

Letters

The nutrient absorption–transportation hypothesis: optimizing structural traits in absorptive roots

Introduction

Plant anatomical structures are important for our understanding of plant ecology, evolution and responses to environmental change, such as shifts in temperature and precipitation regime. In absorptive roots, the cortex (i.e. the tissue between the epidermis and the endodermis) is used for resource absorption, while the stele is responsible for resource transportation (Guo *et al.*, 2008). Absorptive roots with a thicker cortex can provide greater space for mycorrhizal colonization, and hence, a higher absorption rate through mycotrophy (Brundrett, 2002; Comas *et al.*, 2012). However, absorptive roots with a larger stele usually have higher transportation capacity, as the stele can accommodate more and larger conduits (e.g. vessels or tracheids) for transportation. Furthermore, it has been demonstrated that the size ratio of stele radius to cortex thickness is smaller in angiosperms than in gymnosperms (Guo *et al.*, 2008) and that in angiosperms this ratio is larger for evolutionarily late diverged species than for early diverged species (Kong *et al.*, 2014). This suggests that the diversification of the cortex to stele size ratio may also be an unappreciated physiological trait coinciding with shifts in the macroevolution of plant speciation.

Recent studies have shown consistent allometric relationships for the cortex and stele in absorptive roots across a wide variety of species. Across a broad spectrum of angiosperm species, for example, in woody species in (sub)tropical (Kong *et al.*, 2014), temperate (Gu *et al.*, 2014) and mangrove ecosystems (D. L. Kong, unpublished data), as well as in some herbaceous species (Hummel *et al.*, 2007) and ferns (Dong *et al.*, 2015), the slope of the regression line between cortex thickness and root diameter is more than two-fold steeper than the slope of the regression line between stele radius and root diameter. These allometric relationships between cortex thickness and stele radius are remarkably strong and contribute greatly to a key ecological axis of absorptive roots, the root economics spectrum (RES; Kong *et al.*, 2014; Weemstra *et al.*, 2016). However, to date, we know little about what drives this allometric relationship.

Here, we hypothesize that the allometric relationships arise from a functional balance between nutrient absorption and transportation. This hypothesis is posed by comparing two conceptual models

of contrasting ratios of cortex to stele size describing the evolution of interspecific variation in absorptive root diameter. Through this comparison, we show that the model showing an increase in the cortex : stele ratio with increasing root diameter optimally balances nutrient absorption with transportation. We propose that optimizing the balance between these two key root functions may be a leading rule for assembling anatomical structures in absorptive roots. The nutrient absorption–transportation hypothesis can further our understanding of root economic strategies and plant adaptation to changing environments.

Two alternative root models

Recent studies have suggested that absorptive roots of woody angiosperms have evolved from thick to thin diameter over geological time (Comas *et al.*, 2012; Chen *et al.*, 2013). Given similar phylogenetical conservativeness of root cortex thickness and root diameter, and the strong correlation between these two traits (Kong *et al.*, 2014), the early ancestor likely had similar root anatomy to the thick absorptive roots of the *extant* early diverged species, that is, thick roots with a large cortex thickness to stele radius ratio (Fig. 1). However, in providing a broader discussion platform for examining the evolutionary basis for the allometric relationship between root cortex and stele, we alternatively *hypothesize* the evolution of thick-rooted early diverged species with a small cortex thickness to stele radius ratio (Fig. 1). Hence, we present two contrasting models with diverging ratios of cortex thickness to stele radius (Fig. 1). In Model 1, the slope of the regression line of cortex thickness and root diameter is much less steep than the slope of the regression line of stele radius and root diameter (Fig. 1a). In this model, the allometric relationship leads to a smaller proportion of stele tissue in the root cross-sectional area with decreasing root thickness.

By contrast, in Model 2, the slope of the regression line of cortex thickness and root diameter is much steeper than the slope of the regression line of stele radius and root diameter (Fig. 1b). Therefore, in this model the proportion of root cross-sectional area occupied by stele tissue increases with decreasing root thickness. Concurrent with the change in stele radius, the mean number and diameter of vessels in the stele are usually smaller in thinner roots (Kong *et al.*, 2014). Consequently, the slope of the regression line of mean vessel number or diameter and root diameter is much steeper in Model 1 (Fig. 1c) than in Model 2 (Fig. 1d).

