



An integrated framework of plant form and function: The belowground perspective

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*Tansley review***Title: An integrated framework of plant form and function: The belowground perspective**

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Summary

Plant trait variation drives plant function, community composition, and ecosystem processes. However, our current understanding of trait variation disproportionately relies on aboveground observations. Here we integrate root traits into the global framework of plant form and function. We developed and tested an overarching conceptual framework that integrates two recently identified root trait gradients with a well-established aboveground plant trait framework. We confronted our novel framework with published relationships between above- and belowground trait analogues and with multivariate analyses of aboveground and belowground traits of 2510 species. Our traits represent the leaf- and root conservation gradients (specific leaf area, leaf and root nitrogen concentration and root tissue density), the root collaboration gradient (root diameter and specific root length), and the plant size gradient (plant height and rooting depth). We found that an integrated, whole-plant trait space required as much as four axes. The two main axes represented the fast-slow ‘conservation’ gradient on which leaf and fine-root traits were well aligned, and the ‘collaboration’ gradient in roots. The two additional axes were separate, orthogonal plant size axes for height and rooting depth. This perspective on the multi-dimensional nature of plant trait variation better encompasses plant function and influence on the surrounding environment.

Keywords: collaboration gradient, conservation gradient, economic gradient, functional plant strategies, plant size, trade-offs, trait economics

I. Introduction

Vascular plants began to colonize the Earth's land surface ~430 million years ago (Harrison & Morris, 2017; Morris *et al.*, 2018) and emerged as the dominant primary producers in terrestrial systems (Field *et al.*, 1998). Over time, land plants evolved different strategies and growth forms to survive and compete for limited resources. The plant kingdom now spans plants ranging from tiny, short-lived sidewalk weeds (e.g. *Poa annua* L.) with a maximum height of only 30 cm to mighty, long-lived redwood trees (*Sequoia sempervirens* (D.Don) Endl) which stand over 100 m in height and can live to over 2000 years. Seeking to better understand this diversity in plant strategies, ecologists widely adopted trait-based approaches to quantify and interpret global diversity in plant growth, survival and reproduction of individuals in different habitats (Grime, 1977; Westoby *et al.*, 2002; Violle *et al.*, 2014; Bruehlheide *et al.*, 2018; Freschet *et al.*, 2021).

Plant strategies for success have been interpreted in the light of economic theory, but rather than money, plants spend and save the currencies of carbon, nutrients, and water (Box 1). Economic theory suggests that plants invest in organ construction in ways that reflect strategies for rapid growth or enhanced survival and lifespan (Grime, 1977; Oriens & Solbrig, 1977; Tilman, 1982; Lambers & Poorter, 1992). This growth–survival trade-off was further developed following observations on foliar tissues, where the spectrum of strategies ranging from fast-growing, but short-lived, acquisitive leaves to slow-growing, but long-lived and therefore more conservative leaves. This gradient was later coined the leaf economics spectrum (LES) (Reich *et al.*, 1992; Wright *et al.*, 2004). Variation in leaf strategies along the LES has been linked to differences in plant performance (Davis *et al.*, 1998; Poorter & Bongers, 2006), species distributions, interactions (Sterck *et al.*, 2006), and ecosystem processes (Reich *et al.*, 1997; Diaz *et al.*, 2004, 2007; Grigulis *et al.*, 2013).

The success of the LES in explaining variation in leaf traits inspired further application of economic theory in other plant organs such as stems (Poorter & Bongers, 2006; Chave *et al.*, 2009; Zanne *et al.*, 2010) and flowers (Roddy *et al.*, 2020). These investigations largely confirmed trade-offs among investments in tissue construction, longevity, and growth (Niklas, 1995; Poorter *et al.*, 2008; Chave *et al.*, 2009), and led to the conjecture of other gradients of trait variation representing alternate plant strategies. For example, in a large study covering 6 aboveground traits of ~46,000 species, Diaz *et al.* (2016) observed another important axis first highlighted by

Westoby (1998) representing maximum plant size. The possibility that multiple organ strategies would align at the whole-plant level is often referred to as the ‘Plant Economics Spectrum’ (PES; e.g. Wright & Westoby, 1999; Craine, 2005; Kerkhoff *et al.*, 2006; Freschet *et al.*, 2010) or the ‘spectrum of plant form and function’ (Díaz *et al.*, 2016). In his 2014 ‘traits manifesto’ Reich hypothesized that ‘strong selection along trait trade-offs must result in convergence for any taxon on a uniformly fast, medium or slow strategy for all organs (leaves, stems and roots) and all resources (carbon, nitrogen, water).’ However, not all traits seem to fully align with the concept of a whole-plant economy (Brodribb & Feild, 2010; Sack *et al.*, 2013; Kröber *et al.*, 2015; Li *et al.*, 2015; Weemstra *et al.*, 2016).

Furthermore, our understanding of how function follows form in the plant kingdom has developed with a strong bias towards aboveground traits. Several notable studies indicate that belowground trait variation may not follow predictions established aboveground (e.g. Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016). Using an extensive, global database of root trait observations (Guerrero-Ramírez *et al.*, 2021), Bergmann *et al.* (2020) recently expanded the expected uni-dimensional economic spectrum to two main functional gradients belowground. One gradient is defined as the *conservation gradient* and represents the ‘classical’ fast-slow trade-off between traits associated with high metabolic activity, such as root nitrogen concentration, and those associated with tissue investment, such as root tissue density. The other, but equally important, gradient - the *collaboration gradient* - relates to resource acquisition and varies from a ‘do-it-yourself’ strategy to an ‘outsourcing’ strategy, where resource acquisition is primarily delegated to arbuscular mycorrhizal fungal partners. Together, the conservation and the collaboration gradients explain 77% of root trait variation and encompass the so-called root economics space (RES, Box 1).

Here we ask how the two recently discovered dimensions of the RES (Bergmann *et al.*, 2020) relate to aboveground trait variation, i.e. to both the leaf economics spectrum and to the wider framework of global plant form and function *sensu* Díaz *et al.* (2016). First, we present an economic framework that integrates root traits into the global framework of plant form and function by linking the multiple known gradients of plant trait variation - the conservation gradient, the collaboration gradient, and the plant size gradient (Section II). Second, we use a qualitative literature review to reassess the relationships between above- and belowground traits predicted in our framework, focusing on trait pairs that are often intuitively considered

functionally equivalent (e.g. leaf and root tissue density, Sections III and IV). Third, we test our framework with a new analysis, where existing plant trait databases (TRY, Kattge *et al.*, 2020; and GRooT, Guerrero-Ramírez *et al.*, 2021) are combined to assess above- and belowground trait relationships across species (Section V). Fourth, we mirror this global-scale analysis with measurements made within the same individuals or plots to further test the robustness of the trait coordination at the individual plant level (Section VI). Finally, we discuss the implications of our integrated framework and consider future research directions (Section VII).

II. An integrated framework of plant form and function – linking above- and belowground traits

We developed a conceptual framework linking above- and belowground trait variation across species. We envisage three gradients: conservation; collaboration, and plant size, which we expand on below.

