

Review

The origin of bi-dimensionality in plant root traits

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Plant roots show extraordinary diversity in form and function in heterogeneous environments. Mounting evidence has shown global bi-dimensionality in root traits, the root economics spectrum (RES), and an orthogonal dimension describing mycorrhizal collaboration; however, the origin of the bi-dimensionality remains unresolved. Here, we propose that bi-dimensionality arises from the cylindrical geometry of roots, allometry between root cortex and stele, and independence between root cell wall thickness and cell number. Root geometry and mycorrhizal collaboration may both underlie the bi-dimensionality. Further, we emphasize why plant roots should be cylindrical rather than flat. Finally, we highlight the need to integrate organ-, cellular-, and molecular-level processes driving the bi-dimensionality in plant roots to fully understand plant diversity and functions.

The importance of roots

The absorption of resources by roots is fundamental for plant growth and response to environmental changes [1–5]. The absorptive function of plant roots is reflected in a suite of **root functional traits** (see [Glossary](#)) [6–12], encompassing morphology, physiology, architecture, anatomy, chemistry, mechanics, and associations with soil biota. Each of these trait categories (e.g., anatomy) can be subdivided into several subcategories (e.g., size of the **cortex**, **stele**, and vessels) and many finer categories (e.g., cell size and cell number) [6,8,13]. Therefore, there is a large number of root traits related to the absorptive functions of roots [14,15].

Identifying key trait dimensions within the total root trait variation helps to understand how plants coexist and adapt to heterogeneous environments and enables us to predict how changes in vegetation composition and diversity alter the function of ecosystems [2,7,16–20]. Analogous to the well-recognized **leaf economics spectrum (LES)** [21,22], plant root traits were previously considered to be arranged along a **RES** [20,23,24], measured by root tissue density (RTD, root dry mass per unit root volume) and root nitrogen concentration. It has been suggested that the RES aligns with leaf and stem economics, as such forming a whole-plant economics spectrum [23,24]. However, this notion has been challenged by the mounting evidence of another root trait dimension independent of the RES; this dimension is represented by a negative relationship between the root diameter (RD) and specific root length (SRL, root length per unit root biomass), which reflects a trade-off in nutrient acquisition between ‘do-it-yourself’ by high-SRL roots versus low-SRL roots, which outsource nutrient acquisition to mycorrhizal fungi [16,25].

Theoretically, the capacity of root nutrient acquisition relies on how much surface area (i.e., the quantity) of the plant roots is used for nutrient foraging and the physiological activity of the roots taking up nutrients. Currently, the potential decoupling of quantity- and activity-related root traits (see [Box 1](#)), and hence the **bi-dimensionality in root traits**, is the prevailing paradigm that links the form and function of plant roots [7,16,17,26]. Bi-dimensionality in root trait spectra is critical to our understanding of species coexistence and belowground responses to global

Highlights

Plant roots are characterized by a cylindrical nature. The worldwide bi-dimensionality in suites of traits for cylindrical-shaped roots reflects essential plant strategies to cope with different environments.

Of the two dimensions, one is the root economic spectrum, representing a trade-off between nutrient acquisition and conservation, while the second is the gradient of nutrient foraging from mycorrhizal dependence to reliance on roots themselves. However, the origin of this bi-dimensionality remains unknown.

We propose that this bi-dimensionality arises from the cylindrical geometry of roots, the allometric relationship of root anatomical structures, and the independence between root cell wall thickness and cell number.

As such, the cylindrical shape of roots, together with mycorrhizal collaborations, may account for the origin of the bi-dimensionality observed in root traits.

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climate change [16,27]. Yet we know little about the origin of bi-dimensionality in root traits. In this review, we first present a brief introduction to the discovery of root trait bi-dimensionality, then we propose multiple mechanisms that could explain root trait bi-dimensionality, and finally we propose ways forward in this fast-developing field of research.

The discovery of root trait bi-dimensionality

Root trait bi-dimensionality was first empirically demonstrated in 2016 by Kramer-Walter *et al.* [28] in 66 New Zealand tree species, while the bi-dimensional decoupling of root quantity (i.e., SRL) from root activity was observed as early as 2009 [29,30]. Since then, various studies have reported independence of root quantity and activity across different scales, mycorrhiza types, plant growth forms, climatic zones, and successional stages (e.g., Table S1 in the supplemental information online). In 2020, Bergmann *et al.* [16] first proposed the worldwide decoupling between the quantity and activity of **absorptive roots** (i.e., the SRL and RD and the RTD and root nitrogen dimensions) using a global dataset of 1810 plant species. Thus, they conceived the concept of root trait bi-dimensionality, which was further confirmed by Weigelt *et al.* [7], Carmona *et al.* [17], and Klimesova *et al.* [31] using more species.

