Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs

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Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs.

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Contents

Summary

The effects of plants on the biosphere, atmosphere, and geosphere are key determinants of terrestrial ecosystem functioning. However, despite substantial progress made regarding plant belowground components, we are still only beginning to explore the complex relationships between root traits and functions. Drawing on literature in plant physiology, ecophysiology, ecology, agronomy and soil science, we review 24 aspects of plant and ecosystem functioning and their relationships with a number of traits of root systems, including aspects of architecture, physiology, morphology, anatomy, chemistry, biomechanics and biotic interactions. Based on this assessment, we critically evaluate the current strengths and gaps in our knowledge, and identify future research challenges in the field of root ecology. Most importantly, we found that below-ground traits with widest importance in plant and ecosystem functioning are not those most commonly measured. Also, the fair estimation of trait relative importance for functioning requires us to consider a more comprehensive range of functionally-relevant traits from a diverse range of species, across environments and over time series. We also advocate that establishing causal hierarchical links among root traits will provide a hypothesis-based framework to identify the most parsimonious sets of traits with strongest influence on the functions, and to link genotypes to plant and ecosystem functioning.

Keywords: below-ground ecology; ecosystem properties and processes; environmental gradients; plant functions; root traits; spatial and temporal scales; trait covariation; trait causal relationships

I. Introduction

Plants are powerful ecosystem engineers. Extending both above- and below-ground, sometimes to a great height and depth, they shape the biosphere and its interactions with the uppermost lithosphere, the hydrosphere and the atmosphere (de Kroon & Visser, 2003; Schenk & Jackson, 2005). Taken together, the effects of plants on the biosphere, atmosphere, and geosphere are key determinants of terrestrial ecosystem functioning. Below-ground, plant roots and their symbionts are central to the maintenance of multiple ecosystem functions (Bardgett *et al.*, 2014; Freschet & Roumet, 2017): roots play key roles in the transformation and circulation of elements and mineral/organic compounds across the spheres (Prieto *et al.*, 2012; Freschet *et al.*, 2018b), and particularly in the formation, maintenance and stabilisation of soils (Daynes *et al.*, 2013; Dignac *et al.*, 2017). Thus, an advanced mechanistic understanding of the effects of root systems on ecosystem functions has numerous potential applications, such as designing plant mixtures for nutrient retention in agrosystems, for stabilization of hillslopes, etc. (Stokes *et al.*, 2009; Lavorel *et al.*, 2013; Martin & Isaac, 2015).

Root systems, among other plant parts, show a tremendous diversity of forms and properties (Kutschera, 1960; Robinson *et al.*, 2003; Bodner *et al.*, 2013; Iversen *et al.*, 2017). In recent decades, parallel developments in many areas of root research (e.g. morphology, physiology, architecture, biomechanics and anatomy, among others) have brought considerable advances in our understanding of the diversity in root traits and their contribution to plant and ecosystem functioning (Freschet *et al.*, 2020). Such advances are key to strengthening the foundations of current dominating theoretical frameworks, often built on data from the same few easily-measurable traits (McGill *et al.*, 2006; Reich *et al.*, 2014). For example, recent attempts to assemble a diverse set of trait data from a range of disciplines in root science permitted researchers to move from a single root economics spectrum (Reich *et al.*, 2014; Roumet *et al.*, 2016) that only poorly explained root trait variation and its impact on plant performance (Weemstra *et al.*, 2016), towards a multidimensional 'root economics space' that further integrates aspects of symbiotic associations and is supported by traits closely related to functioning (Bergmann *et al.*, 2020). However, despite major progress, numerous gaps remain in our understanding of trait-functioning relationships and we still lack a comprehensive overview of available knowledge that bridges research fields.

Here, sharing expertise from a range of fields in root research, we first synthesise recent advances in our understanding of demonstrated relationships between root traits and plant or ecosystem functioning (section-II, see Tables 1 & 2 and Fig. 1 for an overview of this broad assessment). Additionally, two examples are more comprehensively assessed in order to illustrate the multiple direct and indirect roles of root traits as drivers of i) plant functioning, with an investigation of the relationships between root traits and plant nitrogen (N) uptake capacity, and ii) ecosystem functioning, by examining the linkages between root traits and soil reinforcement against shallow landslides (see Tables 3 & 4 and Fig. 2 for an overview of these comprehensive assessments). Based on this two-step assessment, we critically evaluate the current strengths and gaps in our knowledge, and identify research challenges for the future. Specifically, we address three main research avenues that offer potential to improve our understanding of trait-function relationships. First, we consider the importance of using an informed selection of traits for exploring root trait-functioning relationships and discuss how sets of currently understudied traits may provide more insights than common, easy-to-measure traits (section-III). We then discuss how our understanding of trait-trait relationships and hierarchies among traits can help us to advance our knowledge of the synergistic or antagonistic effects of different traits on plant and ecosystem functioning, and lead us one step further in linking genotypes to function (section-IV). Next, we address the opportunities and pitfalls when generalising trait-functioning patterns across plant species, growth forms, environmental contexts, and temporal and spatial scales (section-V). Our two examples of plant and ecosystem functioning are woven through the remainder of this paper to illustrate our purpose.

II. An overview of trait-functioning relationships: rationale and limitations

To explore relationships between root traits and functions, we performed a broad, multidisciplinary assessment of empirical and demonstrated links between below-ground traits and plant and ecosystem functioning (Tables 1 & 2). To do so, we first identified 15 key plant functions (Table 1) and nine ecosystem processes and properties (Table 2) based on their relevance to the functioning of natural and managed ecosystems. Drawing on literature in the fields of plant physiology, ecophysiology, ecology and soil science, we considered reviews and empirical studies where both root traits and functions were measured or conceptualised. We considered traits relevant for 16 research fields (as distinguished in Freschet *et al.*, 2020; Fig. 1d), taking in aspects of root system architecture, physiology, morphology, anatomy, chemistry, biomechanics and biotic interactions. For each function we report: i) the root trait measured and its relationship to a function (positive or negative); ii) below-ground plant entities (e.g. root type, see Freschet *et al.*, 2020) on which the trait would be most relevant to measure; and iii) contextual information explaining the rationale for and degree of confidence in the relationship (Tables 1 & 2).

Trait selection was motivated by both the presence of a defined mechanistic relationship and empirical observations under controlled conditions or *in situ*. However, Tables 1 & 2 are not consolidated accounts of demonstrated evidence. Most studies reported here cover only a handful of species; as such, they may rely on fortuitous relationships resulting from interactions among traits (as discussed in section-III) and on context-dependent observations that may not be widely generalizable across multiple species and biomes (see section-IV). In addition, we stress that Tables 1 & 2 represent neither an exhaustive list of important traits nor all relevant references, but rather a broad overview of current knowledge where most relationships await confirmation. Highlighted key studies are provided to guide the audience to further reading.

Due to the limited, often contradictory state of current knowledge of root trait-functioning relationships, we do not attempt to estimate the importance of the relationship but merely indicate current evidence for its existence (i.e. a single trait impacts a specific function). Our understanding of results from past studies is particularly limited by a range of methodological issues. This includes the absence of purposeful selection of complementary traits and root entities (see section-III), the lack of accounting for trait covariation and hierarchy (see section-IV), or the lack of knowledge on the influence of genetic diversity, environmental variation and scaling across temporal and spatial scales (see section-V).

Despite these limitations, Tables 1 & 2 are useful because they provide an indication of the range of empirical and theoretical relationships between below-ground traits and plant and ecosystem functioning across research fields; link these relationships to selected references and standardized trait measurement protocols (as described in the handbook of root traits, see Freschet *et al.*, 2020); and highlight a number of rarely considered traits in order to connect different fields.

III. Trait selection

1. Measuring a complementary range of traits: are we focusing on the right ones?

Recent decades have seen the rise of approaches using a few easily measurable traits to capture plant and ecosystem functioning. Given the difficulties associated with specialized measurements of some key physiological, anatomical or chemical traits, most local-scale studies, which later feed global-scale analyses, make use of ‘soft’ traits (i.e. easily measurable traits, often vaguely related to a single or a number of functions) only, rather than a range of soft and 'hard' traits (i.e. those difficult to measure, but often more closely related to a precise function) selected on the basis of a comprehensive review of potentially relevant mechanisms or processes (but see for instance Maire *et al.*, 2009; Belluau & Shipley, 2018; Freschet *et al.*, 2018a; Ros *et al.*, 2018). For example, at the time of this survey, the FRED database (the most extensive fine-root trait database to date; Iversen *et al.*, 2017) comprises a large number of observations for the five traits most easily measured (~5000 entries for root N concentration and classical morphological traits such as root diameter and specific root length, ~3200 for root tissue density), whereas only ~320 entries for indicators of root N uptake (e.g. net ion uptake rate, maximum net ion uptake rate) and ~220 observations for indicators of root exudation (e.g. acid phosphatase activity, carbon exudation rate). Here, we stress that if a trait is widely measured, it does not necessarily mean that it is of key functional importance. During the construction of Tables 1 & 2, many trait-functioning relationships appeared indirect, vaguely justified and/or poorly tested and led us to question the broad relevance of those traits most commonly measured for plant and ecosystem functioning. Moreover, Tables 1 & 2 and Fig. 1 underscore that most ecosystem functions are likely influenced by a wider range of traits than typically assumed (McCormack *et al.*, 2017; Freschet *et al.*, 2020). In this respect, our review strengthens the idea that the search for simplified and generalizable patterns should not be at the expense of the mechanistic understanding of trait-functioning relationships (Shipley *et al.*, 2016; Belluau & Shipley, 2018). As such, we hope that Tables 1 & 2 will stimulate a debate on the merits of the classical notion that we must, by necessity, choose between studying few traits with a clear 'functional importance' or many easily measured traits (Belluau & Shipley, 2018; Freschet *et al.*, 2018a).

Root N concentration, one of the most frequently measured root traits, provides a good illustration of the common discrepancy between the frequency of trait measurements and their functional importance. Clearly important for ecosystem N cycling, root N is often measured for its presumed role in determining the overall metabolic activity (Reich *et al.*, 2008; Roumet *et al.*, 2016) and, by extension, may be assumed to scale up proportionally with specific root uptake activities (e.g. Grassein *et al.*, 2018). For example, above-ground we know that leaf N concentration is indeed strongly linked to leaf photosynthetic capacity, with more than 60% of leaf N contained in leaf photosynthetic compartments (Evans & Seemann, 1989). However, although root N concentration is a good predictor of specific root respiration (Reich *et al.*, 2008, 67 species, R^2 = 0.69; Roumet *et al.*, 2016, 73 species, R^2 = 0.25) (Fig. 2), the multiple functional roles of root N (including nutrient uptake and assimilation, but also transport, defence compounds and stored N) imply that its use as an indicator of specific activities may remain highly speculative (Table 1, Fig. 2a).

Specific root length (SRL) serves as another example of a very commonly measured but little understood 'soft' trait. It is typically interpreted as a large root surface (i.e. equivalent to specific root area) at a low cost of root construction, and is therefore assumed to mirror specific leaf area (Reich, 2014) and act as a gauge for soil resource uptake efficiency (Ostonen *et al.*, 2007). However, while this description is true, it is strongly reductive. First, it is not so much the surface of roots that would matter for below-ground resource uptake, but rather the volume of soil under influence by the root (e.g. the nitrate depletion zone around the root, or the frequency of root encounters during the flow of solutes in the soil), which depends more strongly on the length of roots deployed rather than its surface. Specific root length may thus be better referred to as a proxy for the volume of soil under influence by the root, and will most often be more closely related to soil resource uptake efficiency than specific root area. Second, it is rarely considered that cheaply constructed roots may have a much shorter lifespan (Ryser, 1996), and therefore, as a system, may have limited ability for long-term resource uptake, unless this trait is combined with a high root turnover rate. Third, SRL is a composite trait determined by the variation in root diameter and root tissue density (Fig. 2) and hence under control of complex internal plant construction trade-offs (Kong *et al.*, 2014; Poorter & Ryser, 2015). Fourth, it remains poorly understood to what extent SRL trades-off with root mass fraction (Freschet *et al.*, 2015a; Weemstra *et al.*, 2020, Fig. 2) and mycorrhizal colonization (McCormack & Iversen, 2019; Bergmann *et al.*, 2020), and acts in synergy with root hairs (Forde & Lorenzo, 2001) and root branching density (Eissenstat *et al.*, 2015) to change the volume of soil explored or exploited by roots (*sensu* Lambers *et al.*, 2008; Freschet & Roumet, 2017). A close inspection of these aspects is needed to resolve why SRL has been sometimes found to positively correlate with N uptake rates across species (Reich *et al.*, 1998; Larson & Funk, 2016; Grassein *et al.*, 2018; Hong *et al.*, 2018, 30 species), but not in other cases (Grassein *et al.*, 2015; Bowsher *et al.*, 2016; Ravenek *et al.*, 2016; Freschet *et al.*, 2018a; Ma *et al.*, 2018, 48 species).

Root N concentration and SRL are just two examples of traits where a more correct, mechanistic framing is key to truly understanding the link between traits and plant and ecosystem functioning. This issue may be inherent to below-ground plant ecology, where the relevance of many 'soft' traits was presumed based on the mechanistic understanding of their above-ground counterparts, but with little scrutiny of their actual functional significance below-ground. Ultimately, the identification of key traits for plant and ecosystem functioning needs to come from larger sets of measurements in future studies that include both ‘soft’ and ‘hard’ traits.

2. Estimating the relative importance of traits

Furthering our mechanistic knowledge of trait-functioning relationships requires not only the identification of traits that are relevant for a function (see Tables 1 & 2), but also a consideration of the relative importance of these traits for the function. The relative importance of traits identified in Tables 1 & 2 is sometimes not known and often assumed, but rarely tested. To complicate the picture further, there is ample evidence from case studies that environmental conditions interact to shuffle the relative importance of traits for individual functions, possibly due to variations in costs and benefits of a given plant strategy. For example, the relative importance of a plant’s ability to fix N_2 in symbiosis with microbes strongly increases as soil N availability decreases, while in turn N_2 fixation becomes increasingly constrained as soil P availability decreases (Batterman *et al.*, 2013b). In a second example at the ecosystem level, efficient root hydraulic conductance can rapidly dry wet soil in climates with discontinuous rain events (e.g. Boldrin *et al.*, 2017), and therefore help protect against shallow landslides. However, in climates with prolonged rainy seasons and with soils that are close to saturation for long periods of time, the efficiency of this trait is lost and the mechanical traits become more efficient at reinforcing soil (Kim *et al.*, 2017). Also, there can be distinct thresholds in the ability of traits to serve functions. For example, along a gradient of soil P availability, the dominant plant species strategy tend to shift from the reliance on thin roots at high P levels, towards increasing reliance on high root hair density and mycorrhizal symbiosis at low P levels, and eventually towards the use of highly specialized structures such as cluster roots on severely P-impoverished soils (Lambers *et al.*, 2008).

In summary, few studies to date have quantified comprehensive sets of relevant root traits across a range of species with contrasting ability to perform a function, or replicated such setups along environmental gradients (but see first attempts by Belluau & Shipley, 2018; Freschet *et al.*, 2018a; Ros *et al.*, 2018; Henneron *et al.*, 2020). Moreover, most studies do not measure the actual function of interest, but more easily measurable proxies for the function (e.g. ‘long-term N accumulation in plants’ rather than ‘long-term uptake rate’; ‘centrifuge model estimate’ instead of ‘in-situ measurement’ of soil shear reinforcement; see Tables 3 & 4). Although measuring the actual function often proves challenging, additional efforts may be needed to improve the relatedness of our proxies to the functions.

3. Considering multiple root types

To fully appreciate and understand the impact of root traits on plant or ecosystem functioning, consideration of what portion of the root system and root types are involved is needed (McCormack *et al.*, 2015a; Klimešová *et al.*, 2018). Different parts of a root system may be important for distinct aspects of plant and soil functioning (Freschet & Roumet, 2017). For example, when studying the contribution of vegetation to soil reinforcement against shallow landslides, studying the entire root system is key to capturing the distribution of root diameters that cross the multiple potential shear (rupture) surfaces along a slope (Stokes *et al.*, 2009). Thick structural roots act like soil nails, preventing soil collapse due to their mass, bending strength and stiffness. Thin and fine roots anchor plants to deeper soil layers (beneath the shear surface) and need to be strong when held under tension. Although several geotechnical models have considered the contribution of roots, irrespective of root types, to the reinforcement of potential shear planes that lie parallel to the soil surface (Table 4), these models generally overestimate slope stability, highlighting the need to better differentiate between the effects of distinct root types (Schwarz *et al.*, 2010; Mao *et al.*, 2014).

With respect to N uptake by wheat (*Triticum aestivum*), average rates of uptake per unit length of root may be only a small proportion of predicted uptake rates (Robinson *et al.*, 1991), probably due to a combination of physiological differences between individual roots and spatial clustering of root distribution. Using ion-selective microelectrode techniques, the most rapid N uptake was indeed found between 0 and 40 mm behind the root tip, decreasing between 40 and 60 mm (Plassard *et al.*, 2002; Miller & Cramer, 2004). However, this longitudinal decrease may represent only a 2- to 3-fold difference in uptake rate, with transporter gene expression studies suggesting that mature parts of the root remain significant sites of uptake (Miller & Cramer, 2004; Hawkins *et al.*, 2014). In maize (*Zea mays*), a non-destructive method was developed to fit small chambers around short root segments in hydroponics in order to measure starting and ending nitrate concentration to calculate net influx, which allowed simultaneous measurements of several root types and positions along the roots. By comparing 15-day and 20-day old plants, this study showed that maximum uptake rate may increase as the plant N demand increases, and that variation for this rate exists among lateral roots, basal roots, and shoot-borne roots (York *et al.*, 2016). Overall, despite growing knowledge on how root anatomy differs across root orders, much remains uncertain about how N uptake varies, and how this might differ among herbaceous and woody species (e.g. Hawkins *et al.*, 2014) and across environments (Gessler *et al.*, 2005).

These examples illustrate that much effort is required to further our knowledge of how various plant parts relate to specific functions. The spatial distribution of specific type of roots in the soil, and their ability to perform their function, is clearly dependent on the attributes of the rest of the root system. Focusing on trait-functioning relationships of a single root type may provide an incomplete picture of plant functioning and effects on ecosystem functions.

4. Towards widespread consideration of other types of traits

Our overview of root trait-functioning relationships (Tables 1 & 2), and the visual illustration of their interconnections (Fig. 1), suggests that many understudied traits may be crucial for a range of plant functions and ecosystem properties and processes. Three categories of traits are frequently highlighted (Fig. 1d): those associated with mycorrhizal associations, belowground allocation and the spatial distribution of roots. More specifically, among other traits, mycorrhizal association type and colonization intensity, root length density and root mass fraction, root branching density, root hair length and density, vertical root distribution index and maximum rooting depth are particularly represented in our synthesis of trait-functioning relationships (Fig. 1a-c). Described below, these traits can impact plant and ecosystem functioning in several ways:

i) The reliance of plants on different 'types of mycorrhizal fungi' (e.g. Read & Perez-Moreno, 2003; Phillips *et al.*, 2013) and the 'intensity of root colonization' serve as excellent indicators of the degree to which a plant makes the trade-off between relying on its own functional capability or on symbioses with fungal partners (Kong *et al.*, 2019; McCormack & Iversen, 2019; Bergmann *et al.*, 2020). Such critical determinants of plant resource acquisition and conservation strategies are also increasingly recognized as key drivers of a range of ecosystem properties and processes (Soudzilovskaia *et al.*, 2019).

ii) 'Root mass fraction' (or fine-root mass fraction, rhizome mass fraction, etc.) depicts the relative investment of biomass to specific belowground parts and therefore is a key trait in determining plant performance (Wilson, 1988; Poorter *et al.*, 2012). In association with SRL and total plant biomass, fine-root mass fraction determines total plant investment in fine-root length, which is a key determinant of the potential biophysical interactions between plants and the soil matrix.

iii) 'Root branching density' is increasingly recognized as a key determinant of root system architecture, with high branching density being typical of more clustered root systems favouring soil particle enmeshment and localised soil resource mining, and pre-emption against competitors (Forde & Lorenzo, 2001; Hodge, 2004). Low branching density, on the other hand, favours soil exploration (Eissenstat *et al.*, 2015) and may thus be most effective for the uptake of very mobile soil resources such as nitrate and water (e.g. Pedersen *et al.*, 2010).

iv) Maintaining high 'root hair length and density' is a very efficient way for plants to maintain root contact with soil particles (Carminati *et al.*, 2017), facilitate root anchorage and penetration into dense soils (Haling *et al.*, 2013; Choi & Cho, 2019), as well as reinforcing root interactions with the soil matrix (e.g. for resource uptake, exudation, connection to N_2-fixing symbionts, Holz *et al.*, 2018).

v) 'Vertical root distribution index' and 'maximum rooting depth' are additional descriptors of plant strategies to occupy soil volume and explore different horizons of soil (Freschet *et al.*, 2020). The localization of roots in soil has straightforward implications for the interactions between plants and soil and the transfer of elements, impacting plant resource acquisition and the recycling or sequestration of organic compounds along the soil profile (Jobbágy & Jackson, 2000; Poirier *et al.*, 2018; Mackay *et al.*, 2019).

While this set of traits merits further attention, the primary purpose of drawing up this subjective and non-exhaustive list is to emphasize that many dimensions of root effects on plant and ecosystem functioning require further consideration. Several 'hard' traits important for a range of functions (including some of the above-mentioned traits) present methodological challenges that limit their use (e.g. their study is labour-intensive, is not feasible in the field, requires complex equipment or implies known measurement inaccuracies). These challenges hinder conceptual formalization and testing of trait-functioning relationships, particularly in connection to other traits. Some of these important, but particularly challenging traits include physiological traits such as i) root exudation rate, ii) root exudate composition, iii) root respiration, iv) root enzymatic activities, v) root nutrient absorption (and the synergistic role of mycorrhizal fungi) and vi) root nutrient resorption processes, which are important determinants of nutrient uptake and cycling, chemical and anatomical aspects of vii) root resistance to pathogens and viii) root resistance to mechanical stresses, and aspects of ix) root persistence and turnover in soils that further impact soil nutrient and ecosystem carbon cycling. While an exhaustive review of recent advances in the measurement of these 'hard' traits is beyond the scope of this synthesis, we emphasize that a range of studies are already bringing improvements that facilitate such challenging measurements (see for instance Phillips *et al.,* 2008 for soluble root exudates; Lak *et al.*, 2020, for specific root respiration; Griffiths *et al.*, 2020, for multiple ion-uptake phenotyping; Arnaud *et al.*, 2019, for in-situ root imaging)

IV. Trait-trait relationships

1. Considering trait inter-relations

The individual effects of root traits on plant and ecosystem functioning are not easy to single out (Lavorel & Garnier, 2002; Lavorel *et al.*, 2013) (Fig. 1, 2). The range of trade-offs and synergies typically observed among traits (Poorter *et al.*, 2013; Roumet *et al.*, 2016; Weemstra *et al.*, 2016) suggests that plant internal (construction or evolutionary) constraints are likely to limit the number of possible adaptations of plants to environmental conditions. Figure 2 provides a range of examples where causal relationships between traits during tissue construction leads to trade-offs (e.g. mycorrhizal colonization intensity typically covaries negatively with SRL owing to the opposite effects of root cortex area fraction on the two traits) or synergies (e.g. root bending resistance and root elastic modulus typically covary positively owing to the strong positive influence of lignin and cellulose concentrations on these two traits). The result of these constraints can be seen at both the intra-species and inter-species level. Therefore, a change in the expression of one trait may have several direct consequences for the expression of other traits. This network of inter-relations, as depicted in Fig. 2a and b by causal relationships and trait covariation connectors, is often very complex.

In addition, any trait that helps alleviate a limitation or adapt to a stress, changes the strength of the limitation/stress signal, which may reduce the need for other trait adjustments (Freschet *et al.*, 2018a). As an example of this, Freschet *et al.* (2015a) showed that in a given environment most plant species tend to achieve similar levels of root length per mass of plant by developing either high SRL or high root mass fraction (depicted as causal links in Fig. 2a). This observation holds across several levels of soil N availability (Freschet *et al.*, 2015b). In this context, it appears reasonable to assume that under non-extreme resource limitation or stress conditions, different combinations of root trait values (e.g. high SRL and root hair length and density *versus* high root mass fraction and mycorrhizal colonization intensity) may result in a similar outcome with regard to plant function (e.g. N uptake capacity) (Marks & Lechowicz, 2006; Weemstra *et al.*, 2020).

The variability of plant growth strategies also implies a range of interactions between root traits, with non-additive effects on plant and ecosystem functioning. For example, a species with a deep root system, high reliance on mycorrhiza and low litter decomposability may have a strong positive effect on soil organic carbon stock via deep soil carbon sequestration, whereas a similar species with shallow rooting may have only a marginal effect on soil carbon (e.g. Clemmensen *et al.*, 2013). Similarly, although a deep rooting species may improve resistance to landslides and water uptake at depth, its effect will be noticeable only if a substantial amount of roots is found at depth (e.g. if it has a high index of vertical root distribution) (Stokes *et al.*, 2009).

Overall, it remains largely unknown whether syndromes of traits (i.e. consistent patterns of trait combinations; Bergmann *et al.*, 2020) or syndromes of plastic trait adjustments (i.e. consistent patterns of plastic changes; Freschet *et al.*, 2018) occur along well-characterized resource limitation, stress or disturbance gradients, or whether observed trends are mostly context-dependent (e.g. species-specific, community-specific). The identification of such syndromes may eventually help us summarize the covariation of trait values and their (antagonistic, additive, or synergistic) effects on plant and ecosystem function (Lavorel & Grigulis, 2012; Herben *et al.*, 2018). It would also help us discriminate between mechanistic and fortuitous trait-functioning relationships. Much remains to be done to evaluate the existence and consistency of such inter-relations. First, only a few causal relationships and indirect covariations (as depicted by black and orange connectors, respectively, in Fig. 2) between root traits have been identified (and even less so across traits from the entire plant). Second, our knowledge is biased towards the aforementioned set of widely studied root traits (Fig. 2). Third, in complex natural environments, plants are subjected to many co-occurring environmental factors whose interaction is likely to drive trait expression in multiple directions simultaneously (e.g. Kumordzi *et al.*, 2019; Zhou *et al.*, 2019). This may limit the value of our knowledge of syndromes of traits and plastic trait adjustments recorded across single environmental gradients. Indeed, these trait and environment integrations significantly influence function and fitness landscapes in multidimensional space (York *et al.*, 2013), but more data are required to fully appreciate the complex relationships that are in place.

2. *Accounting for causal relationships among traits*

The functional or categorical grouping of individual root traits as illustrated by the horizontal dimension of Fig. 2 is useful to enhancing our understanding of plant and ecosystem function (McCormack *et al.*, 2017). At the same time, it is important to consider the causal relationships (or hierarchy) among traits, as represented by the vertical dimension of the same Figure (Fig. 2: vertical dimension, Rogers & Benfey, 2015). Many traits, referred to as composite traits, can be broken down into component (i.e. underlying) traits. For example, SRL emerges from the interaction between root diameter and root tissue density, which are themselves influenced by root cortex thickness and stele diameter (Fig. 2a). Root tissue density is further determined by the cortex and stele anatomical and chemical traits (Kong *et al.*, 2019). Composite traits are particularly used because they are seen as concise indicators of plant functioning and often have the most direct influence (i.e. mechanistic link) on ecosystem functioning (see Fig. 2). The drawback is that composite traits are under the influence of several component traits that do not necessarily vary in synchrony (e.g. Poorter & Ryser, 2015), and adjustments to even simple environmental gradients may therefore often be unpredictable. Specific root length is one key example of a trait that may be important for N uptake, but whose response to changes in N availability is highly variable (e.g. Poorter & Ryser, 2015; Freschet *et al.*, 2018a), owing to contrasting responses of its component traits to N availability.