Conservation gradient

The economy along the conservation gradient is a central component of both the leaf economics spectrum (LES) and the root economics space (RES), as both concepts share a trade-off in traits related to a slow versus fast return on resource investment (see Box 1 for terminology). This trade-off differentiates between acquisitive species with short tissue lifespan, high metabolic activity and/or high rates of resource acquisition, and conservative species with longer tissue lifespan, lower metabolic activity and greater protection from herbivory, but slower rates of resource acquisition. The root traits traditionally used to represent this functional trade-off are (1) root nitrogen concentration (RN) as a measure of overall nutrient concentration, physiological activity and palatability (Freschet *et al.*, 2021) and (2) root tissue density (RTD; fine root mass per unit volume) which represents carbon-based construction costs per unit mass (Freschet *et al.*, 2020) including lignification to ensure long lifespan and limited herbivory. Acquisitive or “fast” roots are characterized by high RN concentration and low RTD. The leaf traits traditionally used to represent this functional trade-off are (1) leaf nitrogen concentration (LN) (Wright *et al.*, 2004; Díaz *et al.*, 2016), as fast growth requires high nitrogen concentration to accommodate high photosynthesis rates via high concentrations of proteins associated with light harvesting, CO₂

capture and bioenergetics (Evans & Seemann, 1989), and (2) leaf mass per area (LMA, leaf mass per unit leaf area - the inverse of SLA, specific leaf area), where acquisitive species show low LMA (or high SLA) providing limited construction cost per unit leaf area to achieve a large leaf area and thus “fast” return of carbon on investment. In contrast, conservative, “slow” species are characterized by long-lived leaves with thick cell walls and high construction costs per area (high LMA, low SLA) but low rates of herbivory (low LN) (Poorter *et al.*, 2009). Previous studies have often assumed that SLA (1/LMA) is functionally analogous to specific root length (SRL) because both traits reflect a strategy of cheap construction of absorptive surface area (Reich, 2014). However, recent work from Bergmann *et al.* (2020) has shown that SRL reflects to a large extent an orthogonal belowground collaboration gradient influenced by association with mycorrhizal fungi.

Next to these key traits, there are additional traits related to the conservation gradient (Table 1). The core of the leaf economics spectrum *sensu* Reich *et al.* (1992) and Wright *et al.* (2004) contrasts fast- and slow return on carbon and nutrient investment. The basis for fast return are both high mass-based photosynthetic rates and high leaf respiration rates (Lambers & Poorter, 1992; Reich *et al.*, 1997; Wright *et al.*, 2004), linked with both high LN and leaf phosphorus (LP) concentration, which determines the energy available for plant metabolism (Wright *et al.*, 2004; Güsewell, 2004; Ågren, 2008). In contrast, slow, conservative plants construct dense tissues with thick cell walls that are physically and chemically well-protected from damage and decay. The “slow” end of the conservation spectrum should thus positively relate to tissue density, lignin concentration and lifespan in both leaves and roots. Given the large overlap in conceptual arguments and functioning of both leaf and root conservation gradients, we hypothesize that the traits on the gradients for conservation should be aligned between leaves and roots (Fig. 1). In addition, we hypothesize significant bivariate correlations between leaf and root traits that are assumed to be functionally analogous (Westoby & Wright, 2006; Withington *et al.*, 2006; Freschet *et al.*, 2010; Reich, 2014) such as leaf and root nitrogen or phosphorus concentration and leaf and root tissue density.

Collaboration gradient

Recently, Bergmann *et al.* (2020) demonstrated that SRL is not positioned on the root conservation gradient but on an independent PC-axis related to the ‘collaboration gradient’ that has evolved in

concert with symbiosis with mycorrhizal fungi. This novel global conceptualization of belowground trait space has now also been observed in more local and regional studies (Sun *et al.*, 2021; Spitzer *et al.*, 2021; Sweeney *et al.*, 2021; Williams *et al.*, 2021; Stock *et al.*, 2021). The key traits along this gradient are mean root diameter (RD) and SRL. These traits reflect that thick-rooted species with low SRL are more readily colonized by arbuscular mycorrhizal (AM) fungi due to the larger fungal habitat in the root cortex (Ma *et al.*, 2018; Brundrett & Tedersoo, 2018; Kong *et al.*, 2019; Sweeney *et al.*, 2021). This relationship most likely dominates the root collaboration gradient as about 80% of plant species worldwide are AM (Tedersoo *et al.*, 2020). Other mycorrhizal associations, such as ectomycorrhiza (EcM) or ericoid mycorrhiza (ErM), tend to colonize moderate to thin roots with higher SRL, while non-mycorrhizal species have highest SRL through the construction of very small-diameter roots to maximize the volume of soil that roots explore and exploit by themselves (Bergmann *et al.*, 2020; Freschet *et al.*, 2021).

Inherently related to the functional importance of the collaboration gradient for the symbiosis with mycorrhizal fungi, colonization rates of AM fungi are positively correlated with root diameter (Brundrett, 2002). This is due to an increased fraction of root cortical tissue in thicker roots, providing improved conditions for mycorrhizal association (Kong *et al.*, 2014, 2019; Valverde-Barrantes *et al.*, 2016). This axis of root collaboration leads us to hypothesise that there is no direct functional analogue to SRL and root diameter aboveground and that this axis should therefore be independent of the conservation PC-axis of plant leaves and roots (Fig. 1). Accordingly, we hypothesise that there is no bivariate correlation between SRL and LMA or a functional pairing for thinner leaves (LTh) and thinner root diameter.

Plant size

Plants are more than leaves and fine roots. The analyses of several large data sets have demonstrated that the axis of plant aboveground size forms another independent gradient in multivariate trait space (Díaz *et al.*, 2004; Wright *et al.*, 2007; Díaz *et al.*, 2016). Plant height and overall size represents a coupling of time to reproduction and longevity (Westoby *et al.*, 2002), and is to some extent related to a wide range of differences associated with the dichotomy among herbaceous and woody plants (Díaz *et al.*, 2016). Plants with taller shoots have a greater capacity to compete for light along its predictable vertical gradient (Price *et al.*, 2014). Much in the same way, deeper root systems can be associated with an increased capacity to successfully acquire

water and to a limited extent also nutrients, especially phosphorus, from deeper soil layers (Maeght *et al.*, 2013; Fort *et al.*, 2013; Freschet *et al.*, 2020; Mackay *et al.*, 2020). However, whether maximum rooting depth is directly related to the overall amount of water uptake or merely related to the accessibility of water in deeper soil layers, e.g. under drought conditions, is less clear (Brunner *et al.*, 2015). Further, many belowground resources do not increase with soil depth as nutrient and oxygen availability are often higher in the topsoil (Jobbagy & Jackson, 2001). Successful competition for soil resources may therefore depend to a large extent on horizontal root extent and total root length rather than rooting depth (Postma *et al.*, 2020), but other strategies of soil exploitation may also determine soil resource competition (e.g. Lambers *et al.*, 2008). Ultimately, horizontal extent and total root length are linked to the balance between above- and belowground biomass (e.g. Freschet *et al.*, 2015b; Weemstra *et al.*, 2020) and we thus hypothesize that plant maximum height and maximum root system depth are positively, but weakly related and do not necessarily reflect a single coupled gradient of plant size. Furthermore, both plant maximum height and rooting depth should be independent of leaf and root functional traits (Jiang *et al.*, 2020).

We depicted the main gradients of plant form and function in conceptual Figure 1 which graphically represents our three main hypotheses:

Hypothesis 1: Above- and belowground gradients related to resource investment (conservation gradients) align as a whole-plant fast-slow gradient. Functionally analogous leaf and root traits are well-correlated across this gradient.

Hypothesis 2: Root traits that vary along the belowground collaboration gradient form an orthogonal, independent gradient to the conservation gradient of whole-plant fast-slow traits.

Hypothesis 3: Traits related to overall plant size such as maximum plant height or rooting depth are independent of leaf and root functional trait gradients and form additional gradients in the framework of plant form and function.

III. Methods for current evidence and the analysis of above- and belowground linkages

A detailed methodological description is provided in the supporting information Methods S1.

Qualitative literature review assessing functional trait pairs

We found nearly 100 papers that examined trait correlations among different organs (leaf, stem, root). We selected core traits with key ecological relevance, representing plant *chemistry* (leaf nitrogen concentration, leaf phosphorus concentration, root nitrogen concentration, root phosphorus concentration), *morphology* (leaf tissue density, stem tissue density, leaf thickness, specific leaf area, root tissue density, root diameter, specific root length), *physiology* (leaf photosynthetic capacity, leaf and root respiration), *lifespan* (leaf and root lifespan), *size* (maximum plant height, maximum rooting depth) and *mycorrhization* (i.e., mycorrhizal colonisation rate). We use 1/LMA (equal to SLA) in the literature review as this is most often reported in the literature and is expected to be positively correlated to SRL; in turn we refer to LMA in the remainder of our paper as it is ecologically more intuitive and better reflects the spectrum of plant form and function by Diaz et al. (2016).