The mechanisms of root trait bi-dimensionality

Of the root traits related to the absorptive function, RD is the most easily measured and has been shown to vary substantially among plant species. For example, the diameter of the first-order roots has 115-fold variation from the thinnest, at 40 μm in the highbush blueberry (*Vaccinium corymbosum*, Ericaceae), to the thickest, at 4600 μm in the perennial herb *Cymbidium cyperifolium* (Orchidaceae) [32–34]. There is a strong correlation between SRL and RD but a weak correlation of RTD and root nitrogen with RD [3,16,35,36]; this suggests that the decoupling between quantity (SRL) and activity (RTD, root nitrogen) of plant roots could be due to differing constraints of RD on these two groups of root traits. Here, we propose three inter-related mechanisms that could explain the origin of bi-dimensionality in plant roots.

Mechanism 1: cylindrical geometry of different diameter roots

As absorptive roots are approximately cylindrical [35,37], the SRL of roots is usually calculated as follows: $\text{SRL} = \text{root length}/\text{root mass}$. Mathematically, root mass is the product of RTD (unit: g cm^{-3}) and root volume (unit: cm^3), then SRL can be expressed as in Equation 1 [38].

$$\text{SRL} = \frac{1}{(\text{RTD} \times \pi \times \frac{\text{RD}^2}{4})} = \frac{1}{\text{RTD} \times \text{RD}^2} \times \frac{4}{\pi} \quad [1]$$

To assess the role of RD in shaping the ‘decoupling’ of SRL and RTD, we discuss the relationship for cases of either constant or variable RD across plant species.

Constant RD across species

In this case, variation in SRL would have been determined only by RTD (Figure 1). Then, given that RTD and root nitrogen concentration are closely related to each other and both reflect aspects of root activity, the root quantity and activity dimensions should be closely coupled. As there is great variation in RD across species, this alternatively suggests a key role of variable RD in driving the independence of root quantity and activity. (See Box 1.)

Variable RD across species

To better understand the role of RD in driving the relationship between SRL and RTD, we discuss the following two cases (Figure 1): RTD increasing (and root nitrogen concentration generally

Glossary

Absorptive roots: a few terminal root branches mostly with primary rather than secondary tissues; these root branches are dominantly responsible for nutrient absorption in plant roots (Figure S1 in the supplemental information online).

Bi-dimensionality in root traits: two orthogonal trait syndromes that constitute bi-dimensionality in root traits: one is the root economics spectrum and the other reflects the associations with mycorrhizal fungi.

Cortex: tissues between the epidermis and the vascular system in stems and roots. The cortex in absorptive roots functions as the agent for water and nutrient uptake and the site for mycorrhizal colonization.

Leaf economics spectrum (LES): a trait syndrome in leaves reflecting a trade-off between the capacity and the persistence (i.e., leaf lifespan) in leaf photosynthesis. This spectrum runs from leaves with high photosynthetic rates, short lifespans, and fast growth rates to leaves with low photosynthetic rates, long lifespans, and slow growth rates.

Mycorrhizal associations: the symbiosis between plant roots and mycorrhizal fungi where roots provide carbon to the fungi and, as a reward, the fungi return nutrients to roots.

Root economics spectrum (RES): a trait syndrome in roots, analogous to the leaf economics spectrum, reflecting a trade-off between capacity and persistence (i.e., root lifespan) in root nutrient absorption. Species with this spectrum shift from fast to slow root growth rates.

Root functional traits: characteristics in root morphology, chemistry, physiology, structures, microbial associations, etc., that influence plant performance.

Stele: tissues in the central part of roots and stems consisting of the vascular system and ground tissues. The stele in absorptive roots functions as the agent for water and nutrient transportation upward and photosynthate transportation downward through conduits in the vascular tissues.