An understanding of causal links (or more generally, hierarchical organisation) between root traits is useful for the following three purposes. First, it provides a mechanistic basis (i.e. the hypothesis-based framework) to interpret the outcome of statistical model selection procedures (i.e. the set of variables retained in multivariate models linking traits to functions) or structural equation models. As such, an understanding of trait hierarchical organisation will hold the key to the identification of the most parsimonious sets of traits with strongest influence on the functions. As an example, for defining root N uptake capacity, root diameter is mostly important due to its effect on SRL and its covariation with cortex area fraction (Fig. 2). Second, knowledge of hierarchical relationships aids the identification of component traits whose influence spans several composite traits. With respect to plant N uptake capacity, cortex thickness is one such trait. It was shown to enhance the potential for roots to host mycorrhizal fungi, which is beneficial for root-fungi associations (Kong *et al.*, 2017; Kong *et al.*, 2019). Cortex thickness also influences root diameter and root tissue density, which together determine SRL (Fig. 2). Therefore, despite being rarely measured, root cortex thickness underlies two of the most widely studied and measured morphological root traits and is of critical importance for the capacity to develop mycorrhizal symbiosis. Third, another key aspect of identifying component traits is the likelihood of being directly linked to plant genes. A better understanding of the component traits' genetics—and its regulation under given environmental conditions—will not only provide an evolutionary explanation of key (composite) traits and their selection, but may also foster breeding for root traits beneficial to a specific plant function. In this context, it would be useful to further differentiate between "genuine" composite traits, that are composed by traits with different (sets of) quantitative-trait loci (QTLs) responsible for each different component trait, from "integrated" composite traits where the underlying component traits are varying in a coordinated way as determined by pleiotropic, highly-linked QTLs or tight hormonal control—with nuances between those two extremes.

V. Generalizing across scales

1. Generalizing across species, plant growth forms and biomes

Our review of conceptual, experimental and observational studies of 24 aspects of plant and ecosystem functioning (Tables 1 & 2), and two detailed examples (Fig. 2a,b; Tables 3 & 4), emphasizes that the current knowledge of trait-functioning relationships relies on highly variable numbers of observations covering the range of traits and functions. The majority of these relationships are based on relatively few species from a narrow range of plant growth forms and most have not been replicated along environmental gradients or across contrasting climates and soil types. Some trait-functioning relationships have been established in the field, while others come from pot monoculture or common-garden experiments. In this context, generalising these relationships is hazardous. As discussed above, different sets of species or growth forms may display different syndromes of traits, which further vary along gradients, and may therefore display different trait-function relationships. With respect to direct measurements of soil reinforcement to protect against landslides, only two studies could be found that consider more than three species, and virtually all studies consider only one growth form in one location (Table 4). Regarding N uptake capacity, most studies target herbaceous species at the same growth stage and often grown in hydroponics or pot conditions (Table 3), which questions whether knowledge gained from these highly simplified systems can be generalized to natural systems.

Overall, large differences have been observed across contrasting environmental contexts, such as across biomes. With regard to plant N uptake, we know for example that the importance of N-fixation strongly decreases from early successional to late successional forests of the temperate biome, whereas its importance remains high along similar gradients in the tropics

(Batterman *et al.*, 2013a). Mycorrhizal effects on N uptake also vary strongly across biomes, with ectomycorrhizal fungi transferring less N to their hosts in biomes at higher latitudes than in tropical forests (Mayor *et al.*, 2015). Such examples illustrate that results gained in one system are unlikely to be directly generalizable to other systems.

Generally, further research bridging species from different plant growth forms and growing in contrasting environmental contexts is strongly needed to better inform our knowledge of trait-function relationships.

2. *Meeting the challenge of up-scaling*

Understanding the linkages between functional traits and plant and ecosystem functioning is often most critical at large spatial scales (e.g. entire agroecosystems or natural ecosystems, Suding *et al.*, 2008; Martin & Isaac, 2015). Several functional trait-based up-scaling approaches have been proposed to link plant traits to ecosystem functioning, including the community-weighted-mean trait approach (Lavorel & Garnier, 2002; Violle *et al.*, 2007) and the pooled-species approach (Klumpp & Soussana, 2009; Prieto *et al.*, 2016). In the former, species are individually sampled (or non-destructively analysed), plant traits are measured at the level of individual species and a community trait value is calculated by weighting the trait values measured by the proportion that each species represents in the community (e.g., in terms of biomass or ground area cover). In the latter, pools of plants are sampled (or non-destructively analysed) over given ground area or soil volume and a community trait value is directly measured. In both instances, appropriate sampling resolution is key to capture a mix of plant organs representative of the community (see for example Ottaviani *et al.*, 2020), as biotic and abiotic variations occur at multiple spatial scales, (e.g. changing spatial trophic networks, soil properties, Tscharntke *et al.*, 2005).

Whether in the community-weighted-mean trait approach or pooled-species trait approach, effects on ecosystem functioning are typically assumed to be proportional to abundance (which can be expressed per unit root biomass, length or surface) to determine the functioning of the whole system (Grime, 1998; Garnier *et al.*, 2004). However, there are multiple reasons why such an approach can only capture parts of the plant community and ecosystem functioning. Depending on the system: (i) diversity effects, including competition, complementarity and facilitation, can add to the effect of species taken individually (e.g. Hodge, 2003; Santonja *et al.*, 2017; Mahaut *et al.*, 2019); (ii) some subordinate species can produce disproportionate effects on ecosystem functioning (Mariotte, 2014); (iii) interactions across multiple trophic levels can drive plant community and ecosystem function (Lavorel *et al.*, 2013); (iv) the relative importance of traits shifts depending on the environmental context (e.g. Lambers *et al.*, 2008); (v) small to large scale heterogeneity in ecosystem composition and function can maintain substantial levels of ecosystem function across all scales (Tscharntke *et al.*, 2005); and (vi) feedbacks between biotic and abiotic components, critical for ecosystem functioning and stability (Veldhuis *et al.*, 2018), are not apparent by considering the biotic components alone. For these reasons, scaling up from species traits or pooled-species traits to ecosystem-level functioning must be done with caution, and especially so in natural and semi-natural systems where biotic and abiotic interactions are even more complex than in low-diversity agricultural fields.

Nonetheless, the endeavour of up-scaling from traits to community and ecosystem yields multiple benefits. Most importantly, it provides a mechanistic framework (using or generating causal hypotheses for observed relationships) to test the contributions of traits (from species or pooled-species) to community and ecosystem functioning (Lavorel & Grigulis, 2012). Up-scaling also has the potential to fill in the gap between the small-scale mechanistic understanding of reduced systems and large-scale integrative, but mostly descriptive assessments. In that respect, the community-weighted-mean trait and pooled-species trait approaches represent complementary approaches to tackle the problem at different levels of reductionism. Both approaches have advantages and drawbacks. Clearly, the pooled-species approach is far less time consuming when studying roots and limits the biases associated with estimations of root abundance (Ottaviani *et al.*, 2020) and root species identification. As such, this approach would generally help integrating aspects of both spatial and temporal variation in community trait – ecosystem functioning relationships (as discussed below), especially in ecosystems with large numbers of dominant and subordinate species. However, with respect to ecological modelling, since plant community composition varies across geographical location and time, such measurements of community traits are unlikely to be reused to predict ecosystem functioning from the crossing of community traits with species composition databases; as such, species-level traits might be preferred.

So far, few studies have tested to what extent the knowledge gained on the linkages between single species or pooled-species functional traits and plant and ecosystem functioning can be used to infer such relationships in complex ecosystems (Garnier *et al.*, 2004; Vile *et al.*, 2006; Hales, 2018; De Long *et al.*, 2019). Taking the example of root trait effects on plant N uptake, empirical studies most often measure the physiological ability of distinct species to take up N under controlled conditions (hydroponics or pot experiments, e.g. Maire *et al.*, 2009; Grassein *et al.*, 2015), or quantify community-wide N uptake based on the budgeting approach (e.g. Finzi *et al.*, 2007), ^{15}N labelling (Hong *et al.*, 2018) or even molecular approaches quantifying gene expression (e.g. Kraiser *et al.*, 2011). However, between these two extremes, few studies have attempted to explicitly relate ecosystem-scale measurements to individual species trait values (but see Gessler *et al.*, 1998; Craine *et al.*, 2002; Soussana *et al.*, 2005, 2012 for attempts with planted grass and tree species).

Interestingly, the reverse approach of down-scaling has sometimes been used successfully, starting from the observation of major differences in functioning between systems, and tracking back the causes to individual root traits. As an example, ectomycorrhizal *versus* arbuscular mycorrhizal dominated forests give rise to differences in coupled carbon-nitrogen cycling (see Phillips *et al.*, 2013; Wurzburger & Brookshire, 2017; Zhu *et al.*, 2018). Nonetheless, a species-level approach of root trait-soil function relationships would be useful to further identify the set of mechanistic linkages involved (Wurzburger & Clemmensen, 2018).

Another major challenge of up-scaling lies in the adequate characterization of plant community or ecosystem functioning at large scales. For example, soil reinforcement by roots at small scales (e.g. soil cores) is often used to predict resistance to landslides at the hillslope-scale, using geotechnical slope-scale models (e.g. Genet *et al.*, 2010), but validation of models in the field is usually limited. Although it is possible to perform controlled, slope-scale experimental tests (e.g. Schwarz *et al.*, 2010), and to physically model scaled-slopes in the laboratory (that reproduce the stress-distribution obtained in large-scale slopes, Sonnenberg *et al.*, 2010; Liang *et al.*, 2017), the logistical problems involved render these tests extremely complex to carry out. Nonetheless, whilst these field and laboratory experiments are useful for testing realistic slopes to ultimate-failure, not all important processes or failure mechanisms that operate in the field may be captured. For that reason, future studies need to take particular care to consider the best possible proxies for up-scaling and understanding ecosystem functioning.

Another way to consider scaling belowground trait data within an ecosystem or globally is to improve the representation of root form and function in terrestrial biosphere models (Warren *et al.*, 2015). Simulation modelling translates mechanistic understanding to mathematical relations that can be explored *in silico* (Marshall-Colon *et al.*, 2017). Such models range from the simulation of explicit three-dimensional root architecture and surrounding soil matrix (Dunbabin *et al.*, 2013), to more simple models scaling up trait measurements to the whole plant (Weemstra *et al.*, 2020), agricultural systems (Rosenzweig *et al.*, 2013) or the globe

(Warren *et al.*, 2015). In recent years, several syntheses have called for an appropriate conceptualization of roots and their role in ecosystem functioning in terrestrial biosphere models (Smithwick *et al.,* 2014; Iversen *et al.*, 2015; McCormack *et al.*, 2015b). This approach, sometimes referred to as 'model-experiment' integration (or Mod-Ex) combines current empirical understanding with model conceptualization, parameterization, and validation in an iterative process to improve model representation of the natural world. While much work remains to be done, empirical input into the ways in which models aggregate or generalize across root functional types or plant species, and the way in which models implicitly or explicitly represent root function, can have large impacts on our understanding of ecosystem processes (Zhu *et al.*, 2016; McCormack *et al.,* 2017). In the context of crop breeding, for example, many combinations of root traits can be considered in various environments with regard to their effect on a particular function. These combinations can be validated across a restrained set of real-cases, and being used for prioritizing future research directions, similar to the use of digital prototyping in manufacturing (York, 2019). In global biosphere and climate studies, simulation models can also aid the prioritization of research through sensitivity analyses, for example by identifying key traits whose variation have large consequences for the function of interest (McCormack *et al.*, 2015b). But, most importantly, when tested against empirical data, the results of simulations can discriminate between diverse theoretical models, or reveal (structural or context-dependent) gaps in our mechanistic representation of trait-functioning relationships (Song *et al.*, 2017).

3. *Considering spatial and temporal variation*

A range of methodologies have been developed above-ground, such as eddy covariance towers or remote sensing, that provide large amounts of data on certain plant traits and ecosystem functions at an ecosystem scale and across space and time. However, such approaches have low resolution regarding aspects of spatial variability in functioning and are unlikely to extend to belowground traits. Generally, there is growing evidence of strong small-scale variability in root traits (Defrenne *et al.*, 2019; Kumordzi *et al.*, 2019) that may lead to substantial small-scale variability in functioning. Given the overarching importance of soil properties and biotic (e.g. plant-plant; plant-microbes) interactions, and their typically high heterogeneity at small spatial scales (Jackson & Caldwell, 1993; Ettema & Wardle, 2002), root trait-function relationships might differ strongly over short distances (e.g. centimetres or metres). To date, it remains unclear how the spatial assemblage of species and root traits at small scales might relate to the effects estimated by species averages. Spatially aggregated data may contain little information on the range of trait values occurring within the plant community, the relative abundance of each value, or the existence of several groups of contrasting trait values (e.g. bimodal distributions of trait values), which hampers our ability to understand their consequences for the functioning of ecosystems (e.g., Valencia *et al.*, 2015; Violle *et al.*, 2017).

Likewise, soil properties vary with depth (especially when contrasting soil horizons occur) and characterizing the relative importance of roots and root traits at different depths is therefore necessary to accurately link them to plant and soil functioning (Germon *et al.*, 2016; Fort *et al.*, 2017; Chitra-Tarak *et al.*, 2019). For example, the capacity for N acquisition generally decreases with soil depth due to a decline in the availability of soil N (Wiesler & Horst, 1994; Tückmantel *et al.*, 2017). These patterns can differ across soil types and plant species: in alpine grasslands on Cambisol, the uptake of N was found to decline sharply from 67% in the top 5 cm of soil to 33% in the 5–15 cm layer below (Schleuss *et al.*, 2015), whereas it was only 44% in the top 30 cm, 32% at 30-60 cm and 24% in the 60-120 cm layer for maize in an agricultural field on Luvisol (Wiesler & Horst, 1994). Additionally, changes in trait values typically occur across contrasting soil horizons (McCormack *et al.*, 2017; Trocha *et al.*, 2017), including, for example, the typical patterns of declining root density (Jackson *et al.*, 1996) and physiological activity (Göransson *et al.*, 2008; Tückmantel *et al.*, 2017) with depth. As a consequence, most ecologists assume that (physiological, morphological, etc.) trait measurements made on roots from the topsoil are likely to adequately estimate plant N uptake capacity when N resource is concentrated in the topsoil. However, there are many reasons why such an approximation may be inadequate. First, strong competition for N in the topsoil might make root investment in deeper horizons more profitable, as sometimes observed in biodiversity studies (e.g. Mueller *et al.*, 2013), resulting in more evenly distributed resource uptake across the soil profile. Second, soil N availability interacts with other soil resources, particularly water. Seasonal fluctuations of soil water availability across the soil profile following, for example, changes in water table level and precipitation patterns may reverse the N availability gradient along the profile (Prieto *et al.*, 2012). As such, a good characterization of spatial variations in soil properties (vertically, but also sometimes horizontally; Březina *et al.*, 2019), integrated over long periods of time, might be needed to guide a sound root sampling design (and the measure of e.g., physiological and morphological traits) from the range of soil layers that matter for N uptake. Also, architectural traits or traits representing (vertical and horizontal) root distribution may be important predictors of the match between root presence and N availability (Freschet *et al.*, 2020).

There is also growing evidence that, in parallel to seasonal changes in environmental conditions, such as soil resource availability (Chitra-Tarak *et al.,* 2018; Březina *et al.*, 2019) or soil organism community composition and activity (Bardgett *et al.*, 2005), root trait values vary temporally at both the species and community levels (e.g. Picon-Cochard *et al.*, 2012; Zadworny *et al.*, 2015). For example, seasonal changes in carbohydrate concentration of below-ground organs affects plant resprouting ability during some parts of the growing season in temperate regions, a feature often used to improve the efficiency of mechanical control of weeds (Sosnová *et al.*, 2014). Many root traits are also dependent on the stage of root system development (e.g. architectural traits such as root branching density, coarse to fine root ratio; Freschet *et al.*, 2020) and root age (e.g. Volder *et al.*, 2005). Within a single root axis of maize, for example, tensile strength can vary by about 1.5 orders of magnitude, being greatest in the older root tissue far from the root apex (Loades *et al.*, 2015). This phenomenon is particularly true for woody species, whose architecture and size can change dramatically during their life, with many consequences for trait values and their impact on ecosystem functioning. The importance of ontogenetic stage however also applies to herbaceous species (both annual and perennial) even after reaching maturity, for example due to changes in resource accumulation in roots or rhizomes. Additionally, root phenology differs strongly among species (McCormack *et al.*, 2014), growth forms (Blume-Werry *et al.*, 2016) and biomes (Abramoff & Finzi, 2014). In extreme cases, some species may display no or few absorptive roots at specific times of the year, with periodic flushes of new relatively short-lived fine roots at times of resource availability, as seen in arid climate (Liu *et al.*, 2016). In cold climate with short growing season, however, species with long-lived overwintering root systems may be more successful than species with fall-senescing root systems that are produced for each growing season anew (Courchesne *et al.*, 2020). Similarly, long-lived roots and rhizomes may contribute better to soil reinforcement against landslides than ephemeral roots by providing a more consistent contribution to improve soil strength.

A better understanding of root phenology is therefore key to the meaningful measurement of root trait values (in relation to the focal function) and our understanding of temporal variation in root trait effects on plant and ecosystem functioning. The timing of root sampling must be carefully considered, so as to match the period when the focal function is most relevant. For example, in ecosystems defined by high seasonality, measuring root traits at the peak of plant productivity (sometimes halfway between the seasonal increase and reduction in growth activities) may be a reasonable benchmark for approximating the relationship between root traits and plant nutrient uptake capacity. However, the timing of nutrient uptake is rarely examined (but see Trinder *et al.*, 2012; Jesch *et al.*, 2018; Dovrat & Sheffer, 2019) and may not be directly proportional to plant growth rate. Further, some studies suggest that N can be taken up as soon as it is available (Jackson *et al.*, 2008), suggesting that a good match between plant uptake capacity and the temporality of N fluxes is of critical importance for N uptake (e.g. Edwards & Jefferies, 2010). Regarding the capacity of plants to provide resistance against landslides, it would be best to measure root traits at the time of the year when landslides are most frequent, e.g., when soil is saturated, during the rainy season (in tropical systems) or during snow melt (Stokes *et al.*, 2009), or to differentiate between relationships measured at different times of the year.

Another consideration relates to the temporal variation in species composition within ecosystems, for example during succession or in response to changes in land use. Plant effects on ecosystem functioning can last for long periods after changes in plant community composition have occurred (Fraterrigo *et al.*, 2005) and mismatches between traits and function are therefore likely to be observed in rapidly changing ecosystems (Foster *et al.*, 2003). In the same way, plant species, and their root systems, that established first at a location may not only influence the rooting patterns of other species, but also disproportionately drive the observed relationships between traits and functioning (Delory *et al.*, 2019).

In summary, knowledge of spatial and temporal variation in root traits and their effects, over different spatial and temporal scales, is especially needed to allow more informed recommendation on the location and timing of measurements. Hierarchical spatial sampling and sequential sampling would provide invaluable information on the spatial and temporal fluctuation of root traits and their impact on ecosystem functioning.

4. Of intra- versus interspecific variation and the use of databases

Ecologists have identified and measured phenotypic traits in a wide variety of species, either under laboratory conditions or in the field. Various attempts have been made to include these data into comprehensive/inclusive databases considering plant traits per se (Kleyer *et al.*, 2008; Iversen *et al.*, 2017; Kattge *et al.*, 2020) as well as the plant symbiotic relationships with mycorrhizal fungi (Soudzilovskaia *et al.*, 2020) and with N-fixing bacteria (Tedersoo *et al.*, 2018). Although below-ground traits are still strongly underrepresented in global compilations, especially regarding organs other than fine roots (Klimešová *et al.*, 2018), such databases represent a large amount of trait data that can be related to vegetation composition (Bruelheide *et al.*, 2019) and climate and soil maps. Consequently, relationships between root traits and ecosystem functioning can now be addressed at global scales (e.g. See *et al.*, 2019). However, in global analyses, one trait value per species is generally considered and averaged over all available data, under the assumption that the average will be a good reflection of the 'inherent' trait for a given species. This generalisation is made even though trait expression is adjusted to the specific environmental condition that plants experience (Valladares *et al.*, 2006). Root trait values can strongly differ between plants grown in laboratory versus field experiments (Poorter *et al.*, 2016), for instance as a consequence of different environmental conditions (Li *et al.*, 2017; Kumordzi *et al.*, 2019), along gradients of plant diversity or density with different types of plant-plant interactions (Salahuddin *et al.*, 2018), or with changing interactions between trophic levels (Huber *et al.*, 2016). Ostonen *et al.* (2007) showed for example that intraspecific variation of SRL can be as high as 10-fold across a large environmental gradient. Not accounting for such differences between sites may be one of the key reasons for low predictability of trait-functioning relationships in functional ecology (Shipley *et al.*, 2016).

Due to the potential for large differences between traits and their level of intraspecific variability, getting a clearer view on which traits are most variable or invariant would be critical for data reuse in syntheses of trait-functioning relationships (Funk *et al.*, 2017; McCormack *et al.*, 2017). For above-ground traits, intraspecific variation has only recently begun to be properly addressed across large numbers of species (e.g. Siefert *et al.*, 2015). For root traits, it may be some time before we have a good insight into the contribution of genetic and environmental factors to trait variation (Klimešová *et al.*, 2017). The complexity of the issue is increased further when one considers the importance of genotype-genotype interactions of plants and root-microbial symbionts, which can also have substantial effects on trait expression and key functions (Johnson *et al.*, 2012). Overall, while the characterisation of trait intraspecific variability is critical, it must be stressed that a good characterisation of phenotypic traits also depends on a good characterisation of environmental conditions experienced by plants. This is especially true below-ground where the small-scale heterogeneity of soils limits the value of large-scale databases (Freschet *et al.*, 2017).

VI. Conclusion and perspectives

Our overview of root trait-functioning relationships has raised seven main insights:

1) Below-ground traits with the widest importance in plant and ecosystem functioning are not necessarily those that are the most commonly measured. Meanwhile, the relevance of commonly measured (soft) traits to plant and ecosystem functioning is often indirect and insubstantial, or requiring further testing.

2) Assessing the relative importance of traits for functioning requires quantifying a comprehensive range of functionally relevant traits (on different root entities), including hard traits, from a diverse range of species, as well as replication across environmental gradients or contrasting environmental contexts.

3) Establishing causal links between root traits provides a mechanistic basis (i.e. the hypothesis-based framework) to interpret the outcome of statistical model selection procedure (i.e. the set of variables retained in multivariate models linking traits to functions) or structural equation models. As such, it holds the key to identifying the most parsimonious sets of traits with strongest influence on the functions.

4) Accounting for causal relationships among traits is key to identifying the component traits that link most strongly with a limited set of genes on the one hand, and plant or ecosystem functioning on the other, and therefore to inform us of potential linkages between genotypes and functioning.

5) Investigating syndromes of traits and syndromes of trait plastic adjustments will help us identify the linkages between ‘soft’ and ‘hard’ traits, in order to demonstrate when and to what extent ‘soft’ traits can confidently be used as proxies for ‘hard’ traits.

6) Our ability to scale-up from root, to plant, to species, to community and ecosystem functioning requires more critical investigation and comprehensive experimental/empirical tests, and, in some cases, the incorporation of spatio-temporal variation as well as belowground process conceptualization and testing within the framework of terrestrial biosphere models.

7) Accounting for (the often large) intra-specific variation in trait-functioning relationships in global models requires databases with well contextualized data (e.g. locally measured soil parameters).

Another major contribution of this synthesis lies in the broad overview of root trait-function relationships gathered within Tables 1 & 2. These Tables give an overview of both the range of effects that root traits can have on ecosystem functioning and the range of traits potentially required to adequately capture the effects of roots on most plant functions and ecosystem properties and processes. They provide key references on multiple topics, which should benefit to all who want to broaden their view of root ecology. These Tables further highlight several functionally important, but rarely considered traits from various research fields.

Overall, this synthesis represents a close companion to the recent description of standardized measurement protocols for a substantial set of root traits (Freschet *et al.,* 2020). These two syntheses elucidate connections between the multiple and at times secluded fields of root ecological research and, as such, are meant to inspire novel multidisciplinary approaches. They should encourage researchers more familiar with above-ground aspects of plant ecology to integrate below-ground concepts into their vision of trait-functioning relationships. While we purposely limited our review to below-ground aspects only, we cannot stress enough that these relationships should be considered for entire plants, whenever possible, since plant impacts on (plant and ecosystem) functioning often rely on the integration of both above- and below-ground traits.

Finally, this synthesis brings a range of arguments that call for the design of more comprehensive studies. Studies tackling some, if not all of the above recommendations can be designed that limit the fortuitous, indirect and context-dependent nature of gathered results (as opposed to studies measuring few traits on few species in one single context). We believe that such a set of recommendations will be instrumental in moving towards an integrated, mechanistic knowledge of trait-functioning relationships and open the way to safe applications for ecosystem and agroecosystem management. Achieving a more mechanistic understanding of multivariate trait-functioning relationships will further help us strengthen (or reconsider) the foundations of current dominating theoretical frameworks, often built on data from few soft traits.

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Author Contributions

GTF initiated and coordinated the writing of the manuscript. GTF, CR, MW and AS organized the Workshop and chaired the sessions, with help from LHC. GTF, CR, LHC, MW, GB, BR, RDB, GBD, DJ, JK, ML, MLM, ICM, LP, HP, IP, NW, MZ and AS participated in the Workshop. GTF, CR, AS, MW, GB, LHC, BR, HP, JK, IP, NW, CMI and LY drafted some parts of the manuscript and all authors, including AB-Z, EBB, IB, AG, SEH, LM, CP-C, JAP, LR, PR, MS-L, NAS, TS, OJV and AW, contributed to the writing of the manuscript.

References

Abramoff RZ, Finzi AC. 2015. Are above- and below-ground phenology in sync? *New Phytologist* **205**: 1054-1061.

Arnaud M, Baird AJ, Morris PJ, Harris A, Huck JJ. 2019. EnRoot: a narrow-diameter, inexpensive and partially 3D-printable minirhizotron for imaging fine root production. *Plant Methods* **15**: 101.

Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK. 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution* **20**: 634-641.

Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* **29**: 692-699.

Batterman SA, Hedin LO, van Breugel M, Ransijn J, Craven DJ, Hall JS. 2013a. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature* **502**: 224-227.

Batterman SA, Wurzburger N, Hedin LO. 2013b. Nitrogen and phosphorus interact to control tropical symbiotic N2 fixation: a test in Inga punctata. *Journal of Ecology* **101**: 1400-1408.

Belluau M, Shipley B. 2018. Linking hard and soft traits: Physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. *PLoS ONE* **13**: e0193130.

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM *et al.* 2020. The fungal collaboration gradient dominates the root economics space in plants. *Science Advances 6: eaba3756.*

Blume-Werry G, Wilson SD, Kreyling J, Milbau A. 2016. The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytologist* **209**: 978-986.

Bodner G, Leitner D, Nakhforoosh A, Sobotik M, Moder K, Kaul H-P. 2013. A statistical approach to root system classification. *Frontiers in Plant Science* **4**: 292.

Boldrin D, Leung AK, Bengough AG. 2017. Correlating hydrologic reinforcement of vegetated soil with plant traits during establishment of woody perennials. *Plant and Soil* **416**: 437-451.