In summarizing our results, we counted: (1) the total number of studies reporting a correlation for each trait pair irrespective of the significance of the relationship, (2) number of studies showing a significantly positive relationship, (3) number of studies showing a significantly negative relationship. We report data on 90 bivariate trait pairs in Fig. S1 (see also Methods S2 and Table S1). In the main text, we focus on the set of six above- and belowground traits which we expected to be functional analogues as described in section II (RN-LN, RP-LP, RTD-LTD, RD-LTh, SRL-SLA, depth-height; see abbreviations in Table 1). This detailed review relies on a more conservative selection of 59 studies, that is, only those reporting species-specific trait relationships for a minimum of 15 species (see Methods S2). We tested alternative arbitrary cutoff values for a minimum species number (3 or 20), but the overall outcome was the same (*data not shown*).

Analysis of two global trait datasets to test our conceptual framework

Main database

We used two types of data sets: (1) species-specific mean trait values (804 species) based on global databases (TRY: Kattge *et al.*, 2020; GRooT: Guerrero-Ramírez *et al.*, 2021, additional data sets: supporting information Table S2), (2) species-specific individual trait data (455 species) where root- and shoot traits were measured on the same plant individual or plot to test our inference from global trait databases. However, we did not focus on intraspecific trait variation in

our analysis. Our full data set of species-specific mean traits included all data from the individual trait dataset and all species with data on at least one aboveground and one belowground trait (2510 species). Supporting information Table S3 provides an overview of the full dataset.

We took a three-step approach in our multivariate analyses. *First*, we focused on species with full data on six traits defining the gradients of leaf- and root trait variation, with two traits per gradient: the leaf conservation gradient (LMA, LN), the root conservation gradient (RTD, RN) and the root collaboration gradient (RD, SRL). We performed this analysis for both the species mean trait data set and the individual data set. *Second*, we included maximum plant height (Height, Kattge *et al.*, 2020) and maximum rooting depth (Rdep, Fan *et al.*, 2017) to represent plant stature. There were no species which had observations corresponding to all of the additional traits, so we performed this analysis on the data set of species with mean trait data for at least one aboveground and one belowground trait of the mentioned traits (2,510 species). We used the FungalRoot Database (Soudzilovskaia *et al.*, 2020) and nodDB Database (Tedersoo *et al.*, 2018) to obtain additional information on mycorrhizal association and nitrogen fixation ability, respectively. *Third*, we broadened our analysis to include additional leaf traits characterizing species on the “fast” (leaf phosphorus concentration (LP)) and “slow” (leaf tissue density (LTD), leaf lignin concentration (LL), leaf thickness (Lth)) side of the leaf conservation gradient as well as root traits characterizing species which align with the “fast” (root phosphorus concentration (RP)) and “slow” (root lignin concentration (RL)) end of the conservation gradient. Further, we added traits characterizing “outsourcing” species on the root collaboration gradient (arbuscular mycorrhizal colonization rate (%M), root cortex fraction (CF)).

Data processing

All data processing and analyses were done using R 4.0.3 (R Core Team 2020). Prior to analysis, all trait records were standardized by calculating z-scores. In order to correct trait values for study design and source of publication, we calculated residuals using a linear mixed model for each trait. Scientific names were standardized and matched among data sets using the Taxonomic Name Resolution Service version 4.0 (<http://tnrs.iplantcollaborative.org/>), The Plant List (The Plant List, 2013, Version 1.1), and the Leipzig Catalogue of Vascular Plants (LCVP, Freiberg *et al.*, 2020). Using the backbone phylogeny from Zanne *et al.* (2014), we constructed a phylogenetic tree

including all species using the function ‘phylomatic’ from the package ‘branching’ (Chamberlain, 2020, Version 0.6.0).

Statistical analysis

We used phylogenetically-informed methods for all analyses presented in the main paper and provide results for non-phylogenetically informed analyses in the supporting information. First, we assessed bivariate relationships among the six core traits (RD, SRL, RTD, RN, LMA and LN), where sample sizes ranged from 866 (for RTD vs RN) to 1,497 (for SRL vs LMA) depending on the number of species with respective trait information. We fitted Phylogenetic Generalized Least Squares models to each pair of traits and calculated phylogenetically-corrected correlation coefficients. Second, we performed one phylogenetically-informed Principal Component Analysis (PCA) for all six core traits. In addition, we performed phylogenetically-informed PCAs for subsets of species (mycorrhizal association type, woodiness, or ability to fix atmospheric nitrogen) and used Permutational Multivariate Analysis of Variance (PERMANOVA) to identify significant differences between these subsets. Third, we investigated multiple trait relationships between root traits (RD, SRL, RTD, RN), leaf traits (LMA, LN) and plant size traits (Max Height and Rdep). Fourth, we broadened our analysis to include additional root traits (RP, RL, CF and %M), leaf traits (LL, LP, Lth, LTD), and one stem trait (SSD). We performed a PCA based on pairwise complete correlations using a regularized covariance matrix, where negative eigenvalues were set to small positive values. We used species mean trait data of all 2,510 species to calculate the correlation matrix and subsequently performed a non-phylogenetically corrected PCA.

IV. Current evidence for trait correlations above- and belowground in published literature

First, we tested our integrated framework using a comprehensive literature review to ask to what extent functional analogues, as e.g. LN-RN, LTD-RTD, LTh-RD, SLA-SRL, were supported in previous studies.

Results:

Our literature review documented root-shoot relationships across 36 trait pairs including 147 (53%) non-significant, 86 (31%) significantly positive, and 43 (16%) significantly negative

correlations. However, in only 12 out of the 36 trait pairs were the majority of reported relationships significant; no consistent relationship was detected for the other 24 trait pairs (Fig. 2).

On the “fast” end of the conservation gradient, high LN or LP concentrations were significantly positively correlated to high RN or RP concentrations, as expected based on functional analogues (e.g. Kerkhoff *et al.*, 2006; Geng *et al.*, 2014). On the “slow” end of the conservation gradient, high LTD and RTD were significantly positively correlated in more than half of the studies reporting this relationship (e.g. Wang *et al.*, 2017a; Bergmann *et al.*, 2017). In addition, we found that acquisitive species with high SLA were significantly positively correlated with roots of high RN and RP concentrations (e.g. Holdaway *et al.*, 2011; Kleyer *et al.*, 2019). Further, we found that the majority of reported relationships were significantly negative for RTD compared against LN, LP and SLA (e.g. Shen *et al.*, 2019). Other functional pairs related to the conservation gradient showed mixed results. While leaf and root respiration rates were significantly positively correlated in the majority of studies, we had no data to support potential correlations for leaf and root lifespan (Fig. S1).

Correlations among root traits representing the collaboration gradient (SRL and RD) and purported analogous leaf traits (SLA and LTh) were less clear. Despite 33 studies reporting SRL-SLA correlations on data sets with more than 15 species each, the results were ambiguous: 13 studies reported positive correlations (e.g. Wang *et al.*, 2017b), 17 were non-significant (e.g. Geng *et al.*, 2014), and three were negative (e.g. Li & Bao, 2015). The relationship between SRL and other leaf traits representing the conservation gradient (LN, LP, LTD, LTh) were mostly non-significant as was the relationship between RD and LTh (Fig. 2). Since SRL and SLA are composite traits of RD and RTD and LTh and LTD, respectively, the positive correlation between LTD and RTD appeared to be the underlying reason for the correlation between SRL and SLA, whereas the absence of correlation between RD and LTh appeared to weaken this correlation. The relationships between RD and other aboveground traits were mixed and provided little support for strong coordination between traits along the root collaboration gradient and leaf economics conservation traits. Colonization intensity with mycorrhizal fungi, another important trait characterizing the root collaboration gradient, also showed no significant relationships with leaf traits; however, there was an overall lack of data assessing these relationships (Fig. S1).