Balancing nutrient absorption with transportation

The diameter of absorptive roots often positively correlates with mycorrhizal colonization, a key pathway for nutrient acquisition (Comas *et al.*, 2014; Kong *et al.*, 2014; Eissenstat *et al.*, 2015). In

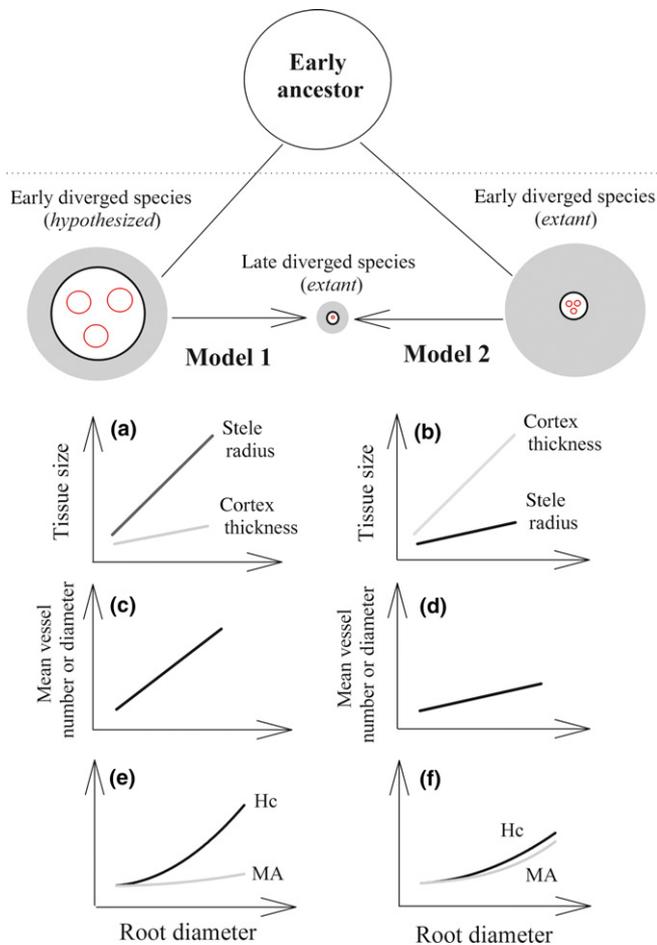


Fig. 1 Conceptual model illustrating the allometric relationships between the size of root stele radius (black circle) and cortex thickness (grey-shaded ring) of absorptive roots in angiosperms as developed over evolutionary time. The red circles represent vessels in the stele. We present two alternative models for the evolution of absorptive root diameter showing how thick roots of a common early ancestor have diverged to thin roots of the extant late diverged species. Model 1 hypothesizes thick roots of the early diverged species with a thick stele, thin cortex and large vessels, while Model 2 depicts the extant early diverged species with a thin stele, thick cortex and small vessels. The panels show changes in (a, b) stele radius and cortex thickness, (c, d) number or diameter of vessels, and (e, f) mycorrhizal association (MA) and hydraulic conductance (Hc) with shifts in root diameter.

both models, it can be expected that mycorrhizal colonization is greater in thicker roots. However, for roots with a similar diameter, those with a higher proportion of cortex can facilitate higher mycorrhizal colonization intensity (i.e. the quantity of mycorrhizal fungi per unit of root cross-sectional area) (Brundrett, 2002; Comas *et al.*, 2012; Valverde-Barrantes *et al.*, 2016b). Therefore, at a similar root diameter, the roots in Model 2 with a thicker cortex (i.e. the grey lines in Fig. 1b vs 1a) would be expected to have greater mycorrhizal colonization than the roots in Model 1 (i.e. the grey lines in Fig. 1f vs 1e).