Bowsher AW, Mason CM, Goolsby EW, Donovan LA. 2016. Fine root tradeoffs between nitrogen concentration and xylem vessel traits preclude unified whole-plant resource strategies in Helianthus. *Ecology and Evolution* **6**: 1016-1031.

Březina S, Jandová K, Pecháčková S, Hadincová V, Skálová H, Krahulec F, Herben T. 2019. Nutrient patches are transient and unpredictable in an unproductive mountain grassland. *Plant Ecology*.

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, Sandel B *et al.* 2019. sPlot – A new tool for global vegetation analyses. *Journal of Vegetation Science* **30**: 161-186.

Carminati A, Benard P, Ahmed MA, Zarebanadkouki M. 2017. Liquid bridges at the root-soil interface. *Plant and Soil* **417**: 1-15.

Chitra-Tarak R, Ruiz L, Dattaraja HS, Mohan Kumar MS, Riotte J, Suresh HS, McMahon SM, Sukumar R. 2018. The roots of the drought: Hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology* **106**: 1495-1507.

Choi H-S, Cho H-T. 2019. Root hairs enhance Arabidopsis seedling survival upon soil disruption. *Scientific Reports* **9**: 11181.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**: 1615-1618.

Courchesne DN, Wilson AZ, Ryser P. 2020. Regional distribution patterns of wetland monocots with different root turnover strategies are associated with local variation in soil temperature. *New Phytologist* **226**: 86-97.

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

Daynes CN, Field DJ, Saleeba JA, Cole MA, McGee PA. 2013. Development and stabilisation of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi and plant roots. *Soil Biology and Biochemistry* **57**: 683-694.

de Kroon H, Visser EJW, eds. 2003. *Root ecology*. Ecological Studies vol. 168. Berlin, Germany: Springer-Verlag.

De Long JR, Jackson BG, Wilkinson A, Pritchard WJ, Oakley S, Mason KE, Stephan JG, Ostle NJ, Johnson D, Baggs EM *et al.* 2019. Relationships between plant traits, soil properties and carbon fluxes differ between monocultures and mixed communities in temperate grassland. *Journal of Ecology* **107**: 1704-1719.

Defrenne CE, McCormack ML, Roach WJ, Addo-Danso SD, Simard SW. 2019. Intraspecific fine-root trait-environment relationships across interior douglas-fir forests of western Canada. *Plants* **8**: 199.

Delory BM, Weidlich EWA, von Gillhaussen P, Temperton VM. 2019. When history matters: The overlooked role of priority effects in grassland overyielding. *Functional Ecology* **33**: 2369-2380.

Dignac M-F, Derrien D, Barré P, Barot S, Cecillon L, Chenu C, Chevallier T, Freschet GT, Garnier P, Guenet B *et al.* 2017. Increasing soil C storage: mechanisms, effects of agricultural practices and proxies. *Agronomy for Sustainable Development* **37**: 1-27.

Dovrat G, Sheffer E. 2019. Symbiotic dinitrogen fixation is seasonal and strongly regulated in water-limited environments. *New Phytologist* **221**: 1866-1877.

Dunbabin VM, Postma JA, Schnepf A, Pagès L, Javaux M, Wu L, Leitner D, Chen YL, Rengel Z, Diggle AJ. 2013. Modelling root-soil interactions using three-dimensional models of root growth, architecture and function. *Plant and Soil* **372**: 93-124.

Edwards KA, Jefferies RL. 2010. Nitrogen uptake by *Carex aquatilis* during the winter–spring transition in a low Arctic wet meadow. *Journal of Ecology* **98**: 737-744.

Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114-124.

Ettema CH, Wardle DA. 2002. Spatial soil ecology. *Trends in Ecology & Evolution* **17**: 177-183.

Evans JR, Seemann JR 1989. The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences, and control. In: Briggs W, Alan R eds. *Towards a broad understanding of photosynthesis*. New York, USA, 183-205.

Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME *et al.* 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences* **104**: 14014-14019.

Forde B, Lorenzo H. 2001. The nutritional control of root development. *Plant and Soil* **232**: 51-68.

Fort F, Volaire F, Guilioni L, Barkaoui K, Navas M-L, Roumet C. 2017. Root traits are related to plant water-use among rangeland Mediterranean species. *Functional Ecology* **31**: 1700-1709.

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* **53**: 77-88.

Fraterrigo JM, Turner MG, Pearson SM, Dixon P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecological Monographs* **75**: 215-230.

Freschet GT, Kichenin E, Wardle DA. 2015a. Explaining within-community variation in plant biomass allocation: a balance between organ biomass and morphology above vs below ground? *Journal of Vegetation Science* **26**: 431-440.

Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA *et al.* 2020. A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements *New Phytologist* **submitted**.

Freschet GT, Roumet C. 2017. Sampling roots to capture plant and soil functions. *Functional Ecology* **31**: 1506-1518.

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

Freschet GT, Valverde-Barrantes OJ, Tucker CM, Craine JM, McCormack ML, Violle C, Fort F, Blackwood CB, Urban-Mead KRU, Iversen CM *et al.* 2017. Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology* **105**: 1182-1196.

Freschet GT, Violle C, Bourget MY, Scherer-Lorenzen M, Fort F. 2018a. Allocation, morphology, physiology, architecture: the multiple facets of plant above and belowground responses to resource stress. *New Phytologist* **219**: 1338-1352.

Freschet GT, Violle C, Roumet C, Garnier E 2018b. Interactions between soil and vegetation: structure of plant communities and soil functioning. In: Lemanceau P, Blouin M eds. *Soils within the critical zone: ecology*. London, UK: ISTE editions.

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* **92**: 1156-1173.

Garnier E, Cortez J, Billes G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630-2637.

Genet M, Stokes A, Fourcaud T, Norris J. 2010. The influence of plant diversity on slope stability in moist evergreen deciduous forest. *Ecological Engineering*, **36**: 265-275.

Germon A, Cardinael R, Prieto I, Mao Z, Kim J, Stokes A, Dupraz C, Laclau J-P, Jourdan C. 2016. Unexpected phenology and lifespan of shallow and deep fine roots of walnut trees grown in a silvoarable Mediterranean agroforestry system. *Plant and Soil* **401**: 409-426.

Gessler A, Jung K, Gasche R, Papen H, Heidenfelder A, Börner E, Metzler B, Augustin S, Hildebrand E, Rennenberg H. 2005. Climate and forest management influence nitrogen balance of European beech forests: microbial N transformations and inorganic N net uptake capacity of mycorrhizal roots. *European Journal of Forest Research* 124: 95-111.

Gessler A, Schneider S, Von Sengbusch D, Weber P, Hanemann U, Huber C, Rothe A, Kreutzer K, Rennenberg H. 1998. Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees. *New Phytologist* **138**: 275-285.

Göransson H, Ingerslev M, Wallander H. 2008. The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature *Quercus robur*, *Fagus sylvatica* and *Picea abies* stands. *Plant and Soil* **306**: 129-137.

Grassein F, Legay N, Arnoldi C, Raphael S, Philippe L, Lavorel S, Clement J-C. 2018. Studies of NH_4^+ and NO_3^- uptake ability of subalpine plants and resource-use strategy identified by their functional traits. *bioRxiv*: 372235.

Grassein F, Lemauviel-Lavenant S, Lavorel S, Bahn M, Bardgett RD, Desclos-Theveniau M, Laîné P. 2015. Relationships between functional traits and inorganic nitrogen acquisition among eight contrasting European grass species. *Annals of Botany* **115**: 107-115.

Griffiths M, Roy S, Guo H, Seethepalli A, Huhman D, Ge Y, Sharp RE, Fritschi FB, York LM. 2020. A multiple ion-uptake phenotyping platform reveals shared mechanisms that affect nutrient uptake by maize roots. *bioRxiv*: 2020.2006.2015.153601.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**: 902-910.

Hales TC. 2018. Modelling biome-scale root reinforcement and slope stability. *Earth Surface Processes and Landforms* **43**: 2157-2166.

Haling RE, Brown LK, Bengough AG, Young IM, Hallett PD, White PJ, George TS. 2013. Root hairs improve root penetration, root–soil contact, and phosphorus acquisition in soils of different strength. *Journal of Experimental Botany* **64**: 3711-3721.

Hawkins BJ, Robbins S, Porter RB. 2014. Nitrogen uptake over entire root systems of tree seedlings. *Tree Physiology* **34**: 334-342.

Henneron L, Cros C, Picon-Cochard C, Rahimian V, Fontaine S. 2020. Plant economic strategies of grassland species control soil carbon dynamics through rhizodeposition. *Journal of Ecology* **108**: 528-545.

Herben T, Klimešová J, Chytrý M. 2018. Effects of disturbance frequency and severity on plant traits: An assessment across a temperate flora. *Functional Ecology* **32**: 799-808.

Hodge A. 2003. Plant nitrogen capture from organic matter as affected by spatial dispersion, interspecific competition and mycorrhizal colonization. *New Phytologist* **157**: 303-314.

Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9-24.

Holz M, Zarebanadkouki M, Kuzyakov Y, Pausch J, Carminati A. 2018. Root hairs increase rhizosphere extension and carbon input to soil. *Annals of Botany* **121**: 61-69.

Hong J, Ma X, Yan Y, Zhang X, Wang X. 2018. Which root traits determine nitrogen uptake by alpine plant species on the Tibetan Plateau? *Plant and Soil* **424**: 63-72.

Huber M, Bont Z, Fricke J, Brillatz T, Aziz Z, Gershenzon J, Erb M. 2016. A below-ground herbivore shapes root defensive chemistry in natural plant populations. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20160285.

Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschleger SD. 2015. The unseen iceberg: Plant roots in arctic tundra. *New Phytologist* **205**: 34-58.

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet GT, Kattge J, Roumet C, Stover DB, Soudzilovskaia NA, Valverde-Barrantes OJ *et al.* 2017. A global Fine-Root Ecology Database to address belowground challenges in plant ecology. *New Phytologist* **215**: 15-26.

Jackson LE, Burger M, Cavagnaro TR. 2008. Roots, nitrogen transformations, and ecosystem services. *Annual Review of Plant Biology* **59**: 341-363.

Jackson R, Caldwell M. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* **81**: 683-692.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411.

Jesch A, Barry KE, Ravenek JM, Bachmann D, Strecker T, Weigelt A, Buchmann N, de Kroon H, Gessler A, Mommer L *et al.* 2018. Below-ground resource partitioning alone cannot explain the biodiversity–ecosystem function relationship: A field test using multiple tracers. *Journal of Ecology* **106**: 2002-2018.

Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423-436.

Johnson D, Martin F, Cairney JWG, Anderson IC. 2012. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytologist* **194**: 614-628.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M *et al.* 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**: 119-188.

Kim JH, Fourcaud T, Jourdan C, Maeght JL, Mao Z, Metayer J, Meylan L, Pierret A, Rapidel B, Roupsard O, de Rouw A, Villatoro Sanchez M, Wang Y, Stokes A. 2017. Vegetation as a driver of temporal variations in slope stability: The impact of hydrological processes. *Geophysical Research Letters* **44**: 4897-4907.

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, Van Groenendael JM, Klimeš L, Klimešová J *et al.* 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* **96**: 1266-1274.

Klimešová J, Janeček Š, Bartušková A, Bartoš M, Altman J, Doležal J, Lanta V, Latzel V. 2017. Is the scaling relationship between carbohydrate storage and leaf biomass in meadow plants affected by the disturbance regime? *Annals of Botany* **120**: 979-985.

Klimešová J, Martínková J, Ottaviani G. 2018. Belowground plant functional ecology: Towards an integrated perspective. *Functional Ecology* **32**: 2115-2126.

Klumpp K, Soussana JF. 2009. Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology* **15**: 2921-2934.

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**: 863-872.

Kong D, Wang J, Wu H, Valverde-Barrantes OJ, 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.

Kong D, Wang J, Zeng H, Liu M, Miao Y, Wu H, Kardol P. 2017. The nutrient absorption–transportation hypothesis: optimizing structural traits in absorptive roots. *New Phytologist* **213**: 1569-1572.

Kraiser T, Gras DE, Gutiérrez AG, González B, Gutiérrez RA. 2011. A holistic view of nitrogen acquisition in plants. *Journal of Experimental Botany* **62**: 1455-1466.

Kumordzi BB, Aubin I, Cardou F, Shipley B, Violle C, Johnstone J, Anand M, Arsenault A, Bell FW, Bergeron Y *et al.* 2019. Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants. *Functional Ecology* **33**: 1771-1784.

Kutschera L. 1960. *Wurzelatlas mitteleuropäischer ackerunkräuter und kulturpflanzen.* Frankfurt-am-Main, Germany: DLG Verlag.

Lak ZA, Sandén H, Mayer M, Rewald B. 2020. Specific root respiration of three plant species as influenced by storage time and conditions. *Plant and Soil* **in press**.

Lambers H, Raven JA, Shaver GR, Smith SE. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* **23**: 95-103.

Larson JE, Funk JL. 2016. Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. *New Phytologist* **210**: 827-38.

Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545-556.

Lavorel S, Grigulis K. 2012. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology* **100**: 128-140.

Lavorel S, Storkey J, Bardgett RD, de Bello F, Berg MP, Le Roux X, Moretti M, Mulder C, Pakeman RJ, Díaz S *et al.* 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science* **24**: 942-948.

Li H, Liu B, McCormack ML, Ma Z, Guo D. 2017. Diverse belowground resource strategies underlie plant species coexistence and spatial distribution in three grasslands along a precipitation gradient. *New Phytologist* **216**: 1140-1150.

Liang T, Bengough AG, Knappett JA, MuirWood D, Loades KW, Hallett PD, Boldrin D, Leung AK, Meijer GJ. 2017. Scaling of the reinforcement of soil slopes by living plants in a geotechnical centrifuge. *Ecological Engineering* **109**: 207-227.

Liu B, He J, Zeng F, Lei J, Arndt SK. 2016. Life span and structure of ephemeral root modules of different functional groups from a desert system. *New Phytologist* **211**: 103-112.

Loades KW, Bengough AG, Bransby MF, Hallett PD. 2015. Effect of root age on the biomechanics of seminal and nodal roots of barley (Hordeum vulgare L.) in contrasting soil environments. *Plant and Soil* **395**: 253-261.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* **555**: 94-97.

Mackay DS, Savoy PR, Grossiord C, Tai X, Pleban JR, Wang DR, McDowell NG, Adams HD, Sperry JS. 2019. Conifers depend on established roots during drought: results from a coupled model of carbon allocation and hydraulics. *New Phytologist* **225**: 679-692.

Mahaut L, Fort F, Violle C, Freschet GT. 2020. Multiple facets of diversity effects on plant productivity: species richness, functional diversity, species identity and intraspecific competition. *Functional Ecology* **34**: 287-298.

Maire V, Gross N, da Silveira Pontes L, Picon-Cochard C, Soussana J-F. 2009. Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology* **23**: 668-679.

Mao Z, Bourrier F, Stokes A, Fourcaud T. 2014. Three-dimensional modelling of slope stability in heterogeneous montane forest ecosystems. *Ecological Modelling* **273**: 11-22.

Mariotte P. 2014. Do subordinate species punch above their weight? Evidence from above- and below-ground. *New Phytologist* **203**: 16-21.

Marks CO, Lechowicz MJ. 2006. Alternative designs and the evolution of functional diversity. *The American Naturalist* **167**: 55-66.

Marshall-Colon A, Long SP, Allen DK, Allen G, Beard DA, Benes B, von Caemmerer S, Christensen AJ, Cox DJ, Hart JC, *et al.* 2017. Crops in silico: generating virtual crops using an integrative and multi-scale modeling platform. *Frontiers in Plant Science* **8**: 786.

Martin AR, Isaac ME. 2015. Plant functional traits in agroecosystems: a blueprint for research. *Journal of Applied Ecology* **56**: 1425-1435.

Mayor J, Bahram M, Henkel T, Buegger F, Pritsch K, Tedersoo L. 2015. Ectomycorrhizal impacts on plant nitrogen nutrition: emerging isotopic patterns, latitudinal variation and hidden mechanisms. *Ecology Letters* **18**: 96-107.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. 2014. Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* **95**: 2224-2235.

McCormack ML, Crisfield E, Raczka B, Schnekenburger F, Eissenstat DM, Smithwick EAH. 2015b. Sensitivity of four ecological models to adjustments in fine root turnover rate. *Ecological Modelling* **297**: 107-117.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015a. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505-518.

McCormack ML, Guo D, Iversen CM, Chen W, Eissenstat DM, Fernandez CW, Li L, Ma C, Ma Z, Poorter H *et al.* 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* **215**: 27-37.

McCormack ML, Iversen CM. 2019. Physical and functional constraints on viable belowground acquisition strategies. *Frontiers in Plant Science* **10**: 1215.

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**: 178-185.

Miller A, Cramer M. 2004. Root nitrogen acquisition and assimilation. *Plant and Soil* **274**: 1-36.

Mueller KE, Tilman D, Fornara DA, Hobbie SE. 2013. Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology* **94**: 787-793.

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Lõhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A *et al.* 2007. Specific root length as an indicator of environmental change. *Plant Biosystems* **141**: 426-442.

Ottaviani G, Molina-Venegas R, Charles-Dominique T, Chelli S, Campetella G, Canullo R, Klimešová J. 2020. The neglected belowground dimension of dominance. *Trends in Ecology and Evolution* **in press.**

Pedersen A, Zhang K, Thorup-Kristensen K, Jensen LS. 2010. Modelling diverse root density dynamics and deep nitrogen uptake—A simple approach. *Plant and Soil* **326**: 493-510.

Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* **199**: 41-51.

Phillips RP, Erlitz Y, Bier R, Bernhardt ES. 2008. New approach for capturing soluble root exudates in forest soils. *Functional Ecology* **22**: 990-999.

Picon-Cochard C, Pilon R, Tarroux E, Pagès L, Robertson J, Dawson L. 2012. Effect of species, root branching order and season on the root traits of 13 perennial grass species. *Plant and Soil* **353**: 47-57.

Plassard C, Guérin-Laguette A, Véry A-A, Casarin V, Thibaud J-B. 2002. Local measurements of nitrate and potassium fluxes along roots of maritime pine. Effects of ectomycorrhizal symbiosis. *Plant, Cell & Environment* **25**: 75-84.

Poirier V, Roumet C, Munson AD. 2018. The root of the matter: Linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry* **120**: 246-259.

Poorter H, Anten NPR, Marcelis LFM. 2013. Physiological mechanisms in plant growth models: do we need a supra-cellular systems biology approach? *Plant, Cell & Environment* **36**: 1673-1690.

Poorter H, Fiorani F, Pieruschka R, Wojciechowski T, van der Putten WH, Kleyer M, Schurr U, Postma J. 2016. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist* **212**: 838-855.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30-50.

Poorter H, Ryser P. 2015. The limits to leaf and root plasticity: what is so special about specific root length? *New Phytologist* **206**: 1188-1190.

Prieto I, Armas C, Pugnaire FI. 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytologist* **193**: 830-841.

Prieto I, Stokes A, Roumet C. 2016. Root functional parameters predict fine root decomposability at the community level. *Journal of Ecology* **104**: 725-733.

Ravenek JM, Mommer L, Visser EJW, van Ruijven J, van der Paauw JW, Smit-Tiekstra A, Caluwe H, de Kroon H. 2016. Linking root traits and competitive success in grassland species. *Plant and Soil*: 1-15.

Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* **157**: 475-492.

Read QD, Henning JA, Sanders NJ. 2017. Intraspecific variation in traits reduces ability of trait-based models to predict community structure. *Journal of Vegetation Science* **28**: 1070-1081.

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

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

Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* **12**: 327-338.

Robinson D, Hodge A, Fitter A 2003. Constraints on the form and function of root systems. In: De Kroon H, Visser EJW eds. *Root ecology*. Berlin Heidelberg: Springer, 1-31.

Robinson D, Linehan DJ, Caul S. 1991. What limits nitrate uptake from soil? *Plant, Cell & Environment* **14**: 77-85.

Rogers ED, Benfey PN. 2015. Regulation of plant root system architecture: implications for crop advancement. *Current Opinion in Biotechnology* **32**: 93-98.

Ros MBH, De Deyn GB, Koopmans GF, Oenema O, van Groenigen JW. 2018. What root traits determine grass resistance to phosphorus deficiency in production grassland? *Journal of Plant Nutrition and Soil Science* **181**: 323-335.

Rosenzweig C, Jones JW, Hatfield JL, Ruane AC, Boote KJ, Thorburn P, Antle JM, Nelson GC, Porter C, Janssen S. 2013. The agricultural model intercomparison and improvement project (AgMIP): protocols and pilot studies. *Agricultural and Forest Meteorology* **170**: 166-182.

Ryser P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**: 717-723.

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

Salahuddin, Rewald B, Razaq M, Lixue Y, Li J, Khan F, Jie Z. 2018. Root order-based traits of Manchurian walnut & larch and their plasticity under interspecific competition. *Scientific Reports* **8**: 9815.

Santonja M, Rancon A, Fromin N, Baldy V, Hättenschwiler S, Fernandez C, Montès N, Mirleau P. 2017. Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland. *Soil Biology and Biochemistry* **111**: 124-134.

Schenk HJ, Jackson RB. 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma* **126**: 129-140.

Schleuss P-M, Heitkamp F, Sun Y, Miehe G, Xu X, Kuzyakov Y. 2015. Nitrogen uptake in an alpine Kobresia pasture on the Tibetan Plateau: localization by 15N labeling and implications for a vulnerable ecosystem. *Ecosystems* **18**: 946-957.

Schwarz M, Lehmann P, Or D. 2010. Quantifying lateral root reinforcement in steep slopes – from a bundle of roots to tree stands. *Earth Surface Processes and Landforms* **35**: 354-367.

See CR, Luke McCormack M, Hobbie SE, Flores-Moreno H, Silver WL, Kennedy PG. 2019. Global patterns in fine root decomposition: climate, chemistry, mycorrhizal association and woodiness. *Ecology Letters* **22**: 946-953.

Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. 2016. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* **180**: 923-931.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406-1419.

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

Song X, Hoffman FM, Iversen CM, Yin Y, Kumar J, Ma C, Xu X. 2017. Significant inconsistency of vegetation carbon density in CMIP5 Earth System Models against observational data. *Journal of Geophysical Research - Biogeosciences* **122**: 2282-2297.

Sonnenberg R, Bransby MF, Hallett PD, Bengough AG, Mickovski SB, Davies MCR. 2010. Centrifuge modelling of soil slopes reinforced with vegetation. *Canadian Geotechnical Journal* **47**: 1415-1430.

Sosnová M, Herben T, Martínková J, Bartušková A, Klimešová J. 2014. To resprout or not to resprout? Modeling population dynamics of a root-sprouting monocarpic plant under various disturbance regimes. *Plant Ecology* **215**: 1245-1254.

Soudzilovskaia NA, van Bodegom PM, Terrer C, Zelfde Mvt, McCallum I, Luke McCormack M, Fisher JB, Brundrett MC, de Sá NC, Tedersoo L. 2019. Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* **10**: 5077.

Soudzilovskaia NA, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett MC, Gomes SIF, Merckx V, Tederesoo L. 2019. FungalRoot: global online database of plant mycorrhizal associations. *New Phytologist* **in press**.

Soussana J-F, Maire V, Gross N, Bachelet B, Pagès L, Martin R, Hill D, Wirth C. 2012. Gemini: A grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation. *Ecological Modelling* **231**: 134-145.

Soussana J-F, Teyssonneyre F, Picon-Cochard C, Dawson L. 2005. A trade-off between nitrogen uptake and use increases responsiveness to elevated CO2 in infrequently cut mixed C3 grasses. *The New Phytologist* **166**: 217-230.

Stokes A, Atger C, Bengough A, Fourcaud T, Sidle R. 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil* **324**: 1-30.

Suding KN, Lavorel S, Chapin FS, III, Cornelissen JHC, Diaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas M-L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125-1140.

Tedersoo L, Laanisto L, Rahimlou S, Toussaint A, Hallikma T, Pärtel M. 2018. Global database of plants with root-symbiotic nitrogen fixation: NodDB. *Journal of Vegetation Science* **29**: 560-568.

Trinder CJ, Brooker RW, Davidson H, Robinson D. 2012. A new hammer to crack an old nut: interspecific competitive resource capture by plants is regulated by nutrient supply, not climate. *PLoS ONE* **7**: e29413.

Trocha LK, Bułaj B, Kutczyńska P, Mucha J, Rutkowski P, Zadworny M. 2017. The interactive impact of root branch order and soil genetic horizon on root respiration and nitrogen concentration. *Tree Physiology* **37**: 1055-1068.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* **8**: 857-874.

Tückmantel T, Leuschner C, Preusser S, Kandeler E, Angst G, Mueller CW, Meier IC. 2017. Root exudation patterns in a beech forest: Dependence on soil depth, root morphology, and environment. *Soil Biology and Biochemistry* **107**: 188-197.

Valencia E, Maestre FT, Le Bagousse-Pinguet Y, Quero JL, Tamme R, Börger L, García-Gómez M, Gross N. 2015. Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist* **206**: 660-671.

Valladares F, Sanchez-Gomez D, Zavala MA. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* **94**: 1103-1116.

Veldhuis MP, Berg MP, Loreau M, Olff H. 2018. Ecological autocatalysis: a central principle in ecosystem organization? *Ecological Monographs* **88**: 304-319.

Vile D, Shipley B, Garnier E. 2006. Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecology Letters* **9**: 1061-1067.

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

Violle C, Thuiller W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, Livingstone SW, Mouillot D. 2017. Functional rarity: the ecology of outliers. *Trends in Ecology & Evolution* **32**: 356-367.

Volder A, Smart DR, Bloom AJ, Eissenstat DM. 2005. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytologist* **165**: 493-502.

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

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

Weemstra M, Kiorapostolou N, van Ruijven J, Mommer L, de Vries J, Sterck F. 2020. The role of fine-root mass, specific root length and life span in tree performance: a whole-tree exploration. *Functional Ecology* **34**: 575-585.

Wiesler F, Horst WJ. 1994. Root growth and nitrate utilization of maize cultivars under field conditions. *Plant and Soil* **163**: 267-277.

Wilson JB. 1988. A review of evidence on the control of shoot: root ratio, in relation to models. *Annals of Botany* **61**: 433-449.

Wurzburger N, Brookshire ENJ. 2017. Experimental evidence that mycorrhizal nitrogen strategies affect soil carbon. *Ecology* **98**: 1491-1497.

Wurzburger N, Clemmensen KE. 2018. From mycorrhizal fungal traits to ecosystem properties – and back again. *Journal of Ecology* **106**: 463-467.

York LM, Nord EA, Lynch JP. 2013. Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science* **4**: 1-15.

York LM, Silberbush M, Lynch JP. 2016. Spatiotemporal variation of nitrate uptake kinetics within the maize (*Zea mays* L.) root system is associated with greater nitrate uptake and interactions with architectural phenes. *Journal of Experimental Botany* **67**: 3763-3775.

York LM. 2019. Functional phenomics: an emerging field integrating high-throughput phenotyping, physiology, and bioinformatics. *Journal of Experimental Botany* **70**: 379-386.

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

Zhou M, Wang J, Bai W, Zhang Y, & Zhang W. 2019. The response of root traits to precipitation change of herbaceous species in temperate steppes. *Functional Ecology* **33**: 2030-2041.

Zhu K, McCormack ML, Lankau RA, Egan JF, Wurzburger N. 2018. Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. *Journal of Ecology* **106**: 524-535.