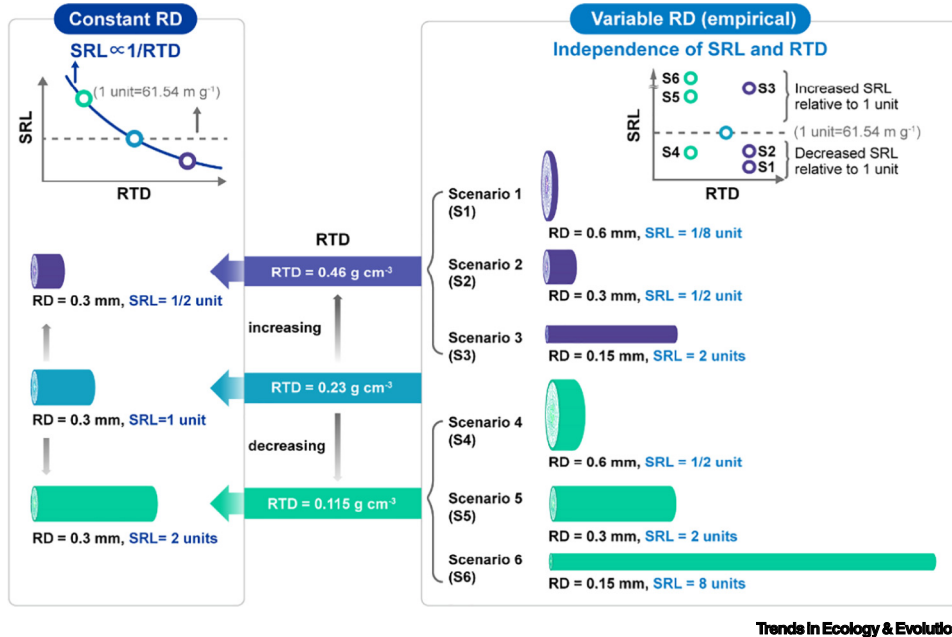


Figure 1. The cylinder shape and root trait bi-dimensionality. Conceptual diagram illustrating how shifts in root diameter (RD) can shape the independent variation of specific root length (SRL) and root tissue density (RTD). Roots are simplified as cylinders with different diameters and SRL can be calculated using Equation 2 in the main text. As an example, the initial RD and RTD values are set at 0.3 mm and 0.23 g cm^{-3} , respectively, using the median trait value of the first-order roots from the Fine-Root Ecology Database (FRED) 3.0 [15], and the resulting SRL value of 61.54 m g^{-1} is considered as 1 unit of SRL. In the left panel, assuming a constant RD, SRL is negatively correlated with RTD. The right panel shows two cases for the effect of increasing RTD (e.g., in dry and infertile soils) and decreasing RTD (e.g., in wet and fertile soils) on SRL and each case includes three scenarios showing increasing, constant, and decreasing values of RD (i.e., Scenarios 1–3 and Scenarios 4–6). Scenario 1: doubling in RD; SRL decreases from 1 unit to 1/8 unit. Scenario 2: constant RD; SRL decreases from 1 unit to 1/2 unit. Scenario 3: a 50% decrease in RD; SRL increases from 1 unit to 2 units. Scenario 4: doubling in RD; SRL decreases from 1 unit to 1/2 unit. Scenario 5: constant RD; SRL increases from 1 unit to 2 units. Scenario 6: a 50% decrease in RD; SRL increases from 1 unit to 8 units.

decreasing) or RTD decreasing (and root nitrogen concentration generally increasing) from an initial value of RTD and RD. Theoretically, the initial RTD and RD can be randomly assigned a value. As an example, we use the median value of RTD and RD (i.e., 0.23 g cm^{-3} and 0.3 mm, respectively) for the first-order roots (the root segment most active in absorptive function [39]) in the Fine-Root Ecology Database (FRED 3.0) [15], currently the largest root trait database. In FRED 3.0, RD varies largely independently of RTD (Figures S2 and S3 in the supplemental information online). For simplicity, we consider the case of increasing RTD by onefold and the case of decreasing RTD by 50%. For each of these two cases, we examine how SRL changes under three scenarios, corresponding to doubling in RD, constant RD, and a 50% decrease in RD, respectively (Scenarios 1–6, Figure 1).

These scenarios show greater sensitivity of SRL to changes in RD than to changes in RTD. That is, in each case of RTD being doubled or halved, shifts in RD allow relatively free variation of SRL (i.e., increasing, decreasing, or remaining constant; Figure 1). In other words, SRL varies independently from RTD, indicating the decoupling of the quantity and activity of absorptive roots. Therefore, such decoupling or root bi-dimensionality can result from varying diameters of the cylindrical geometry of the roots, regardless of the interior structures of the roots (e.g., assembly of the cortex and the stele, see mechanism 2, and cell wall thickness of these tissues, see mechanism 3).

Box 1. Quantity-related and activity-related root traits

The terms 'quantity' and 'activity' in root traits are inspired by the terms of 'quantity' and 'efficiency' of the ecosystem traits proposed by He *et al.* [90,91]. Here, 'quantity'-related root traits refer to the root mass or surface area per unit land area and describe the capacity for nutrient foraging [78]. Whereas the 'activity'-related root traits refer to root mass- or surface area-normalized traits that are directly or indirectly related to nutrient uptake efficiency from the root surface. These include root biochemical contents (e.g., nutrients, proteins, and hormones), enzyme activity (e.g., phosphatase activity), and rates of physiological processes (e.g., root respiration and exudation) [6,25,92,93]. All else being equal, the longer the total absorptive root length, the larger surface area these roots have contacting the soil for nutrient foraging. Therefore, the root length per unit root biomass (i.e., SRL) can be taken as the trait reflecting the quantity of absorptive surface area for a given root biomass. However, the activity of roots for nutrient uptake is usually represented by two common traits at opposite ends of the root economics spectrum [i.e., root nitrogen concentration and root tissue density (RTD)] [28,58]; other activity-related root traits are infrequently measured [82,92]. Root nitrogen is closely and positively related to root respiration [94]. The higher RTD that is common in dry or infertile soils is usually associated with higher investment in root cell walls, which, in turn, reduces the resources allocated for nutrient uptake [46,95]. If quantity-related root traits are coordinated with activity-related root traits (e.g., high SRL is associated with low RTD or high root nitrogen concentration), plants would run along the fast- to slow-growing continuum both above- and belowground and thus form the assumed plant economics spectrum [24].

