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# Incorporating belowground traits: avenues towards a whole-tree perspective on performance

**Monique Weemstra, Thomas W. Kuyper, Frank J. Sterck and María Natalia Umaña**

*M. Weemstra (https://orcid.org/0000-0002-6994-2501) ✉ (moniqueweemstra@hotmail.com) and M. N. Umaña, Dept of Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI, USA. – T. W. Kuyper, Soil Biology Group, Wageningen Univ. and Research Centre, Wageningen, the Netherlands. – F. J. Sterck, Forest Ecology and Forest Management Group, Wageningen Univ. and Research Centre, Wageningen, the Netherlands.*

**Oikos**
**2022: e08827**
doi: 10.1111/oik.08827
Subject Editor: Deliang Kong
Editor-in-Chief: Dries Bonte
Accepted 20 May 2022

Tree performance depends on the coordinated functioning of interdependent leaves, stems and (mycorrhizal) roots. Integrating plant organs and their traits, therefore, provides a more complete understanding of tree performance than studying organs in isolation. Until recently, our limited understanding of root traits impeded such a whole-tree perspective on performance, but recent developments in root ecology provide new impetuses for integrating the below- and aboveground. Here, we identify two key avenues to further develop a whole-tree perspective on performance and highlight the conceptual and practical challenges and opportunities involved in including the belowground. First, traits of individual roots need to be scaled up to the root system as a whole to determine belowground functioning, e.g. total soil water and nutrient uptake, and hence performance. Second, above- and belowground plant organs need to be mechanistically connected to account for how they functionally interact and to investigate their combined impacts on tree performance. We further identify mycorrhizal symbiosis as the next frontier and emphasize several courses of actions to incorporate these symbionts in whole-tree frameworks. By scaling up and mechanistically integrating (mycorrhizal) roots as argued here, the belowground can be better represented in whole-tree conceptual and mechanistic models; ultimately, this will improve our estimates of not only the functioning and performance of individual trees, but also the processes and responses to environmental change of the communities and ecosystems they are part of.

Keywords: leaf traits, mycorrhizal fungi, root traits, tree performance, whole-tree frameworks

## Introduction

Plants regulate important ecological processes across spatial scales through their physiology and performance (see Box 1 for definitions). For example, differences in leaf photosynthetic rates (reflecting a physiological process) underlie interspecific differences in tree growth (a component of organism performance) (Poorter et al. 2006, Sterck et al. 2006, Janse-Ten Klooster et al. 2007) that further drive community

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dynamics (Franklin et al. 2020), up to the primary productivity of ecosystems (Chen and Coughenour 2004). Plant physiology and performance are often determined using functional traits (hereafter: traits; Box 1) as proxies, e.g. variations in photosynthetic capacities and plant growth rates can be predicted from leaf chemical traits (e.g. leaf nitrogen concentration; Evans 1989, Poorter and Bongers 2006) or morphological traits (e.g. specific leaf area (SLA, leaf area per unit leaf dry mass)); Reich et al. 1998, Wright and Westoby 2001). While these traits are most frequently measured on isolated organs, and mostly leaves, plant performance eventually results from combinations of interdependent leaf, stem and (mycorrhizal) root traits, their associated functions and underlying physiology (Marks and Lechowicz 2006, Sobral 2021, Weemstra et al. 2021, Yang et al. 2021). Rather than studying them separately, integrating the functioning of different organs, therefore renders a more complete understanding of plant performance, and ultimately, community and ecosystem processes. A key bottleneck regarding such whole-plant integration lays belowground (McCormack et al. 2017), where (mycorrhizal) root traits play critical but often unclear roles in plant performance by determining rates of water and nutrient uptake and plant tissue losses, and by anchoring the plant. Fortunately, recent conceptual and technological advances in root ecology provide important impetuses for belowground integration at the whole-tree level (Defrenne et al. 2021). Here, we propose and discuss key avenues to including (mycorrhizal) roots in whole-tree frameworks.

Until recently, roots were considered the ‘black hole’ in plant ecology, and the availability of data on root traits still lags behind that of leaf traits (Bardgett et al. 2014, Iversen et al. 2017). However, the last years have seen a strong interest in the belowground parts of plants. Recent developments include the standardization of (mycorrhizal) root and mycorrhizal–fungal trait measurement protocols (Freschet et al. 2021a), the establishment of multidimensional root trait frameworks (Kramer-Walter et al. 2016, Weemstra et al. 2016, Liese et al. 2017, Ma et al. 2018, Li et al. 2019, Bergmann et al. 2020) and how these relate to aboveground traits (Carmona et al. 2021, Weigelt et al. 2021), clearer definitions of, and links between root traits and root functions (Freschet and Roumet 2017, McCormack et al. 2017, Freschet et al. 2021b), and the expansion of global root and mycorrhizal–fungal trait datasets (Chaudhary et al. 2016, Iversen et al. 2017, Flores-Moreno et al. 2019, Soudzilovskaia et al. 2020, Zanne et al. 2020, Guerrero-Ramírez et al. 2021), with particular improvements in underrepresented study areas, like the tropics (Cusack et al. 2021). Technological progress provides new insights in processes that used to be largely invisible to the eye; for instance, while minirhizotrons have been important tools to observe in situ root growth, development and mortality since the 1930s (Bates 1937), newer, high-resolution cameras used with minirhizotrons provide even more detailed observations of roots and mycorrhizal–fungal dynamics (Defrenne et al. 2020). These advances shine new lights on (mycorrhizal) roots, their traits and how these

### Box 1. Obtaining a whole-plant perspective on performance definitions

- *Functional trait.* Any morphological, physiological or phenological feature that influences fitness indirectly via their effects on individual performance. For example, root $K_m$, the root Michaelis–Menten constant, i.e. the nutrient concentration where 50% of the maximum net ion uptake is observed.
- *Function.* The action for which an organ, organism or object is specially fitted or used. For example, root nutrient uptake.
- *Organ-level trait.* A functional trait that is measured at a single organ. For example, specific root length (i.e. root length per unit root dry mass) is measured on a (or several pooled) individual root(s).
- *Organism-level trait.* A functional trait measured at the organism level. For example, total root biomass is the root biomass of the plant as a whole.
- *Performance.* The growth, survival or reproductive rate of an organism.
- *Physiology.* Chemical and physical processes behind an organ or organism’s function. For example, root nutrient uptake kinetics, i.e. the concentration-dependent net uptake rates of a given nutrient of a root that is described by two functional traits: $I_{max}$ (the amount of ions accumulated per unit root biomass and time under conditions of nonlimiting nutrient concentration) and $K_m$ (see example of functional trait).