Our literature review provided limited evidence to broaden our perspective on plant form and function to include the relationship between plant height and rooting depth as suggested functional analogues. In fact, our survey, focusing on reports containing more than 15 species per study, resulted in only one study reporting a positive correlation between plant height and rooting depth (Burton *et al.*, 2020), though we are aware of some other studies - particularly in smaller stature plants - that have also found positive correlations between height and rooting depth (Violle *et al.*, 2009). Our full database contained two additional studies analysing plant height and rooting depth (Leuschner & Meier, 2018; Miedema *et al.*, 2019), both with non-significant results (Fig. S1). Clearly, any generalization regarding this trait pair based on our survey would be premature.

From this literature review we conclude that reported bivariate correlations provided some evidence that traits along the conservation gradient of the RES are correlated with traits of the LES. Yet, many of the root-shoot pair correlations were non-significant except for leaf and root chemical traits, leaf chemical traits and RTD, and LTD and RTD. Bivariate correlations between root traits along the collaboration gradient (SRL and RD) and all leaf traits were mostly non-significant, except perhaps the correlation between SRL and SLA - though there was no consensus on whether the correlation was positive or negative, and conclusions remain ambiguous despite the large amount of studies. Overall, our literature review provided some evidence for relationships between above- and belowground traits, but they seemed less straightforward than expected from previous synthesis papers (Reich, 2014), presumably due to the multidimensional trait space belowground (Bergmann *et al.*, 2020).

V. The global spectrum of plant form and function – evidence from a global data set of above- and belowground species mean trait values

In the *second step* testing our integrated framework for global form and function in plants we utilized a data set of six core traits quantified as species means for each of 804 species. The six traits selected represented the leaf and root conservation gradients (LN, LMA, RTD, RN) and the root collaboration gradient (RD, SRL). Results of the principal components analysis (Fig. 3, Table S4) supported our conceptual framework. The belowground root conservation PC-axis was closely aligned with the aboveground leaf conservation PC-axis (*Hypothesis 1*), while the collaboration-related root traits belowground (RD and SRL) formed a separate PC-axis that was orthogonal to the conservation-associated traits (*Hypothesis 2*). While most traits were best captured by PC1 and

PC2, RTD most strongly loaded onto PC3 indicating that in addition to its relevance for root economics, RTD shows additional variation potentially related to other root functions that is not captured elsewhere (also see Fig. S2 for pairwise trait correlations, and Fig. S3 and Table S5 for non-phylogenetically informed results).

Results from the main PCA were consistent when conducted separately within woody and non-woody plants (Fig. S4). The main difference between the two growth forms is that RTD was less strongly loaded on PC1 in the non-woody plants leading to a weakening of the correlation between LMA and RTD in these species compared to trees and shrubs (Fig. S4, Table S6). While there was substantial overlap there were significant differences in the trait space occupied by common subgroups including growth form, mycorrhizal association, and N-fixing status (Fig. 3; Table S7). Woody species generally encompassed a larger trait space while non-woody species were more concentrated towards the acquisitive side of the leaf- and root conservation axes. Likely reflecting their larger global diversity and wider distribution, plants forming relationships with AM fungi encompassed the full trait space. In contrast, plants that formed relationships with EM and ErM were more concentrated around higher RTD and LMA values. While the species in our data set with AM associations spanned the plant kingdom, the species with EM and ErM associations were limited to three plant orders: the Fagales (EM), Pinales (EM) and the Ericales (ErM). As a result, the more conservative leaf and root traits associated with these groups may be related to both their mycorrhizal association and their phylogeny. Non-mycorrhizal plants were more concentrated towards higher SRL on the collaboration axis, representing smaller-diameter roots which maximize their absorptive surface area in order to exploit soil resources by themselves (Fig. 3b, Table S7). Finally, N-fixers were strongly associated with higher LN and RN (Fig. 3c, Table S7).

Next, we extended our data set to include measures of plant size, namely plant height and rooting depth, using a PCA based on a matrix of pairwise relationships across 2,510 species. Here we focused initially on 8 traits so that each gradient proposed in our conceptual framework would be equally represented by two traits. The addition of plant size traits did not alter the alignment of leaf and root traits (Fig. 4, Fig. S5). Consistent with our conceptual framework, rooting depth and plant height were unrelated to all other traits and were poorly related to PCs 1 and 2 (*Hypothesis 3*; Fig. 4, Fig. S5, Table S8). Rooting depth and plant height were instead best captured by PCs 3 and 4, respectively. As expected, these traits were only weakly aligned, demonstrating a significant

bivariate correlation ($p = 0.03$, *data not shown*) but without meaningful predictive power ($r = 0.09$).

In a *final* step of our analysis we used an expanded set of 14 leaf and root traits to determine if these traits aligned with the conservation or collaboration gradient as hypothesized in our conceptual framework (Fig. 1). High CF and %M were closely associated with high RD on the ‘outsourcing’ end of the collaboration PC-axis, opposite from greater SRL (Fig. S6, Table S9). The inclusion of additional leaf- and root conservation traits was generally consistent with our expectations as high phosphorous concentrations (LP and RP) remained aligned with high LN and RN representing a ‘fast’ strategy while high lignin concentrations (LL and RL), LMA, and LTD were oriented along the same PC-axis representing a ‘slow’ strategy. One notable exception to these trends was that leaf thickness (LTh) was partly separated from the traditional LES, being most strongly associated with PCs 3 and 4 (Table S9). As in the literature review, the bivariate relationship between composite traits LMA and SRL appeared to be driven more by the association between LTD and RTD than between RD and LTh (Fig. S6). Results from this expanded set of 14 leaf and root traits were consistent with results including also size related traits (17 traits, Fig. S7, Table S10, also see Fig. S8 and Tables S11 and S12 for a sensitivity analysis of this data).

VI. The robustness of above- and belowground trait coordination at the level of individual plants: are individual-based measurements consistent with database composites of species mean traits?

The comparison of mean traits values calculated from observations across different environments and sites are highly useful to allow standardized species comparisons over large, spatial scales (Section V). However, local site conditions drive within-species phenotypic variation in traits and may thus obscure global patterns of trait relationships as well as above- belowground coordination which might be co-adapted to a local environment. To account for potential cross-site variation we conducted an additional set of tests utilizing trait values where above- and belowground traits were measured within individuals or within the same plot across individuals experiencing the same edaphic and climatic conditions for 455 species. Results from our individual-based analysis are consistent with those made using the global, species-mean database and support the robustness of

our conceptual framework (Fig. 1). The overall pattern of trait alignment in our individual-based analysis (Fig. 5, Table S13) was consistent with that observed using the larger species mean data sets with 6 core traits (Fig. 3) and the expanded set of 14 root and leaf traits (Fig. S6). In the individual-based analysis, root diameter (RD) and specific root length (SRL) formed a clear PC-axis representing the root collaboration gradient that was orthogonal to a separate PC-axis where both leaf- and root conservation traits were reasonably well aligned (Fig. 5, Table 13, also see Fig. S9 and Table S14 for non-phylogenetically informed results).

Permutational multivariate analysis again highlighted distinct differences among common plant groups, though these differences were less consistent and less striking compared with the global species-averaged data set (see Figs. 3 and 5). Plants associated with N₂-fixing bacteria differed significantly from plants without this symbiosis (Table S15). There were also significant differences between the most common types of mycorrhizal associations (Fig. 5, Table S15). However, unlike the species-averaged data set, there was not a significant difference between woody and non-woody species in the individual-based data set (Table S15).