Thus, the cylindrical shape could be an important driver for root trait bi-dimensionality, which enables multiple root strategies in coping with different environments belowground [17].

Mechanism 2: allometry between root cortex and stele

There is a common allometry between root cortex and stele (hereafter, root allometry), that is, the cortical thickness increases at a faster rate than the stele radius with increasing RD across plant species (Figure 2, Model 1) [35,40,41]. The allometric relationship between the root cortex and stele is not a coincidence, but is rather to balance root nutrient uptake and transport as well as balance root carbon supply and consumption [42–44]. This relationship can lead to a negative correlation between RD and RTD (Figure 2, Model 1) [35] as the proportion of root cross-sectional area occupied by the high mass-density stele decreases with increasing RD (Figure 2, Model 1) [45].

According to the Equation 2 the negative effect of increasing RD on SRL, in conjunction with a shift to thicker absorptive roots, could be offset by the positive effect of decreasing RTD on SRL.

$$SRL = \frac{1}{RTD \times RD^2} \times \frac{4}{\pi}, \quad [2]$$

This offset effect would greatly reduce the variation in SRL with changing RD, while RTD, as mentioned earlier, decreases with increasing RD. The different trends of SRL and RTD with increasing RD could thus result in the decoupling of SRL and RTD (Figure 2, Model 1) [35]. For a better understanding of the root allometry-induced bi-dimensionality in root traits, we consider a hypothetical case of root allometry. In this hypothetical case, if the stele radius increases much faster than the cortex thickness with increasing RD (Figure 2, Model 2), then RTD would increase (Figure 2, Model 2) with increasing RD. In this case both RTD and RD would negatively affect SRL rather than offsetting each other, creating a negative relationship between SRL and RTD (Figure 2, Model 2). That is, the quantity (SRL) and activity (RTD) of absorptive roots could be coupled in this hypothetical case. Together, by comparing the extant (Figure 2, Model 1) and hypothesized (Figure 2, Model 2) root allometry, it is reasonable to deduce that the independence of the quantity and the activity of absorptive roots (i.e., root trait bi-dimensionality) also arises from the allometric relationship between root cortex and stele in extant plants [35].

Mechanism 3: independent variation in cell wall thickness and cell number

The allometry between root cortex and stele has a profound impact on RTD [35,45]. Nevertheless, we still observe considerable variation in RTD around the predicted RTD from the root