#### ***Highlights: three lines for future research***

- Traits of individual roots need to be scaled up to the entire root system to estimate belowground functioning (e.g. total nutrient uptake rate) and, by extension, performance (e.g. growth) at the whole-tree level.
- Because plant functions involve the integrated work of above- and belowground organs, connecting them at the whole-plant level requires accounting for their functional interdependencies to determine how they together determine tree performance.
- The integration of mycorrhizal fungi based on their traits, their functioning and interactions with their host tree from a myco- and phytocentric perspective forms one of the main frontiers to improve belowground representation in conceptual and mechanistic whole-tree frameworks.

influence plant performance, and offer promising opportunities to incorporate them at the whole-plant level.

We propose two avenues that are key to the development of a whole-plant framework that includes roots. Firstly, trait information is mostly obtained at the organ level with e.g. SLA or specific root length (SRL, root length per unit root dry mass) representing the absorptive area and thus potential resource uptake of a single leaf or root per unit biomass invested. However, plant performance relies on the total amount of water and nutrients acquired, conserved and lost, and is hence reflected by trait information at the organism rather than the organ level. Here, we plea for scaling up traits from a single root to the root system as a whole as a first opportunity to generate more accurate and complete estimates of whole-tree functions and performance. In this context, it should be noted that when distinguishing organ- and organism-level traits (Box 1), we refer to the concept of 'trait' in a broader sense, that is, any morphological, physiological or phenological feature that influences fitness indirectly via their effects on individual performance (i.e. growth, survival, reproduction) (Arnold 1983, Violle et al. 2007) without reference to its heritability (i.e. 'trait' sensu Garnier et al. 2015). Using this broader definition precludes addressing evolutionary questions regarding the traits that drive whole-plant performance but does allow the inclusion of organism-level traits, like total root mass or length, that have a minor heritable component but are critical determinants of e.g. total soil resource uptake and thus, tree performance.

A second avenue concerns connecting the below- and aboveground to explore and understand how plants function as a whole. Previous studies sought to link them using a plant economics framework that assumes that leaf and root traits covary in a (one-dimensional) leaf and root economics spectrum, respectively, ranging from species with acquisitive traits that allow fast resource uptake, to species with conservative traits that permit long-term resource retention (Reich et al. 1997, Wright et al. 2004, Reich 2014). These leaf and root traits spectra were further expected to run in parallel to each other: species with 'fast,' acquisitive leaves with high photosynthetic rates would have fast, acquisitive roots to rapidly supply the crown with water and nutrients, and species with slow, conservative leaves would have slow, conservative roots to retain plant resources both above- and belowground (Reich 2014). Belowground, however, reality proves more complicated than assumed: root resource economics requires a broader interpretation because root traits do not only covary along a single fast–slow continuum, but also along a second 'collaboration axis' involving associations with mycorrhizal fungi (Bergmann et al. 2020). This collaboration axis separates species with thin roots and high SRL that rely on their roots themselves to acquire nutrients, from species with thick roots and low SRL that allow high colonization by mycorrhizal fungi to which they outsource nutrient acquisition (Bergmann et al. 2020). Because this collaboration axis has no aboveground equivalent, leaf and root traits do not necessarily covary (Fortunel et al. 2012, Hogan et al. 2020), and only recently has this belowground multidimensionality been accounted for when correlating leaf and root traits (Carmona et al. 2021, Weigelt et al. 2021). While offering novel insights into above–belowground trait connections, these recent studies do not account for or provide information on the mechanistic interplay between plant organs and how this drives performance. For example, carbon gain not only depends on leaf chemistry and morphology but also on (mycorrhizal) fine-root (hereafter referred to as root) traits that determine the acquisition of nutrients and water required for photosynthesis, and whose functioning requires carbon fixed by the leaves. As the functioning of one organ is contingent on the functioning of another, we here call for accounting for these functional interdependencies to provide more accurate insights into how organs relate and together drive whole-plant performance.

An implication and further complication of this belowground multidimensionality relates to the fact that for the vast majority (> 80%) of plant species, and almost all trees, the role of roots in whole-plant performance is co-determined by their ecto- (EcM) or arbuscular mycorrhizal (AM) associations that are in turn involved in different plant functions. Their best-known and most frequently studied function is nutrient transfer to the host plant (Newsham et al. 1995, Delavaux et al. 2017), and both types of mycorrhizal symbiosis strongly enlarge the plant's belowground absorptive area and extend the depletion zone for poorly mobile elements by producing thin (emanating) hyphae. Both AM and EcM fungi contribute to phosphorus uptake and that of other well-buffered nutrients and especially EcM fungi with long emanating hyphae and long rhizomorphs (i.e. thick bundles of extramatrical mycelia) can transport nitrogen and phosphorus over ecologically significant distances (Agerer 1995, Tedersoo and Bahram 2019). Ectomycorrhizal fungi can also access organic nutrients by excreting enzymes that oxidize organic matter (Rineau et al. 2012, Lindahl and Tunlid 2015), whereas AM fungi generally have no or limited capacity to do this (Hodge 2001, Read and Perez-Moreno 2003). Mycorrhizal (especially EcM) fungi further contribute to plant water uptake and through hydraulic lift, they redistribute water among individual plants through mycelial networks (Querejeta et al. 2003, Egerton-Warburton et al. 2007). They can also improve plant water status through indirect impacts on stomatal conductance and photosynthesis; for instance, enhanced (AM and EcM fungal) hyphal length can maintain conductivity and thus plant water status by filling drought-induced air pockets between root and soil (Augé 2001). Mycorrhizal fungi further affect the plant carbon balance by 1) receiving up to 20% of photosynthetic carbon of the plant (Hobbie and Hobbie 2006), especially EcM fungi that have greater carbon requirements than AM fungi due to their larger hyphal networks (Leake et al. 2004, Hobbie 2006, Brzostek et al. 2015, Lu and Hedin 2019); 2) serving as an important carbon sink driving plant photosynthetic rates (Hobbie and Hobbie 2006, Kaschuk et al. 2009); and 3) allowing the transfer of carbon between individual plants through common mycelial networks (Simard et al. 1997, Klein et al. 2016), although most of this carbon might be retained by the fungus and hence may not impact plant performance (Robinson and Fitter 1999). Finally, plant resource conservation is influenced through (local and systemic) physical and chemical protection of plant tissue by AM and EcM fungi (Marx 1972, Gange and West 1995, Newsham et al. 1995, Pozo and Azcón-Aguilar 2007, Kempel et al. 2010), e.g. by EcM hyphal mantles that envelop root tips and protect them from antagonists (Marx 1972); by mycorrhizal-induced plant production of protective compounds (Frew et al. 2021); or by plant–plant transfer of herbivore defense signals through mycorrhizal networks (Simard et al. 2012, Babikova et al. 2013, Song et al. 2014). As mycorrhizal fungi not only have pronounced impacts on these different plant functions and performance, but also directly modify root traits, such as diameter, SRL, nitrogen concentrations and lifespan (Berta et al. 1995, King et al. 2002, Heijden and Kuyper 2003, Ostonen et al. 2009, Ouimette et al. 2013), their integration in a whole-plant framework is essential.