VII. Conclusions and ecological considerations

After years of vigorous scientific debate, we asked whether above- and belowground plant traits were coordinated across the whole plant using a qualitative literature review combined with analyses of a global plant trait database spanning leaf, stem, and fine-root traits. We found that key leaf- and fine-root traits were aligned along the expected ‘conservation’ gradient of plant economic investment, but decoupled from an additional ‘collaboration’ gradient for fine roots, explaining a similar amount of trait variation. Together the two respective PCA-axes explained 58% of the variation across leaf and root traits. In turn, whole-plant traits such as plant height and rooting depth each formed additional, separate gradients; we observed similar patterns using both species trait means and above- and belowground trait data collected from individual plants. This large-scale data synthesis and analysis highlights that the trait space for whole-plant form and function is multidimensional, and that the capability for fine roots to collaborate with mycorrhizal fungi for plant resource acquisition adds an important and ecologically-relevant dimension to this trait space.

Traits along the ‘conservation’ gradient

The currencies of economics in plants are the carbon, water and nutrient inputs required to construct and maintain tissues that explore the environment for a resource return on this investment. Plants with an acquisitive strategy - a high metabolic rate, fast growth and fast turnover - need to invest in leaves and roots that are capable of delivering high amounts of resources. We observed that these strategies - as reflected in leaf and root traits - are coordinated in air and soil within a plant, as predicted by Reich (2014) and shown by many others as documented in the literature review (Section IV).

The higher metabolic activity that comes with higher mass-based rates of leaf photosynthesis, root nutrient uptake and growth in both organs should be reflected in the respiration rates of leaves and stems (Reich *et al.*, 1998b,a). Although root respiration measurements are complicated, especially *in situ*, we found good concordance between leaf and root respiration rates (Fig. S1). However, studies comparing both the physiology of leaves and roots are scarce (but see Loveys *et al.*, 2003; Reich *et al.*, 2008) and limited by methodological constraints to accurately quantify traits like nutrient uptake capacity and root respiration (Freschet *et al.*, 2020). We hope the near future will see improved capabilities to scale up physiological root measurements, both in lab and field measurements (Griffiths & York, 2020).

However, this fast-slow continuum does not capture all of the variation in plant strategies, and not all above-belowground trait analogues were well coordinated. In particular, the composite traits of LMA and SRL have been previously assumed to be functionally analogous. However, our analyses indicate that SRL is related to the collaboration gradient (Kong *et al.*, 2019; Bergmann *et al.*, 2020; Sweeney *et al.*, 2021), and ambiguous relationships between LMA and SRL observed in previous studies are likely confounded by positive correlation between functional analogues LTD and RTD; yet no correlation between LTh and RD.

Traits along the 'collaboration' gradient

The collaboration gradient refers to the symbiosis with mycorrhizal fungi via the investment of carbon in a fungal partner for the return of limiting soil resources (Kong *et al.*, 2019; Bergmann *et al.*, 2020). Plant collaboration strategies range from “do-it-yourself” with thin, high SRL roots for efficient resource uptake to “outsourcing” with more cortex volume and hence a larger root diameter to harbor fungal structures. While a parallel can be made with the microbial phyllosphere

communities of leaves aboveground, which can fix atmospheric N₂ to the benefit of the plant (Stone *et al.*, 2018), the magnitude of this outsourcing strategy is unique for the soil environment.

Apart from increasing SRL, there are other conceivable options to realize a “do-it-yourself” resource acquisition. Eissenstat *et al.* (2015) found root branching to be positively correlated with SRL and negatively with mycorrhizal colonization, though evidence for linked architectural and morphological traits is mixed (Comas & Eissenstat, 2009; Kong *et al.*, 2014; Liese *et al.*, 2017). Plants can also release exudates to chemically enhance inorganic phosphorus availability (Lambers *et al.*, 2006). Furthermore, root hairs are known as major structure for resource uptake (Peterson & Farquhar, 1996). They mimic the beneficial effect of mycorrhizal fungi (Schweiger *et al.*, 1995; Maherali, 2017) and could conceptually be linked to a “do-it-yourself” strategy (e.g. Yang *et al.*, 2017).

Traits along the ‘size’ gradients

We found that traits related to plant size, above- and belowground, were independent from the conservation and collaboration gradients (as in Díaz *et al.*, 2016). Further, plant height and rooting depth were aligned on separate PC-axes from one another, and the assumption that tall plants also root deeply was not supported by our data. This lack of correlation may be expected for several reasons. First, while greater height achieves greater access to light, changes in rooting depth can be important for multiple returns on investment, including water acquisition, nutrient uptake, and anchorage. Furthermore, these belowground functions can also be achieved by adjustments in other traits, potentially diluting singular relationships above- and belowground (Ennos & Pellerin, 2000; Lambers *et al.*, 2006; Maeght *et al.*, 2013; Freschet *et al.*, 2021). Second, while growing taller may be associated with increased transpiration-induced water demand and photosynthesis-related nutrient demand, growing deeper does not necessarily improve access to water if water is not limiting, nor does it increase nutrient uptake if nutrients are concentrated in shallow soil layers. However, other metrics of plant size may be more closely aligned. For example, above- and belowground biomass pools (e.g. root:shoot ratios) may reveal more consistent coordination in whole-plant size (see next section below).

Although seed mass has received considerable attention in the trait literature (Westoby, 1998; Moles & Westoby, 2004; Díaz *et al.*, 2016) and has been suggested to be closely linked to plant

size (Díaz *et al.*, 2016; but see Westoby, 1998), we did not focus on this trait here because there was no first approximation of a logical belowground analogue. However, recent evidence indicates that seed mass may be associated with the belowground collaboration axis (Bergmann *et al.* 2017) and this is a tantalizing avenue for further study.

Further widening of the traits capturing plant form and function

While the traits of individual roots and leaves are crucially important, how these structures are displayed (i.e. their branching architecture; Lynch, 2005) or deployed through the soil (vertical and lateral distribution; Niinemets, 2010), together with total biomass allocated to different plant tissues (Poorter *et al.*, 2012), will ultimately determine the overall growth and functioning of a plant. Biomass allocation over different organs is a highly plastic trait as plants adapt and respond to local conditions (Poorter *et al.*, 2012; Freschet *et al.*, 2018). However, allocation is challenging to measure in the field, particularly belowground (Freschet *et al.*, 2020), but revealing relationships between biomass pools of fine roots vs. leaves (or total belowground vs. aboveground biomass) could lead to more consistent trait coordination in whole-plant size than we observed between plant height and rooting depth (but see Freschet *et al.*, 2015a).

Coordination of hydraulic traits above- and belowground seems vital to ensure efficient overall plant hydraulic conductance, photosynthetic rates and plant growth (Brodribb *et al.*, 2002; Fan *et al.*, 2012; Smith & Sperry, 2014). Indeed, recent reviews have compiled strong evidence for correlations between rooting depth and root conductivity and leaf and stem conductivity in woody species (Bartlett *et al.*, 2016; Brum *et al.*, 2017; Mursinna *et al.*, 2018; McCulloh *et al.*, 2019). However, data on herbaceous species and the importance of other root hydraulic traits for leaf hydraulic traits is limited (Zhou *et al.*, 2021). Furthermore, hydraulic traits tend to be decoupled from the LES and RESpectrum (Kong *et al.*, 2014; Li *et al.*, 2015) and work on hydraulic trait coordination still merits more attention from the trait research community.

Constraints on and potential limitations of plant form and function

There are a number of factors with the potential to alter the above- belowground trait correlations predicted by our conceptual thinking (Fig. 1), but three stand out to us: (1) trait correlations potentially differ between species mean traits and those measured on individual plants; (2) traits

and trait correlations can change in different environments, and (3) trait correlations likely manifest in different ways across the phylogenetic tree.