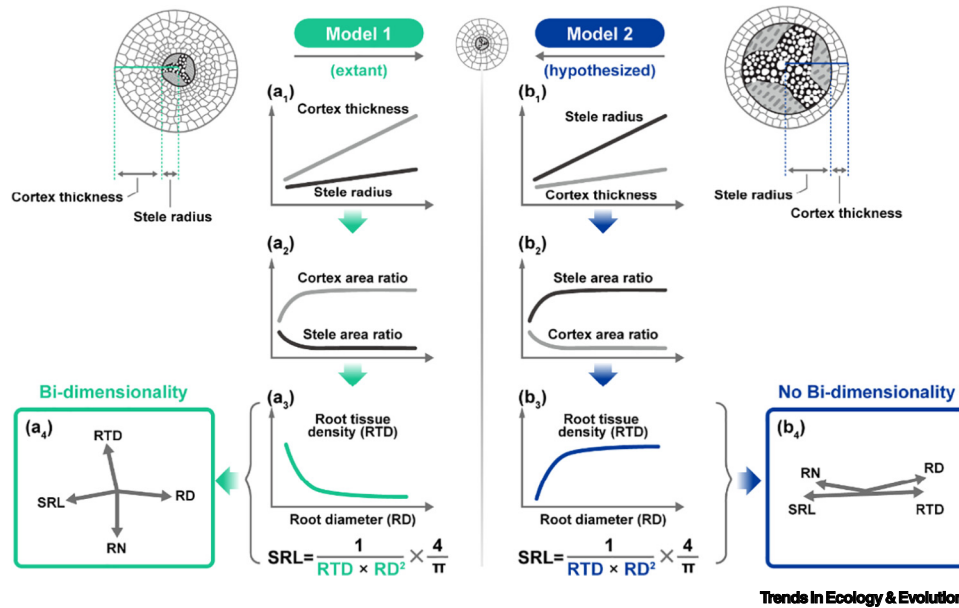
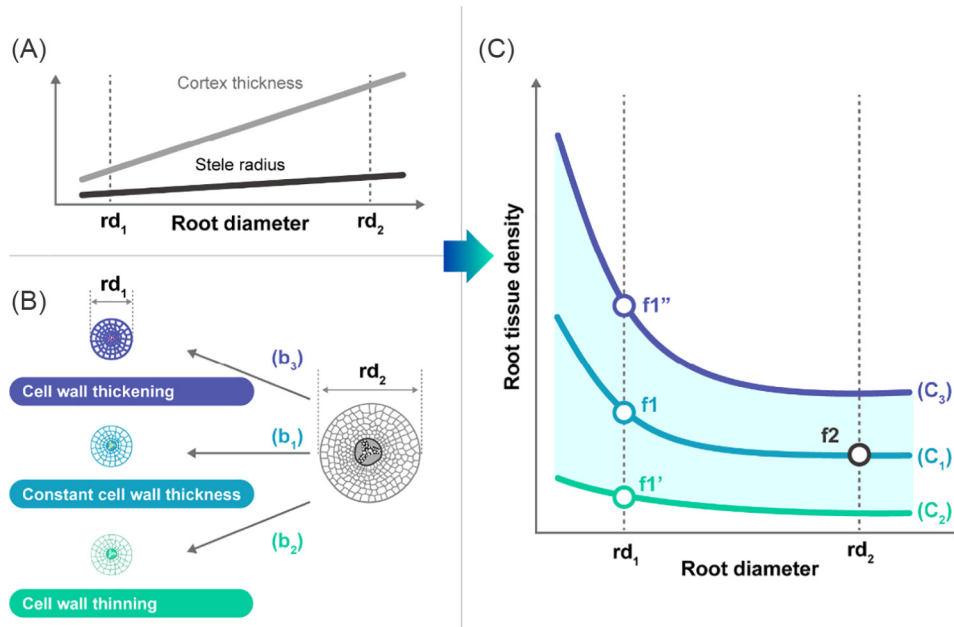


Figure 2. Allometry in root structural components and root trait bi-dimensionality. Models 1 (a₁) and 2 (b₁) represent the extant and hypothesized allometry between root cortex and stele, respectively. The two allometric models and the panels a₁ and b₁ are based on Figure 1 in a previous study [35]. The known and hypothesized allometry lead to different patterns of cortex and stele area ratio (i.e., the proportion of root cross-sectional area occupied by the cortex and the stele) with increasing root diameter (RD) (a₂, b₂), and a negative (a₃) and positive (b₃) relationship between RD and root tissue density (RTD). Given the calculation of SRL using Equation 2 in the main text, the negative RTD-RD relationship (a₃) could cause an offset effect of RTD and RD on SRL, eventually leading to root trait bi-dimensionality (a₄); alternatively, the positive RTD-RD relationship (b₃) would cause no such offset effect and, hence, no root trait bi-dimensionality (b₄). Cortex is shown as the area of layers of open cells; stele is the open circle surrounded by the cortex; vessels are the small open circles inside the stele. Abbreviations: RN, root nitrogen concentration; SRL, specific root length.

allometric equation [16,35]. The deviation of RTD is largely due to changes in cell walls of root cortex and stele [46–48]. The rationale is that cell walls of the cortex and stele, in particular vessels and fibers in the stele, are enriched in chemical components with high specific density, such as cellulose (1.53–1.57 g cm⁻³), hemicellulose (1.50–1.54 g cm⁻³), and/or lignin (1.26–1.41 g cm⁻³) [49,50]. All of these have a higher specific density than the cytoplasm (about 1.00 g cm⁻³) [51,52]. Therefore, changes in cell wall thickness of the cortex and the stele can have a great impact on RTD [46,48,53–55].

Considering the root allometric relationship (Figure 3A), increasing RD is accompanied by a significant increase in cell numbers of root cortex and stele [43,55,56]. Therefore, a change in RTD depends on both cell number and cell wall thickness of the root cortex and stele. If we assume constant cell wall thickness of root cortex and stele alongside an increasing RD (Figure 3B), RTD shows a nonlinear decrease according to root allometry across plant species (curve c₁ in Figure 3C) [35]. Alternatively, if cell wall thickness becomes thinner (Figure 3B), for example, in nutrient-rich habitats [28,57], the actual RTD value for any given RD (curve c₂ in Figure 3C) would be lower than that predicted from the root allometric equation [34]. By contrast, an increase in cell wall thickness, for example, in nutrient-poor habitats [58–60], could increase the RTD value (curve c₃ in Figure 3C) relative to that predicted from the root allometric equation.