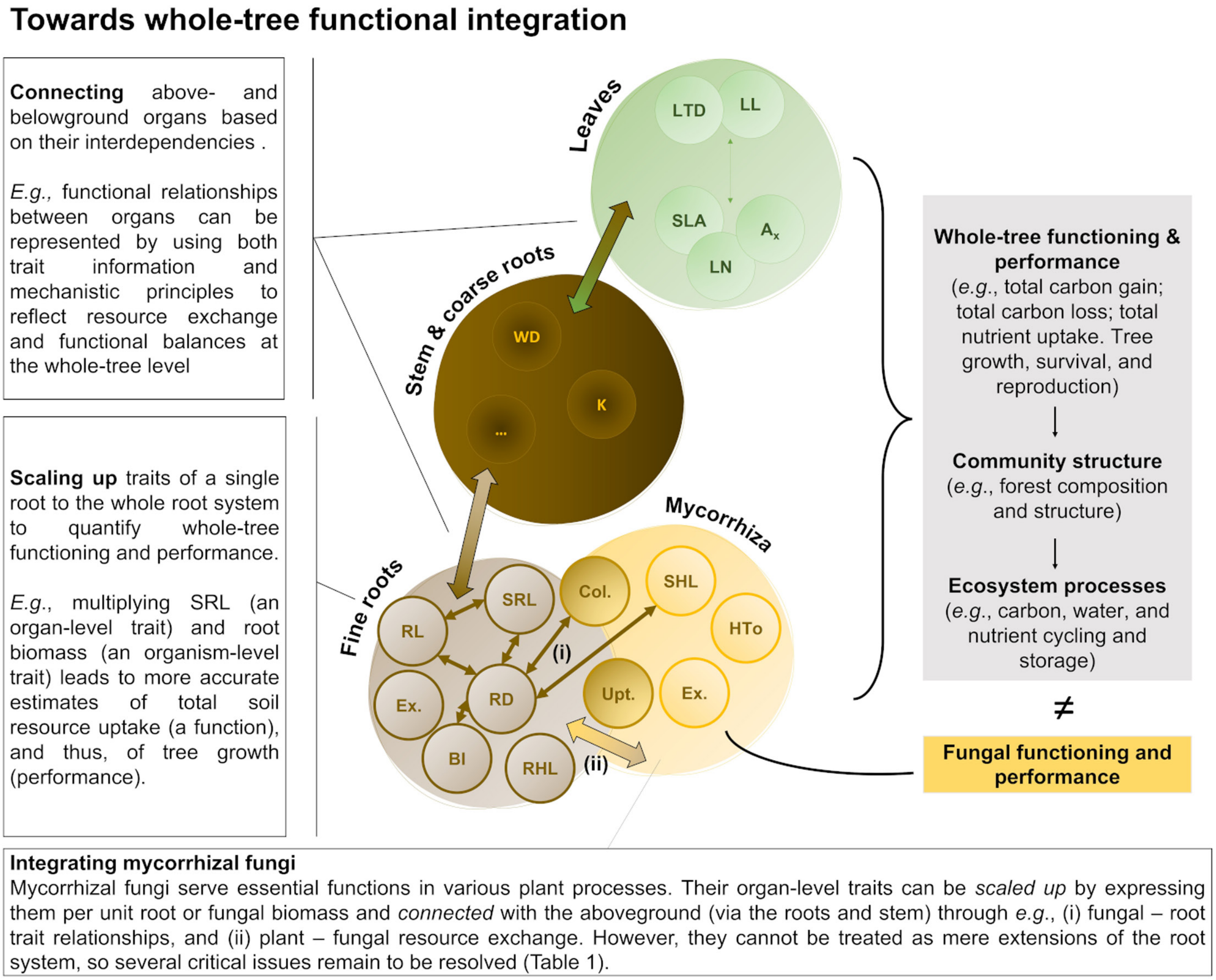
In the next sections, we discuss the state-of-the-art and important considerations of these two key avenues: 1) scaling up belowground traits, and 2) mechanistically connecting the below- and aboveground, to advance the development of a whole-plant perspective on functioning and performance. We further highlight opportunities and knowledge gaps for mycorrhizal integration at the whole-plant level as they play indispensable roles in plant functioning. We conclude with the implications of our proposed approaches and whole-tree framework to improve our understanding of ecological processes on spatial scales beyond the individual tree. This study focuses on trees because woody and non-woody plants may differ in their root trait coordination (Roumet et al. 2016, Weemstra et al. 2016) which may have different implications for how the belowground is integrated at the whole-plant level.

## Scaling up from single roots to the root system as a whole

A first avenue to gain a more accurate and complete understanding of whole-tree performance involves scaling up single-root traits to the root system as a whole (Fig. 1). An important recent development in plant ecology has been the assembly of root trait data in large-scale databases (e.g. 'FRED' (Iversen et al. 2017) and 'GRooT' (Guerrero-Ramírez et al. 2021)). Most of these traits are determined at the organ level (i.e. on individual roots, see examples in the fine-root circle in Fig. 1) and serve as important proxies for plant resource use and uptake strategies. For example, high values of SRL (an organ-level trait) have been generally interpreted to reflect a resource-acquisitive strategy by maximizing the root absorptive area per unit biomass, and as such, is expected to be associated with high tree growth rates (Comas and Eissenstat 2004, Reich 2014). As such, SRL and other organ-level traits can be highly useful relative measures to compare e.g. belowground strategies across species and/or environments, but they do not provide absolute information about total belowground resource use and uptake, and therefore about performance, because these processes also depend on the size of the root system (Yang et al. 2018). An aboveground example illustrates that combinations of SLA (an organ-level trait) and leaf mass fraction (an organism-level trait) better predicted seedling growth rates than SLA alone (Umaña et al. 2021). Similarly, SRL values may be multiplied by measurements of the total root biomass of trees (resulting in total root length) to estimate the potential for soil resource uptake more accurately than either SRL or total root mass by themselves. Other traits, e.g. reflecting root physiological activity, such as uptake kinetics, respiration and exudation rates expressed per unit root biomass, can be similarly integrated at the root system level to further explain belowground plant functioning.

