on soils with suboptimal availability of nitrogen, phosphorus, and potassium. *Plant Physiology*, *156*(3), 1190–1201. <https://doi.org/10.1104/pp.111.175489>
- Poulter, B., MacBean, N., Hartley, A., Khlystova, I., Arino, O., Betts, R., Bontemps, S., Boettcher, M., Brockmann, C., Defourny, P., Hagemann, S., Herold, M., Kirches, G., Lamarche, C., Lederer, D., Otlé, C., Peters, M., & Peylin, P. (2015). Plant functional type classification for earth system models: results from the European Space Agency's Land Cover Climate Change Initiative. *Geoscientific Model Development*, *8*(7), 2315–2328. <https://doi.org/10.5194/gmd-8-2315-2015>
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Rousard, O., Thammahacksa, C., & Stokes, A. (2015). Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology*, *103*(2), 361–373. <https://doi.org/10.1111/1365-2745.12351>
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K. fang, & Stokes, A. (2016). Root structure-function relationships in 74 species: Evidence of a root economics spectrum related to carbon economy. *New Phytologist*, *210*(3), 815–826. <https://doi.org/10.1111/nph.13828>
- Ryser, P. (2006). The mysterious root length. *Plant and Soil*, *286*(1–2), 1–6. <https://doi.org/10.1007/s11104-006-9096-1>
- Schenk, H. J., & Jackson, R. B. (2002a). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, *90*(3), 480–494. <https://doi.org/10.1046/j.1365-2745.2002.00682.x>
- Schenk, H. J., & Jackson, R. B. (2002b). THE GLOBAL BIOGEOGRAPHY OF ROOTS. In *Ecological Monographs* (Vol. 72, Issue 3). [https://doi.org/doi.org/10.1890/0012-9615\(2002\)072\[0311:TGBOR\]2.0.CO;2](https://doi.org/doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2)
- Schenk, H. J., & Jackson, R. B. (2005). Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma*, *126*(1–2), 129–140. <https://doi.org/10.1016/j.geoderma.2004.11.018>
- Shao, X., Wang, L., Zhang, Q., Liu, Y., & Yang, X. (2019). Future direction of searching for root economics spectrum: focusing on the fibrous roots “absorptive unit.” *Ecosphere*, *10*(5). <https://doi.org/10.1002/ecs2.2716>
- Shipley, B., de Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, *180*(4), 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Sperry, J. S., Adler, F. R., Campbell, G. S., & Comstock, J. P. (1998). Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment*, *21*(4), 347–359. <https://doi.org/10.1046/j.1365-3040.1998.00287.x>
- Streit, R. P., & Bellwood, D. R. (2022). To harness traits for ecology, let's abandon 'functionality.' *Trends in Ecology & Evolution*. <https://doi.org/10.1016/j.tree.2022.11.009>
- Thakur, M. P., & Wright, A. J. (2017). Environmental Filtering, Niche Construction, and Trait Variability: The Missing Discussion.

- Trends in Ecology & Evolution*, 32(12), 884–886. <https://doi.org/10.1016/j.tree.2017.09.014>
- Toussaint, A., Brosse, S., Bueno, C. G., Pärtel, M., Tamme, R., & Carmona, C. P. (2021). Extinction of threatened vertebrates will lead to idiosyncratic changes in functional diversity across the world. *Nature Communications*, 12(1), 5162. <https://doi.org/10.1038/s41467-021-25293-0>
- Valverde-Barrantes, O. J., Freschet, G. T., Roumet, C., & Blackwood, C. B. (2017). A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist*, 215(4), 1562–1573. <https://doi.org/10.1111/nph.14571>
- van der Plas, F., Schröder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R. L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., ... Wirth, C. (2020). Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology and Evolution*, 4(12), 1602–1611. <https://doi.org/10.1038/s41559-020-01316-9>
- Vincent, C., Ebert, R., & Hermans, C. (2022). Root hair quantification is an accessible approach to phenotyping important functional traits. *Journal of Experimental Botany*, 73(11), 3304–3307. <https://doi.org/10.1093/jxb/erac102>
- Vincent, C., Rowland, D., Na, C., & Schaffer, B. (2017). A high-throughput method to quantify root hair area in digital images taken in situ. *Plant and Soil*, 412(1–2), 61–80. <https://doi.org/10.1007/s11104-016-3016-9>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! In *Oikos* (Vol. 116, Issue 5, pp. 882–892). <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Volaire, F., Gleason, S. M., & Delzon, S. (2020). What do you mean “functional” in ecology? Patterns versus processes. *Ecology and Evolution*, 10(21), 11875–11885. <https://doi.org/10.1002/ece3.6781>
- Wahl, S., & Ryser, P. (2000). Root tissue structure is linked to ecological strategies of grasses. *New Phytologist*, 148(3), 459–471. <https://doi.org/10.1046/j.1469-8137.2000.00775.x>
- Weemstra, M., Freschet, G. T., Stokes, A., & Roumet, C. (2021). Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. *Functional Ecology*, 35(2), 342–356. <https://doi.org/10.1111/1365-2435.13723>
- Weemstra, M., Mommer, L., Visser, E. J. W., van Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: a tree root review. *New Phytologist*, 211(4), 1159–1169. <https://doi.org/10.1111/nph.14003>
- Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C., Meier, I. C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F. M., Semchenko, M., ... McCormack, M. L. (2021). An integrated framework of plant form and function: The belowground perspective. *New Phytologist*, nph.17590. <https://doi.org/10.1111/nph.17590>
- Weiherr, E., & Keddy, P. A. (1999). Assembly rules as general constraints on community composition. In E. Weiherr & P. Keddy (Eds.), *Ecological assembly rules: perspectives, advances, retreats* (pp. 251–271). Cambridge University Press.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-

Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>

Wright, I. J., & Westoby, M. (1999). Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology*, 87(1), 85–97. <https://doi.org/10.1046/j.1365-2745.1999.00330.x>

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91(12), 3664–3674. <https://doi.org/10.1890/09-2335.1>

Yamauchi, T., Abe, F., Tsutsumi, N., & Nakazono, M. (2019). Root cortex provides a venue for gas-space formation and is essential for plant adaptation to waterlogging. *Frontiers in Plant Science*, 10. <https://doi.org/10.3389/fpls.2019.00259>

Yamauchi, T., Pedersen, O., Nakazono, M., & Tsutsumi, N. (2021). Key root traits of Poaceae for adaptation to soil water gradients. *New Phytologist*, 229(6), 3133–3140. <https://doi.org/10.1111/nph.17093>

Zhu, J., Brown, K. M., & Lynch, J. P. (2010). Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant, Cell & Environment*, 33(5), 740–749. <https://doi.org/10.1111/j.1365-3040.2009.02099.x>