Comparison of global mean vs individual-based trait data - Trait variation driven by local conditions and within-species phenotypic diversity may obscure global patterns. At the same time, global averages may also mask important above- belowground relationships that are only observed when trait sets are adapted to a common environment. Here, we observed very similar trade-offs between global species-means and individual-based data sets. While we deem our results to be generally robust, substantial uncertainty remains surrounding the amount and importance of intraspecific variation and plasticity in trait analyses (Sultan, 2000; Weemstra *et al.*, 2021). Additional work is needed to investigate the ranges of variation within and across species and, given the focus of the current study, it would be particularly interesting to know whether there is more variation in above- or belowground traits.

Environmental constraints can synchronize or decouple plant form and function - Above-belowground trait correlations may shift under different environmental constraints given that traits vary along environmental and climatic gradients. Trait-environment variation is well known for aboveground traits, e.g. in responses to light (Reich *et al.*, 1998a,b; Poorter & Bongers, 2006), temperature and precipitation (Moles *et al.*, 2014; Maire *et al.*, 2015), but also for root traits along changing soil resource availability (Holdaway *et al.*, 2011; Freschet *et al.*, 2017; de la Riva *et al.*, 2018; Fort & Freschet, 2020). Yet, evidence on whether above-belowground traits are coordinated or decoupled along environmental gradients is mixed and depends on the traits (e.g. Craine & Lee, 2003; Freschet *et al.*, 2013; de la Riva *et al.*, 2016; Chen *et al.*, 2016; Kramer-Walter *et al.*, 2016; Hu *et al.*, 2019; Zadworny *et al.*, 2021). Overall, shifting environmental constraints will likely cause trait adjustments within organs or shifts in allocation to different organs (e.g. Prescott *et al.*, 2020) and both changes could strengthen, weaken, or fully decouple aboveground-belowground trait correlations. With the whole-plant trait framework developed here we hope to inspire new work to unravel patterns of trait coordination across environmental gradients more effectively.

Trait variation among clades and across phylogenetic scales - Patterns of trait variation observed across all higher plant groups will likely vary among individual clades and at different phylogenetic scales. For example, variations in leaf- and root nitrogen content are decoupled in monocots and caryophyllales, yet are closely coupled within other major plant clades (Kerkhoff *et*

al., 2006; Valverde-Barrantes *et al.*, 2017). Similarly, root and leaf trait relationships observed within a genus or single species (e.g. Isaac *et al.*, 2017; McCormack *et al.*, 2020) often differ from those reported here and other studies based on more diverse cross-species surveys. Moreover, strong phylogenetic conservatism observed in many collaboration-related traits (e.g. RD, SRL, root cortex, mycorrhizal colonization; (Kong *et al.*, 2014; Ma *et al.*, 2018)) and the comparatively weak phylogenetic conservatism of LMA (Flores *et al.*, 2014) make it more likely that these trait pairs are not tightly coupled. Importantly, the degree to which traits are conserved also varies widely among different groups. For example, root diameter is highly conserved in some groups with species in the Fagaceae often having relatively thin roots and those in the Magnoliaceae relatively thick roots. Yet, Kong *et al.* (2014) observed a greater range in first-order root diameter in the family Euphorbiaceae alone than across all other families of surveyed subtropical plants. Here again, targeted studies are needed to untangle how phylogeny and evolution have shaped above- and belowground trait coordination.

Future directions

Our study provides a comprehensive understanding of how plant trait variation above- and belowground can be integrated at the whole-plant level. Still, despite our best efforts, we were able to assemble root trait data for only ~2,500 species with at least one trait measured above- and belowground. In comparison, the most comprehensive aboveground trait analysis included ~46,000 species (Díaz *et al.*, 2016). This illustrates the need to focus our attention on the neglected ‘hidden half’ of the plant. Yet, future efforts should not only broaden the number of observations in global root trait databases (e.g. Iversen *et al.*, 2017), but deliberately strive to fill gaps identified in this review. One such gap is the need to better understand belowground physiological processes (i.e., actual measurements of root functions like root respiration or resource uptake that we aim to predict based on root form) where true progress is currently limited by methodological constraints.

Our framework opens up a range of perspectives in plant ecology and plant biology. Future studies should scrutinize the relevance of trait gradients for individual plant performance and upscale these findings to the community level. Past attempts to verify the ecological value of traits on different scales showed mixed success (Robinson *et al.*, 1999; Schroeder-Georgi *et al.*, 2016; Ravenek *et al.*, 2016; Fort *et al.*, 2017; van der Plas *et al.*, 2020); but the new framework might provide new insights. These insights could also help to unravel the importance of trait gradients

for stress responses as shown for flooding (Mommer *et al.*, 2006; Wright *et al.*, 2017), drought (Gupta *et al.*, 2020), herbivore attack (Stam *et al.*, 2014) or interactions thereof (Pierik *et al.*, 2013; Vries *et al.*, 2019). Especially community-level gradients of plant trait variation might allow us to better predict ecosystem functioning under climate change.

Another challenge is to reveal how environmental gradients drive trait changes. So far, studies on regional or global scales were restricted to climatic gradients for leaves (e.g. Bruelheide *et al.*, 2018) or roots (Holdaway *et al.*, 2011; Laughlin *et al.* 2021) because we lack the data to link traits with local environmental conditions, especially soil physical and chemical properties. Abiotic conditions drive plant form and function and are underpinning integrated trait variation and coordination. In order to advance our understanding of trait-environment relationships, we encourage all to provide meta-data on abiotic parameters together with trait information.

Our work provides the plant trait community with an integrated above- and belowground framework to build on and better understand plant growth and function under different conditions in a changing world. This framework hopefully moves beyond the trait community *per se*, as it has implications for agronomists developing crop systems, breeders incorporating root traits into breeding programs, forestry, plant growth and climate modelers who are connecting above- and belowground worlds.

Box 1 - Callout box

The sROOT working group had extensive discussions at the iDiv Synthesis Center on the meanings of plant trait terminology. Some of us initially perceived these discussions as tedious, but later realised that taking the time to reflect on the terms and their meaning would deepen our understanding of the trait framework concept we were building. It was doubly important to make sure we were all on the same page given that among the core group of 22 participants, we spoke seven different languages. We decided to share some of our thoughts here in case it helps others to understand our reasoning and conceptual framework.

Axis, Gradient, Spectrum, or Space?

Wright et al. (2004) introduced the leaf economics *spectrum* (LES). Following the Oxford dictionary, the word spectrum is used to classify the position of an object on a scale between two extreme points. The leaf economics spectrum is therefore considered to be unidimensional, and mathematically, a spectrum is described by one axis. In this paper, we only use the term *spectrum* when referring to the leaf economics spectrum, and the term PC-axis when referring to the axes of a principal component analysis. In other, more generalized discussions, we use the term *gradient* to describe gradual linear changes between two opposed ecological strategies.

The next question was how to address multi-dimensional trait coordination. A spectrum is a single gradient from A to B, so that term does not suffice. Bergmann et al. (2020) therefore decided to term two-dimensional root trait coordination the ‘Root economics *space*’, where we think of *space* as an area or volume which is spanned by two or more unidimensional gradients. Confusingly, both, the root economics *spectrum* (as in Weemstra et al., 2016) and the root economics *space* (Bergmann et al., 2020) are abbreviated as RES. We use RES to abbreviate *root economics space* and will refer to RESpectrum otherwise. The RESpectrum, as an analogue of the fast-slow LES, is just one aspect of RES.

The naming of the axes in the RES

As long as there was just one axis described, terminology was simple: LESpectrum or RESpectrum, was sufficient to refer to the fast-slow or acquisitive - conservative gradient. Now that there were two- or more independent axes defining the trait space we needed additional names.

Our rationale to name the fast-slow spectrum the conservation gradient was based on the strong functional link to lifespan. Despite a comparably low initial investment, the fast strategy comes with the expense of short-lived structures; in turn, the slow strategy allows a longer rate of return on investments by conserving invested carbon in better-protected structures.