Several critical issues need to be considered prior to scaling up root traits and processes, and technological advances and novel scientific insights from the belowground allow (at least partly) resolving them. Firstly, even more than aboveground, belowground organism-level traits like total root mass or length are not always easy to quantify or interpret. For seedlings and saplings, (above- and) belowground traits are feasible to scale up, since their organ- and organism-level traits can be more easily quantified (e.g. by destructive harvesting in pot or mesocosm studies), but data or insights acquired from seedlings in pots cannot be extrapolated to large trees in natural systems due to ontogenetic and soil environmental effects on root trait expressions (Tobner et al. 2013). The excavation and measurement of complete root systems of mature trees, however, is far more difficult and time-consuming, especially for the more fragile roots at the distal ends of a root system, so that upscaling to the level of the tree-root system remains challenging at present. In monocultures, extensive root sampling at the population level (through soil coring) can be used to infer root biomass information for individual trees (Valverde-Barrantes et al. 2007, Weemstra et al. 2017, 2020), but in mixed stands where roots cannot be easily distinguished between species, this proves more difficult. Novel techniques may however be developed or improved that would lead to more certain estimates of total root biomass or length for an individual tree. For example, advances in molecular techniques and improved DNA barcoding may allow better root biomass estimates at least at the species level in species mixtures (Mommer et al. 2010, Luo et al. 2021). At the same time, roots may overlap in their depletion zones, so whether total root mass or length measurements actually scale linearly with root system resource uptake needs to be carefully considered.

A second consideration is the multidimensionality of belowground trait variation. The availability of aboveground resources (light, $CO_2$) follows a rather even and predictable gradient throughout the canopy, so that leaf traits are in general tightly coordinated in suites associated with either resource acquisition or resource conservation (represented by the thin arrows in Fig. 1) (Reich et al. 1997, Wright et al. 2004). Roots, in contrast, need to simultaneously acquire multiple resources (i.e. water and a variety of nutrients)


**Towards whole-tree functional integration**

**Connecting** above- and belowground organs based on their interdependencies .

*E.g.,* functional relationships between organs can be represented by using both trait information and mechanistic principles to reflect resource exchange and functional balances at the whole-tree level

**Scaling up** traits of a single root to the whole root system to quantify whole-tree functioning and performance.

*E.g.*, multiplying SRL (an organ-level trait) and root biomass (an organism-level trait) leads to more accurate estimates of total soil resource uptake (a function), and thus, of tree growth (performance).

**Whole-tree functioning & performance** (*e.g.*, total carbon gain; total carbon loss; total nutrient uptake. Tree growth, survival, and reproduction)

↓

**Community structure** (*e.g.*, forest composition and structure)

↓

**Ecosystem processes** (*e.g.*, carbon, water, and nutrient cycling and storage)

≠

**Fungal functioning and performance**

**Integrating mycorrhizal fungi**
Mycorrhizal fungi serve essential functions in various plant processes. Their organ-level traits can be *scaled up* by expressing them per unit root or fungal biomass and *connected* with the aboveground (via the roots and stem) through *e.g.*, (i) fungal – root trait relationships, and (ii) plant – fungal resource exchange. However, they cannot be treated as mere extensions of the root system, so several critical issues remain to be resolved (Table 1).

Figure 1. Conceptual model of a whole-tree perspective on plant functioning where traits and functions are integrated across organs. Large circles represent the different organs of plants: leaves, stems and coarse roots, and fine roots, and mycorrhizal fungi, and their organism-level traits (e.g. total biomass of leaves, stem and coarse roots, fine roots and mycorrhizal fungi). Stems and coarse roots are combined since they provide similar functions: resource transport and storage, and mechanical support, that are represented by similar (stem and coarse-root) wood traits. Small circles illustrate examples of organ-level traits related to resource uptake and conservation, i.e. measured on individual leaf, stem, fine-root or fungal subsamples, including leaf tissue density (LTD), leaf lifespan (LL), specific leaf area (SLA), leaf nitrogen (LN), maximum photosynthetic rate ($A_x$), wood density (WD), wood hydraulic conductivity (K), specific root length (SRL), root lifespan (RL), root diameter (RD), root branching intensity (BI), root hair length (RHL), root or mycorrhizal–fungal exudation (Ex.), root or mycorrhizal water or nutrient uptake rates (Upt.), mycorrhizal colonization rate (Col.), specific hyphal length (SHL) and hyphal turnover rates (HTo). Wide, filled arrows indicate fluxes of resources (water, nutrients and carbon) between plant organs and mycorrhizal fungi with carbon fixed by the leaves (partially) being transported to the roots and mycorrhizal fungi through the stem and coarse roots to maintain wood, root and fungal functional processes; water and nutrients acquired by the (mycorrhizal) roots are (partly) transferred to coarse roots, stem and crown where they (among others) drive photosynthesis. Thin arrows indicate (examples of) trait relationships. Leaf traits are generally tightly correlated (represented by partially overlapping trait circles) in acquisitive or conservative trait syndromes that tradeoff. Root traits however can correlate in multiple ways, and can tradeoff with fungal traits (e.g. root diameter and mycorrhizal colonization rate, or hyphal length), giving rise to multiple adaptive belowground trait combinations that determine plant resource use and uptake. Some mycorrhizal traits are often measured on root and fungi, such as colonization rates and resource uptake rates, while others, like hyphal length and turnover, are determined on the mycorrhizal fungi alone. While mycorrhizal traits may reflect mycorrhizal functioning and performance (yellow box), they may not necessarily be indicative of whole-tree function and performance as emphasized by the '≠' sign. Understanding of whole-tree functioning and performance can ultimately be used to infer ecological processes at larger spatial scales as indicated in the grey box.

that can be highly heterogeneously and unpredictably distributed throughout the soil in time and space, and vary in their mobility with important implications for studying root system functions like total resource uptake. Firstly, these multiple resources in turn place different constraints on root traits, e.g. (mineral) nitrogen uptake may be enhanced by producing long, thin roots to maximize the root absorptive area, but this comes at the expense of water transport rate which increases with root diameter (Eissenstat 1992). To balance these various constraints, root trait variation is multidimensional: a large diversity of belowground traits exists (that are not necessarily organized in clearcut trait syndromes as exemplified by the multiple thin arrows in the fine-root circle in Fig. 1) to improve belowground resource acquisition and conservation. For example, besides increasing SRL, trees can enlarge root diameter to facilitate high mycorrhizal colonization rates (Comas et al. 2014); increase root branching intensity (i.e. the number of root laterals (often root tips) per unit root length; Liese et al. 2017, Freschet et al. 2021a); and alter other root architectural (e.g. root hair density), chemical (e.g. concentrations of secondary metabolites) or physiological (e.g. nutrient uptake rates, exudation rates) traits (Sun et al. 2020). Similar resource limitations may therefore not select for similar root trait expressions. Secondly, the functional relevance of a root trait is contingent on the resource to be acquired, e.g. traits like nodulation, the ability to form cluster roots, and the density of root passage cells are important for nitrogen, phosphorus and water acquisition, respectively, but are not directly associated with the uptake of other resources (Freschet et al. 2021b). Even a single nutrient like phosphorus may select for different belowground trait strategies, such as mycorrhizal associations, the formation of cluster roots and root exudation rates and profiles, depending on the form in which it occurs within the soil, e.g. orthophosphates, phosphomonoesters or phytates (Dallstream et al. 2022). In other words, belowground resource uptake is not a single function that roots need to fulfill, but instead poses a complex optimization challenge to the production of an efficient root system for the uptake of water and different nutrient elements (Weemstra et al. 2016). This resultant multidimensionality of root traits implies that in order to quantify even a single belowground function of interest at the root system level, a large variety of potentially relevant root organ-level traits in specific environmental contexts needs to be carefully identified and scaled up (Fig. 1).