When absorbed nutrients are transported to vessels, the volumetric flow rates are proportional to the fourth power of vessel diameter according to the Hagen–Poiseuille law (Feild & Arens, 2007). If vessel diameter varies at a similar rate to cortex thickness with root diameter, the fourth power relationship of

nutrient transportation with vessel diameter could result in a remarkable ‘lag’ of nutrient absorption behind nutrient transportation. The reason is that even if the root cross-sectional area were to be completely occupied by the cortex, nutrient absorption through mycorrhizal associations could only be in a quadratic relationship with root diameter. Here, we assume that mycorrhizal colonization (y) is proportional to the root cortex cross-sectional area (x) (Brundrett, 2002; Comas *et al.*, 2012), and that their relationship, as such, can be expressed as $y = kx$, where k is a constant. When the root cross-sectional area is completely occupied by the cortex, the earlier described relationship becomes: $y = k\pi r^2$, where r is root radius. One effective way to reduce the nutrient absorption lag would be to widen the difference between the slope of cortex and stele size with root diameter, that is, a steeper slope of the regression line between cortex thickness and root diameter and a much less steep slope of the regression line between stele radius and root diameter (Fig. 1b). As indicated in Model 2, this could greatly enhance (or decrease) nutrient absorption with increasing (or decreasing) root diameter and constrain the drastic increase (or decrease) in nutrient transportation capacity based on the Hagen–Poiseuille law, thus more optimally balancing the two processes (Fig. 1f). By contrast, in Model 1, the greater increase (or decrease) of transportation capacity of vessels concurs with a much smaller increase (or decrease) of nutrient acquisition through mycorrhizal association (Fig. 1e).

Thus, based on the Hagen–Poiseuille law and strong dependence on mycotrophy, we pose that the functional balance between nutrient absorption and transportation could be an important factor in explaining the widely demonstrated allometric relationship between the size of root stele and cortex in mycorrhizal woody angiosperms.

Implications

The nutrient absorption–transportation balance hypothesis may have important implications for our understanding of the ecology and evolution of woody angiosperms. In absorptive roots, the cortex constitutes a dominant component of hydraulic resistance of water transportation from the root surface to the vessels in the stele (Steudle & Peterson, 1998). Greater cortex thickness may bring greater hydraulic resistance through the cortex (Huang & Eissenstat, 2000). Hence, to ensure sufficient water transportation through the cortex to the vessels, species with a thicker root cortex should be mainly restricted to areas with ample water supply, such as rain forests (Baylis, 1975; Holdaway *et al.*, 2011). However, species with a relatively thin cortex and, hence, lower hydraulic resistance through the cortex may have a competitive advantage in drier environments.

Furthermore, recent studies using extant species have proposed that the evolution of absorptive roots in woody angiosperms from thick to thin (Fig. 1) could have resulted from the physiological drought caused by the decline in atmospheric CO_2 during the Cretaceous (Comas *et al.*, 2012; Chen *et al.*, 2013; Gu *et al.*, 2014). Producing thin and ephemeral roots has been suggested to be cost-effective in coping with periodic water stress (Chen *et al.*, 2013). However, besides reducing root diameter, the allometric

relationship between root cortex and stele size, as mentioned earlier, may also have driven plant adaptation to the progressively drier environment, that is, reduced cortex to stele ratio may be more favourable for water and nutrient transportation under dry conditions. Therefore, the nutrient absorption–transportation balance hypothesis adds further insights into the mechanisms of plant evolution and responses to climate change.