RD and associated root cell number are phylogenetically conserved, while RTD and associated root cell wall thickness strongly vary across species with environmental conditions, such as soil



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Figure 3. Independent variation in root cell number and cell wall thickness and root trait bi-dimensionality. (A) Root allometry between the cortex and stele. (B) Different scenarios for the change in cell wall thickness from thick (rd_2) to thin (rd_1) absorptive roots: constant (b_1), thinning (b_2), and thickening (b_3). Cortex is shown as the area of layers of open cells; stele is the open circle surrounded by the cortex; vessels are the small open circles inside the stele. (C) Different relationships (curves c_1 – c_3) between root tissue density (RTD) and root diameter (RD), corresponding to constant (c_1), thinning (c_2), and thickening (c_3) of the root cell wall thickness, when roots are built according to the allometric relationship depicted in (A). The light blue area between curve c_2 and curve c_3 is shaped by the combined effects of changes in root cell number and root cell wall thickness on RTD. For example, from a thick absorptive root ($RD = rd_2$) to a thin absorptive root ($RD = rd_1$), the RTD may not necessarily shift from f_2 to f_1 but could shift to an even smaller value of f_1' due to thinning of root cell walls or a greater value of f_1'' due to thickening of root cell walls.

fertility, moisture, and soil compaction [27,28,47] (Table S1 in the supplemental information online). Moreover, the responses of cell wall thickness to environmental changes differ between root cortex and stele [46–48,60]. The actual RTD value deviates substantially from that predicted by the root allometric equation (see the light gray area in Figure 3C). This, in turn, suggests that variation in root cell wall thickness can be independent of both RD and root cell number. The hypothesized independence is partially supported by the lack of relationships between RD and cell wall thickness in root exodermis [55] and root stele [46] and by the large amount of variation in cell wall thickness for plant species with a similar RD [48,61]. The independence could also be supported by a strong root allometry ($R^2 = 0.60$ – 0.98) [35] but a weak root allometry-derived relationship between RTD and RD in both Kong *et al.* [35] ($R^2 = 0.16$) and Bergmann *et al.* [16] ($R^2 = 0.01$).

In the case of independent variation in root cell wall thickness and cell number, the effect of RTD on SRL (by changing root cell wall thickness) can increase, be cancelled out, or be reversed by adjusting the RD (i.e., root cell number) because of the larger effect of RD on SRL than on RTD (under the formula, in Equation 2; see mechanism 1). Consequently, this could lead to bi-dimensionality in root traits. Given the close relationship of cell wall thickness with cell metabolic activity (e.g., thicker cell walls usually indicate lower cell metabolic activity) [47,62,63], root trait bi-dimensionality could originate from the independence between root cell activity (i.e., root cell wall thickness) and cell number. For nutrient acquisition, the organ-level independence of the root quantity

(SRL) and activity (RTD) could be explained by the cellular-level independence of root cell activity and cell number. This supports the general idea in ecology that patterns and processes observed at coarser scales originate essentially from those at finer scales [48,58,64].

Relationships among the three mechanisms

The three mechanisms (Figure 4) differ in how they perceive the role of the allometry between root cortex and stele in driving root trait bi-dimensionality. As for mechanism 2, the bi-dimensionality arises primarily from the allometry-derived negative relationship between RTD and RD (Figure 2, Model 1a₃ or curve c₁ in Figure 3C). Different from mechanism 2, with a default assumption of constant root cell wall thickness, mechanism 3 accounts for variations in root cell wall thickness, allowing higher variability of RTD (the area between curve c₂ and curve c₃ in Figure 3C).

In contrast to mechanisms 2 and 3, mechanism 1 accounts for factors underlying variations in RTD (i.e., root allometry and/or the variation of root cell wall thickness). Even in few cases with no observable root allometry [39,65], mechanism 1 can still explain bi-dimensionality in root traits. Therefore, mechanism 1 basically covers all cases in mechanisms 2 and 3. Moreover, both mechanisms 2 and 3 hold under the prerequisite of cylindrically-shaped roots as well as their components (i.e., cortex and stele). Collectively, we propose that the bi-dimensionality in root traits could originate from the cylindrical geometry of plant roots with variable diameter (i.e., mechanism 1).

Why are roots cylindrically shaped?

Although absorptive roots can deviate from a perfect cylindrical shape, the deviation is small. We define a roundness value for an elliptical shape as the ratio of the minor to the major axis (i.e., the