When scaling up functions and traits of individual roots to the root system, the relevant part of the root system also needs to be defined, because – unlike leaves – different parts of the same root system are involved in different functions. When studying nutrient uptake, coarse roots (≥ 2 mm diameter) that play no or at best a marginal role are already discarded, but even within the fine, absorptive roots (< 2 mm diameter), there still is considerable variation in traits and functioning (Pregitzer 2002, McCormack et al. 2015, Valverde-Barrantes et al. 2016). For example, determining nutrient uptake requires separate measurements on the first three root orders (i.e. the roots actively engaged in nutrient uptake) (Freschet and Roumet 2017), so these data are to be combined with the biomass of only the first- to third-order roots to scale them up to the root system level. Studying other functions, however, may require sampling differ root entities, e.g. root growth requires data of only the root tips as these are the fragments with apical growth (Freschet and Roumet 2017), so for scaling up, trait data should be combined with the total biomass of only the functionally relevant fractions of the root system.

Furthermore, both leaf and root organ- and organism-level traits vary at different organizational scales, e.g. intra-versus interspecifically. Despite sometimes considerable intraspecific variation (Siefert et al. 2015), traits generally vary more between than within species (Garnier et al. 2001, Westoby et al. 2002, Weemstra et al. 2021). However, this is more often the case for organ- than organism-level traits that are generally less genetically conserved and more controlled by environmental variation (Siefert et al. 2015, Umaña et al. 2018, Yang et al. 2021). For example, along soil environmental gradients, SRL often remains constant within species (George et al. 1997, Espeleta and Donovan 2002, Leuschner et al. 2004, Meier and Leuschner 2008) whereas total root mass can show great intraspecific differences (Weemstra et al. 2017, although it can vary interspecifically as well (Valverde-Barrantes et al. 2007, Weemstra et al. 2020)). The interspecific robustness of organ-level traits makes them highly useful e.g. to compare relative resource acquisition or conservation rates across species, but not to reflect more absolute rates of plant functioning. In fact, measures of plant performance are often poorly explained by organ-level traits (Paine et al. 2015, Yang et al. 2018) and can be more strongly related to traits expressed at the individual rather than the species level (Liu et al. 2016) or at both organizational levels (Umaña et al. 2021). While organ-level trait measurements may be appropriate (for comparisons) at the species level, scaling up belowground functioning from the single root to the whole root system should thus recognize and quantify the degree of intra-specific variation in organism-level traits.

Ultimately, whole-tree performance is not only a function of resource uptake but also of resource losses – through tissue turnover and respiration – at the root system level. For example, trees can combine high-SRL roots with low total root biomass or low-SRL roots with high total root biomass to arrive at equal total root lengths and hence, resource uptake. However, because high-SRL roots have higher turnover rates (McCormack et al. 2012, Weemstra et al. 2016), differences in traits that underlie total root length (SRL and total root mass) may still cause variations in tree performance (Weemstra et al. 2020). Besides carbon expended to root production, additional belowground processes, like root respiration and exudation, make up for a large part of the plant's carbon budget. For example, Kong and Fridley (2019) demonstrated that root mass fraction alone does not well represent belowground carbon allocation, as plants with low root mass fraction still invested a large proportion of carbon belowground due to their higher respiration rates than plants with high root mass fraction. Not accounting for these additional carbon losses leads to poor estimates of plant performance (Kong and Fridley 2019). Further scaling up belowground functioning from the root system to the whole-tree level therefore requires additional considerations, for example of the underlying properties of composite traits like total root length, and additional determinants of tree performance, like belowground resource losses, that are less frequently quantified.

## Scaling up mycorrhizal traits to the root system level

The close associations that almost all trees form with mycorrhizal fungi have important implications for determining traits and functions at the root system level, and ultimately, the whole tree. For example, simply multiplying SRL and root biomass to determine the total root absorptive area and hence, total soil resource uptake potential discounts the large role of mycorrhizal fungi in resource acquisition. More accurate estimates of total belowground resource uptake would therefore account for the total fungal absorptive area as well, e.g. represented by measures of mycorrhizal hyphal mass or length, especially for EcM fungi that produce large hyphal networks (Agerer 2001). To relate mycorrhizal traits to root system functions, they would need to be scaled up from the organ level (e.g. a mycorrhizal root (tip), or fungal hyphae; see trait examples in the mycorrhizal circle in Fig. 1) to the root system level, as we argued above for root traits. Mycorrhizal traits directly expressed on a root mass, length or tip basis (e.g. fractional colonization) could thus be extrapolated through measurements of the whole root system (or the relevant fraction thereof) (Fig. 1).

Incorporating such mycorrhizal fungal traits at the root system level still requires, however, careful consideration and resolution of different issues (Table 1). Firstly, even more than for roots, fungal organism-level traits like total hyphal length are much easier quantified in pots than in natural systems where the spatial boundaries of hyphal networks would be near-impossible to demarcate and the hyphal system virtually impossible to extract as a whole. Also, even if such practical difficulties were to be resolved (e.g. in pot experiments), when depletion zones around hyphae overlap, data on hyphal length do not scale linearly with mycorrhizal and thus, total soil resource uptake by trees. Secondly, many of the relevant mycorrhizal fungal traits are yet to be identified and quantified. Some traits are more readily measured and linked to the functioning of the fungus: for example, high specific hyphal length (i.e. hyphal length per hyphal biomass) could be hypothesized to be associated with faster fungal nutrient uptake. Other traits, like hyphal diameter (with a separation between thin, branched hyphae and wider runner hyphae for AM fungi (Friese and Allen 1991) or rhizomorphs for EcM fungi), hyphal tissue density or physiological parameters of the uptake system (like $C_{min}$ (i.e. the minimum nutrient concentration required for mycorrhizal fungal uptake) or $K_m$ (i.e. the Michaelis–Menten constant)), and exudation rate and