Zhu Q, Iversen CM, Riley WJ, Slette IJ, Vander Stel HM. 2016. Root traits explain observed tundra vegetation nitrogen uptake patterns: Implications for trait-based land models. *Journal of Geophysical Research - Biogeosciences* **121**: 3101-3112.

Supporting Information

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

Notes S1. Full list of references for papers cited in Tables 1, 2, 3 & 4.

Tables

Table 1. Broad, multidisciplinary assessment of theoretical and demonstrated links between below-ground traits and 15 aspects of plant functioning. CC: colour code, in dark blue: trait of prime importance for performing the plant function in at least some environmental conditions; medium blue: trait of secondary importance in at least some environmental conditions; light blue: trait of potential but unknown importance due to missing or low experimental evidence. * refers to traits whose measurement protocols are described in Freschet *et al.* (2020). (+) versus (-) refers to the positive or negative effect of one trait on the function, respectively. (explorative) versus (exploitative) refers to traits that increase the overall volume of soil explored or improve the exploitation of a more limited volume of soil, respectively. ‘Entity of interest’ refers to a range of plant belowground parts as described in Freschet *et al.* (2020). The full list of references is available as Supplementary Notes S1.

PLANT FUNCTIONS				
CC	Belowground traits	Entity of interest	References (examples of)	Rationale
Soil space occupancy (from explorative to exploitative strategies)				This function includes both exploration and exploitation strategies (whose traits generally trade-off).
🟦	Maximum rooting depth* (explorative)	Whole root system	Thorup-Kristensen, 2001; Maeght *et al.*, 2013; Fan *et al.*, 2017	Reflects the potential range of soil layers colonized by roots.
🟦	Lateral rooting extent* (explorative)	Whole root system	Schenk & Jackson, 2002a	Reflects the potential area of ground colonized by roots.
🟦	Horizontal* and vertical root distribution index* (explorative)	Whole root system, fine-roots	Gale & Gringal, 1987; Jackson *et al.*, 1996	A homogeneous distribution below the soil surface and across depths is typical of an explorative rather than an exploitative strategy.
🟦	Root length density* (exploitative)	Whole root system, fine-roots	Eissenstat, 1992; Robinson *et al.*, 1994; Reich *et al.*, 1998; Ravenek *et al.*, 2016	Increases the spatial coverage of a given soil volume.
🟦	Root mass fraction* (exploitative)	Whole root system, fine-roots	Poorter *et al.*, 2012; Freschet *et al.*, 2015	Increases the proportional investment of plants towards the root system or specific parts of the root system.

🟦	Specific root length* (explorative or exploitative)	Whole root system, fine-roots	Bauhus & Messier, 1999; Ostonen *et al.,* 2007	Increases the length of root exploring or exploiting the soil per unit root mass invested.
🟦	Root branching density* (exploitative)	Whole root system, absorptive roots	Wiersum, 1958; Fitter & Stickland 1991; Larigauderie & Richards, 1994; Eissenstat *et al.,* 2015; Zhao *et al.*, 2018 ; Lynch *et al.*, 2019	Typically increases with soil resource patchiness as very thin roots tend to proliferate (strong increase in root branching density) in nutrient-rich hotspots. While higher branching density increases local soil exploitation, lower branching might enable larger soil volume exploration.
🟦	Root elongation rate* (explorative or exploitative)	First-order roots	Forde & Lorenzo 2001; Rewald & Leuschner, 2009; Eissenstat *et al.,* 2015	On pioneer roots, measures the capacity of root systems to send roots to depth (explorative). On absorptive roots, characterizes the capacity of root systems to respond to fluctuating resource availability (exploitative).
🟦	Time of root growth initiation*	First-order roots	Langlois *et al.*, 1983; Eissenstat & Caldwell, 1988	Measures the capacity of root systems to pre-occupy soil patches before competitors.
🟦	Root branching angle* (explorative)	Highest order roots	Trachsel *et al.,* 2013; Lynch, 2013; Miguel *et al.,* 2015	Larger (i.e. steeper) root branching angles promote exploration of deep soil and increase soil volume explored in conditions of competition with neighbouring plants.
🟦	Persistence of connection between ramets* (explorative)	Rhizomes, stolons, shoot-bearing roots	Jónsdóttir & Watson, 1997; Weiser *et al.,* 2016; Klimešová *et al.*, 2018	Longer lifespan of rhizomes and shoot bearing roots enables sharing of resources among ramets in a clone over longer period and larger area and enables also longer on-spot occupancy. Longer persistence of connections is also generally related to longer root lifespan.
🟦	Lateral spread* (explorative)	Rhizomes, stolons, shoot-bearing roots	Weiser & Smyčka, 2015; Klimešová *et al.*, 2018	The longer lateral spread by clonal growth organ (stolon, rhizome) the farther away (from older roots) new roots must be established.
Plant N acquisition				
🟦	See traits associated to "Soil space occupancy" (+)	Whole root system, absorptive roots	Maire *et al.,* 2009; Simon *et al.*, 2017; Freschet *et al.,* 2018	Most "Soil space occupancy" traits can be important for this function as they determine the temporal and spatial localisation of roots in soil and the efficiency of soil exploration and exploitation.
🟦	Net N uptake rate* (+)	Whole root system, absorptive roots	Garnier, 1991; Poorter *et al.,* 1991; Garnier *et al.,* 1998	When measured on short time periods (from hours to days), this measure primarily represents plant N uptake. Over longer periods (days to months) this measure also takes into account N loss due to leaching, herbivory and senescence.
🟦	Michaelis-Menten constant (Km)* (+)	Whole root system, absorptive roots	Robinson *et al.,* 1994; Miller *et al.*, 2007; Grassein *et al.*, 2015	The Km is a measure of the affinity of a transport system for its substrate; the lower the Km the faster nutrients can be taken up at low availability.
🟦	Ability to fix N* (+)	Nodules	Sprent, 2009; Afkhami *et al.,* 2018; Tedersoo *et al.,* 2018	Provides N to the plant from atmospheric source N_2 via microbial root symbionts.
🟦	Nitrogen fixation rate* (+)	Nodules	Carlsson & Huss-Danell, 2003; Batterman *et al.,* 2013a; Yelenik *et al.,* 2013; Ament *et al.,* 2018	Increases the rate of atmospheric N acquisition.
🟦	Mycorrhizal association type*	Absorptive roots	Read & Perez Moreno, 2003; Read *et al.,* 2004; Lambers *et al.*, 2009; Phillips *et al.,* 2013; Liese *et al.*, 2018; Pellitier & Zak, 2018	Different mycorrhizal types have different enzymatic capacities and ability to explore soil volumes and thereby different abilities to take up N. Also, AM, ECM, and ERM fungi represent a gradient from limited saprotrophic capabilities and greater reliance on inorganic N as primary N source to the ability to produce extracellular enzymes and greater use of increasingly complex organic N forms.
🟦	Root hair length* and density* (+)	Absorptive roots	Robinson & Rorison, 1987; Freschet *et al.,* 2018	Root hairs increase the absorptive surface area of non-woody roots, which is important for N uptake as well as uptake of other nutrients.

	Ratio of absorptive to transport roots* (+/-)	Fine-roots	Schneider *et al.*, 2017; Zadworny *et al.*, 2017	Increases N uptake rate. However, root cortical senescence can also increase N reallocation from senescing tissue and reduce root respiration and root N requirements.
	Mycorrhizal colonization intensity* (+)	Absorptive roots	Miller *et al.*, 1995; Hodge *et al.,* 2003; Treseder, 2013	Mycorrhizal fungi are physiologically and morphologically well-adapted to acquire N from soil. The colonization intensity provides a first approximation of the association between the plant and mycorrhizal partner. However, it should be noted that there is still significant variation in the potential benefit provided by the fungi based on the fungi identity, the total hyphal production and the local environmental context.
	Root cortical aerenchyma (+/-)	Absorptive roots	Postma & Lynch, 2011; Schneider *et al.*, 2017	Decreases radial N transport but increases nutrient uptake efficiency by decreasing metabolic costs.
	Maximum net uptake capacity (Imax)* (+)	Absorptive roots	Robinson *et al.,* 1994; Garnier *et al.,* 1998; Grassein *et al.,* 2018	Imax represents a potential rate at non-limiting substrate availability that might, however, not be fully expressed under in situ conditions.
	Mycorrhizal hyphal length (+)	Absorptive roots	Miller *et al.*, 1995; Chen *et al.*, 2016; McCormack & Iversen, 2019	The hyphal length associated with a colonized root provides a closer approximation of both the potential benefit and cost of the mycorrhizal symbiosis than colonization intensity alone.
	Specific root respiration* (+)	Absorptive roots	Poorter *et al.,* 1991; Reich *et al.,* 1998; Rewald *et al.*, 2016	Root respiration is related simultaneously to maintenance, growth and nutrient uptake of roots and is therefore inconsistently linked to nutrient uptake. It also varies with N form.
	Root N concentration (+)	Absorptive roots	Loqué & von Wirén, 2004; Grassein *et al.,* 2015; Grassein *et al.,* 2018	Root nitrogen is involved in all metabolic processes related to N uptake but is also stored in roots and included in root defence compounds and is therefore inconsistently linked to nutrient uptake.
Plant P acquisition				
	See traits associated to "Soil space occupancy" (+)	Whole root system, absorptive roots	Lynch *et al.,* 2011; Laliberté *et al.,* 2015; Ros *et al.,* 2018	Most "Soil space occupancy" traits can be important for this function.
	Net P uptake rate* (+)	Whole root system, absorptive roots	Itoh, 1987; Föhse *et al.,* 1988	When measured on short time periods (from hours to days), this measure primarily represents plant P uptake. Over longer periods (days to months) this measure also takes into account P loss due to leaching, herbivory and senescence.
	Mycorrhizal association type*	Absorptive roots	Read, 1991; Read & Perez-Moreno, 2003; Philipps *et al.,* 2013; Lambers *et al.,* 2009	Distinct mycorrhizal types have differing capacity to extract P from soils. AM fungi have greater influence on plant P acquisition (representing up to 90% of plant P uptake) than ECM fungi (up to 70%). AM fungal extramatrical mycelia express specific transporters to take up P_i from the periarbuscular space (i.e., they bypass roots). ECM and ERM fungi can access organic forms of P that are not available to AM fungi.
	Ability to grow cluster and dauciform roots (+)	First-order roots	Neumann & Martinoia, 2002; Shane *et al.,* 2006	Cluster and dauciform roots are specialized organs efficient in mining P from nutrient-impoverished soils.
	Root hair length* and density* (+)	Absorptive roots	Wissuwa & Ae, 2001; Brown *et al.,* 2013; Haling *et al.,* 2013	Root hairs can be more effective than mycorrhiza in facilitating P acquisition.
	Ratio of absorptive to transport roots* (+/-)	Fine-roots	Schneider *et al.*, 2017; Zadworny *et al.*, 2017	Increases P uptake rate. However, root cortical senescence can also increase P reallocation from senescing tissue and reduce root respiration and root P requirements.
	Rhizospheric phytase and phosphatase activity (+)	First-order roots	Spohn & Kuzyakov, 2013; Meier *et al.,* 2015	Roots can release (acid) phosphatases (sometimes phytases) directly or exude organic substances that act as substrate for microorganisms which in turn produce phytases and (acid or alkaline) phosphatases.

🟦	Mycorrhizal colonization intensity* (+)	Absorptive roots	Treseder, 2013; Elumeeva *et al.,* 2018	Mycorrhizal fungi are physiologically and morphologically better adapted than roots to extract P from soils thereby increasing host plant nutrient concentrations.
▒	Mycorrhizal genetic diversity* (+)	Absorptive roots	Plassard & Dell, 2010; Plassard *et al.,* 2011; Köhler *et al.,* 2018	P uptake efficiency increases with increasing ECM fungi species richness and diversity. Increased ECM fungi diversity is associated with greater variability in soil exploration types among ECM fungi species, which increases the explored soil volume for P.
▒	Root cortical aerenchyma (+/-)	Absorptive roots	Hu *et al.*, 2014; Schneider *et al.*, 2017	Decreases radial P transport but increases nutrient uptake efficiency by decreasing metabolic costs.
░	Root exudation rate* (+)	Absorptive roots	Lopez-Bucio *et al.,* 2000; Lambers *et al.,* 2012; Ryan *et al.,* 2014; Zhang *et al.,* 2016	Excretion of acidifying/chelating compounds (e.g., citric acid, malic acid) enhances the solubility of inorganic P, although evidence exists mostly for Proteaceae and crops.
░	Mycorrhizal hyphal length (+)	Absorptive roots	Miller *et al.*, 1995; Laliberté *et al.*, 2015; Chen *et al.*, 2016; McCormack & Iversen, 2019	The amount of hyphal length associated with a colonized root provides a closer approximation of both the potential benefit and cost of the mycorrhizal symbiosis than colonization intensity alone.
░	Michaelis-Menten constant (Km)* (+)	Whole root system, absorptive roots	Itoh, 1987; Lambers *et al.*, 2006	The Km is a measure of the affinity of a transport system for its substrate; the lower the Km the faster nutrients can be taken up at low availability. However, the diffusion of inorganic phosphate in soil is the key limiting factor for P uptake so that kinetic parameters of the P-uptake system may have only small effects on the overall uptake capacity of plants.
Plant water acquisition				
🟦	**See traits associated to "Soil space occupancy" (+)**	Whole root system, absorptive roots	Fort *et al.,* 2017; Chitra-Tarak *et al.,* 2019	Most "Soil space occupancy" traits can be important for this function, especially in soils with heterogeneous water distribution.
🟦	Root hair length* and density* (+)	Absorptive roots	Segal *et al.*, 2008; Carminati *et al.,* 2017	Improve the contact of roots with water films of soil particles.
🟦	Cortical thickness* (-)	Absorptive roots	Huang & Eissenstat, 2000; Comas *et al.,* 2012	Thinner cortex resulting in less impedance to water movement towards the stele.
🟦	Fraction of passage cells in exodermis* (+)	Absorptive roots	Enstone & Peterson, 1992; Peterson & Enstone, 1996; Huang *et al.,* 1995; Peterson & Waite, 1996	Higher density of passage cells enhances water movement towards the stele.
🟦	Mycorrhizal colonization intensity* (+)	Absorptive roots	Augé *et al.,* 2001; Querejeta *et al.,* 2003; Querejeta *et al.,* 2012; Prieto *et al.,* 2016	Allows water transfer to the plant and improves root contact with the soil.
🟦	Hydraulic conductance* (+)	Whole root system, fine-roots	Muhsin & Zwiazek, 2002; Eldhuset *et al.,* 2013; Zadworny *et al.,* 2018	Increases the potential flow of water from the roots to upper parts of the plant.
🟦	Vulnerability to embolism (-)	Whole root system	Domec *et al.*, 2006	Occurrence of embolism limits the potential flow of water from roots to upper parts of the plant
🟦	Type and frequency of root entities	Whole root system	North, 2004; Draye *et al.*, 2010; Rewald *et al.*, 2011, 2012; Ahmed *et al.*, 2018	Distribution of the root hydraulic properties between root entities determines root system hydraulic architecture.
🟦	**See traits associated to "Soil water holding capacity" (+)**	Fine-roots	Feddes *et al.*, 2001	Soil water holding capacity acts as a buffer against periodic rainfall events, particularly in places where rainfall evens are irregular.
▒	Suberin concentration (-)	Whole root system	Steudle & Peterson, 1998; Schreiber *et al.*, 2005; Gambetta *et al.*, 2013	Not only deposition of suberin lamellae but also chemical composition of suberin would affect radial water flow from cell to cell (i.e. decrease root hydraulic conductivity).

▦	Xylem lumen area (+)	Whole root system, fine-roots	Hummel *et al.,* 2007; Valenzuela-Estrada *et al.,* 2008; Long *et al.,* 2013; Kong *et al.*, 2014	Greater conduit lumen area may exhibit enhanced hydraulic conductance.
▦	Aquaporin expression (+)	Absorptive roots	Johnson *et al.*, 2014	Facilitates radial, symplastic conductance of water.
░	Lignin concentration* (-)	Absorptive roots	Ranathunge *et al.,* 2003, 2004; Naseer *et al.,* 2012	Lignins may act as apoplastic barriers limiting radial water transport across roots.
Root penetration of soil				
🟦	Root growth pressure (+)	First-order roots	Dexter, 1987; Clark & Barraclough, 1999	Root growth pressure is essential to root penetration, although there is limited evidence of its variation as a trait.
🟦	Mean root diameter* (+)	First-order roots	Materechera *et al.,* 1992	Thicker roots are generally better at penetrating hard soils to greater depth.
▦	Number of main root axes (+)	Whole root system	Jakobson & Dexter, 1987; Landl *et al.,* 2017	In structured soils containing many cracks and biopores, plants with many main axes may penetrate more effectively.
░	Root buckling resistance (+)	First-order roots	Clark *et al.,* 2008; Burr-Hersey *et al.,* 2017	Species and genotypes differ substantially in their ability to penetrate hard soils without buckling or altering their growth trajectory.
░	Root cap friction coefficient (-)	First-order roots	Bengough & McKenzie, 1997; Iijima *et al.,* 2003	Sloughing of root border cells and root exudate production decreases the mechanical resistance to root growth and aids root penetration.
Plant nutrient and C conservation				
🟦	Lifespan* (+)	Whole root system, rhizomes	McCormack *et al.,* 2012; Liu *et al.,* 2016; Klimešová *et al.,* 2018	Decreases losses associated to root turnover.
🟦	Root resorption efficiency and proficiency (+)	Whole root system, absorptive roots	Gordon & Jackson, 2000; Freschet *et al.,* 2010	Decreases losses associated to root senescence.
🟦	Specific respiration rate* (-)	Whole root system	Walk *et al.*, 2006; Rewald *et al.*, 2014, 2016	Respiration is a major driver of C loss.
🟦	Ratio of absorptive to transport roots* (-)	Fine-roots	Lynch, 2019; Schneider *et al.*, 2017	Root cortical senescence reduces metabolic maintenance costs.
🟦	See traits associated to “Plant protection against pathogens and herbivory” (+)	Whole root system	Kaplan *et al.,* 2008; Moore & Johnson, 2017	Traits providing “Plant protection against pathogens and herbivory” are important for this function.
░	Root tissue density* (+)	Whole root system	Ryser, 1996; Liu *et al.,* 2016; Bumb *et al.,* 2018; Lynch, 2019	Increases root lifespan, plant mechanical resistance and decreases plant palatability. Evidence gathered aboveground for leaf tissue density (e.g. leaf dry matter content) theoretically applies belowground. However, reduced tissue density due to aerenchyma formation, increase in cortical cell sizes or decrease in cortical cell numbers may also reduce metabolic costs.
Plant storage				
🟦	Ability to produce storage structures (+)	Tubers, rhizomes, tap roots, corms, bulbs	Klimešová *et al.*, 2018; Pausas *et al.*, 2018	Substantially improves the overall capacity of plants to store C and nutrients.
🟦	Total belowground carbohydrate storage* (+)	Tubers, rhizomes, tap roots, corms, bulbs	Janeček & Klimešová, 2014; Martínez-Vilalta *et al.,* 2016	Storage in specialized organs represents the largest part of C storage and, in contrast to storage in other types of roots, represents an active storage strategy rather than passive accumulation due to limitation of growth (e.g. by nutrients, cold).

Plant regeneration				
🟦	Bud bank size* (+)	Whole root system, rhizomes	Klimešová & Klimeš, 2007; Ott *et al.*, 2019	Belowground bud bank allows plant regeneration after aboveground disturbance
🟦	Depth of buds in bud bank (+)	Whole root system, rhizomes	Lubbe & Henry, 2019; Ott *et al.*, 2019	Deeper buds are more resistant to disturbance like fire or ploughing. On the other hand, deeper buds require more resource storage and time to produce new aboveground shoots.
▨	**See traits associated to "Plant storage" (+)**	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016	Most "Plant storage" traits can be important for this function. Storage organs support regrowth of new aboveground parts.
▨	Ability to produce adventitious shoots on roots (+)	Whole root system	Klimešová *et al.*, 2017a	Adaptation of plants to soil disturbance (numerous perennial weeds of arable land possess ability to resprout from roots). Some species may produce adventitious shoots spontaneously, some only in response to disturbance.
Plant lateral spread and belowground dispersal				
🟦	Ability to produce rhizomes (+)	Rhizomes	Groff & Kaplan, 1988	Rhizomes (belowground stems with adventitious roots) allow the colonization of new ground while relying to some extent on resources from well-established ramets.
🟦	Lateral spread* (explorative)	Rhizomes, stolons, shoot-bearing roots	Weiser & Smyčka, 2015; Klimešová *et al.*, 2018	The longer lateral spread by clonal growth organ (stolon, rhizome) the farther away (from older roots) new roots must be established.
🟦	Ability to produce adventitious roots (+)	Whole root system, rhizomes	Groff & Kaplan, 1988	Facilitates establishment of new rooted areas along belowground (rhizomes) or aboveground (stolons, decumbent shoots) stems and splitting a clone to physically independent parts.
🟦	Lateral rooting extent* (explorative)	Whole root system	Schenk & Jackson, 2002a	Reflects the potential area of ground colonized by roots.
🟦	Ability to produce adventitious shoots on roots (+)	Shoot-bearing roots	Groff & Kaplan, 1988; Klimešová *et al.*, 2017a	Common among species of dry and disturbed areas to extend plant spread and to overcome bud bank limitation.
▨	**See traits associated to "Plant storage" (+)**	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016; Klimešová *et al.*, 2017b	Most "Plant storage" traits can be important for this function as they often serve both functions.
░	**See traits associated to "Root penetration force in soil" (+)**	Root and rhizome apices	Klimešová *et al.*, 2012	Facilitates movement of roots and rhizomes into new areas.
░	Persistence of connection between ramets* (+)	Rhizomes, shoot bearing roots	Jónsdóttir & Watson, 1997	Longer lifespan of rhizomes and shoot bearing roots enables sharing of resources among ramets in a clone over a longer period and larger area and enables longer on-spot occupancy.
Initiation and establishment of mycorrhizal symbioses				This function refers to mycorrhizal fungi as well as pathogenic hyphae.
🟦	Root cortex thickness* (+)	Absorptive roots	Brundrett, 2002; Comas *et al.*, 2012; Zadworny *et al.*, 2016; Kong *et al.*, 2017	Larger parenchyma cortex enhances associations with mycorrhizal colonization by providing larger space for mycorrhizal fungal hyphae and arbuscules.
🟦	**See traits associated to "Plant P acquisition" (-)**	Absorptive roots	Oldroyd, 2013; Raven *et al.*, 2018	Most "Plant P acquisition" traits can be important for this function. Plants with higher P acquisition capacities and therefore higher P status are less likely to establish symbioses.
▨	Root cortex area fraction* (+)	Absorptive roots	Comas *et al.*, 2012; Burton *et al.*, 2013; Gu *et al.*, 2014; Valverde-Barrantes *et al.*, 2016	A large cortex area fraction theoretically implies a higher possibility for connection to symbionts by providing larger space for mycorrhizal fungal hyphae and arbuscules.

	Fraction of passage cells in exodermis* (+)	Absorptive roots	Kamula *et al.,* 1994; Peterson & Enstone, 1996; Sharda & Koide, 2008; Zadworny & Eissenstat, 2011	Exodermal passage cells provide the major penetration sites for the colonization of mycorrhizal and pathogenic hyphae.
	Concentration of compounds controlling the degree of colonization: e.g. lignin, suberin, phenolic compounds, phytohormones, 'reactive oxygen species', branching factors (-)	Absorptive roots	Nicholson & Hammerschmidt, 1992; Matern *et al.,* 1995; Fester & Hause 2005; López-Ráez *et al.,* 2010	Roots contain and produce anti-fungal compounds (i.e. lignin deposition, suberization, high tannin content and 'reactive oxygen species') that control fungi (pathogenic and mycorrhizal) entry and development.
	Carbon translocation to symbionts (+)	Whole root system	Tuomi *et al.,* 2001; Hogberg & Hogberg, 2002; Hobbie, 2006; Nehls *et al.,* 2010	Symbiosis establishment require plant resources such as photosynthetically assimilated carbon; the symbiosis affects the rate of photosynthesis and influences the carbon assimilation and allocation
Plant protection against pathogens and herbivory				
🟦	Secondary metabolites (alkaloids, glucosinolates, phenolics, terpenoids, furanocoumarins, cardenolides) (+)	Whole root system, absorptive roots	Zangerl & Rutledge, 1996; Bezemer *et al.,* 2004; Kaplan *et al.,* 2008; Rasmann *et al.,* 2009; Moore & Johnson, 2018	Decreases plant palatability.
🟦	Mycorrhizal colonization intensity* (+)	Absorptive roots	Newsham *et al.,* 1995; Jung *et al.,* 2012; Babikova *et al.,* 2014	Provides protection against some herbivores and pathogens.
🟦	Fraction of passage cells in exodermis* (-)	Absorptive roots	Kamula *et al.*, 1994	Exodermal passage cells provide the major penetration sites for the colonization of pathogenic fungi.
🟦	See traits associated to "Plant resistance to uprooting" (+)	Whole root system	Ennos, 2000; Burylo *et al.,* 2009	Prevents uprooting during grazing by aboveground herbivores and total root system disruption during grazing by belowground herbivores.
🟦	Root lignin concentration* (+)	Whole root system, absorptive roots	Johnson *et al.,* 2010	Lignin concentration and composition contribute to root toughness acting as an effective barrier to root herbivory.
🟦	Root silica and calcium oxalate content (+)	Absorptive roots	Korth *et al.,* 2006; Park *et al.,* 2009; Moore & Johnson, 2017	These deposits are hard and can abrade insect mouthparts and reduce the digestibility of food via a physical action.
	Root tissue density* (+)	Whole root system, absorptive roots	Bumb *et al.,* 2018	Decreases plant palatability. Evidence gathered aboveground for leaf tissue density (e.g. leaf dry matter content) theoretically applies belowground.
	Root N concentration* (-)	Whole root system, absorptive roots	Brown & Gange, 1990; Dawson *et al.,* 2002; Agrawal *et al.,* 2006	Low levels of N limit the nutritional value of the root tissue, as evidenced aboveground.
	Root hair length* and density* (+)	Absorptive roots	Johnson *et al.,* 2016; Moore & Johnson, 2017	Root hairs offer some protection by preventing very small herbivores from reaching and penetrating the root epidermis or by providing refuge for natural enemies of herbivores such as entomopathogenic nematodes.
Plant resistance to vertical uprooting				This applies particularly to herbaceous species (e.g. under conditions of large herbivore grazing).
🟦	Root length density* (+)	Whole root system	Ennos, 1989.	Particularly important across a range of soil horizons. Increasing root length augments the pull-out resistance up to a critical root axis length, above which roots will break in tension instead of slipping out of the soil.
🟦	Root mass fraction* (+)	Whole root system	Ennos, 1993	Low investment in belowground parts increases chances of uprooting.