Finally, the absorption–transportation balance hypothesis has consequences for the RES, which broadly depicts a tradeoff between resource acquisition and conservation (e.g. fast resource acquisition capacity and growth rates tradeoff with short root lifespan and reduced survival under stress conditions) (Reich, 2014; Weemstra *et al.*, 2016). In our hypothesis, the relatively thick cortex in absorptive roots of early diverged species in Model 2 is primarily used to promote nutrient absorption for balancing nutrient transportation. However, the thicker cortex roots may be associated with greater nutrient acquisition through mycotrophy as well as a longer lifespan because of higher costs of root construction and maintenance of mycorrhizal associations (Liu *et al.*, 2015, 2016; Weemstra *et al.*, 2016). As such, the optimization of uptake of different limiting resources (i.e. water and nutrients) would lead to a weak, or lack of, RES in absorptive roots of woody angiosperms (Valverde-Barrantes *et al.*, 2015; Kong *et al.*, 2016; Weemstra *et al.*, 2016). Hence, our hypothesis further emphasizes the impacts of mycorrhizal colonization on RES and contributes to the recently proposed multiple dimensions of root trait variation (Valverde-Barrantes *et al.*, 2016a; Weemstra *et al.*, 2016).

The way forward

The nutrient absorption–transportation hypothesis, as presented here, provides a stepping stone for future studies on root ecology and plant evolution. One of the main challenges is to determine how much plants with varying root anatomy benefit from mycorrhizal associations in terms of nutrient uptake, that is, the rate of nutrient absorption through mycorrhizal fungi. The nutrient flux through mycotrophy could be investigated by using stable isotope methods (Hodge & Fitter, 2009; Kiers *et al.*, 2011), or quantum dots (Whiteside *et al.*, 2012). Furthermore, along the lines of studies on leaf structure and anatomy by use of artificial leaves (Noblin *et al.*, 2008), our hypothesis may also be tested by constructing artificial roots consisting of stele, vessels, cortex, and mycorrhizal fungi and monitoring nutrient absorption and transportation rates. Other experimental approaches may include testing physiological and competitive responses of phylogenetically divergent plant species varying in root cortex to stele ratio to factorial combinations of water and nutrient availability.

Finally, we note that the allometric relationships for root anatomical structures are largely derived from arbuscular mycorrhizal (AM), woody angiosperms. It remains unclear whether similar allometric relationships exist in other plant lineages such as monocots (Hummel *et al.*, 2007), gymnosperms (Guo *et al.*, 2008), and ferns (Dong *et al.*, 2015). Notably, gymnosperms and ferns transport water by means of tracheids (a primitive form of

water-conducting conduits) which usually have lower hydraulic conductance than the vessels evolved in woody angiosperms (Esau, 1977). In addition, the relationships between root anatomical structures and mycorrhizal colonization can vary among mycorrhizal types (Brundrett, 2002; Comas *et al.*, 2014) with, for example, stronger relationships for AM than for ectomycorrhizal (EM) species (Kong *et al.*, 2014). Also, although experimental evidence is scarce, it has been suggested that the nutritional benefits of mycorrhizal associations may be higher for EM than for AM species (Ouimette *et al.*, 2013). Therefore, testing our hypothesis across plant lineages and mycorrhizal types is important in unravelling drivers of the emerging multiple dimensions of trait variation in absorptive roots. This will eventually advance our understanding of the linkages between plant aboveground and belowground parts (Li *et al.*, 2015; Valverde-Barrantes *et al.*, 2015), plant evolution (Comas *et al.*, 2012), species coexistence (Li *et al.*, 2015; Liu *et al.*, 2015) and responses to future climate change (Bardgett *et al.*, 2014).

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Author contributions

D.K., J.W. and H.Z. conceived the idea for the study. D.K., Y.M., M.L. analysed data from the literature. D.K., J.W., Y.M., M.L., H.W., P.K. wrote the manuscript.

**Deliang Kong^{1*}, Junjian Wang², Hui Zeng³, Mengzhou Liu⁴,
Yuan Miao⁴, Huifang Wu⁴ and Paul Kardol⁵**

¹College of Bioscience and Biotechnology, Shenyang Agricultural University, Shenyang 110866, China;

²Department of Physical and Environmental Sciences, University of Toronto, Toronto M1C 1A4, Canada;

³Key Laboratory for Urban Habitat Environmental Science and Technology, Peking University Shenzhen Graduate School, Shenzhen 518005, China;

⁴School of Life Sciences, Henan University, Kaifeng 475004, China;

⁵Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå 90183, Sweden

(*Author for correspondence: tel +86 024 88492799; email deliangkong1999@126.com)

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