Table 1. Challenges and opportunities for integrating mycorrhizal fungi at the tree level to determine whole-tree functioning and performance.

| Challenge | Example(s) | Opportunities |
|---|---|---|
| Mycorrhizal–fungal traits are difficult to scale up to belowground tree functioning. | 1) Scaling up specific hyphal length requires data on total hyphal biomass which is near impossible to measure in the field. 2) If hyphal length is larger than required by the host tree to improve fungal performance, it does not scale linearly with root system functioning. | Pot and mesocosm studies offer useful first opportunities to quantify both fungal organ- and organism level traits and scale up mycorrhizal functioning to the whole tree. Measuring leaf nutrient concentrations and/or in situ root uptake rates accounts for mycorrhizal functioning. |
| Mycorrhizal fungi contribute to multiple plant functions that drive whole-tree performance, and the fungal traits involved are not yet well defined. | Mycorrhizal fungal traits that characterize their contributions to plant tissue protection are unknown. | Whole-tree research foci can be expanded from mycorrhizal roles in nutrient acquisition to other plant functions, and explore the relevant fungal traits involved, using or contributing to existing fungal trait datasets. |
| Mycorrhizal–fungal performance interests may not align with tree performance interests. | Fungi can increasingly retain nitrogen to promote fungal performance at the expense of plant nutrition. | Future research should be directed towards 1) studying mycorrhizal contributions to tree functioning from a myco- and phytocentric perspective; 2) identifying the environmental conditions under which the fungal trap occurs and 3) establishing direct relationships between fungal traits and tree functioning and performance, rather than assuming tree functioning from fungal functioning. |
| Mycorrhizal fungi cannot be treated as roots in conceptual or mechanistic models | 1) Carbon allocation to mycorrhiza may not be a relevant cost to the host tree; 2) mycorrhizal fungi can retain and allocate resources to their own performance; 3) root, AM and EcM traits play differential roles in (inorganic) nitrogen and phosphorus uptake. | Whole-tree conceptual and mechanistic models that include mycorrhizal fungi should be revisited to 1) focus less on carbon and more on nutrient costs and benefits of the symbiosis; 2) separate nutrient elements based on their mobility; 3) account for asymmetrical fungal and plant performance interests (under certain environmental conditions); and 4) implement fungal traits relevant for (multiple) tree functions and performance and not just fungal performance, as they may not be aligned. |

composition may also be important drivers of fungal nutrient uptake and transport (Agerer 2001, Aguilar-Trigueros et al. 2015, Zanne et al. 2020), but are measured far less frequently. Thirdly, while advances in trait-based (mycorrhizal) fungal frameworks (Aguilar-Trigueros et al. 2015, Zanne et al. 2020) and accompanying datasets (Chaudhary et al. 2016, Flores-Moreno et al. 2019) contribute to scaling up mycorrhizal fungal traits to the root system as a whole, these frameworks are, to date, mostly interpreted from a mycocentric view, that is, they are linked to fungal functions. However, as we discuss in greater detail below, the performance interests of the mycorrhizal partners are often but not always aligned, so that fungal traits involved in fungal functioning may not (to the same extent) benefit root system functioning. Clear tasks for future research lie therefore in further identifying the relevant mycorrhizal traits for fungal performance and their (potentially different) contribution to plant belowground functioning.

At present, there are several promising opportunities to scale root organ to root system functions while accounting for mycorrhizal symbiosis (Table 1). For instance, some physiological processes can be measured directly on the roots or leaves of mycorrhizal plants thereby circumventing the need to quantify the entire fungal system: e.g. by measuring leaf nutrient concentrations, or by quantifying in situ nutrient uptake rates on intact mycorrhizal roots, i.e. without disrupting the mycorrhiza. These measurements can then be linked to the relevant organism-level traits (e.g. determining mycorrhizal root nutrient uptake rate per unit root mass and combining this with total mycorrhizal root mass, or combining nutrient concentrations of individual leaves with the total leaf biomass of plants) to scale up to the root system as a whole. Ultimately, this will provide absolute rather than relative measures of the belowground function(s) of interest (e.g. total tree nitrogen uptake instead of organ-level SRL values), which can in turn be used to better explain tree performance from belowground properties. Furthermore, the traits and functioning of mycorrhizal fungi depend on the mycorrhizal fungal community colonizing the root (which may consist of hundreds of fungal taxa), and this may change with host species identity and environmental conditions. As mycorrhizal fungal community composition can be quantified with increasing accuracy and be linked with fungal functional traits and forest tree growth (Anthony et al. 2022), integrating the mycorrhizal fungal community into the plant trait framework can be one of the key future directions to improve our understanding of holistic root system, tree and ecosystem functions.

## Connecting the below- and aboveground at the whole-tree level

While scaling up traits from individual roots to the entire root system can provide better estimates of belowground functioning, whole-tree performance ultimately relies on the integrated functioning of all plant parts. A second avenue towards a whole-tree perspective on performance therefore involves connecting above- and belowground organs and their functioning because these are interdependent (Fig. 1). Root functioning (e.g. root production) depends on aboveground physiological processes (e.g. carbon assimilated by the leaves and allocated belowground), while leaf functioning (e.g. carbon gain) is simultaneously constrained by water and nutrient uptake by (mycorrhizal) roots. At the same time, organizing traits along parallel resource fast–slow continua does not suffice to make these leaf and root linkages, because leaf traits covary along a one-dimensional resource economics spectrum, while root trait variation is multidimensionally structured and can reflect widely diverse belowground strategies (Carmona et al. 2021, Weigelt et al. 2021).

Recent whole-tree models started to mechanistically integrate above- and belowground plant traits and functions to explain performance at the organism level. Rather than only relying on (single) trait information, mechanistic models also include functions (e.g. nutrient uptake). For example, Weemstra et al. (2020) applied a model that mechanistically incorporated root traits and physiology to test how root functioning impact whole-tree performance through their interactions with aboveground plant parts. Specifically, the model computed the root absorptive area for different combinations of SRL and total root biomass, where an increase in the root absorptive area led to faster uptake of water and nutrients (in this model: inorganic nitrogen), allowing a higher leaf area index (LAI, leaf area per unit ground area) and hence, faster carbon gain in the crown. At the same time, these changes in root and aboveground traits caused carbon losses: an increase in SRL meant faster root turnover and increases in LAI and root biomass led to greater leaf and root (mass-based) turnover and respiration (Weemstra et al. 2020). The model then simulated the net daily carbon gain – a proxy of whole-tree performance – as the difference between carbon gained (through photosynthesis) and carbon lost (through above- and belowground tissue turnover and respiration) based on the coupled uptake, loss and exchange of water, nutrients and carbon between the leaves and roots. Traits involved in resource uptake and loss were thus combined with mechanistic principles to reflect the functional interdependencies between organs (in this model: resource fluxes). This way, an adaptive root-trait strategy alternative to having high-SRL roots was identified: trees with a high total root biomass and low SRL (associated with slow root turnover) had the highest performance because they best balanced the loss of carbon by constructing long-lived roots and the supply of water and nitrogen to the crown by producing sufficient root biomass (Weemstra et al. 2020).