The second spectrum - which we only observe belowground - reflects on the importance of collaboration with mycorrhizal fungi. Collaboration strategies range from ‘do it yourself’ resource acquisition to outsourcing a large portion of resource acquisition to mycorrhizal fungi. The

conservation and collaboration gradients vary along orthogonal principal component axes in global root trait variation (Bergmann *et al.*, 2020) and are hence independent - meaning that a fast or slow plant strategy can be combined with a range of collaboration strategies with mycorrhizal fungi.

Reflections on Plant Economics

Plant trait coordination is based on economic theory, where the currency is not money but instead photoassimilates, nutrients, and water - the building blocks of plant tissues. We discussed two aspects regarding this concept.

How to interpret the term '*economy*' in plants? Some considered the economy as optimising the absolute scarcity of resources (i.e. the most limiting factor). Others coined it as the 'decisions' that plants have to make towards investing resources in different tissues with a certain return on investments (i.e. more the operational level). If the term economy related to the actual limiting factor that needs optimisation in trait space, it would require a debate on the most limiting resource for plant growth (e.g., carbon, nitrogen or other resources like phosphorus or water). Since there is an ongoing discussion to what extent carbon currently is, and under future climate change will be, limiting plant growth (Prescott et al. 2020, Millard et al. 2007), the framing of the whole-plant economics space as a carbon economy would potentially be problematic. Therefore, it seemed more relevant to coin the term '*economy*' as plant investment in tissue construction with a return on investment of resource acquisition. Along the conservation gradient, the returns on investment range from fast to slow, and along the collaboration gradient, carbon is either invested in a high root surface area or traded for resource acquisition with mycorrhizal fungi.

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Data availability

The RCode to compile the final dataset as well as the RCode and data to reproduce all figures and analyses of this paper can be accessed at <http://doi.org/10.5281/zenodo.5006671>

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Table 1: Above- and belowground traits included in the current analyses.

Traits	Abbreviation	Units	Associated gradient
Leaf mass per area	LMA	mg mm ⁻²	Leaf conservation
Leaf tissue density	LTD	g cm ⁻³	Leaf conservation
Leaf thickness	Lth	mm	Leaf conservation
Leaf nitrogen concentration	LN	mg g ⁻¹	Leaf conservation
Leaf phosphorus concentration	LP	mg g ⁻¹	Leaf conservation
Leaf lignin concentration	LL	mg g ⁻¹	Leaf conservation
Specific stem density	SSD	kg m ⁻³	Plant size
Maximum vegetative plant height	Height	m	Plant size
Maximum rooting depth	Rdep	m	Plant size
Root tissue density	RTD	g cm ⁻³	Root conservation
Root nitrogen concentration	RN	mg g ⁻¹	Root conservation
Root phosphorus concentration	RP	mg g ⁻¹	Root conservation
Root lignin concentration	RL	mg g ⁻¹	Root conservation
Root diameter	RD	mm	Root collaboration
Specific root length	SRL	m g ⁻¹	Root collaboration
Mycorrhizal colonization intensity	%M	%	Root collaboration
Root cortex fraction	CF	ratio	Root collaboration

Figure 1. The integrated framework of plant form and function based on knowledge and expectations from separate findings of the leaf economics spectrum (LES), the root economics space (RES) and the spectrum of whole-plant form and function. We hypothesize a strong coordination of leaf and root conservation gradients representing a gradient of species from fast resource return on investment to slow resource return on investment both above- and belowground. Further we expect an orthogonal collaboration gradient of root traits representing a gradient of species from “do it yourself” resource uptake strategies to strategies where resource acquisition is outsourced to collaborative fungal partners. We do not necessarily expect a single gradient of plant size for maximum height and rooting depth. Figure courtesy of Nathan Armistead, ORNL Graphics based on Kramer-Walter et al. (2016).

Figure 2: Results of qualitative literature review of 59 papers with 276 reported root-leaf trait relationships among a minimum of 15 species presented as pie charts. LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; LTD, leaf tissue density *or* leaf dry matter content; Lth, leaf thickness; LMA, leaf mass per area; Height, maximum vegetative plant height; RN, root nitrogen concentration; RP, root phosphorus concentration; RTD, root tissue density *or* root dry matter content; RD, average root diameter; SRL, specific root length; Rdep, maximum rooting depth. * We use 1/LMA (equal to SLA) as this is most often reported in literature and expected to be positively correlated to SRL. Pie content: grey is the percentage of overall studies with non-significant relationship, blue is the percentage of overall studies with significantly negative correlations, green is the percentage of overall studies with significant positive correlation. Green box color highlights the diagonal root-shoot trait pairs which are assumed to be functional analogues and positively correlated. The outer ring color of the pie indicates the direction of hypothesized relationships based on our new framework of plant form and function (see Fig. 1); grey if no significant correlation was expected, blue for negative and green for positive expected correlations between trait pairs. Where the color of the outer ring matches the main color of the pie content our new framework is supported by a majority of studies in the literature. The size of the pie relates to the number of studies reporting a correlation between the trait pair: smallest size is 0 studies, second size is 1-5 studies, third size is 6 - 10 studies, largest size is greater than or equal to 10 studies. As an example, leaf and root nitrogen are expected to be functional analogues (green box). A trait correlation between the pair was reported in 26 studies

(biggest circle), 21 of which were significantly positive (81% green); no study was significantly negative (0% blue), and 5 studies reported non-significant results (19% gray). See Fig. S1 for full results.

Figure 3: Phylogenetically-informed principal component analyses of the core species set ($n = 804$) based on species mean trait values for (a) woody ($n = 480$) and non-woody ($n = 324$) plant species; (b) arbuscular mycorrhizal species (AM, $n = 630$), ectomycorrhizal mycorrhizal species (EM, $n = 84$), arbuscular and ectomycorrhizal species (EM-AM, $n = 15$), ericoid mycorrhizal species (ErM, $n = 12$), or non-mycorrhizal species (NM, $n = 63$); (c) non-N-fixing ($n = 739$) and N-fixing plant species ($n = 65$, corresponding data in Supporting Information **Tables S4**). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length. Permutational multivariate analysis reveals significant differences between all subgroups and can be found in **Table S7**.

Figure 4: Principal component analysis based on a correlation matrix of species mean values of root and leaf traits (species $n = 2510$) representing the six core traits (see Fig. 3) together with overall plant size for (a) the first and second axes and (b) the third and fourth axis (corresponding data in Supporting Information **Table S8**). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length; Height, maximum vegetative plant height; Rdep, maximum rooting depth. A 3-D version of this figure is available as **Fig. S5**. A PCA of all 17 traits based on pairwise correlations (**Fig. S7, Table S10**) very closely resembled the result of 14 traits as in **Fig. S6**.

Figure 5: Phylogenetically-informed principal component analysis of traits measured on the same individual showing arbuscular mycorrhizal species (AM, $n = 372$), ericoid mycorrhizal species (ErM, $n = 3$), ectomycorrhizal mycorrhizal species (EM, $n = 42$), ectomycorrhizal/ arbuscular mycorrhizal species (EM-AM, $n = 5$) or non-mycorrhizal species (NM, $n = 33$) associated plant species (total $n = 455$, corresponding data in Supporting Information **Tables S13 and S15**). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length.

Supporting Information:

Additional supporting information may be found in the online version of this article.

Methods S1 Detailed description of all methods for sections III, IV and V.

Methods S2 PRISMA flowchart of qualitative literature review.

Table S1 List of 140 papers and extracted information used for qualitative literature review.

Table S2 List of additional data sources for the main database.

Table S3 Quantitative description of all plant traits in the main database.

Table S4 Results of the phylogenetically-informed PCA on the core species set ($n = 804$) for the six core traits based on species mean trait data (as shown in Fig. 3).

Table S5 Results of the non-phylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species mean trait data (as shown in Fig. S3).

Table S6 Results of the phylogenetically-informed PCA on the core species set ($n = 804$) for the six core traits based on species mean trait data of woody and non-woody species (as shown in Fig. S4).