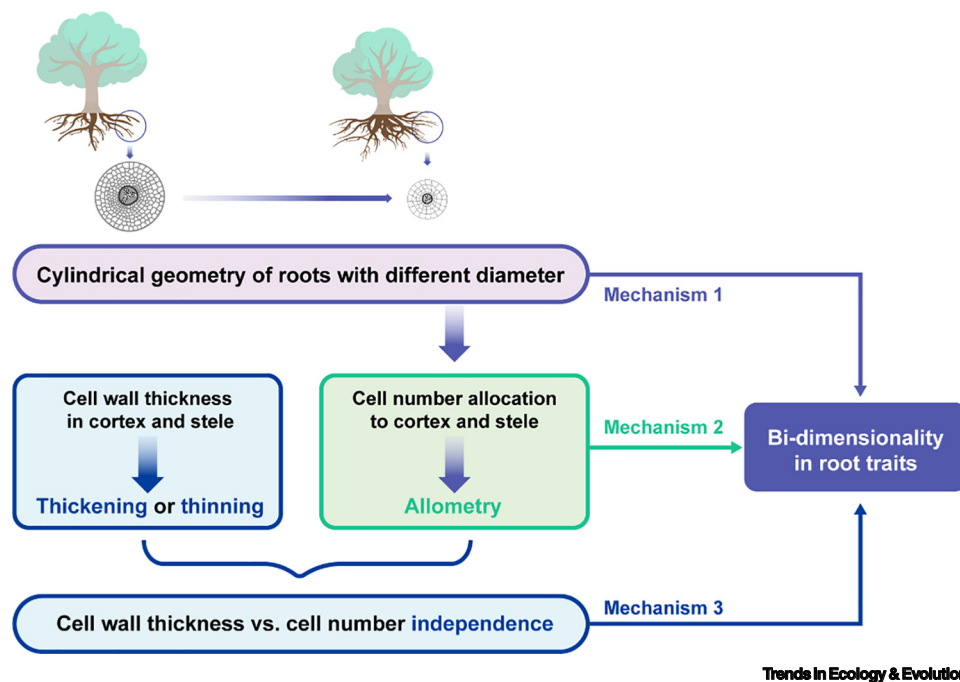


Figure 4. Relationships among the three mechanisms underpinning bi-dimensionality in plant root traits. Mechanisms are indicated by squares linked with arrowed lines in different colors: cylindrical geometry of roots (mechanism 1), allometry between root cortex and stele (mechanism 2), and independence variation in root cell wall thickness and cell number (mechanism 3). See Figures 1–3 in the main text for details on the three mechanisms. Typical cross-sectional areas of a thick and thin absorptive root are presented. Cortex is shown as the area of layers of open cells; stele is the open circle surrounded by the cortex; vessels are the small open circles inside the stele.

roundness value) of the ellipse. We find that the average roundness value of 0.96 ($n = 36$, Table S2 in the supplemental information online) is very close to 1, which signifies an almost perfectly round shape. Therefore, absorptive roots can generally be characterized by a cylindrical nature.

When plants colonized terrestrial habits more than 400 million years ago, they formed rhizomes and, later, true roots in the cylindrical shape [66,67]. As argued earlier, the innate bi-dimensionality of the cylindrical roots and, hence, multiple nutrient acquisition strategies of plant roots, might be why plant roots evolved cylindrically.

However, why roots in reality are cylindrical (and not flat, as leaves are) also lies in several characteristics of the soils that plant roots grow in. First, given the porous nature of soils [68,69], flat roots would be confronted with substantial physical resistance both horizontally and vertically [44,70], consequently prohibiting root extension. Second, soils are rich in pathogens and root herbivores, such as nematodes [70–73]. While flat roots, if we assume them flattened from cylinder-shaped roots of the same dry mass, would greatly enhance soil nutrient acquisition because of increased root surface area, they would also suffer from increased infection by soil pathogens and herbivory [71]. This would require increased investment in defense and, hence, a reduction in plant growth.

Alternatively, although a spherical shape favors nutrient foraging in all directions of soil space, it is also understandable why the absorptive roots are not spherical. If the absorptive roots were spherical, there would be high physical resistance as well as great carbon cost in building the roots to obtain nutrients over distances. Furthermore, given the same volume, the spherical shape has the least surface contact with soils and thus the highest carbon cost of nutrient foraging.

Root trait bi-dimensionality and mycorrhizal associations

Mycorrhizal associations may produce a root trait dimension different from the RES. For example, thick absorptive roots (low SRL) that typically have long lifespan are expected to have low nutrient acquisition abilities according to the RES; however, they can, in fact, have high nutrient acquisition rates through high mycorrhizal associations [3,42,74]. Therefore, mycorrhizal associations potentially contribute to the formation of bi-dimensionality in root traits [74–76]. Different to this perspective, root trait bi-dimensionality, as we have argued, could simply result from the cylindrical geometry of the roots. That is, given a cylindrical geometry of roots with varying diameters, root trait bi-dimensionality is an inevitable outcome, irrespective of mycorrhizal associations.