The strength of such mechanistic studies is that they can estimate whole-tree performance by combining the size and dimensions of different organs, their key traits, and, building on biochemical and -physical principles, the total acquisition, use, loss and exchange of resources among organs. As such, scaling up traits – that is, the first avenue we identified in this study – is an essential element since the resource fluxes that functionally connect organs depend on the absolute uptake and use of water, nutrients and carbon by plant parts. In addition, mechanistic models are useful for testing the adaptiveness of different alternative designs (sensu Marks and Lechowicz 2006) that encompass a range of possible trait combinations through which plants as a whole can perform equally well. This opportunity is particularly relevant when integrating the belowground at the whole-tree level, because for roots, a greater variety of trait combinations can be adaptive compared to leaves (compare the thin arrows between syndromes of leaf traits with the various thin arrows between individual root traits in Fig. 1) (Kramer-Walter et al. 2016, McCormack and Iversen 2019). While above- and belowground traits may not be coordinated across (Carmona et al. 2021, Weigelt et al. 2021) or within (Weemstra et al. 2022) species, their functioning and underlying physiological processes (e.g. photosynthesis, water and nutrient uptake) must be balanced at the whole-tree level in order for trees to grow and survive (Cannell and Dewar 1994). Based on this premise, improving our understanding of tree performance, therefore, calls for mechanistic perspectives that take these functional processes and interactions into account when connecting the above- and belowground.

At the same time, several challenges are yet to be addressed for the improvement of such mechanistic approaches. For instance, the model by Weemstra et al. (2020) is restricted to root acquisition of inorganic nitrogen, but as we discussed above, the multidimensionality of root traits implies that the uptake of other nutrient forms may select for (partially) different root traits. Determining the optimal combination of root traits (i.e. leading to the highest performance) and their functional feedbacks with the aboveground thus requires accounting for different (soil) environmental constraints that select for different belowground trait combinations. Another, yet related, caveat pertains to the conceptual and mechanistic inclusion of mycorrhizal symbiosis. In the model by Weemstra et al. (2020), for example, mycorrhizal fungi were lacking, but they form an important additional way through which the belowground absorptive area and, by extension, soil resource uptake, aboveground carbon fixation and whole-tree performance, are strongly enhanced. Connecting leaves and roots at the whole-plant level therefore needs to explicitly address the mechanisms through which mycorrhizal fungi impact above- and belowground plant functioning, as we further discuss below.

## Integrating mycorrhizal fungi at the whole-tree level

Connecting mycorrhizal fungi to the aboveground may benefit from the same mechanistic approach as proposed for roots since they too supply the crown with water and nutrients in return for carbon fixed by the leaves (Fig. 1). This exchange of resources is used e.g. to explain the relative advantage of associating with EcM or AM fungi across soil environments: compared to AM fungi, EcM fungi may have greater carbon requirements to maintain their larger hyphal network, but these carbon costs may be offset by their greater resource uptake potential, especially on soils with high amounts of soil organic matter in which nutrients are stored and where nitrogen is the main limiting nutrient. Due to qualitative similarities between plant roots and mycorrhizal fungal mycelia in the exchange of resources, it may be tempting to treat mycorrhizas as simple extensions of the root system (empirically or in models, de Vries et al. 2021), for example by adding fungal traits analogous to the root traits to the model by Weemstra et al. (2020), e.g. specific hyphal length (i.e. hyphal length per unit hyphal biomass), hyphal biomass and their relevant physiological rates (hyphal uptake, respiration and turnover rates). However, even when these mycorrhizal trait data are readily available, there are some key differences between the functioning of mycorrhizal fungi and roots and their interactions with aboveground organs, which preclude mechanistically integrating fungal traits in a similar way as root traits (Table 1).

Firstly, unlike roots, mycorrhizal symbiosis may not invoke carbon costs but may present nutrient limitations to the host plant, with consequences for aboveground physiology and whole-tree performance. While mycorrhizal fungi rely on carbon supply from their host, this is not necessarily a relevant cost to the plant: studies show that carbon allocation to the fungus and consequently fungal growth can be merely a way to divest excess carbon to prevent downregulation of photosynthesis, stimulate higher photosynthetic rates due to larger sink activity, and may not come at the expense of plant growth (Kaschuk et al. 2009, Corrêa et al. 2012, Gavito et al. 2019, Prescott et al. 2020). Instead of by draining carbon that cannot be invested in plant growth, under nutrient limitations, mycorrhization was found to mostly affect plant growth due to enhanced nutrient (nitrogen and phosphorus) uptake (Corrêa et al. 2008, 2012), which explains how fungal-induced progressive nitrogen limitation reduces plant growth (Alberton et al. 2007). For example, fungal traits that enhance fungal growth (e.g. greater hyphal length) and thus fungal nutrient demands may coincide with greater nitrogen immobilization in fungal mycelium so that less nitrogen is transferred to the host plant and plant growth rates decrease (Alberton et al. 2007, Corrêa et al. 2008, 2012, Alberton and Kuyper 2009, Näsholm et al. 2013, Franklin et al. 2014). Experimental work showed further evidence of such a ‘fungal trap’ where (arbuscular) mycorrhizal fungi were able to take up nitrogen but transferred only a (small) part of this to the host plant and used another part of this for their own growth (Hodge and Fitter 2010, Püschel et al. 2016). Such mycorrhizal-induced nutrient retention is largely unaccounted for but deserves greater attention in studies that connect mycorrhiza to aboveground or whole-tree performance. The phenomenon may be particularly relevant in the context of tree performance along environmental gradients because the mycorrhizal fungal trap may occur predominantly on nitrogen-poor soils (Näsholm et al. 2013) where plants allocate more carbon to their fungal partner(s) (Högberg et al. 2003), or when associating with mycorrhizal fungi with specific traits, e.g. EcM fungal species with extensive extramatrical hyphae (that often co-occur with low soil nitrogen status (Kjøller et al. 2012)).