Table S7 Results of the permutational multivariate analysis on the core species set ($n = 804$) including variation between different groups of species based on species mean trait data (as shown in Fig. 3).

Table S8 Results of the PCA based on the correlation matrix of all species ($n = 2510$) for the six core traits and plant height and rooting depth (as shown in Fig. 4).

Table S9 Results of the PCA based on the correlation matrix using complete pairwise data of all species ($n = 2510$) expanding the six core traits to a set of 14 leaf and root traits (as shown in Fig. S6).

Table S10 Results of the PCA based on the correlation matrix using complete pairwise data of all species ($n = 2510$) for all traits (as shown in Fig. S7).

Table S11 Results of the PCA based on the correlation matrix using complete pairwise data for species corresponding to the full data set ($n = 804$) for all traits (as shown in Fig. S8a).

Table S12 Results of the PCA based on the correlation matrix using complete pairwise data for all species ($n = 2510$) for only the six core traits (as shown in Fig. S8b).

Table S13 Results of the phylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (as shown in Fig. 5).

Table S14 Results of the non-phylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (as shown in Fig. S9).

Table S15 Results of the permutational multivariate analysis of traits measured on the individual plant level ($n = 455$) for the six core traits including variation between different mycorrhizal types (as shown in Fig. 5).

Fig. S1 Results of the full quantitative literature review of 98 papers with 550 reported root-leaf-stem trait relationships presented as pie charts.

Fig. S2 Pairwise correlation of all traits used in the analysis based on the full dataset ($n = 2510$ species).

Fig. S3 Non-phylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species mean trait data (corresponding to phylogenetically informed Fig. 3b, corresponding data in Table S5).

Fig. S4 Phylogenetically-informed PCA on the core species set ($n = 804$) separated for non-woody and woody plant species for the six core traits based on species mean trait data (corresponding to Fig. 3, corresponding data in Table S6).

Fig. S5 Three-dimensional representation of Fig. 4.

Fig. S6 PCA based on correlation matrix of species mean traits ($n = 2510$) expanding the six core traits (see Fig. 3) to a set of 14 leaf and root traits (corresponding data in Table S9).

Fig. S7 PCA based on correlation matrix based on species mean trait data of all traits ($n = 2510$, corresponding data in Table S10).

Fig. S8 Sensitivity analysis for data shown in Fig. 3 to test if using different combinations of species numbers and traits would affect the results (corresponding data in Tables S11 and S12).

Fig. S9 Non-phylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (corresponding to phylogenetically-informed Fig. 5, corresponding data in Table S14).

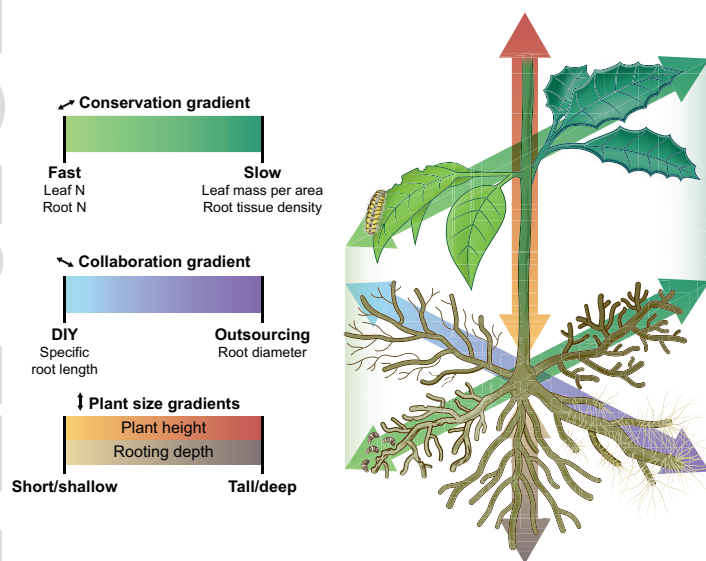


Figure 1

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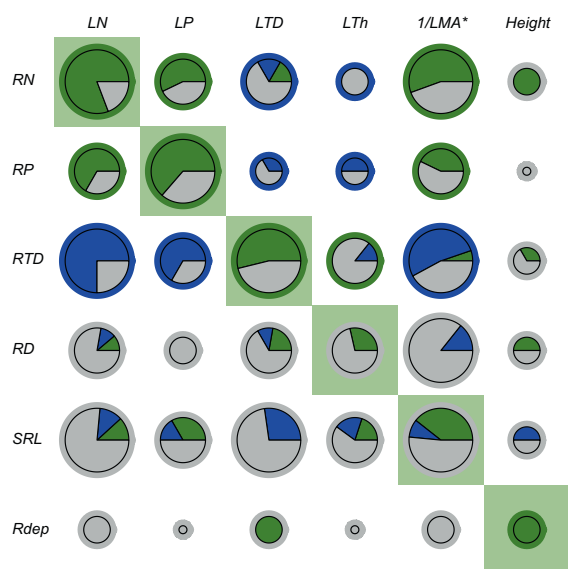


Figure 2

Tansley Review 36271

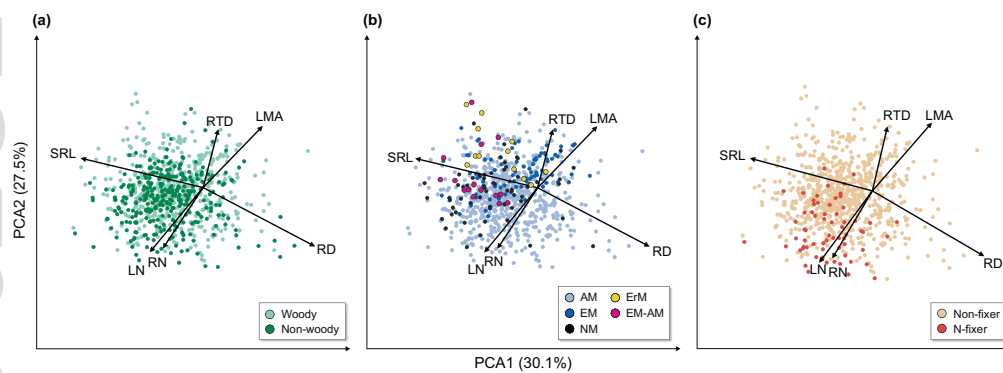


Figure 3

Tansley Review 36271

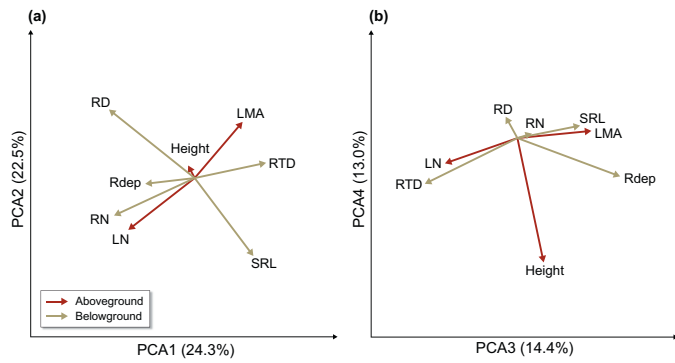


Figure 4

Tansley Review 36271

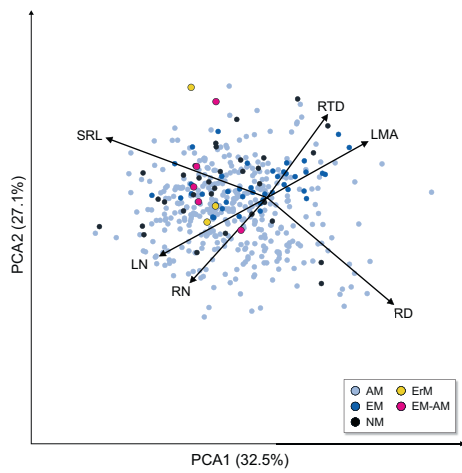


Figure 5

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