Nevertheless, for most terrestrial plants, mycorrhizal associations are greatly influenced by RD [3]. This is because thick absorptive roots with low SRL usually have little absorptive area for a given amount of root biomass. Hence, mycorrhizal associations of thick absorptive roots would be favored by natural selection in nutrient-limiting environments [3,77]. Meanwhile, a single thick absorptive root has a large surface area and, as such, a high chance to ‘meet’ and be colonized by mycorrhizal fungi [40]. Therefore, mycorrhizal associations can be seen to coevolve with the cylindrical geometry of the roots varying in diameter, as such, co-contributing to the bi-dimensionality in root traits. We note there are species with no mycorrhizal association or no positive mycorrhizal association with RD (e.g., ectomycorrhiza) that still exhibit root trait bi-dimensionality [7,16,78,79]. Here, the bi-dimensionality can mainly be attributed to the cylindrical geometry of the roots.

Concluding remarks

In light of the widely recognized bi-dimensionality in root traits, we proposed three inter-related mechanisms. Of these, the cylindrical geometry of roots is likely to be the most straightforward and most powerful in explaining the origin of root trait bi-dimensionality. However, all three

Outstanding questions

At the level of bulk roots, what is the relationship between overlooked quantity traits, such as absorptive root biomass, and dominating root traits in a multidimensional root trait space? For instance, the assumed positive correlation between specific root length and nutrient absorption, a fundamental assumption in root economics space, can be impacted by variations in absorptive root biomass, which is often ignored. By uncovering the coupled or decoupled association between absorptive root biomass and specific root length, a better understanding of the form, function, and evolution of the whole plant can be obtained.

At the cellular level, is there independent variation across species in both cell activity and quantity in absorptive roots? The thickness or chemical composition of root cell walls can indicate cell activity, while cell number indicates cell quantity. Investigating cellular independence can clarify how individual root activity and quantity become decoupled, leading to the formation of bi-dimensionality in root traits.

At the biochemical level, is the bi-dimensionality of root traits the result of the autonomous regulation of certain key genes governing cell wall thickening and cell mitosis in absorptive roots? Conducting empirical tests to explore this hypothesis would provide further evidence supporting the long-standing idea that macro-scale processes, such as species coexistence and plant diversity, inherently arise from micro-scale processes like molecular interactions.

Is there an abrupt functional transition between coarse roots (or rhizomes) and absorptive roots (e.g., transport/storage/mechanics versus absorption) along root branches? Despite the functional transition, all these tissues are intimately connected for plant belowground functioning. Therefore, do coarse roots and rhizomes have the bi-dimensionality in their traits and is the bi-dimensionality, if it exists, underlain by the cylindrical geometry?

mechanisms help in understanding the form and function of plant roots. Here, we propose three top-priority directions for further research (see [Outstanding questions](#)).

First, in the framework of root trait bi-dimensionality, SRL (root length per unit root biomass) is typically used as a proxy, reflecting the quantity of root surface area for a given root biomass in nutrient foraging. However, root foraging depends not only on the SRL of the absorptive roots but also on the quantity of plant biomass allocated to the absorptive roots and mycorrhizal fungi (e.g., ectomycorrhizas) [75,80,81]. Hence, in understanding whole-plant performance, it would be interesting to test whether the root and mycorrhizal biomass-based quantity traits are coordinated with or vary independently with the SRL-based quantity traits.

Second, we put forward the idea of independent variation in root cell activity and cell number at the cellular level and that this cellular-level independence could explain the organ-level root trait bi-dimensionality (see mechanism 3). To test the cellular level independence, it is necessary to know how the cell activity and cell number vary within and across different plant functional groups that possess contrasting root traits (e.g., woody versus non-woody species or arbuscular mycorrhizal species versus ectomycorrhizal species versus ericoid mycorrhizal species) [82,83]. Furthermore, one could evaluate how the chemical composition of cell walls covaries with the cell wall thickness in absorptive roots, as both are important determinants of root metabolic activity and mycorrhizal associations [84,85].

Third, if the cellular independence of cell activity and number in plant roots is widely supported, we can dig deeper (e.g., how is all of this shaped at the molecular level?). It has been shown that cell numbers are controlled by some transcription factors [84] and that cell wall thickness is genetically controlled through regulating gene expression of cellulose, hemi-cellulose, or lignin [48,86]. It is possible that the cell activity- and cell number-related processes are regulated independently through different molecular pathways or networks with little crosstalk [87–89]. This interesting hypothesis links molecular-level processes with cylindrical geometry-derived bi-dimensionality in root traits. The molecular-level processes-based bi-dimensionality, if tested, will offer valuable insights into how the macro-scale plant community complexity and diversity, since the first appearance of land plants from sea, can arise from the interactions of organic-, cellular-, and molecular-level processes.

Data availability

The data used in Figures S2 and S3 in the supplemental information online are available from the Fine-Root Ecology Database (FRED), <http://roots.ornl.gov>.

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Author contributions

Y.Z. and D.K. conceived the idea. Y.Z. wrote the first draft of the manuscript. D.K., J.C., G.F., M.L., J.W., and P.K. contributed to the further writing of the final manuscript.

Declaration of interests

The authors declare no competing interests.

Supplemental information

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