Secondly, as we outlined in the introduction, mycorrhizal fungal traits drive various whole-tree functions beyond carbon and nutrient exchange between the above- and belowground, such as leaf (and root) protection against pathogens and herbivores, which are often overlooked (Frew et al. 2021). To some extent, the same fungal traits may be relevant for different plant functions, e.g. mycorrhizal fungal traits that contribute to plant nutrition may also indirectly enhance plant tolerance to herbivory by facilitating compensatory plant growth (Chagnon et al. 2013, Frew et al. 2021). Other fungal traits that may relate to these additional plant functions are less clearly defined. For example, specific fungal traits have not yet been identified to characterize mycorrhizal priming of the plant defense system both below- and aboveground, and the contributions of common mycelial networks and associated mycorrhizal traits to plant water status and drought tolerance are not easily captured and mostly demonstrated through high-tech physiological and molecular experiments (including stable-isotope labeling and image analysis, as summarized by Simard et al. (2012)). Since whole-tree performance is a function of various simultaneous and interdependent physiological processes above- and belowground (Laughlin and Messier 2015), increased research efforts into whole-tree performance should be directed towards further exploring and unraveling how and to what degree mycorrhizal fungi and their traits contribute to these diverse plant functions.

Finally, recent studies captured whole-tree form and function in multiple (partially independent) axes of leaf and root trait variation by accounting for mycorrhizal symbiosis (i.e. the belowground collaboration axis, sensu Bergmann et al. 2020, Carmona et al. 2021, Weigelt et al. 2021). However, the limiting nutrient, its mobility, and how it is acquired by roots versus mycorrhizal fungi call for a more nuanced perspective on these recently established above–belowground trait spaces. A recent study applied a mechanistic model to simulate the acquisition of nitrogen (nitrate) versus phosphorus (orthophosphate) of AM plants with different root traits, accounting for the much lower mobility of orthophosphate throughout the soil matrix compared to nitrate (de Vries et al. 2021). The authors showed that plants with AM associations benefited from having thick, unbranched roots for the uptake of (immobile) orthophosphate, but not of (mobile) nitrate. These results support the 'collaboration tradeoff' (Bergmann et al. 2020) but further demonstrate that the benefits of the 'do-it-yourself' strategy (high SRL) versus the 'outsourcing' strategy (high root diameter) are contingent on which nutrient is limiting (de Vries et al. 2021): for phosphorus (and potentially organic nitrogen), this tradeoff indeed represents two alternative uptake strategies, but for inorganic nitrogen, the 'do-it-yourself' strategy is always more efficient, as it can move freely to the root and no nitrogen needs to be invested in the symbiosis. Separating these limiting nutrients based on their mobility, or more generally, classes of nutrients that are mass-flow or diffusion-limited, thus reveals the (ir)relevance of the collaboration axis for the acquisition of different nutrients. In turn, this distinction may have consequences for establishing and interpreting whole-tree conceptual frameworks like the 'global spectrum of plant form and function' (sensu Díaz et al. 2016, Carmona et al. 2021) and can contribute to the further development of whole-tree models to include mycorrhizal fungi.

## General conclusions

This study highlights the importance, opportunities and challenges towards integrating the belowground (that is, roots and associated mycorrhizal fungi) in whole-tree frameworks and improve our understanding, explanatory and ultimately predictive power of performance variation across trees. We propose two important avenues towards estimating performance at the whole-tree level and thirdly, identify the incorporation of mycorrhizal fungi as a crucial next frontier to further improve these predictions (Box 1). Specifically, scaling up traits from a single root to the entire root system likely leads to more accurate and complete estimates of specific belowground functions (e.g. total nutrient uptake) and, more generally, of tree performance. Scaling up (mycorrhizal) root traits and functioning, however, involves explicit consideration of belowground multidimensionality because depending on the environment, trees can adopt a variety of belowground traits to fulfill the same function(s). We further highlight the importance of mechanistically connecting the below- and aboveground to reflect their functional interactions because these are what drives tree performance. An important next frontier towards further completing whole-tree frameworks pertains to the conceptual and mechanistic integration of mycorrhizal fungi (Table 1). They fulfill qualitatively similar functions to the plant (e.g. nutrient and water supply) as roots, but owing to pronounced differences in their functioning, e.g. pertaining to the fungal trap, a mycocentric alongside a phytocentric perspective on the symbiosis is warranted. By highlighting these functional differences and potentially asymmetrical fitness interests between roots and mycorrhizal fungi, we stress the need to further explore mycorrhizal fungal traits and functioning and their actual relevance to trees.

We call for implementing these three research lines to improve the representation of the belowground in whole-tree frameworks that can further advance our understanding of processes on spatial scales beyond individual trees. Some specific insights that we highlight here, e.g. derived from distinguishing nutrients based on their mobility, will be particularly relevant to expand our insights on whole-tree functioning from e.g. temperate to tropical forests where phosphorus is generally the limiting nutrient (Vitousek 2004), as currently our concepts are biased by the dominance of studies on temperate trees in nitrogen-limited environments (Cusack et al. 2021). It will also be increasingly important as due to global change, vegetation in the temperate zone might shift towards phosphorus rather than nitrogen limitation and hence shift forests from being dominated by EcM trees to being dominated by AM trees (Suz et al. 2021). More generally, more accurate measures of tree total resource use and uptake (e.g. by scaling up from individual roots to the root system or by accounting for nitrogen retention by mycorrhizal fungi) can lead to better estimates of tree growth and survival, which in turn, drive forest structure and composition, or of water, carbon and nutrient cycling and storage at the ecosystem level. Furthermore, insights on how to functionally integrate different plant organs and symbionts – e.g. through resource fluxes between aboveground plant parts, roots and mycorrhizal fungi – at the individual plant level can feed into larger-scale models, such as terrestrial ecosystem models, vegetation models or species distribution models. Finally, whole-tree empirical and modeling studies that scale up and/or connect both traits (and functioning) across organs and tree performance can expand whole-tree conceptual models that currently link leaf and (some) belowground traits but are not validated against actual performance data. As such, connecting whole-tree functioning to the environment in both conceptual frameworks and in modeling approaches by 1) scaling up belowground functioning, 2) mechanistically connecting it to the aboveground and 3) accounting for mycorrhiza by recognizing their functional differences from roots, will have important implications for our predictions of forest functioning under environmental change.

*Acknowledgements* – We thank Dr Deliang Kong for critical and constructive comments on earlier versions of this manuscript.
*Funding* – MNU was supported by the National Science Foundation (DEB-2016678).

## Author contributions

**Monique Weemstra**: Conceptualization (lead); Writing – original draft (lead). **Thomas Kuyper**: Writing – review and editing (supporting). **Frank Sterck**: Writing – review and editing (supporting). **María Natalia Umaña**: Conceptualization (supporting); Writing – review and editing (supporting).

## Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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