■	Root branching density* (+)	Whole root system	Dupuy *et al.,* 2005a; Devkota *et al.,* 2006; Burylo *et al.,* 2009	The tensile force required to uproot whole plants is positively related to the root branching density and number of root tips per unit volume of soil.
■	Tensile strength* (+)	Whole root system	Ennos & Pellerin, 2000; Chimungu *et al.,* 2015; Mao *et al.,* 2018	An estimation of total anchorage strength can be obtained by summing the basal tensile strengths of all the roots.
■	Modulus of elasticity* (-)	Whole root system	Mao *et al.,* 2018	If a root has a small elastic modulus, it will be able to deform further without failing under a given load, thus improving plant anchorage.
□	Ability to produce rhizomes (+)	Rhizomes	Bankhead *et al.,* 2017	The force required to cause rhizome failure can be high, thus improving overall plant anchorage.
□	Lateral rooting extent* (+)	Whole root system	Ennos, 1989; Mickovski *et al.,* 2005	Lateral roots increase the weight of the root-soil plate enmeshed by roots. Increasing root length augments the pull-out resistance up to a critical root axis length, above which roots will break in tension instead of slipping out of the soil.
□	Specific root length (+)	Whole root system	Ennos, 1993; Edmaier *et al.,* 2015	High specific root length often implies more numerous thinner roots improving anchorage whereas low specific root length implies less but thicker roots.
Plant resistance to overturning				This function applies particularly to tree species (e.g. under conditions of lateral wind loading).
■	Root area ratio (+)	Whole root system	Dupuy *et al.,* 2005b	The greater the root area ratio of coarse and fine roots (although roots > 2 cm in diameter contribute less) crossing the potential failure zone (edges of soil-root plate), the more the soil shear strength is increased around the root-soil plate.
■	Vertical root length distribution index* (+)	Whole root system	Bruce *et al.,* 2006; Fourcaud *et al.,* 2008	Deeper root systems are better anchored because the anchorage force provided by roots is proportional to their length up to a critical length, beyond which roots will break before more distal regions are stretched.
■	Root length density* (+)	Whole root system	Danquechin Dorval *et al.,* 2016	The higher the density of roots, either tap, sinker or lateral roots, the greater the resistance to overturning.
■	Root mass fraction* (+)	Whole root system	Danquechin Dorval *et al.,* 2016	Proportionally low investment in below-ground parts increases chances of overturning.
□	Root bending strength (+)	Lateral roots, sinker roots	Nicoll & Ray, 1996; Stokes & Mattheck, 1996	Increases resistance to failure due to root bending during lateral sway.
□	Presence of sinker roots along lateral roots (+)	Lateral roots	Danjon *et al.,* 2005	Sinker roots capture a mass of soil and so increase the weight of the root-soil plate. During lateral sway, a heavier root-soil plate will improve resistance to overturning.
□	Presence of a taproot (+)	Taproot	Ennos, 1993; Fourcaud *et al.,* 2008; Burylo *et al.,* 2010; Yang *et al.,* 2017	If shallow lateral roots are growing horizontally from the taproot, then the taproot constitutes the main root element that contributes to anchorage rigidity. Longer taproots anchor the plant better in soil.
Plant tolerance to waterlogging				
■	Presence of aerenchyma tissue (+)	Absorptive roots, adventitious roots, rhizomes	Kohl *et al.*, 1996; Colmer, 2003; Colmer & Voesenek, 2009; Abiko *et al.,* 2012; Sauter, 2013	Improves root tissue oxygenation by conducting air along the roots (and rhizomes).
■	Presence of pneumatophores (+)	Pneumatophores	Purnobasuki & Suzuki, 2005; Zhang *et al.,* 2015; da Ponte *et al.,* 2019	Pneumatophores (i.e. aerial roots) are morpho-anatomical adaptations of roots with negative geotropism that emerge above the water surface to take up oxygen.

🟦	Root tissue porosity (+)	Whole root system	Gibberd *et al.,* 2001; Purnobasuki & Suzuki, 2004; Ding *et al.,* 2017; Striker & Colmer, 2017	Enhances the internal movements of gases and increases root oxygenation in anaerobic soils.
▢	Tolerance to high ethanol concentration (+)	Whole root system	Jackson *et al.,* 1982; Boamfa *et al.,* 2005; Maricle *et al.,* 2014	Ethanol toxicity is a prime cause of the injury and death of flooded plants.
▢	Fine root regrowth rate (+)	Whole root system	Vidoz *et al.,* 2010; Luo *et al.,* 2011; Sauter 2013; Dawood *et al.,* 2014	Adventitious roots functionally replace primary root systems that may deteriorate during flooding due to oxygen deficiency.
▢	Specific root respiration* (-)	Whole root system	Moog & Brugemann, 1998; Nakamura & Nakamura, 2016	Reduces root oxygen requirements.
Plant resistance to and avoidance of drought				
🟦	Critical tension for conduit collapse* (+)	Whole root system	Hacke *et al.,* 2001	Decrease the risk of conduit collapse during drought.
🟦	**See traits associated to "Plant water acquisition" (+)**	Whole root system, absorptive roots	Brunner *et al.*, 2015	Most "plant water acquisition" traits, including "soil space occupancy" traits, are important for plant resistance to drought.
🟦	**See traits associated to "Plant regeneration" (+)**	Whole root system, tubers, rhizomes, tap roots, corms, bulbs	Qian *et al.*, 2017	Plant regeneration capacity provides plants with the ability to survive intense drought periods despite the loss of aboveground biomass.
▢	**See traits associated to "Plant storage" (+)**	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016	Most "Plant storage" traits can be important for this function. Storage organs support regrowth of new aboveground parts.

Table 2. Broad, multidisciplinary assessment of theoretical and demonstrated links between below-ground traits and nine aspects of ecosystem functioning. CC: colour code, in dark blue: trait of prime importance for performing the ecosystem process or property in at least some environmental conditions; medium blue: trait of secondary importance in at least some environmental conditions; light blue: trait of potential but unknown importance due to missing or low experimental evidence. * refers to traits whose measurement protocols are described in Freschet *et al.* (2020). (+) versus (-) refers to the positive or negative effect of one trait on the function, respectively. 'Entity of interest' refers to a range of plant belowground parts as described in Freschet *et al.* (2020). The full list of references is available as Supplementary Notes S1.

ECOSYSTEM PROCESSES AND PROPERTIES				
CC	Belowground traits	Entity of interest	References (examples of)	Rationale
Ecosystem C cycling				This process includes C inputs, losses, retention and transformation. Its complexity may not be meaningfully simplified into traits that accelerate versus decelerate the element cycling.
🟦	See traits associated to "Soil space occupancy"	Whole root system, absorptive roots, rhizomes	Jastrow *et al.*, 1998; Jobbagy & Jackson, 2000; Rasse *et al.*, 2005; De Deyn *et al.*, 2008; Wang *et al.*, 2010; Clemmensen *et al.*, 2013; Pérès *et al.*, 2013; Cornelissen *et al.*, 2014; Liao *et al.*, 2014; Gould *et al.*, 2016; Poirier *et al.*, 2018	Most "Soil space occupancy" traits can be important for this process because they determine the location (i.e. biotic and abiotic conditions) of root effects on soil, influences the amount of contact surface between roots and soil (e.g. physical enmeshment of soil aggregates), influences the amount of root-derived C inputs to soil (e.g. litter, exudates), soil moisture and nutrient availability.
🟦	Mycorrhizal association type*	Absorptive roots	Langley *et al.*, 2006; Phillips *et al.*, 2013; Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2015, 2019	Ecosystems dominated by arbuscular mycorrhizal, ericoid mycorrhizal and ectomycorrhizal fungi plants are characterized by different carbon and mineral nutrient cycles due to the different enzymatic capacities of the symbionts. Ecosystems dominated by plants in symbiosis with ectomycorrhizal fungi store 70% more C in soils than ecosystems dominated by arbuscular mycorrhizal-associated plants.
🟦	Specific root respiration*	Absorptive roots	Bond-Lamberty *et al.*, 2004; Reich *et al.*, 2008; Bardgett *et al.*, 2014	The contribution of root respiration represents on average 40-50% of the total soil CO_2 efflux but varies strongly among species.
🟦	Mycorrhizal colonization intensity*	Absorptive roots	Rillig *et al.*, 2001; Gleixner *et al.*, 2002; Kögel-Knabner, 2002; Allen *et al.*, 2003; Langley & Hungate, 2003; Fernandez *et al.*, 2016; Poirier *et al.*, 2018	Mycorrhizal fungi synthesize hydrophobic and recalcitrant compounds, such as chitin and melanin, respectively, which are discussed to be less biodegradable and to accumulate in soils (at least in ecosystems experiencing cold climates).
🟦	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.*, 1997; Fan & Guo, 2010; McCormack *et al.*, 2015; Klimešová *et al.*, 2018	Root lifespan regulates the quantity and quality of root-derived organic matter transferred into the soil organic matter pool. Fine-roots and low-order roots, which have a short lifespan and turnover rapidly, represent a substantial input of C into the soil.
🟦	Root litter mass loss rate*	Whole root system, fine-roots	Silver & Miya, 2001; Zhang & Wang, 2015; See *et al.*, 2019	Determines the rate at which C from litters is released into the atmosphere or enters the soil in the form of particulate organic matter or dissolved organic matter.

🟦	Root exudation rate*	Fine-roots	Tisdall & Oades, 1982; Kuzyakov, 2010; Phillips *et al.,* 2011; Keiluweit *et al.,* 2015; Tückmantel *et al.,* 2017; Henneron *et al.*, 2020	Enhanced root exudation increases the microbial activity and accelerates the breakdown of soil organic matter in the rhizosphere (priming effect). Meanwhile root exudates can act as binding agents to stabilize soil aggregates and thus enhance the stabilization of occluded soil organic matter.
🟦	Root hair length and density*	First-order roots	Gould *et al.,* 2016; Poirier *et al.,* 2018	Root hairs can physically attach soil particles and contribute to the formation of stable soil aggregates enriched in C.
🟦	Mycorrhizal hyphal length	Absorptive roots	Miller & Jastrow, 1990; Degens, 1997; Wilson *et al.,* 2009; Wu *et al.,* 2014	Increased hyphal length leads to greater enmeshment of soil particles and increases soil aggregate stability and soil organic C stabilisation.
🟦	Ability to fix N*	Nodules	Cole *et al.,* 1995; Binkley, 2005; Kaye *et al.,* 2000; Fornara & Tilman, 2008; De Deyn *et al.,* 2011	The biological fixation of N_2 by N_2-fixing root symbiotic bacteria generally increases the plant belowground and aboveground primary productivity. The presence of N_2-fixing species also tends to increase soil organic C accumulation.
▒	Root branching density*	Absorptive roots	Poirier *et al.,* 2018	A high branching density contributes to stabilizing soil aggregates through enmeshment of soil particles and higher production of exudates by root tips.
▒	**See traits associated to "Hydraulic redistribution" (+)**		Domec *et al.*, 2010	Affects topsoil organic matter and litter decomposition.
Ecosystem N cycling				This process includes N inputs, losses, retention and transformation. Its complexity may not be meaningfully simplified into traits that accelerate versus decelerate the element cycling.
🟦	**See traits associated to "Soil space occupancy"**	Whole root system, absorptive roots	Fornara *et al.,* 2011; Abalos *et al.,* 2014; De Vries *et al.,* 2016	Most "Soil space occupancy" traits can be important for this process. The density and distribution of roots determines the location of root exudates, litter inputs and nutrient uptake.
🟦	**See traits associated to "Plant N acquisition"**	Whole root system, absorptive roots	van der Krift & Berendse, 2001; Scherer-Lorenzen *et al.,* 2003; Personeni & Loiseau, 2005; Batterman *et al.,* 2013b; Leroux *et al.,* 2013; Moreau *et al.,* 2019	Most traits associated to "Plant N acquisition" can be important for this process. The capacity of plants to acquire N from soil, and compete with microorganisms, across a range of locations in the soil influences N cycling.
🟦	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.,* 1997; Fan & Guo, 2010; McCormack *et al.,* 2015	Influences the input of litter (and N-containing compounds) into the soil.
🟦	Root litter nutrient release rate*	Whole root system, fine-roots	Parton *et al.,* 2007	Determines the rate at which N is transferred from litter to soil.
🟦	Root N concentration*	Whole root system, absorptive roots	Hobbie *et al.,* 2006; Parton *et al.,* 2007; Legay *et al.,* 2014; Cantarel *et al.,* 2015; Thion *et al.,* 2016	Root N is positively related to litter N release rate (lower N immobilization rate), N mineralisation and nitrification (e.g. archaeal ammonia oxidisers are more abundant in the rhizosphere of high N roots than low N roots).
🟦	Mycorrhizal association type*	Absorptive roots	Phillips *et al.,* 2013; Lin *et al.,* 2017; Wurzburger & Brookshire, 2017; Zhu *et al.,* 2018	Ecosystems dominated by AM, ERM and ECM plants are characterized by different C and mineral nutrient cycles due to the different enzymatic capacities of the symbionts. AM, ECM, and ERM fungi represent a gradient from limited saprotrophic capabilities and greater reliance on inorganic N as primary N source to the ability to produce extracellular enzymes and greater use of increasingly complex organic N forms.
▒	Root exudation rate*	Fine-roots	Phillips *et al.,* 2011; Meier *et al.,* 2017; Moreau *et al.,* 2019	Enhanced root exudation increases soil microbial activity and accelerates the breakdown of (fast-cycling) organic N forms in the rhizosphere. Roots can exude/secrete nitrification and denitrification inhibitors.

Ecosystem P cycling				
■	**See traits associated to "Plant P acquisition"**	Whole root system, absorptive roots	Lambers *et al.,* 2008; Ros *et al.,* 2018	Most traits associated to "Plant P acquisition", including traits associated to "Soil space occupancy", can be important for this process. The capacity of plants to acquire P from soil, with or without mycorrhizal symbiosis, across a range of locations in the soil influences P cycling.
■	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.,* 1997; Fan & Guo, 2010; McCormack *et al.,* 2015	Influences the input of litter (and P-containing compounds) into the soil.
■	Root litter nutrient release rate*	Whole root system, fine-roots	Fujii & Takeda, 2010	Determines the rate at which P is transferred from litter to soil.
■	Root P concentration*	Whole root system, fine-roots	Seastedt, 1988; McGrath *et al.,* 2000; Manzoni *et al.,* 2010	Can be a major driver of soil P availability in P-limited soils.
Soil water holding capacity				
■	**See traits associated to " Ecosystem C cycling"**	Fine-roots	Rillig & Mummey, 2006; Poirier *et al.,* 2018	Root and mycorrhizal traits favouring C accumulation in soil and improving soil aggregate stability, improve soil water holding capacity.
▨	Root mass and length density* (+)	Fine-roots	Noguchi *et al.,* 1997	After death and decay, roots leave empty galleries and pores favourable to water retention. Roots also contribute to organic matter accumulation, which increases soil water holding capacity.
▨	Root turnover* (+)	Fine-roots	Noguchi *et al.,* 1997; Perillo *et al.,* 1999	After death and decay, roots leave empty galleries and pores favourable to water retention. Roots also contribute to organic matter accumulation, which increases soil water holding capacity.
□	Mean root diameter*	First-order roots	Norton *et al.,* 2004; Ghestem *et al.,* 2011; Soto-Gomez *et al.,* 2018	Larger roots leave larger pores that, depending on the context, may be favourable or detrimental to water retention.
Bedrock weathering				
■	Root exudation rate* (+)	Fine-roots	Ochs *et al.,* 1993; Hinsinger, 1998; Phillips *et al.,* 2009; He *et al.,* 2012; Houben & Sonnet, 2012	Exudation of organic acids and enzymes by roots enhance bedrock weathering. Additionally, C flux to the rhizosphere stimulates the weathering activity of root microbiome.
■	Maximum rooting depth* (+)	Whole root system	Richter & Markewitz, 1995; Schwinning, 2010; Maeght et al., 2013	Deep-rooted species are most likely to reach bedrock.
■	Root mass and length density* (+)		Hinsinger *et al.,* 1992	Increases root overall impact on bedrock.
■	**See traits associated to "Root penetration of soil" (+)**	Whole root system	Bengough, 2012; Kolb *et al.,* 2012	Root growth pressures may help to extend cracks in weathering bedrock. Root elongation within a rock crack depends on the balance of axial and radial pressures.
□	Mycorrhizal association type*	Fine-roots	Taylor *et al.,* 2009; Pawlik *et al.,* 2016	There is stronger evidence for bedrock weathering from ECM activity than this of AM.
□	Mycorrhizal fungi identity*	Fine-roots	Jongmans *et al.,* 1997; Hoffland *et al.,* 2004; Schwinning, 2010.	Due to differences in rates of chemical exudation, hyphal production, and exploration distances among species of mycorrhizal fungi, species identity is likely to be an important determinant for faster or slower weathering rates.

◻	Root secondary growth (+)	Whole root system	Misra *et al.,* 1986; Richter & Markewitz, 1995	The radial force widening a crack is the product of the radial pressure and the contact area of root surface in the crack.
Hydraulic redistribution				
🟦	Diverse root growth angles* (+)	Whole root system	Hultine *et al.,* 2003a; Hultine *et al.,* 2003b Scholz *et al.,* 2008; Siqueira *et al.,* 2008	Extensive distribution of roots in higher and lower soil horizons allows connection between wet and drier soil layers.
🟦	Maximum rooting depth* (+)	Whole root system	Burgess *et al.,* 1998; Burgess, 2000; Scholz *et al.,* 2008; Maeght *et al.*, 2013	Presence of roots at depth allows access to wetter soil layers in soils experiencing drying of the upper horizons, which is critical for hydraulic lift.
🟦	**See traits associated to "Plant resistance and survival to drought" (+)**	Whole root system, absorptive roots	Domec *et al.,* 2004; McElrone *et al.,* 2007; Warren *et al.,* 2008; Grigg *et al.,* 2010; Prieto *et al.,* 2012a ;Prieto *et al.,* 2014	Most traits favouring "Plant resistance to drought", including traits favouring "Plant water acquisition", will contribute to maintaining a functional root system during periods of soil drying and therefore allow hydraulic redistribution.
🟦	**See traits associated to "Plant water acquisition" (+)**	Whole root system, absorptive roots	Egerton-Warburton *et al.*, 2008; Prieto *et al.*, 2012b	Root and mycorrhizal traits favouring "plant water acquisition" increase water flow through the root system.
◻	Vertical root mass distribution index* (+)	Whole root system	Schenk & Jackson, 2002a, 2002b	High proportion of roots in deeper soil horizons may reinforce hydraulic lift.
◻	Root turnover* (+)	Absorptive roots	Espeleta *et al.,* 2004	Determines the presence of active roots in soil layers that absorb and redistribute water.
◻	**See traits associated to "Plant lateral spread and belowground dispersal" (+)**	Whole root system	Jónsdóttir & Watson, 1997; Stuefer, 1998	Redistribution of water can occur in the horizontal plane via plant clonal connectors.
Ecosystem evapotranspiration				
🟦	**See traits associated to "Plant water acquisition" (+)**	Whole root system, absorptive roots	Nepstad *et al.,* 1994; Augé *et al.,* 2008; Fort *et al.,* 2017	Most traits associated to "Plant water acquisition" facilitate the transfer of water from the soil to the plant and favour evapotranspiration.
🟦	**See traits associated to "Hydraulic redistribution" (+)**		Domec *et al.*, 2010	Facilitates the transfer of water from deep soils to shallower soil horizons.
Soil inter-particle cohesion				This property relates to soil surficial erosion.
🟦	**See traits associated to "Soil space occupancy" (+)**	Whole root system, fine-roots	Angers & Caron, 1998; Gould *et al.,* 2016; Poirier *et al.,* 2018	Most traits increasing "Soil space occupancy" contribute to stabilizing soil macroaggregates through entanglement of soil particles, production of exudates, binding and compressing soil particles, and root-induced wetting and drying cycles.
🟦	Root exudation rate* (+)	Fine-roots	Carminati *et al.*, 2016; Baumert *et al.,* 2018; Poirier *et al.,* 2018	Exudates (especially polysaccharides and cations) act as binding agents to initiate microaggregate formation and stabilize macroaggregates. Exudates also clog aggregate pores and induce water repellency.
🟦	Mycorrhizal colonisation intensity* (+)	Absorptive roots	Rillig *et al.,* 2015; Poirier *et al.,* 2018	Mycorrhizal fungi produce exopolymers and proteins that glue and bind soil particles. The release of hydrophobins by ECM increases aggregate hydrophobicity. In addition, hypha enmesh soil fine particles within micro and macro aggregates.
🟦	Root hemicellulose content (+)	Whole root system	Poirier *et al.,* 2018	Hemicellulose contains pentoses and uronics acids that stabilize soil aggregates.

🟦	Root suberin content (+)	Whole root system	Bachman *et al.,* 2008; Poirier *et al.,* 2018	Suberin increases aggregate hydrophobicity and soil water repellency.
🟦	**See traits associated to “Plant water acquisition” (+)**	Whole root system, absorptive roots	Czarnes *et al.,* 2000	Soil inter-particle cohesion is affected by wetting-drying cycles that increase the strength of organic binding agents.
Soil reinforcement against shallow landslides				
🟦	Maximum rooting depth* (+)	Whole root system	van Beek *et al.,* 2005	Deep growing roots are more likely to cross the potential soil shear surface (zone within the soil where failure initiates), which enhances soil reinforcement.
🟦	Vertical root length distribution index* (+)	Whole root system	Ghestem *et al.,* 2014	A greater number of branched roots below the shear plane will enhance root anchorage and so improve soil shear resistance.
🟦	Root area ratio (+)	Whole root system	Wu, 1976; Bischetti *et al.*, 2005; Mao *et al.*, 2012	The greater the root area ratio of coarse and fine-roots (although roots > 2 cm in diameter contribute less) crossing the potential failure zone, the more the soil shear strength is increased, thus improving soil reinforcement.
🟦	Root length density* (+)	Whole root system	Ennos, 1993; Stokes *et al.,* 2009	Increasing root length augments the pull-out resistance up to a critical length, from which roots will break in tension instead of slipping out of the soil.
🟦	Root branching angle* (+)	Tap and sinker roots	Ghestem *et al.,* 2014	Vertically oriented roots increase soil shear resistance.
🟦	Tensile strength* (+)	Whole root system	Chimungu *et al.,* 2015; Giadrossich *et al.,* 2017, 2019; Mao *et al.,* 2018	A higher tensile strength will enable a root to mobilise its full strength as it is pulled out of soil, thereby increasing soil shear strength.
🟦	Modulus of elasticity* (+)	Whole root system	Cohen *et al.,* 2009; Mao *et al.,* 2018	Roots with large elastic modulus can remain anchored in soil, even after soil failure has occurred, thus holding vegetation in place and retarding or preventing mass substrate failure.
🟦	Root bending resistance (+)	Tap, sinker and lateral roots	Goodman *et al.*, 2001	During landslide, thick structural roots act like soil nails that bend, preventing soil collapse, before breaking.
🟦	**See traits associated to “Plant water acquisition”**	Whole root system, absorptive roots	Boldrin *et al.,* 2017	Rapid water acquisition will maintain soil in a drier state that offers greater resistance to deformation.

Table 3. Overview of studies testing the relationships between root traits and plant N uptake capacity. The full list of references is available as Supplementary Notes S1.

Reference	**Function measured**	**Units**	**Method used**	**Temporal scale**	**Spatial scale**	**Root or plant traits measured (and relationship found)**	**Root entities**	**Number of species**	**Growth forms**	**Biome**
Bowsher *et al.,* 2016	Short-term net uptake rate	µmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	30 h	Pot	Specific root length (ns), root tissue density (ns)	Whole root system	6	Forbs (6)	
Craine *et al.,* 2003	Long-term net uptake rate	mg N kg^{-1}	Soil NH_4^+ and NO_3^- sampling		Pot	Fine root mass density (+), coarse root mass density (ns)	Fine roots (<2mm)	11	Graminoids (6), forbs (3), Legumes (2)	Temperate
de Vries & Bardgett, 2016	Long-term net uptake rate	kg N ha^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	48 h	Pot	Root biomass (+), specific root length (ns), root tissue density (-), root N concentration (ns)	Whole root system	24	Graminoids (12), forbs (12)	Temperate
Dybzinski *et al.,* 2019	Long-term net uptake rate	g N m^{-2} day^{-1}	Whole plant N increment	95-110 days	Pot	Fine root mass (ns in 62% of cases; linear + in 5% of cases; saturated in 33% of cases)	Fine roots (<1mm)	18	Graminoids (5), Forbs (2) Tree (11)	
Dybzinski *et al.,* 2019	Long-term net uptake rate	g N m^{-2} day^{-1}	Whole plant N increment		Field	Fine root mass (ns: 5 studies; linear +: 2 studies)	Fine roots (<1mm)	7	Tree (7)	
Ficken & Wright, 2019	Long-term net uptake rate	mg N g^{-1} leaf	^{15}N tracers of NH_4^+ and NO_3^-	10 days	Pot	Root tip number per biomass (+), fine:coarse root volume (+), leaf nitrogen content (+)	Whole root system	4	Shrub (3), Tree (1)	Temperate
Freschet *et al.,* 2018	Short-term net uptake rate	µg N m^{-1} root h^{-1} and µg N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	6 h	Pot	Root mass fraction (ns), deep root fraction (ns), specific root length (ns), root hair length (ns), root interbranch distance (ns), root N concentration (ns), leaf mass fraction (ns), specific leaf area (ns), maximum leaf photosynthetic capacity (ns), plant height (-)	Absorptive roots	9	Graminoids (3), forbs (3), Legumes (3)	Temperate
Garnier *et al.,* 1989	Long-term net uptake rate	mg N g^{-1} root day^{-1}	Whole plant N increment	28 days	Hydro-ponics	Relative growth rate (+)	Whole root system	14	Graminoids (4), forbs (10)	Temperate
Garnier *et al.,* 1989	Short-term net uptake rate	mg N g root^{-1} day^{-1}	NO_3^- depletion in nutrient solution	90 min	Hydro-ponics	Relative growth rate (+)	Whole root system	7	Graminoids (2), forbs (5)	Temperate
Garnier, 1991	Long-term net uptake rate	mg N g root^{-1} day^{-1}	Whole plant N increment	17-28 days	Hydro-ponics	Relative growth rate (+)	Whole root system	21	Graminoids (9), forbs (12)	Temperate

Grassein *et al.,* 2015	Imax, Km	µmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+	5 min	Common garden	Imax NH_4^+: Specific root length (ns), root dry matter content (ns), root N concentration (+), specific leaf area (+), leaf dry matter content (ns), shoot N content (ns), shoot:root ratio (+) Km NH_4^+: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (ns), leaf dry matter content (+), shoot N content (ns), shoot:root ratio (ns)	Whole root system	8	Graminoids (8)	Temperate
Grassein *et al.,* 2015	Imax, Km	µmol N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	5 min	Common garden	Imax NO_3^-: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (+), leaf dry matter content (ns), shoot N concentration (ns), shoot:root ratio (ns) Km NO_3^-: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (-), leaf dry matter content (+), shoot N concentration (ns), shoot:root ratio (ns)	Whole root system	8	Graminoids (8)	Temperate grassland
Grassein *et al.,* 2018	Imax	nmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+	1 h	Field + excised roots	Specific root length (ns), root dry matter content (-), root N concentration (+), specific leaf area (ns), leaf dry matter content (ns), leaf N content (+)	Absorptive roots	3	Graminoids (3)	Temperate
Grassein *et al.,* 2018	Imax	nmol N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	1 h	Field + excised roots	Specific root length (+), root dry matter content (-), root nitrogen concentration (+), specific leaf area (ns), leaf dry matter content (ns), leaf N content (+)	Absorptive roots	3	Graminoids (3)	Temperate grassland
Hodge, 2003	Long-term net uptake rate	mg N (^{14}N+^{15}N)	^{15}N tracers of labelled ^{15}N shoot material	22 days	Pot	In mixtures: Root length (+), mycorrhizal inoculation (+) In monocultures: Root length (ns), mycorrhizal inoculation (ns)	Whole root system	2	Graminoids (1), forbs (1)	Temperate
Hodge *et al.,* 1998	Long-term net uptake rate	µg N	^{15}N tracers of labelled organic material in patches	39 days	Pot	Root biomass (ns), root length (ns)	Whole root system	5	Graminoids (5)	Temperate
Hodge *et al.,* 1999	Long-term net uptake rate	µg N	^{15}N tracers of labelled organic material in patches	56 days	Pot	Root length density (+)	Whole root system	2	Graminoids (2)	Temperate grasslands
Hong *et al.,* 2018	Short-term net uptake rate	µg N m^{-1} root h^{-1}	^{15}N tracers of NH_4^+ or NO_3^- or Glycine or (NH_4^+ + NO_3^- + Glycine)	24 h	Field	Root surface area (+), specific root length (+), root diameter (-), root biomass (-)	Whole root system	10	Graminoids (3), forbs (4), legumes (3)	Alpine grassland

Kulmatiski *et al.,* 2017	Short-term net uptake rate	% cm^{-1} root	^{15}N tracers of NH_4^+ and NO_3^-	72 h	Field	Root biomass (ns)	Whole root system (absorptive)	5	Graminoids (3), forbs (1), Shrub (1)	
Larson & Funk, 2016	Long-term net uptake rate	µg N day^{-1}	Whole plant N increment	28-58 days	Pot	Root growth rate (+), root elongation rate (+), root mass fraction (-), specific root length (+), root diameter (-)	Whole root system (absorptive)	18	Graminoids (4), forbs (7), Trees (7)	Temperate
Leffler *et al.,* 2013	Short-term net uptake rate	µg N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	2 h	Pot	Root mass (+), root length (+), specific root length (+)	Whole root system	5	Graminoids (5)	Temperate
Levang-Brilz & Biondini, 2003	Long-term net uptake rate	g N m^{-2} root day^{-1}	Whole plant N increment	60-90 days	Pot	Root:shoot ratio (+), relative growth rate (saturated relationship)	Whole root system	55	Graminoids (17), forbs (29), legumes (7), shrubs (2)	Temperate
Liu & Kleunen, 2019	Long-term net uptake rate	g N g^{-1} root day^{-1}	Whole plant N increment	26 days	Pot	Root mass fraction (-)	Whole root system (absorptive)	41	Graminoids (11), forbs (26), Legumes (4)	Temperate
Ma *et al.,* 2018	Short-term net uptake rate	µg N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	90 min	Field	Specific root length (ns), root diameter (ns)		17	Trees (17)	Grassland, boreal, temperate, subtropical, tropical
Ma *et al.,* 2018	Long-term net uptake rate	µg N g^{-1} root h^{-1}	Whole plant N increment	7 days	Field	Specific root length (ns), root diameter (ns)		17	Trees (17)	Grassland, boreal, temperate, subtropical, tropical
Maire *et al.,* 2009	Imax, Km	mg N g^{-1} root h^{-1}	NH_4^+ and NO_3^- depletion in nutrient solution	90 min	Common garden	Imax: Root dry mass (ns), root area (-), leaf N concentration (+)	Absorptive roots	13	Graminoids (13)	Temperate
Maire *et al.,* 2009	Long-term net uptake rate	g N m^{-3} y^{-1}	Shoot plant N increment	209-212 days	Common garden	Root dry mass (+), leaf N concentration (ns)	Absorptive roots	13	Graminoids (13)	Temperate
Osone *et al.,* 2008	Long-term net uptake rate	g N g^{-1} root day^{-1}	Whole plant N increment		Pot	Relative growth rate (+), root:shoot ratio (-), specific leaf area (+), leaf N concentration per area (-), net assimilation rate (+)	Whole root system (absorptive)	11	Forbs (6), Trees (5)	
Poorter *et al.,* 1991	Long-term net uptake rate	nmol N g root^{-1} day^{-1}	Whole plant N increment	17 days	Hydro-ponics	Relative growth rate (+)	Whole root system	24	Graminoids (11), forbs (13)	Temperate

Ravenek *et al.,* 2016	Short-term net uptake rate	µmol N m^{-1} root h^{-1}	Li and Rb uptake rate (surrogate tracers)	46 h	Pot	Relative growth rate (ns), selective root placement (ns), root length density (ns), specific root length (ns)	Absorptive roots	8	Graminoids (4), forbs (4)	Temperate
Reich *et al.,* 1998	Long-term net uptake rate	mg N g^{-1} root day^{-1}	Whole plant N increment	61 days	Pot	Specific root length (+), root length ratio (+), root respiration (+), relative growth rate (+)	Whole root system	9	Trees (9)	Boreal forest
Robinson *et al.,* 1991	Long-term net uptake rate		Whole plant N increment	97 days	Pot	Root length density (ns)	Whole root system (absorptive)	1 (13 karyo-types)	Graminoids (1)	Temperate
Wiesler & Horst, 1994	Long-term net uptake rate	kg N ha^{-1}	Soil NO_3^- depletion and shoot uptake rate		Field	Root length density (+)	Whole root system	1 (10 maize cultivars)	Graminoids (1: crop)	Temperate
Zerihun & Bassirirad, 2001	Imax, Km	µmol N g^{-1} root h^{-1}	NO_3^- and NH_4^+ depletion	12 h	Pot	Imax NH_4^+: Relative growth rate (+), biomass allocation (ns) Km NH_4^+: Relative growth rate (+)	Fine (<1mm) & coarse roots	6	Trees (6)	Temperate

Table 4. Overview of studies testing the relationships between root traits and soil reinforcement against shallow landslides. The full list of references is available as Supplementary Notes S1.

References	Property measured	Method used	Soil type	Soil moisture content	Root or plant traits measured (and relationship found)	Root entities	Number of species	Growth forms	Biomes
Docker & Hubble, 2008	Increase in shear stress in soil matrix due to roots (kPa)	In-situ testing with a large shear box (ranged from 0.4 x 0.4 to 0.5 x 0.5 at the base and 0.21 - 0.44 m in height)	Brown loam and sandy loam	Saturated	Root area ratio of roots crossing the shear plane (+)	Whole root system	4	Trees (4)	Subtropical rainforest, subtropical dry forest
Fan & Chen, 2010	Soil matrix shear strength (kPa)	In-situ testing with a large shear box (0.3 x 0.3 x 0.2 m)	Clayey and sandy soils	12-14%	Cumulated tensile strength of all roots per unit area of soil (+), cumulated tensile strength of all roots crossing the shear plane (+)	Roots < 20 mm	5	Trees (5)	Tropical rainforest
Ghestem *et al.*, 2014; Veylon *et al.*, 2015	Tangential shear stress at yield point (kPa) of soil matrix	Laboratory testing with a large shear box (0.5 x 0.5 x 0.3 m)	Alluvial silty clay	9-21%	Roots crossing the shear plane: cross-sectional area of coarse roots (+), number of coarse roots (+), fine root mass (+), number of coarse root branches per unit length (ns), coarse root length (ns), coarse root diameter, coarse root volume (ns), fine root mass density (ns) Roots above the shear plane: coarse root length (+), number of coarse root branches per unit length (+), number of coarse roots (ns), cross-sectional area of coarse roots (ns), diameter of coarse roots (ns), coarse root volume (ns), fine root mass (ns), fine root mass density (ns) Roots below the shear plane: number of coarse root branches per unit length (+), coarse root volume (+), fine root mass (+), number of coarse roots (ns), cross-sectional area of coarse roots (ns), coarse root diameter (ns), coarse root length (ns), fine root mass density (ns).	Whole root system	3	Trees (3)	Subtropical rainforest
Normaniza *et al.*, 2008; Ali & Osman, 2008	Soil matrix shear strength (kPa)	Laboratory testing with a large shear box (0.3 x 0.3 x 0.2 m)	Silty sand	Not known	Root length density (+), root diameter (+)	Whole root system	3	Trees (2), Shrubs (1)	Tropical rainforest

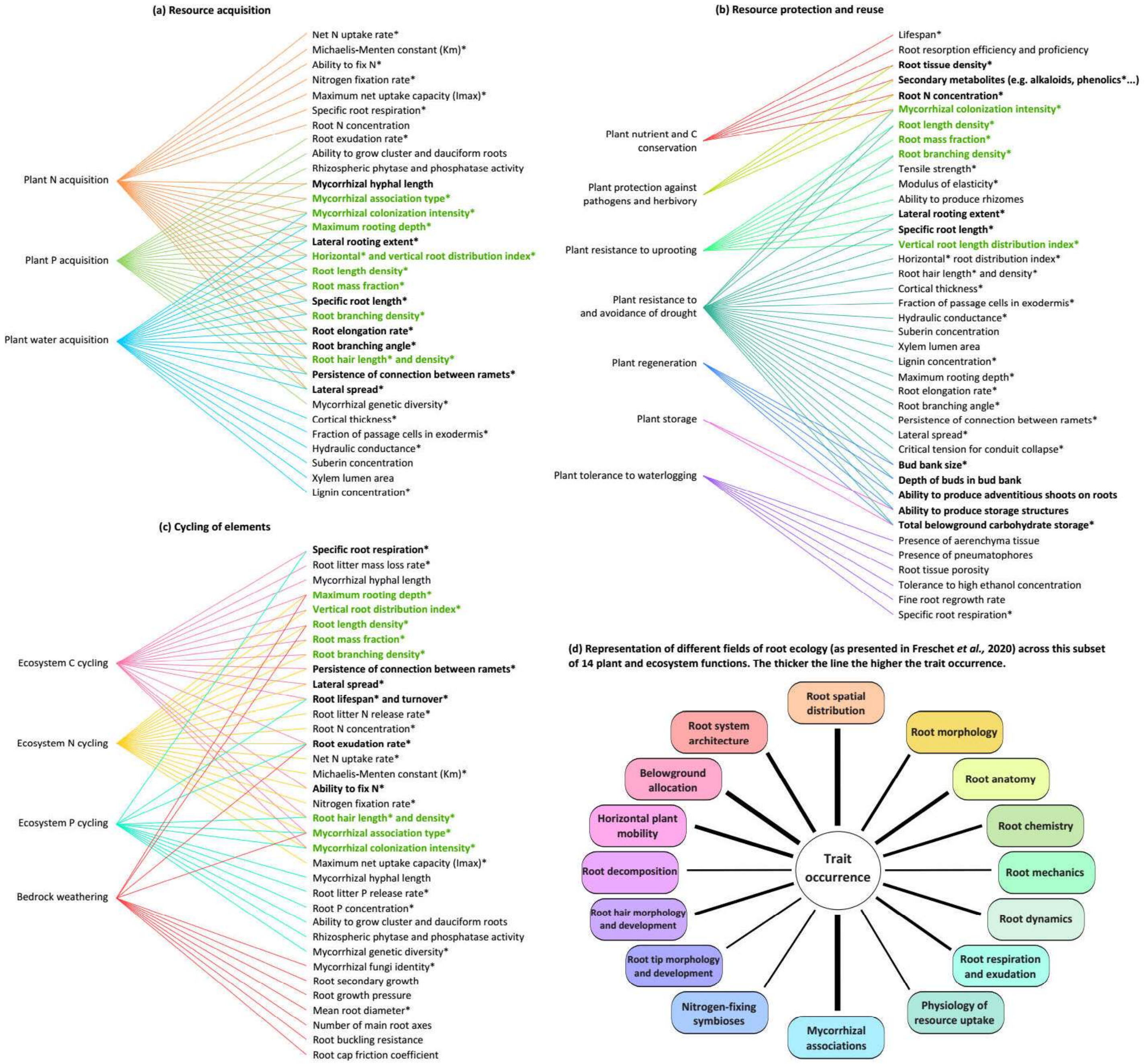
Wu *et al.*, 1988	Force applied to shear soil matrix (N)	In-situ testing with a large shear box (0.6 x 0.3 x 0.3 m)	Sandy silt, gravelly silt, silty clay and sand	Partially saturated	Cumulated tensile force of all roots crossing the shear plane (+ in sandy and gravelly silt soils only, 2 species). Cumulated tensile force of all roots crossing the shear plane (ns in silty clay, 1 species).	Whole root system	3	Trees (3)	Boreal forest, temperate forest

Figure captions

Figure 1. Plant and ecosystem functioning typically relate to a wide range of root traits (a, b, c) from a wide range of fields of root ecology (d). Meanwhile, some traits play multiple roles in a range of functions, as illustrated by a subset of functions associated to (a) resource acquisition and (b) resource protection and use by plants, and the (c) cycling of elements in ecosystems; as well as a (d) compilation of the relative occurrence of traits from several sub-disciplines of root ecology in these three examples. Traits with an * refer to traits whose measurement protocols are described in Freschet *et al.* (2020). Traits connected to at least two functions are shown in bold font and those highly represented across all three panels (a, b and c) are further highlighted in green font. Colours of lines and text boxes are only for visual effects.

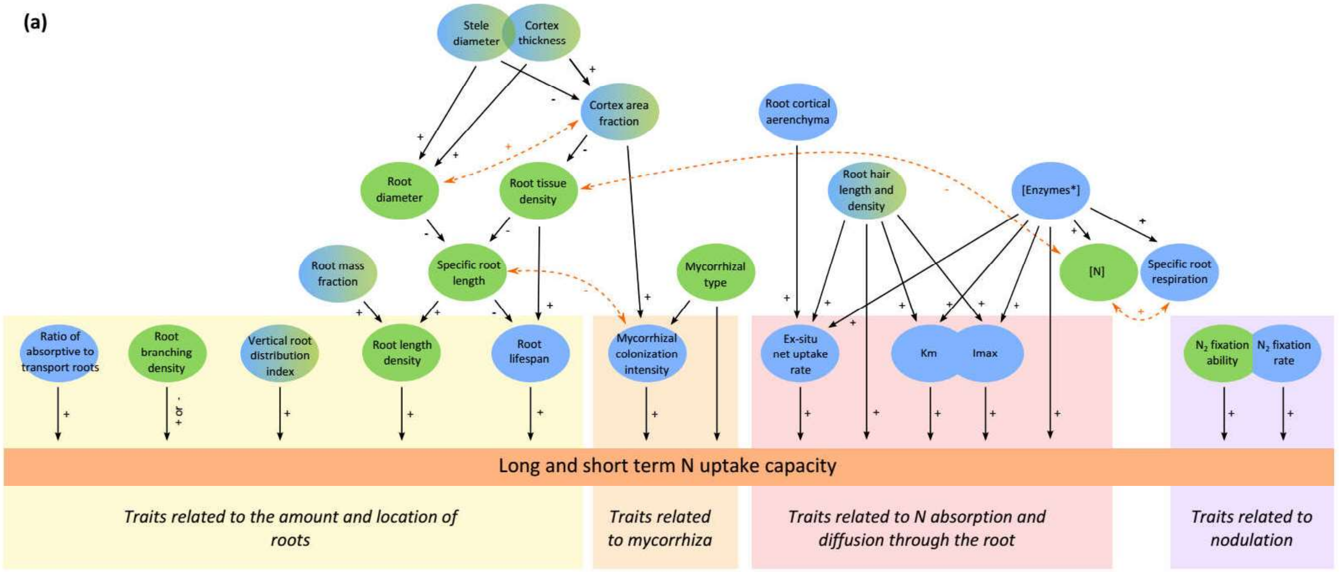
Figure 2. Direct, indirect and hierarchical relationships between the (non-exhaustive) range of root traits that have been linked to (a) long- and short-term N uptake and (b) soil reinforcement against shallow landslides. Black arrows represent causal relationships. + and - represent the direction of the relationship. Trait position along the vertical axis depicts trait hierarchical relationships, with lower levels representing 'composite' traits and upper levels representing 'underlying' traits (see main text). Major trait covariations are also shown with orange dotted arrows. The ease of trait measurement is approximated by colour ranging from blue ('hard' traits) to green ('soft' traits). * 'Enzymes' refers to the range of enzymes related to N uptake, assimilation and transport in roots. Imax stands for ‘root maximum net ion uptake rate’ and Km for ‘root Michaelis-Menten constant’.

Figure 1.

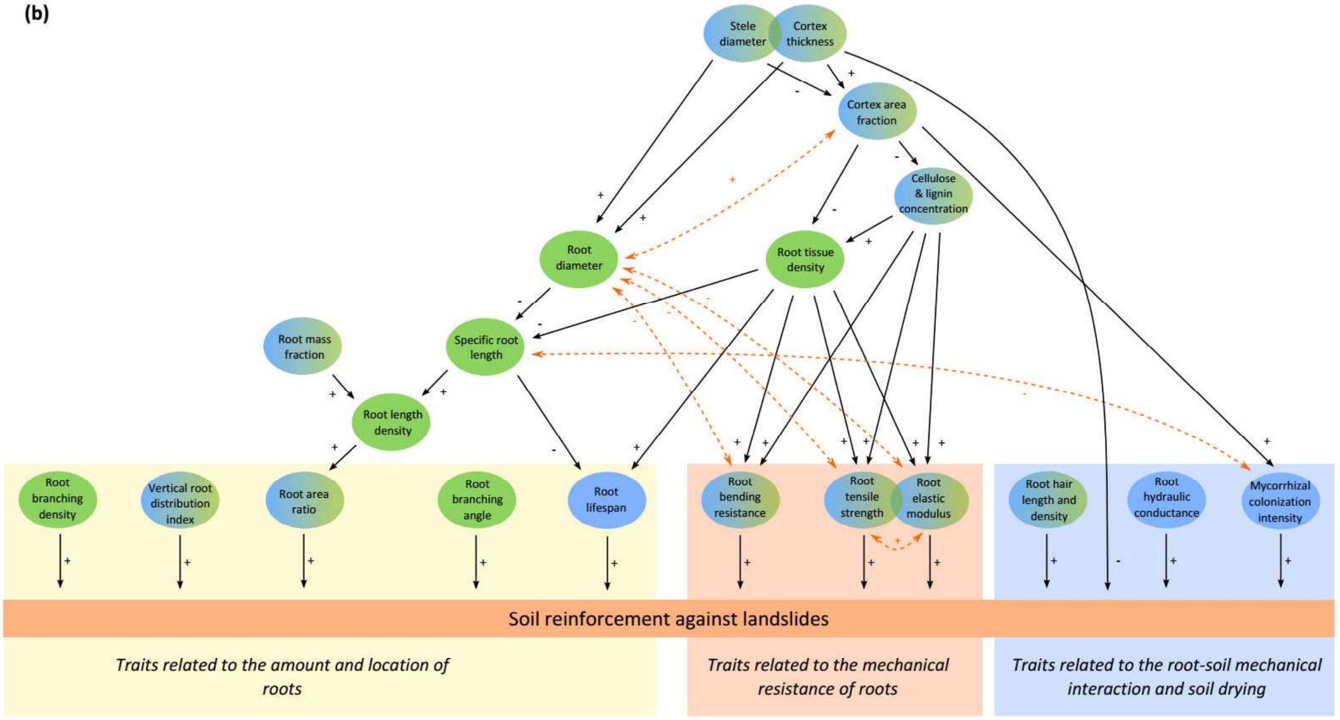


(d) Representation of different fields of root ecology (as presented in Freschet *et al.*, 2020) across this subset of 14 plant and ecosystem functions. The thicker the line the higher the trait occurrence.

Figure 2.



Uptake capacity is greatest when the soil volume is efficiently explored and/or exploited, and when the root is metabolically active towards N absorption or promote active resource exchange via symbiotic associations.



Reinforcement is greatest when a number of roots cross a potential shear plane, when the root tissue is mechanically strong and with a large elastic modulus, and when roots are strongly bonded to the soil and dry the soil rapidly.

New Phytologist Supporting Information

Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs.

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Supplementary Notes S1. References cited in Tables 1, 2, 3 and 4.

Abalos D, De Deyn GB, Kuyper TW, van Groenigen JW. 2014. Plant species identity surpasses species richness as a key driver of N_2O emissions from grassland. *Global Change Biology* **20**: 265-275.

Abiko T, Kotula L, Shiono K, Malik AI, Colmer TD, Nakazono M. 2012. Enhanced formation of aerenchyma and induction of a barrier to radial oxygen loss in adventitious roots of *Zea nicaraguensis* contribute to its waterlogging tolerance as compared with maize (*Zea mays ssp mays*). *Plant Cell and Environment* **35**: 1618-1630.

Afkhami ME, Mahler DL, Burns JH, Weber MG, Wojciechowski MF, Sprent J, Strauss SY. 2018. Symbioses with nitrogen-fixing bacteria: nodulation and phylogenetic data across legume genera. *Ecology* **99**: 502-502

Agrawal AA, Fishbein M. 2006. Plant defense syndromes. *Ecology* **87**: 132-149.

Ahmed MA, Zarebanadkouki M, Meunier F, Javaux M, Kaestner A, Carminati A. 2018. Root type matters: measurement of water uptake by seminal, crown, and lateral roots in maize. *Journal of Experimental Botany* **69**: 1199-1206.

Ali FH, Osman N. 2008. Shear strength of a soil containing vegetation roots. *Soils and Foundations* **48**: 587-596.

Allen MF, Swenson W, Querejeta JI, Egerton-Warburton LM, Treseder KK. 2003. Ecology of mycorrhizae: A conceptual framework for complex interactions among plants and fungi. *Annual Review of Phytopathology* **41**: 271-303.

Ament MR, Tierney JA, Hedin LO, Hobbie EA, Wurzburger N. 2018. Phosphorus and species regulate N_2 fixation by herbaceous legumes in longleaf pine savannas. *Oecologia* **187**: 281-290.

Angers D, Caron J. 1998. Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry* **42**: 55-72.

Augé RM, Stodola AJW, Tims JE, Saxton AM. 2001. Moisture retention properties of a mycorrhizal soil. *Plant and Soil* **230**: 87-97.

Augé RM, Toler HD, Sams CE, Nasim G. 2008. Hydraulic conductance and water potential gradients in squash leaves showing mycorrhiza-induced increases in stomatal conductance. *Mycorrhiza* **18**: 115-121.

Averill C, Turner BJ, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**: 543-545.

Babikova Z, Gilbert L, Bruce TJA, Dewhirst SY, Pickett JA & Johnson D. 2014. Arbuscular mycorrhizal fungi and aphids interact by changing host plant quality and volatile emission. *Functional Ecology* **28**: 375-385.

Bachmann J, Guggenberger G, Baumgartl T, Ellerbrock RH, Urbanek E, Goebel MO, Kaiser K, Horn R, Fischer WR. 2008. Physical carbon-sequestration mechanisms under special consideration of soil wettability. *Journal of Plant Nutrition and Soil Science* **171**: 14-26.

Bankhead NL, Thomas RE, Simon A. 2017. A combined field, laboratory and numerical study of the forces applied to, and the potential for removal of, bar top vegetation in a braided river. *Earth Surface Processes and Landforms* **42**: 439-459.

Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* **29**: 692-699.

Batterman SA, Hedin LO, van Breugel M, Ransijn J, Craven DJ, Hall JS. 2013a. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature* **502**: 224-227.

Batterman SA, Wurzburger N, Hedin LO. 2013b. Nitrogen and phosphorus interact to control tropical symbiotic N_2 fixation: a test in *Inga punctata*. *Journal of Ecology* **101**: 1400-1408.

Bauhus J, Messier C. 1999. Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Canadian Journal of Forest Research* **29**: 260-273.

Baumert VL, Vasilyeva N, Vladimirov AA, Meier IC, Kögel-Knabner I, Mueller CW. 2018. Root exudates induce soil macroaggregation facilitated by fungi in subsoil. *Frontiers in Environmental Science* **6**: 140.

Bengough AG, McKenzie BM. 1997. Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth. *Journal of Experimental Botany* **48**: 885-893.

Bengough AG. 2012. Root elongation is restricted by axial but not by radial pressures: so what happens in field soil? *Plant and Soil* **360**: 15-18.

Bezemer TM, Wagenaar R, van Dam NM, Van Der Putten WH, Wackers FL. 2004. Above- and below-ground terpenoid aldehyde induction in cotton, *Gossypium herbaceum*, following root and leaf injury. *Journal of Chemical Ecology* **30**:53-67.

Binkley D. 2005. How nitrogen-fixing trees change soil carbon. In: Binkley D, Menyailo O eds. *Tree species effects on soils: implications for global change.* Dordrecht, The Netherlands: Kluwer Academic Publishers, 155-164.

Bischetti GB, Chiaradia EA, Simonato T, Speziali B, Vitali B, Vullo P, Zocco A. 2005. Root strength and root area ratio of forest species in Lombardy (Northern Italy). *Plant and Soil* **278**: 11-22

Boamfa EI, Veres AH, Ram PC, Jackson MB, Reuss J, Harren FJM. 2005. Kinetics of ethanol and acetaldehyde release suggest a role for acetaldehyde production in tolerance of rice seedlings to micro-aerobic conditions. *Annals of Botany* **96**: 727-736.

Boldrin D, Leung AK, Bengough AG. 2017. Correlating hydrologic reinforcement of vegetated soil with plant traits during establishment of woody perennials. *Plant and Soil* **416**: 437-451.

Bond-Lamberty B, Wang C, Gower S. 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* **10**: 1756-1766.

Bowsher AW, Miller BJ, Donovan LA. 2016. Evolutionary divergences in root system morphology, allocation, and nitrogen uptake in species from high-versus low-fertility soils. *Functional plant biology* **43**: 129-40.

Brown LK, Geoge TS, Barrett GE, Hubbard SF, White PJ. 2013. Interactions between root hair length and arbuscular mycorrhizal colonisation in phosphorus deficient barley (*Hordeum vulgare*). *Plant and Soil* **372:** 195-205.

Brown VK, Gange AC. 1990. Insect herbivory below ground. *Advances in Ecological Research* **20:** 1-58.

Bruce C, Nicoll BC, Gardiner A, Rayner Bl, Peace AJ. 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Canadian Journal of Forest Research* **36**: 1871-1883.

Brundrett MC. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* **154**: 275-304.

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C. 2015. How tree roots respond to drought. *Frontiers in Plant Science* **6**: 547.

Bumb I, Garnier E, Coq S, Nahmani J, Del Rey Granado M, Gimenez O, Kazakou E. 2018. Traits determining the digestibility–decomposability relationships in species from Mediterranean rangelands. *Annals of Botany* **121**: 459-469.

Burgess SSO, Adams MA, Turner NC, Ong CK. 1998. The redistribution of soil water by tree root systems. *Oecologia* **115**: 306-311.

Burgess SSO, Pate JS, Adams MA, Dawson TE. 2000. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany* **85**: 215-224.

Burgess SSO, Adams MA, Bleby TM. 2000. Measurement of sap flow in roots of woody plants: a commentary. *Tree Physiology* **20**: 909-913.

Burr-Hersey JE, Mooney SJ, Bengough AG, Mairhofer S, Ritz K. 2017. Developmental morphology of cover crop species exhibit contrasting behaviour to changes in soil bulk density, revealed by X-ray computed tomography. *PLoS ONE* **12**: e0181872.

Burton AL, Lynch JP, Brown KM. 2013. Spatial distribution and phenotypic variation in root cortical aerenchyma of maize (*Zea mays* L.). *Plant and Soil* **367**: 263-274.

Burylo M, Rey F, Roumet C, Buisson E, Dutoit T. 2009. Linking plant morphological traits to uprooting resistance in eroded marly lands (Southern Alps, France). *Plant and Soil* **324**: 31-42.

Cantarel AAM, Pommier T, Desclos-Theveniau M, Diquélou S, Dumont M, Grassein F, Kastl E-M, Grigulis K, Laîné P, Lavorel S *et al.* 2015. Using plant traits to explain plant–microbe relationships involved in nitrogen acquisition. *Ecology* **96**: 788-799.

Carlsson G, Huss-Danell K. 2003. Nitrogen fixation in perennial forage legumes in the field. *Plant and Soil* **253**: 353-372

Carminati A, Zarebanadkouki M, Kroener E, Ahmed MA, Holz M. 2016. Biophysical rhizosphere processes affecting root water uptake. *Annals of Botany* **118**: 561-571.

Carminati A, Benard P, Ahmed MA, Zarebanadkouki M. 2017. Liquid bridges at the root-soil interface. *Plant and Soil* **417**: 1-15.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences* **113**: 8741-8746.

Chimungu JG, Loades KW, Lynch JP. 2015. Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea mays*). *Journal of Experimental Botany* **66**: 3151-3162.

Chitra-Tarak R, Ruiz L, Dattaraja HS, Kumar MM, Riotte J, Suresh HS, McMahon SM, Sukumar R. 2018. The roots of the drought: Hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology* **106**: 1495-1507.

Clark LJ, Barraclough PB. 1999. Do dicotyledons generate greater maximum axial root growth pressures than monocotyledons? *Journal of Experimental Botany* **50**: 1263-1266.

Clark LJ, Price AH, Steele KA, Whalley WR. 2008. Evidence from near-isogenic lines that root penetration increases with root diameter and bending stiffness in rice. *Functional Plant Biology* **35**: 1163-1171.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**: 1615-1618.

Cohen D, Lehmann P, Or D. 2009. Fiber bundle model for multiscale modelling of hydromechanical triggering of shallow landslides. *Water Resources Research* **45**: W10436.

Colmer TD. 2003. Aerenchyma and an inducible barrier to radial oxygen loss facilitate root aeration in upland, paddy and deep-water rice (*Oryza sativa* L.). *Annals of Botany* **91**: 301-309.

Colmer TD, Voesenek L. 2009. Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology* **36**: 665-681.

Comas LH, Mueller KE, Taylor LL, Midford PE, Callahan HS, Beerling DJ. 2012. Evolutionary patterns and biogeochemical significance of angiosperm root traits. *International Journal of Plant Sciences* **173**: 584-595.

Cornelissen JHC, Song YB, Yu FH, Dong M. 2014. Plant traits and ecosystem effects of clonality: A new research agenda. *Annals of Botany* **114**: 369-376.

Craine JM, Wedin DA, Chapin FS, Reich PB. 2003. Relationship between the structure of root systems and resource use for 11 North American grassland plants. *Plant Ecology* **165**: 85-100.

Czarnes S, Dexter A, Bartoli F. 2000. Wetting and drying cycles in the maize rhizosphere under controlled conditions. Mechanics of the root-adhering soil. *Plant and Soil* **221**: 253-271.

da Ponte NHT, Santos RIN, Lopes WRL, Cunha RL, Magalhaes MM, Pinheiro HA. 2019. Morphological assessments evidence that higher number of pneumatophores improves tolerance to long-term waterlogging in oil palm (*Elaeis guineensis*) seedlings. *Flora* **250**: 52-58.

Danjon F, Fourcaud T, Bert D. 2005. Root architecture and wind-firmness of mature *Pinus pinaster*. *New Phytologist* **168**: 387-400.

Danquechin Dorval A, Meredieu C, Danjon F. 2016. Anchorage failure of young trees in sandy soils is prevented by a rigid central part of the root system with various designs. *Annals of Botany* **118**: 747-762.

Dawood T, Rieu I, Wolters-Arts M, Derksen EB, Mariani C, Visser EJW. 2014. Rapid flooding-induced adventitious root development from preformed primordia in *Solanum dulcamara*. *Aob Plants* **6**: plt058

Dawson LA, Grayston SJ, Murray PJ, Pratt SM. 2002. Root feeding behaviour of *Tipula paludosa* (Meig.) (Diptera: Tipulidae) on *Lolium perenne* (L.) and *Trifolium repens* (L.). *Soil Biology and Biochemistry* **34**: 609-615.

De Deyn GB, Cornelissen JHC, Bardgett RD. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* **11**: 516-531.

De Deyn G, Shiel R, Ostle N, McNamara N, Oakley S, Young I, Freeman C, Fenner N, Quirk H, Bardgett RD. 2011. Additional carbon sequestration benefits of grassland diversity restoration. *Journal of Applied Ecology* **48**: 600-608.

De Moraes MG, Carvalho MAM, Franco AC, Pollock CJ, Figueiredo-Ribeiro RCL. 2016. Fire and drought: soluble carbohydrate storage and survival mechanisms in herbaceous plants from the Cerrado. *Bioscience* **66**: 107-117

de Vries FT, Bardgett RD. 2016. Plant community controls on short-term ecosystem nitrogen retention. *New Phytologist* **210**: 861-874.

Degens BP, Harris JA. 1997. Development of a physiological approach to measuring the catabolic diversity of soil microbial communities. *Soil Biology and Biochemistry* **29**: 1309-1320.

Devkota BD, Omura H, Kubota T, Paudel P, Inoue S. 2006. Revegetation condition and morphological characteristics of grass species observed in landslide scars, Shintategawa Watershed, Fukuoka, Japan. *Journal of Applied Sciences* **6**: 2238-2244.

Dexter A. 1987. Compression of soil around roots. *Plant and Soil* **97**: 401-406.

Ding XH, Zou JF, Li YZ, Yao X, Zou DS, Zhang CM, Yang N, Niu YD, Bian HL, Deng JJ, Ge ZX. 2017. Acclimation of *Salix triandroides* cuttings to incomplete submergence is reduced by low light. *Aquatic Ecology* **51**: 321-330.

Docker BB, Hubble TCT. 2008. Quantifying root-reinforcement of river bank soils by four Australian tree species. *Geomorphology* **100**: 401-418.

Domec JC, Warren JM, Meinzer FC. 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and Ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* **141**: 7-16.

Domec JC, Scholz FG, Bucci SJ, Meinzer FC, Goldstein G, Villalobos-Vega R. 2006. Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status. *Plant, Cell and Environment* **29**: 26-35.

Domec JC, King JS, Noormets A, Treasure E, Gavazzi MJ, Sun G, McNulty SG. 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. *New Phytologist* **187**: 171-183.

Draye X, Kim Y, Lobet G, Javaux M. 2010. Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. *Journal of Experimental Botany* **61**: 2145-2155.

Dupuy L, Fourcaud T, Stokes A. 2005a. A numerical investigation into factors affecting the anchorage of roots in tension. *European Journal of Soil Science* **56**: 319-327.

Dupuy L, Fourcaud T, Stokes A. 2005b. A numerical investigation into the influence of soil type and root architecture on tree anchorage. *Plant and Soil* **278**: 119-134

Dybzinski R, Kelvakis A, McCabe J, Panock S, Anuchitlertchon K, Vasarhelyi L, McCormack ML, McNickle GG, Poorter H, Trinder C *et al.* 2019. How are nitrogen availability, fine-root mass, and nitrogen uptake related empirically? Implications for models and theory. *Global Change Biology* **25**: 885-899.

Edmaier K, Crouzy B, Perona P. 2015. Experimental characterization of vegetation uprooting by flow. *Journal of Geophysical Research: Biogeosciences* **120**: 1812-1824.

Egerton-Warburton LM, Querejeta JI, Allen MF. 2008. Efflux of hydraulically lifted water from mycorrhizal fungal hyphae during imposed drought. *Plant Signalling & Behaviour* **3**: 68-71.

Eissenstat DM, Caldwell MM. 1988. Seasonal timing of root-growth in favorable microsites. *Ecology* **69**: 870-873.

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

Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114-124.

Eldhuset TD, Nagy NE, Volarik D, Borja I, Gebauer R, Yakovlev IA, Krokene P. 2013. Drought affects tracheid structure, dehydrin expression, and above- and belowground growth in 5-year-old Norway spruce. *Plant and Soil* **366**: 305-320.

Elumeeva TG, Onipchenko VG, Cornelissen JHC, Semenova GV, Perevedentseva LG, Freschet GT, van Logtestijn RSP, Soudzilovskaia NA. 2018. Is intensity of plant root mycorrhizal colonization a good proxy for plant growth rate, dominance and decomposition in nutrient poor conditions? *Journal of Vegetation Science* **29**: 715-725.

Ennos AR. 1989. The mechanics of anchorage in seedlings of sunflower, *Helianthus annuus* L. *New Phytologist* 113: 185-192.

Ennos AR. 1993. The scaling of root anchorage. *Journal of Theoretical Biology* **161**: 61-75

Ennos AR. 2000. The mechanics of root anchorage. *Advances in Botanical Research* **33**: 133-157.

Ennos AR, Pellerin S. 2000. Plant anchorage. In: Smit AL, Bengough AG, Engels C, van Noordwijk M, Pellerin S, van de Geijn SC eds. *Root Methods*. Berlin & Heidelberg, Germany: Springer, 545-565.

Enstone DE, Peterson CA. 1992. The apoplastic permeability of root apices. *Canadian Journal of Botany* **70**: 1502-1512.

Espeleta JF, West JB. Donovan LA. 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. *Oecologia* **138**: 341-349.

Fan CC, Chen YW. 2010. The effect of root architecture on the shearing resistance of root-permeated soils. *Ecological Engineering* **36**: 813-826.

Fan P, Guo D. 2010. Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. *Oecologia* **163**: 509-515.

Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C. 2017. Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences* **114**: 10572-10577.

Feddes RA, Hoff H, Bruen M, Dawson T, De Rosnay P, Dirmeyer P, Jackson RB, Kabat P, Kleidon A, Lilly A, *et al.* 2001. Modeling root water uptake in hydrological and climate models. *Bulletin of the American Meteorological* Society **82**: 2797-2810.

Fernandez CW, Langley JA, Chapman S, McCormack ML, Koide RT. 2016. The decomposition of ectomycorrhizal fungal necromass. *Soil Biology and Biochemistry* **93**: 38-49.

Fester T, Hause G. 2005. Accumulation of reactive oxygen species in arbuscular mycorrhizal roots. *Mycorrhiza* **15**:373-379.

Ficken CD, Wright JP. 2019. Nitrogen uptake and biomass resprouting show contrasting relationships with resource acquisitive and conservative plant traits. *Journal of vegetation science* **30**: 65-74.

Fitter AH, Stickland TR. 1991. Architectural analysis of plant root systems 2. Influence of nutrient supply on architecture in contrasting plant species. *New Phytologist* **118**: 383-389.

Föhse D, Claassen N, Jungk A. 1988. Phosphorus efficiency of plants. *Plant and Soil* **110**: 101-109.

Forde B, Lorenzo H. 2001. The nutritional control of root development. *Plant and Soil* **232**: 51-68.

Fornara DA, Tilman D. 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology* **96**: 314-322.

Fornara DA, Bardgett R, Steinbeiss S, Zak DR, Gleixner G, Tilman D. 2011. Plant effects on soil N mineralization are mediated by the composition of multiple soil organic fractions. *Ecological Research* **26**: 201-208.

Fort F, Volaire F, Guilioni L, Barkaoui K, Navas M-L, Roumet C. 2017. Root traits are related to plant water-use among rangeland Mediterranean species. *Functional Ecology* **31**: 1700-1709.

Fourcaud T, Ji J, Zhang Z, Stokes A. 2008. Understanding the impact of root morphology on overturning mechanisms: a modeling approach. *Annals of Botany* **101**: 1267-1280

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

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

Freschet GT, Violle C, Bourget MY, Scherer-Lorenzen M, Fort F. 2018. Allocation, morphology, physiology, architecture: the multiple facets of plant above and belowground responses to resource stress. *New Phytologist* **219**: 1338-1352.

Fujii S, Takeda H. 2010. Dominant effects of litter substrate quality on the difference between leaf and root decomposition process above- and belowground. *Soil Biology and Biochemistry* **42**: 2224-2230.

Gale MR, Gringal DF. 1987. Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research* **17**: 829-834

Gambetta GA, Fei J, Rost TL, Knipfer T, Matthews MA, Shackel KA, Walker MA, McElrone AJ. 2013. Water uptake along the length of grapevine fine roots: Developmental anatomy, tissue-specific aquaporin expression, and pathways of water transport. *Plant Physiology* **163**: 1254-1265.

Garnier E, Koch GW, Roy J, Mooney HA. 1989. Responses of wild plants to nitrate availability. *Oecologia* **79**: 542-550.

Garnier E. 1991. Resource capture, biomass allocation and growth in herbaceous plants. *Trends in Ecology & Evolution* **6**: 126-131.

Ghestem M, Sidle RC, Stokes A. 2011. The influence of plant root systems on subsurface flow: Implications for slope stability. *BioScience* **61**: 869-879.

Ghestem M, Veylon G, Bernard A, Vanel Q, Stokes A. 2014. Influence of plant root system morphology and architectural traits on soil shear resistance. *Plant and Soil* **377**: 43-61

Giadrossich F, Schwarz M, Cohen D, Cislaghi A, Vergani C, Hubble TC, Phillips C, Stokes A. 2017. Methods to measure the mechanical behaviour of tree roots: A review. *Ecological Engineering* **109**: 256-271

Giadrossich F, Cohen D, Schwarz M, Ganga A, Marrosu R, Pirastru M, and Capra GF. 2019. Large roots dominate the contribution of trees to slope stability. *Earth Surface Processes and Landforms* **44**: 1602-1609.

Gibberd MR, Gray JD, Cocks PS, Colmer TD. 2001. Waterlogging tolerance among a diverse range of Trifolium accessions is related to root porosity, lateral root formation and 'aerotropic rooting'. *Annals of Botany* **88**: 579-589.

Gleixner G, Poirier N, Bol R, Balesdent J. 2002. Molecular dynamics of organic matter in a cultivated soil. *Organic Geochemistry* **33**:357-366.

Goodman AM, Crook MJ, Ennos AR. 2001. Anchorage mechanics of the tap root system of winter-sown oilseed rape (*Brassica napus* L.). *Annals of Botany* **87**: 397-404.

Gould IJ, Quinton JN, Weigelt A, De Deyn GB, Bardgett RD. 2016. Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters* **19**: 1140-1149.

Grassein F, Lemauviel-Lavenant S, Lavorel S, Bahn M, Bardgett RD, Desclos-Theveniau M, Laîné P. 2015. Relationships between functional traits and inorganic nitrogen acquisition among eight contrasting European grass species. *Annals of Botany* **115**: 107-115.

Grassein F, Legay N, Arnoldi C, Raphael S, Philippe L, Lavorel S, Clement J-C. 2018. Studies of NH_4^+ and NO_3^- uptake ability of subalpine plants and resource-use strategy identified by their functional traits. *bioRxiv*: 372235.

Grigg A, Lambers H, Veneklaas E. 2010. Changes in water relations for *Acacia ancistrocarpa* on natural and mine-rehabilitation sites in response to an experimental wetting pulse in the Great Sandy Desert. *Plant and Soil* **326**: 75-96.

Groff PA, Kaplan DR. 1988. The relation of root systems to shoot systems in vascular plants. *The Botanical Review* **54**: 387-422

Gu J, Xu Y, Dong X, Wang H, Wang Z. 2014. Root diameter variations explained by anatomy and phylogeny of 50 tropical and temperate tree species. *Tree Physiology* **34**: 415-425.

Haling RE, Brown LK, Bengough AG, Young IM, Hallett PD, White PJ, George TS. 2013. Root hairs improve root penetration, root–soil contact, and phosphorus acquisition in soils of different strength. *Journal of Experimental Botany* **64**: 3711-3721.

He H, Bleby TM, Veneklaas EJ, Lambers H. 2012. Arid-zone Acacia species can access poorly soluble iron phosphate but show limited growth response. *Plant and Soil* **358**: 119-130.

Henneron L, Cros C, Picon-Cochard C, Rahimian V, Fontaine S. 2020. Plant economic strategies of grassland species control soil carbon dynamics through rhizodeposition. *Journal of Ecology* **108**: 528-545.

Hinsinger P, Jaillard B, Dufey JE. 1992. Rapid weathering of a trioctahedral mica by the roots of Ryegrass. *Soil Science Society of America Journal* **56**: 977-982

Hinsinger P. 1998. How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. *Advances in Agronomy* **64**: 225-265

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* **87**: 2288-2297.

Hobbie EA. 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology* **87**: 563-569.

Hodge A, Stewart J, Robinson D, Griffiths BS, Fitter AH. 1998. Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. *New Phytologist* **139**: 479-494.

Hodge A, Robinson D, Griffiths B, Fitter A. 1999. Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. *Plant, Cell & Environment* **22**: 811-820.

Hodge A. 2003. Plant nitrogen capture from organic matter as affected by spatial dispersion, interspecific competition and mycorrhizal colonization. *New Phytologist* **157**: 303-314.

Hoffland E, Kuyper TW, Wallander H, Plassard C, Gorbushina AA, Haselwandter K, Holmström S, Landeweert R, Lundström US, Rosling A *et al.* 2004. The role of fungi in weathering. *Frontiers in Ecology and the Environment* **2**: 258-264.

Högberg MN, Högberg P. 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytologist* **154**:791-795.

Hong J, Ma X, Yan Y, Zhang X, Wang X. 2018. Which root traits determine nitrogen uptake by alpine plant species on the Tibetan Plateau? *Plant and Soil* **424**: 63-72.

Houben D, Sonnet P. 2012. Zinc mineral weathering as affected by plant roots. *Applied Geochemistry* **27**: 1587-1592.

Hu B, Henry A, Brown KM, Lynch JP. 2014. Root cortical aerenchyma inhibits radial nutrient transport in maize (*Zea mays*). *Annals of Botany* **113**:181-189.

Huang B, Eissenstat DM, Achor D. 1995. Root hydraulic conductivity in relation to its morphological and anatomical characteristics for citrus root stocks. In: Topa MA, Rygiewicz PT, Cumming JR, eds. *Dynamics of Physiological Processes in Woody Roots, proceedings.* Ithaca, NY, USA: Boyce Thompson Institute for Plant Research, 80.

Huang B, Eissenstat DM. 2000. Linking hydraulic conductivity to anatomy in plants that vary in specific root length. *Journal of the American Society for Horticultural Science* **125**: 260-264.

Hultine KR, Cable WL, Burgess SSO. Williams DG. 2003. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353-360.

Hultine KR, Williams DG, Burgess SSO, Keefer TO. 2003. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* **135**: 167-175.

Hummel I, Vile D, Violle C, Devaux J, Ricci B, Blanchard A, Garnier É, Roumet C. 2007. Relating root structure and anatomy to whole-plant functioning in 14 herbaceous Mediterranean species. *New Phytologist* **173**: 313-321.

Iijima M, Higuchi T, Barlow PW, A. Glyn Bengough AG. 2003. Root cap removal increases root penetration resistance in maize (*Zea mays* L.). *Journal of Experimental Botany* **54**: 2105-2109

Itoh S. 1987. Characteristics of phosphorus uptake of chickpea in comparison with pigeonpea, soybean, and maize. *Soil Science and Plant Nutrition* **33**: 417-422.

Jackson MB, Herman B, Goodenough A. 1982. An examination of the importance of ethanol in causing injury to flooded plants. *Plant, Cell & Environment* **5**: 163-172.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411.

Jackson RB, Mooney HA, Schulze E-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* **94**: 7362-7366.

Jakobson BF, Dexter AR. 1987. Effect of soil structure on wheat root growth, water uptake and grain yield. A computer simulation model. *Soil Tillage Research* **10**: 331-345.

Janeček S, Klimešová J. 2014. Carbohydrate storage in meadow plants and its depletion after disturbance: do roots and stem-derived organs differ in their roles? *Oecologia* **175**: 51-61.

Jastrow J, Miller R, Lussenhop J. 1998. Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biology and Biochemistry* **30**: 905-916.

Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423-436.

Johnson DM, Sherrard ME, Domec J-C, Jackson RB. 2014. Role of aquaporin activity in regulating deep and shallow root hydraulic conductance during extreme drought. *Trees* **28**: 1323-1331.

Johnson SN, Hallett PD, Gillespie TL, Halpin C. 2010. Below-ground herbivory and root toughness: a potential model system using lignin-modified tobacco. P*hysiological Entomology* **35**: 186-191.

Johnson SN, Benefer CM, Frew A, Griffiths BS, Hartley SE, Karley AJ, Rasmann S, Schumann M, Sonnemann I, Robert CAM. 2016. Frontiers in belowground ecology for plant protection from root-feeding insects. *Applied Soil Ecology* **108**: 96-107.

Jongmans AG, Van Breemen N, Lundström US, Van Hees PAW, Finlay RD, Srinivasan M, Unestam T, Giesler R, Melkerud P-A, Olsson M. 1997. Rock-eating fungi. *Nature* **389**: 682-683.

Jónsdóttir IS, Watson M. 1997. Extensive physiological integration: An adaptive trait in resource-poor environments? In: de Kroon H, van Groenendael J, eds. *The ecology and evolution of clonal plants*. Leiden, The Netherlands: Backhuys publishers, 109-136.

Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ. 2012. Mycorrhiza-induced resistance and priming of plant defenses. *Journal of Chemical Ecology* **38**: 651-664.

Kamula SA, Peterson CA, Mayfield CI. 1994. Impact of the exodermis on infection of roots by *Fusarium culmorum*. *Plant and Soil* **167**: 121-126.

Kaplan I, Halitschke R, Kessler A, Sardanelli S, Denno RF. 2008. Constitutive and induced defenses to herbivory in above-and belowground plant tissues. *Ecology* **89**: 392-406.

Keiluweit M, Bougoure JJ, Nico PS, Pett-Ridge J, Weber PK, Kleber M. 2015. Mineral protection of soil carbon counteracted by root exudates. *Nature Climate Change* **5**: 588-595.

Klimešová J, Klimeš L. 2007. Bud banks and their role in vegetative regeneration-a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **8**: 115-129

Klimešová J, Doležal J, Prach K, Košnar J. 2012. Clonal growth forms in Arctic plants and their habitat preferences: a study from Petuniabukta, Spitsbergen. *Polish Polar Research* **33**: 421-442

Klimešová J, Herben T, Martínková J. 2017a. Disturbance is an important factor in the evolution and distribution of root-sprouting species. *Evolutionary Ecology* **31**: 387-399.

Klimešová J, Janeček Š, Bartušková A, Bartoš M, Altman J, Doležal J, Lanta V, Latzel V. 2017b. Is the scaling relationship between carbohydrate storage and leaf biomass in meadow plants affected by the disturbance regime? *Annals of Botany* **120**: 979-985.

Klimešová J, Martínková J, Ottaviani G. 2018. Belowground plant functional ecology: Towards an integrated perspective. *Functional Ecology* **32**: 2115-2126.

Kögel-Knabner I. 2017. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on. *Soil Biology and Biochemistry* **105**: A3-A8.

Kohl JG, Henze R, Kühl H. 1996. Evaluation of the ventilation resistance to convective gas-flow in the rhizomes of natural reed beds of *Phragmites australis* (Cav.) Trin. ex Steud.. *Aquatic Botany* **54**: 199-210.

Köhler J, Yang N, Pena R, Raghavan V, Polle A, Meier IC. 2018. Ectomycorrhizal fungal diversity increases P uptake efficiency of European beech. *New Phytologist* **220**: 1200-1210.

Kolb E, Hartmann C, Genet P. 2012. Radial force development during root growth measured by photoelasticity. *Plant and Soil* **360**: 19-35.

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**: 863-872.

Kong D, Wang J, Zeng H, Liu M, Miao Y, Wu H, Kardol P. 2017. The nutrient absorption–transportation hypothesis: optimizing structural traits in absorptive roots. *New Phytologist* **213**: 1569-1572.

Korth KL, Doege SJ, Park SH, Goggin FL, Wang Q, Gomez SK, Liu G, Jia L, Nakata PA. 2006. *Medicago truncatula* mutants demonstrate the role of plant calcium oxalate crystals as an effective defense against chewing insects. *Plant Physiology* **141**:188-195.

Kulmatiski A, Adler PB, Stark JM, Tredennick AT. 2017. Water and nitrogen uptake are better associated with resource availability than root biomass. *Ecosphere* **8**: e01738.

Kuzyakov Y. 2010. Priming effects: Interactions between living and dead organic matter. *Soil Biology and Biochemistry* **42**: 1363-1371.

Laliberté E, Lambers H, Burgess TI, Wright SJ. 2015. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist* **206**: 507-521.

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ. 2006. Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits. *Annals of Botany* **98**: 693-713.

Lambers H, Raven JA, Shaver GR, Smith SE. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* **23**: 95-103.

Lambers H, Mougel C, Jaillard B, Hinsinger P. 2009. Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. *Plant and Soil* **321**: 83-115

Lambers H, Bishop JG, Hopper SD, Laliberté E, Zúñiga-Feest A. 2012. Phosphorus-mobilization ecosystem engineering: the roles of cluster roots and carboxylate exudation in young P-limited ecosystems. *Annals of Botany* **110**: 329-348.

Landl M, Huber K, Schnepf A, Vanderborght J, Javaux M, Bengough AG, Vereecken H. 2017. A new model for root growth in soil with macropores. *Plant and Soil* **415**: 99-116

Langley JA, Hungate BA. 2003. Mycorrhizal controls on belowground litter quality. *Ecology* **84**: 2302-2312.

Langley JA, Chapman SK, Hungate BA. 2006. Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecology Letters* **9**: 955-959.

Langlois CG, Godbout L, Fortin JA. 1983. Seasonal-variation of growth and development of the roots of 5 2nd year conifer species in the nursery. *Plant and Soil* **71**: 55-62.

Larigauderie A, Richards JH. 1994. Root proliferation characteristics of seven perennial arid-land grasses in nutrient-enriched microsites. *Oecologia* **99**: 102-111.

Larson JE, Funk JL. 2019. Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. *New Phytologist* **210**: 827-38.

Le Roux X, Schmid B, Poly F, Barnard RL, Niklaus PA, Guillaumaud N, Habekost M, Oelmann Y, Philippot L, Salles JF, *et al.* 2013. Soil environmental conditions and microbial build-up mediate the effect of plant diversity on soil nitrifying and denitrifying enzyme activities in temperate grasslands. *PLoS One* **8**: e61069.

Leffler AJ, James JJ, Monaco TA. 2013. Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia* **171**: 51-60.

Legay N, Baxendale C, Grigulis K, Krainer U, Kastl E, Schloter M, Bardgett RD, Arnoldi C, Bahn M, Dumont M *et al.* 2014. Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. *Annals of Botany* **114**: 1011-1021.

Levang-Brilz N, Biondini ME. 2003. Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains Grasslands, USA. *Plant Ecology* **165**: 117-144.

Liao Y, McCormack ML, Fan H, Wang H, Wu J, Tu J, Liu W, Guo D. 2014. Relation of fine root distribution to soil C in a *Cunninghamia lanceolata* plantation in subtropical China. *Plant and Soil* **381**: 225-234.

Liese R, Lübbe T, Albers NW, Meier IC. 2018. The mycorrhizal type governs root exudation and N uptake of temperate tree species. *Tree Physiology* **38**: 83-95.

Lin G, McCormack ML, Ma C, Guo D. 2017. Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist* **213**: 1440-1451.

Liu B, He J, Zeng F, Lei J, Arndt SK. 2016. Life span and structure of ephemeral root modules of different functional groups from a desert system. *New Phytologist* **211**: 103-112.

Liu Y, van Kleunen M. 2019. Nitrogen acquisition of Central European herbaceous plants that differ in their global naturalization success. *Functional ecology* **33**: 566-75.

Long Y, Kong D, Chen Z, Zeng H. 2013. Variation of the linkage of root function with root branch order. *PLoS One* **8**: e57153

Lopez-Bucio J, de la Vega OM, Guevara-García A, Herrera-Estrella L. 2000. Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. *Nature Biotechnology* **18**: 450-453.

López-Ráez JA, Verhage A, Fernandez I, Garcia JM, Azcon-Aguilar C, Flors V, Pozo MJ. 2010. Hormonal and transcriptional profiles highlight common and differential host responses to arbuscular mycorrhizal fungi and the regulation of the oxylipin pathway. *Journal of Experimental Botany* **61**: 2589-2601.

Loqué D, von Wirén N. 2004. Regulatory levels for the transport of ammonium in plant roots. *Journal of Experimental Botany* **55**: 1293-1305.

Lubbe FC, Henry HA. 2019. The cost of depth: frost avoidance trade-offs in herbaceous plants. *Plant and Soil* **444**: 213–224.

Luo FL, Nagel KA, Scharr H, Zeng B, Schurr U, Matsubara S. 2011. Recovery dynamics of growth, photosynthesis and carbohydrate accumulation after de-submergence: a comparison between two wetland plants showing escape and quiescence strategies. *Annals of Botany* **107**: 49-63.

Lynch JP. 2011. Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. *Plant Physiology* **156**: 1041-1049.

Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* **112**: 347-357.

Lynch JP. 2019. Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. *New Phytologist* **223**: 548-564.

Ma Z, Walk TC, Marcus A, Lynch JP. 2001. Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: A modeling approach. *Plant and Soil* **236**: 221-235.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* **555**: 94-97.

Maeght J-L, Rewald B, Pierret A. 2013. How to study deep roots – and why it matters. *Frontiers in Plant Science* **4**: 299.

Maire V, Gross N, da Silveira Pontes L, Picon-Cochard C, Soussana J-F. 2009. Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology* **23**: 668-679.

Manzoni S, Trofymow JA, Jackson RB, Porporato A. 2010. Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. *Ecological Monographs* **80**: 89-106.

Mao Z, Saint-André L, Genet M, Mine FX, Jourdan C, Rey H, Courbaud B, Stokes A. 2012. Engineering ecological protection against landslides in mountain forests: choosing cohesion models. *Ecological Engineering* **45**: 55-69.

Mao Z, Wang Y, McCormack ML, Rowe N, Deng X, Yang X, Xia S, Nespoulous J, Sidle RC, Guo D *et al.* 2018. Mechanical traits of fine roots as a function of topology and anatomy. *Annals of Botany* **122**: 1103-1116.

Maricle BR, White SJ, Meraz A, Maforo NG, Biggs TN, Martin NM, Caudle KL. 2014. Effect of ethanol toxicity on enzyme activity in anaerobic respiration in plants. *Transactions of the Kansas Academy of Science (1903-)* **117**: 237-244.

Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F. 2016. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecological Monographs* **86**: 495-16.

Materechera SA, Alston AM, Kirby JM, Dexter AR. 1992. Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil* **144**: 297-303.

Matern U, Grimmig B, Kneusel RE. 1995. Plant-cell wall reinforcement in the disease resistance response - molecular composition and regulation. *Canadian Journal of Botany-Revue Canadienne De Botanique* 73: S511-S517.

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

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D,

Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505-518.

McCormack ML, Iversen CM. 2019. Physical and functional constraints on viable belowground acquisition strategies. *Frontiers in Plant Science* **10**: 1215.

McElrone AJ, Bichler J, Pockman WT, Addington RN, Linder CR, Jackson RB. 2007. Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant Cell and Environment* **30**: 1411-1421.

McGrath DA, Comerford NB, Duryea ML. 2000. Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. *Forest Ecology and Management* **131**: 167-181.

Meier IC, Pritchard SG, Brzostek ER, McCormack ML, Phillips RP. 2015. Rhizosphere and hyphosphere differ in their impacts on carbon and nitrogen cycling in forests exposed to elevated CO_2. *New Phytologist* **205**: 1164-1174.

Meier IC, Finzi AC, Phillips RP. 2017. Root exudates increase N availability by stimulating microbial turnover of fast-cycling N pools. *Soil Biology & Biochemistry* **106**: 119-128.

Mickovski SB, Van Beek LPH, Salin F. 2005. Uprooting resistance of vetiver grass (*Vetiveria zizanioides*). *Plant and Soil* **278**: 33–41.

Miguel MA, Postma JA, Lynch JP. 2015. Phene synergism between root hair length and basal root growth angle for phosphorus acquisition. *Plant Physiology* **167**: 1430-1439.

Miller AJ, Fan XR, Orsel M, Smith SJ, Wells DM. 2007. Nitrate transport and signalling. *Journal of Experimental Botany* **58**: 2297-2306.

Miller RM, Jastrow JD. 1990. Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biology and Biochemistry* **22**: 579-584.

Miller RM, Jastrow JD, Reinhardt DR. 1995. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* **103**: 17-23.

Misra RK, Dexter AR, Alston AM. 1986. Maximum axial and radial growth pressures of plant roots. *Plant and Soil* **95**: 315-326

Moog PR, Bruggemann W. 1998 Flooding tolerance of Carex species. II. Root gas-exchange capacity. *Planta* **207**: 199-206.

Moore BD, Johnson SN. 2017. Get tough, get toxic, or get a bodyguard: identifying candidate traits conferring belowground resistance to herbivores in grasses. *Frontiers in Plant Science* 7: 1925.

Moreau D, Bardgett RD, Finlay RD, Jones DL, Philippot L. 2019. A plant perspective on nitrogen cycling in the rhizosphere. *Functional Ecology* **33**: 540-552.

Muhsin TM, Zwiazek JJ. 2002. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. *New Phytologist* 153: 153-158.

Nakamura T, Nakamura M. 2016. Root respiratory costs of ion uptake, root growth, and root maintenance in wetland plants: efficiency and strategy of O_2 use for adaptation to hypoxia. *Oecologia* **182**: n667-678.

Naseer S, Lee Y, Lapierre C, Franke R, Nawrath C, Geldner N. 2012. Casparian strip diffusion barrier in Arabidopsis is made of lignin polymer without suberin. *Proceedings of the National Academy of Sciences USA* **109**: 10101-10106.

Nehls U, Gohringer F, Wittulsky S, Dietz S. 2010. Fungal carbohydrate support in the ectomycorrhizal symbiosis: a review. *Plant Biology* **12**: 292-301.

Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negralros OH, da Silva ED, Stone TA, Trumbore SE, Vieira S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**: 666-669.

Neumann G, Martinoia E. 2002. Cluster roots – an underground adaptation for survival in extreme environments. *Trends in Plant Science* **7**: 162-167.

Newsham KK, Fitter AH, Watkinson AR. 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology & Evolution* **10**: 407-411.

Nicholson RL, Hammerschmidt R. 1992. Phenolic-compounds and their role in disease resistance. *Annual Review of Phytopathology* **30**: 369-389.

Nicoll BC, Ray D. 1996. Adaptive growth of tree root systems in response to wind action and site conditions. *Tree Physiology* **16**: 891-898.

Noguchi S, Nik AR, Kasran B, Tani M, Sammori T, Morisada K. 1997. Soil physical properties and preferential flow pathways in tropical rain forest, Bukit Tarek, Peninsular Malaysia. *Journal of Forest Research* **2**: 115-120.

Normaniza O, Faisal HA, Barakbah SS. 2008. Engineering properties of *Leucaena leucocephala* for prevention of slope failure. *Ecological Engineering* **32**: 215-221.

Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* **57**: 445-466.

Ochs M, Brunner I, Stumm W, Cosovic B. 1993. Effects of root exudates and humic substances on weathering kinetics. *Water Air and Soil Pollution* **68**: 213-229.

Oldroyd GED. 2013. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nature Reviews Microbiology* **11**: 252-263.

Osone Y, Ishida A, Tateno M. 2008. Correlation between relative growth rate and specific leaf area requires associations of specific leaf area with nitrogen absorption rate of roots. *New Phytologist* **179**: 417-427.

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Lõhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A *et al.* 2007. Specific root length as an indicator of environmental change. *Plant Biosystems* **141**: 426-442.

Park SH, Doege SJ, Nakata PA, Korth KL. 2009. *Medicago truncatula*-derived calcium oxalate crystals have a negative impact on chewing Insect performance via their physical properties. *Entomologia Experimentalis et Applicata* **131**: 208-215.

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC *et al.* 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**: 361-364.

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A. 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* **2017**: 1435-1448

Pellitier PT, Zak DR. 2018. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. *New Phytologist* **217**: 68-73.

Pérès G, Cluzeau D, Menasseri S, Soussana JF, Bessler H, Engels C, Habekost M, Gleixner G, Weigelt A, Weisser WW *et al.* 2013. Mechanisms linking plant community properties to soil aggregate stability in an experimental grassland plant diversity gradient. *Plant and Soil* **373**: 285-299.

Perillo CA, Gupta SC, Nater EA, Moncrief JF. 1999. Prevalence and initiation of preferential flow paths in a sandy loam with argillic horizon. *Geoderma* **89**: 307-331.

Personeni E, Loiseau P. 2004. How does the nature of living and dead roots affect the residence time of carbon in the root litter continuum? *Plant and Soil* **267**: 129-141.

Peterson CA, Enstone DE. 1996. Functions of passage cells in the endodermis and exodermis of roots. *Physiologia Plantarum* **97**: 592-598.

Peterson CA, Waite JL. 1996. The effect of suberin lamellae on the vitality and symplasmic permeability of the onion root exodermis. *Canadian Journal of Botany* **74**: 1220-1226.

Phillips LA, Greer CW, Farrell RE, Germida JJ. 2009. Field-scale assessment of weathered hydrocarbon degradation by mixed and single plant treatments. *Applied Soil Ecology* **42**: 9-17.

Phillips RP, Finzi AC, Bernhardt ES. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO_2 fumigation. *Ecology Letters* **14**: 187-194.

Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* **199**: 41-51.

Plassard C, Dell B. 2010. Phosphorus nutrition of mycorrhizal trees. *Tree Physiology* **30**: 1129-1139.

Plassard C, Louche J, Ali MA, Duchemin M, Legname E, Cloutier-Hurteau B. 2011. Diversity in phosphorus mobilisation and uptake in ectomycorrhizal fungi. *Annals of Forest Science* **68**: 33-43.

Poirier V, Roumet C, Munson AD. 2018. The root of the matter: Linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry* **120**: 246-259.

Poorter H, Van der Werf A, Atkin OK, Lambers H. 1991. Respiratory energy requirements of roots depend on the potential growth rate of a plant species. *Physiologia Plantarum* **83**: 469-475.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30-50.

Postma JA, Lynch JP. 2011. Root cortical aerenchyma enhances growth of *Zea mays* L. on soils with suboptimal availability of nitrogen, phosphorus and potassium. *Plant Physiology* **156**: 1190-1201.

Prieto I, Armas C, Pugnaire FI. 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytologist* **193**: 830-841.

Prieto I, Armas C, Pugnaire FI. 2012a. Hydraulic lift promotes selective root foraging in nutrient-rich soil patches. *Functional Plant Biology* **39**: 804-812.

Prieto I, Ryel RJ. 2014. Internal hydraulic redistribution prevents the loss of root conductivity during drought. *Tree Physiology* **34**: 39-48.

Prieto I, Roldán A, Huygens D, del Mar Alguacil M, Navarro-Cano JA, Querejeta JI. 2016. Species-specific roles of ectomycorrhizal fungi in facilitating interplant transfer of hydraulically redistributed water between *Pinus halepensis* saplings and seedlings. *Plant and Soil* **406**: 15-27.

Purnobasuki H, Suzuki M. 2004. Aerenchyma formation and porosity in root of a mangrove plant, *Sonneratia alba* (Lythraceae). *Journal of Plant Research* **117**: 465-472.

Purnobasuki H, Suzuki M. 2005. Functional anatomy of air conducting network on the pneumatophores of a mangrove plant, *Avicennia marina* (Forsk.) Vierh. *Asian Journal of Plant Sciences* **4**: 334-347.

Qian J, Wang Z, Klimešová J, Lü X, Kuang W, Liu Z, Han X. 2017. Differences in below-ground bud bank density and composition along a climatic gradient in the temperate steppe of northern China. *Annals of Botany* **120**: 755-764.

Querejeta J, Egerton-Warburton LM, Allen MF. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* **134**: 55-64.

Querejeta JI, Egerton-Warburton LM, Prieto I, Vargas R, Allen MF. 2012. Changes in soil hyphal abundance and viability can alter the patterns of hydraulic redistribution by plant roots. *Plant and Soil* **355**: 63-73.

Ranathunge K, Steudle E, Lafitte R. 2003. Control of water uptake by rice (*Oryza sativa* L.): role of the outer part of the root. *Planta* **217**: 193-205.

Ranathunge K, Kotula L, Steudle E, Lafitte R. 2004. Water permeability and reflection coefficient of the outer part of young rice roots are differently affected by closure of water channels (aquaporins) or blockage of apoplastic pores. *Journal of Experimental Botany*

55: 433-447.

Rasmann S, Agrawal AA, Cook SC, Erwin AC. 2009. Cardenolides, induced responses, and interactions between above- and belowground herbivores in the milkweeds *(Asclepias spp.)*. *Ecology* **90**: 2393-404.

Rasse DP, Rumpel C, Dignac M-F. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* **269**: 341-356.

Raven JA, Lambers H, Smith SE, Westoby M. 2018. Costs of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. *New Phytologist* **217**: 1420-1427.

Ravenek JM, Mommer L, Visser EJW, van Ruijven J, van der Paauw JW, Smit-Tiekstra A, Caluwe H, de Kroon H. 2016. Linking root traits and competitive success in grassland species. *Plant and Soil* **407**: 39-53.

Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* **47**: 376-391.

Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* **157**: 475-492.

Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany* **82**: 1243–1263.

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* **12**: 395-405.

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

Rewald B, Leuschner C. 2009. Belowground competition in a broad-leaved temperate mixed forest: pattern analysis and experiments in a four-species stand. *European Journal of Forest Research* **128**: 387-398.

Rewald B, Ephrath JE, Rachmilevitch S. 2011. A root is a root is a root? Water uptake rates of Citrus root orders. *Plant, Cell & Environment* **34**: 33-42.

Rewald B, Raveh E, Gendler T, Ephrath JE, Rachmilevitch S. 2012. Phenotypic plasticity and water flux rates of Citrus root orders under salinity. *Journal of Experimental Botany* **63**: 2717-2727.

Rewald B, Rechenmacher A, Godbold DL. 2014. It's complicated: Intraroot system variability of respiration and morphological traits in four deciduous tree species. *Plant Physiology* **166**: 736-745.

Rewald B, Kunze ME, Godbold DL. 2016. NH_4:NO_3 nutrition influence on biomass productivity and root respiration of poplar and willow clones. *Global Change Biology Bioenergy* **8**: 51-58.

Richter DD, Markewitz D. 1995. How deep is soil? *Bioscience* **45**: 600-609.

Rillig MC, Wright S, Nichols K, Schmidt W, Torn M. 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant and Soil* **233**: 167-177.

Rillig MC, Mummey DL. 2006. Mycorrhizas and soil structure. *New Phytologist* **171**: 41-53.

Rillig MC, Aguilar-Trigueros CA, Bergmann J, Verbruggen E, Veresoglou SD, Lehmann A. 2015. Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytologist* **205**: 1385-1388.

Robinson D, Rorison IH. 1987. Root hairs and plant growth at low nitrogen availabilities. *New Phytologist* **107**: 681-693.

Robinson D, Linehan DJ, Caul S. 1991. What limits nitrate uptake from soil? *Plant, Cell & Environment* **14**: 77-85.

Robinson D, Linehan DJ, Gordon DC. 1994. Capture of nitrate from soil by wheat in relation to root length, nitrogen inflow and availability. *New Phytologist* **128**: 297-305.

Ros MBH, De Deyn GB, Koopmans GF, Oenema O, van Groenigen JW. 2018. What root traits determine grass resistance to phosphorus deficiency in production grassland? *Journal of Plant Nutrition and Soil Science* **181**: 323-335.

Ryan PR, James RA, Weligama C, Delhaize E, Rattey A, Lewis DC, Bovill WD, McDonald G, Rathjen TM, Wang E, *et al.* 2014. Can citrate efflux from roots improve phosphorus uptake by plants? Testing the hypothesis with near-isogenic lines of wheat. *Physiologia Plantarum* **151**: 230-242.

Ryser P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**: 717-723.

Sauter M. 2013. Root responses to flooding. *Current Opinion in Plant Biology* **16**: 282-286.

Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480-494.

Schenk HJ, Jackson RB. 2002. The global biogeography of roots. *Ecological Monographs* **72**: 311-328.

Scherer-Lorenzen M, Palmborg C, Prinz A, Schulze E-D. 2003. The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology* **84**: 1539-1552.

Schneider H, Postma JA, Wojciechowski T, Kuppe C, Lynch J. 2017. Root cortical senescence improves growth under suboptimal availability of N, P, and K. *Plant Physiology* **174**: 2333-2347.

Scholz FG, Bucci SJ, Goldstein G, Moreira MZ, Meinzer FC, Domec J-C, Villalobos-Vega R, Franco AC, Miralles-Wilhelm F. 2008. Biophysical and life-history determinants of hydraulic lift in Neotropical savanna trees. *Functional Ecology* **22**: 773-786.

Schreiber L, Franke R, Hartmann K, Ranathunge K, Steudle E. 2005. The chemical composition of suberin in apoplastic barriers affects radial hydraulic conductivity differently in the roots of rice (*Oryza sativa* L. cv. IR64) and corn (*Zea mays* L. cv. Helix). *Journal of Experimental Botany* **56**: 1427-1436.

Schwinning S. 2010. The ecohydrology of roots in rocks. *Ecohydrology* **3**:238-245.

Seastedt TR. 1988. Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology* **69**: 59-65.

See CR, Luke McCormack M, Hobbie SE, Flores-Moreno H, Silver WL, Kennedy PG. 2019. Global patterns in fine root decomposition: climate, chemistry, mycorrhizal association and woodiness. *Ecology Letters* **22**: 946-953.

Segal E, Kushnir T, Mualem Y, Shani U. 2008. Water uptake and hydraulics of the root hair rhizosphere. *Vadose Zone Journal* 7: 1027-1034.

Shane MW, Cawthray GR, Cramer MD, Kuo J, Lambers H. 2006. Specialised 'dauciform' roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. *Plant, Cell and Environment* **29**: 1989-1999.

Sharda JN, Koide RT. 2008. Can hypodermal passage cell distribution limit root penetration by mycorrhizal fungi? *New Phytologist* **180**: 696-701.

Silver W, Miya R. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* **129**: 407-419.

Simon J, Dannenmann M, Pena R, Gessler A, Rennenberg H. 2017. Nitrogen nutrition of beech forests in a changing climate: importance of plant-soil-microbe water, carbon, and nitrogen interactions. *Plant and Soil* **418**: 89-114.

Siqueira M, Katul G, Porporato A. 2008. Onset of water stress, hysteresis in plant conductance, and hydraulic lift: Scaling soil water dynamics from millimeters to meters. *Water Resources Research* **44**: W01432.

Soto-Gómez D, Pérez-Rodríguez P, Vázquez-Juiz L, López-Periago JE, Paradelo M. 2018. Linking pore network characteristics extracted from ct images to the transport of solute and colloid tracers in soils under different tillage managements. *Soil and Tillage Research* **177**: 145-154.

Soudzilovskaia NA, van der Heijden MGA, Cornelissen JHC, Makarov MI, Onipchenko VG, Maslov MN, Akhmetzhanova AA, van Bodegom PM. 2015. Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling. *New Phytologist* **208**: 280-293.

Soudzilovskaia NA, van Bodegom PM, Terrer C, Zelfde Mvt, McCallum I, Luke McCormack M, Fisher JB, Brundrett MC, de Sá NC, Tedersoo L. 2019. Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* **10**: 5077.

Spohn M, Kuzyakov Y. 2013. Distribution of microbial- and root-derived phosphatase activities in the rhizosphere depending on P availability and C allocation - Coupling soil zymography with C-14 imaging. *Soil Biology and Biochemistry* **67**: 106-113

Sprent J. 2009. *Legume nodulation: A global perspective*. Oxford, UK: John Wiley & Sons.

Steudle E, Peterson CA. 1998. How does water get through roots? *Journal of Experimental Botany* **49**: 775-788.

Stokes A, Atger C, Bengough A, Fourcaud T, Sidle R. 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil* **324**: 1-30.

Stokes A, Mattheck C. 1996. Variation of wood strength in tree roots. *Journal of Experimental Botany* **47**: 693-699.

Striker GG, Colmer TD. 2017. Flooding tolerance of forage legumes. *Journal of Experimental Botany* **68**: 1851-1872.

Stuefer JF. 1998. Two types of division of labour in clonal plants: benefits, costs and constraints. *Perspectives in Plant Ecology, Evolution and Systematics* **1**: 47-60.

Taylor LL, Leake JR, Quirk J, Hardy K, Banwart SA, Beerling DJ. 2009. Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. *Geobiology* **7**: 171-191.

Tedersoo L, Laanisto L, Rahimlou S, Toussaint A, Hallikma T, Pärtel M. 2018. Global database of plants with root-symbiotic nitrogen fixation: NodDB. *Journal of Vegetation Science* **29**: 560-568.

Thion CE, Poirel JD, Cornulier T, De Vries FT, Bardgett RD, Prosser JI. 2016. Plant nitrogen-use strategy as a driver of rhizosphere archaeal and bacterial ammonia oxidiser abundance. *FEMS Microbiology Ecology* **92**: fiw091.

Thorup-Kristensen K. 2001. Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant and Soil* **230**: 185-195.

Tisdall JM, Oades JM. 1982. Organic matter and water-stable aggregates in soils. *Journal of Soil Science* **33**: 141-163.

Trachsel S, Kaeppler SM, Brown KM, Lynch JP. 2013. Maize root growth angles become steeper under low N conditions. *Field Crops Research* **140**: 18-31.

Treseder KK. 2013. The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content. *Plant and Soil* **371**: 1-13.

Tückmantel T, Leuschner C, Preusser S, Kandeler E, Angst G, Mueller CW, Meier IC. 2017. Root exudation patterns in a beech forest: Dependence on soil depth, root morphology, and environment. *Soil Biology & Biochemistry* **107**: 188-197.

Tuomi J, Kytoviita MM, Hardling R. 2001. Cost efficiency of nutrient acquisition and the advantage of mycorrhizal symbiosis for the host plant. *Oikos* **92**: 62-70.

Valenzuela-Estrada LR, Vera-Caraballo V, Ruth LE, Eissenstat DM. 2008. Root anatomy, morphology, and longevity among root orders in *Vaccinium corymbosum* (Ericaceae). *American Journal of Botany* **95**: 1506-1514.

Valverde-Barrantes OJ, Horning AL, Smemo KA, Blackwood CB. 2016. Phylogenetically structured traits in root systems influence arbuscular mycorrhizal colonization in woody angiosperms. *Plant and Soil* **404**: 1-12.

van Beek L, Wint J, Cammeraat L, Edwards J. 2005. Observation and simulation of root reinforcement on abandoned Mediterranean slopes. *Plant and Soil* **278**: 55-74.

van Der Krift TAJ, Berendse F. 2001. The effect of plant species on soil nitrogen mineralization. *Journal of Ecology* **89**: 555-561.

Veylon G, Ghestem M, Bernard A, Stokes A. 2015. Quantification of mechanical and hydric components of soil reinforcement by plant roots. *Canadian Geotechnical Journal* **52**: 1839-1849.

Vidoz ML, Loreti E, Mensuali A, Alpi A, Perata P. 2010. Hormonal interplay during adventitious root formation in flooded tomato plants. *The Plant Journal* **63**: 551-562.

Walk TC, Jaramillo R, Lynch JP. 2006. Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. *Plant and Soil* **279**: 347-366.

Wang Y, Li Y, Ye X, Chu Y, Wang X. 2010. Profile storage of organic/inorganic carbon in soil: From forest to desert. *Science of the Total Environment* **408**: 1925-1931.

Warren JM, Brooks JR, Meinzer FC, Eberhart JL. 2008. Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. *New Phytologist* **178**: 382-394.

Weiser M, Smyčka J. 2015. A simple model for the influence of habitat resource availability on lateral clonal spread. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20150327.

Weiser M, Koubek T, Herben T. 2016. Root foraging performance and life-history traits. *Frontiers in Plant Science* **7**: 779.

Wiersum LK. 1958. Density of root branching as affected by substrate and separate ions. *Acta botanica neerlandica* **7**: 174-190.

Wiesler F, Horst WJ. 1994. Root growth and nitrate utilization of maize cultivars under field conditions. *Plant and Soil* **163**: 267-277.

Wissuwa M, Ae N. 2001. Genotypic variation for tolerance to phosphorus deficiency in rice and the potential for its exploitation in rice improvement. *Plant Breeding* **120**: 43-48.

Wu QS, Cao MQ, Zou YN, He X. 2014. Direct and indirect effects of glomalin, mycorrhizal hyphae, and roots on aggregate stability in rhizosphere of trifoliate orange. *Scientific Reports* **4**: 5823.

Wu TH. 1976. *Investigation of landslides on Prince of Wales Island, Alaska*. Geotechnical Engineering Report 5, Ohio State University, Department of Civil Engineering, Columbus, Ohio, USA: 94

Wu TH, Beal PE, Lan C. 1988. In-situ shear test of soil-root systems. *Journal of Geotechnical Engineering* **114**: 1376-1394.

Wurzburger N, Brookshire ENJ. 2017. Experimental evidence that mycorrhizal nitrogen strategies affect soil carbon. *Ecology* **98**: 1491-1497.

Yang M, Défossez P, Danjon F, Dupont S, Fourcaud T. 2017. Which root architectural elements contribute the best to anchorage of *Pinus* species? Insights from in silico experiments. *Plant and Soil* **411**: 275-291.

Yelenik S, Perakis S, Hibbs D. 2013. Regional constraints to biological nitrogen fixation in post-fire forest communities. *Ecology* **94**: 739-750.

Zadworny M, Eissenstat DM. 2011. Contrasting the morphology, anatomy and fungal colonization of new pioneer and fibrous roots. *New Phytologist* **190**: 213-221.

Zadworny M, Jagodziński AM, Łakomy P, Ufnalski K, Oleksyn J. 2014. The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought. *Forest Ecology and Management* **318**: 133-141.

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

Zadworny M, Comas LH, Eissenstat DM. 2018. Linking fine root morphology, hydraulic functioning and shade tolerance of trees. *Annals of Botany* **122**: 239-250.

Zangerl AR, Rutledge CE. 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. *The American Naturalist* **147**: 599-608

Zerihun A, Bassirirad H. 2001. Interspecies variation in nitrogen uptake kinetic responses of temperate forest species to elevated CO_2: potential causes and consequences. *Global Change Biology* 7: 211-22.

Zhang D, Zhang C, Tang X, L, H, Zhang F, Rengel Z, Whalley WR, Davies WJ, Shen J. 2016. Increased soil phosphorus availability induced by faba bean root exudation stimulates root growth and phosphorus uptake in neighbouring maize. *New Phytologist* **209**: 823-831.

Zhang X, Wang W. 2015. The decomposition of fine and coarse roots: their global patterns and controlling factors. *Scientific Reports* **5**: 9940.

Zhang XF, Chua VP, Cheong HF. 2015. Geometrical and material properties of *Sonneratia alba* mangrove roots. *Trees-Structure and Function* **29**: 285-297.

Zhao J, Sykacek P, Bodner G, Rewald B. 2018. Root traits of European *Vicia faba* cultivars - Using machine learning to explore adaptations to agro-climatic conditions. *Plant, Cell & Environment* **41**: 1984-1996.

Zhu K, McCormack ML, Lankau RA, Egan JF, Wurzburger N. 2018. Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. *Journal of Ecology* **106**: 524-535.