REVIEW ARTICLE

Interplay between developmental cues and rhizosphere signals from mycorrhizal fungi shape root anatomy, impacting crop productivity

Alexandre Grondin · Meng Li · Rahul Bhosale · Ruairidh Sawers · Hannah M. Schneider

Abstract

Background The rhizosphere is the interface between roots and the soil and the site of nutrient and water uptake for plant growth. Root anatomy and the physical, chemical, and biological components of the rhizosphere interact to influence plant growth. Several root developmental and rhizosphere signals combine in the patterning of root cortical anatomy and have implications for the plant's hydro-mineral nutrition and carbon partitioning and therefore crop productivity, especially in edaphic stress.

Scope Here, we highlight how mutualistic mycorrhizal fungi from the rhizosphere mobilize plant molecular actors controlling root anatomical traits, including cortical cell size, to facilitate their establishment and accommodation within the cortex. We explore the effects on plant growth and stress tolerance that may result from the changes in root anatomy driven by interactions with arbuscular mycorrhizal fungi, including altering the metabolic efficiency required for nutrient exploitation. We also discuss opportunities for understanding the genetic control of root anatomy and rhizosphere interactions to enable a comprehensive understanding of the benefits and trade-offs of root-rhizosphere interactions for more productive crops.

Keywords Root anatomy · Rhizosphere · Genetic control · Mycorrhizal fungi · Crop productivity

A. Grondin
UMR DIADE, IRD, Université de Montpellier,
Montpellier, France

M. Li · R. Sawers
Department of Plant Science, Pennsylvania State
University, University Park, PA, USA

R. Bhosale
Future Food Beacon and School of Biosciences, University
of Nottingham, Loughborough LE12 5RD, UK

H. M. Schneider (✉)
Department of Physiology & Cell Biology, Leibniz-
Institute of Plant Genetics and Crop Plant Research (IPK),
OT Gatersleben Corrensstr 3, 06466 Seeland, Germany
e-mail: schneiderh@ipk-gatersleben.de

Introduction

In the next 25 years, food production needs to be doubled to meet the demands of the growing population (Hunter et al. 2017). This challenge is further complicated by climate change, where altered weather patterns, increasing temperature, degrading soil quality, and depletion of freshwater resources will reduce the regions and growing seasons suited for agricultural production (IPCC 2021). Thus, we urgently need novel strategies to develop crops with improved resource efficiency. Roots play a critical role in the efficiency of soil resource acquisition and dynamically interact with the soil matrix around the root (defined as the rhizosphere)

to influence stress adaptation and yield. One promising approach for the development of crops with improved resource efficiency is selecting varieties with root anatomical traits that enhance interactions with beneficial microorganisms from the rhizosphere, with positive effects on plant hydro-mineral nutrition and abiotic stress tolerance (Galindo-Castañeda et al. 2022).

Root anatomy differs substantially both within and among species (Enstone et al. 2003; Lynch et al. 2021). Optimization of root anatomical traits such as root cortical cell size, root cortical cell wall thickness, root cortical cell file number, or root cortical aerenchyma can reduce the nutrient and respiratory demands of root tissues, enabling greater acquisition of soil resources for a given level of metabolic investment and improving yield under stress (reviewed in Lynch et al. 2021). In addition, anatomical traits can influence root oxygen availability (Kotula et al. 2009), and exudation of chemical signals (Canarini et al. 2019), impacting root associations with microorganisms in the rhizosphere (as reviewed in Lynch et al. 2021; Galindo-Castañeda et al. 2022).

Root and rhizosphere interactions can be beneficial, neutral, or antagonistic in terms of plant fitness. Root associations with arbuscular mycorrhizal fungi are one such example of potential positive interplay between the root and rhizosphere. The arbuscular mycorrhizal fungi develop an extensive network of hyphae that grow both in the rhizosphere and intercellularly in the root cortex, thereby functionally extending the root system. In the root, hyphae grow into individual cortical cells where they develop highly branched hyphal structures, arbuscules, where inorganic nitrogen, phosphorus, and other minerals are unloaded for plant growth in exchange for photosynthetically derived lipids and carbohydrates. Arbuscular mycorrhizal symbiosis can provide up to 40% nitrogen and 80% phosphorus uptake in rice and increase yield by 30% in maize (Yang et al. 2012; Ramírez-Flores et al. 2020; Wang et al. 2021).

There has been significant progress in understanding the signaling associated with the early stages of arbuscular mycorrhizal symbiosis (e.g., Kosuta et al. 2003; Besserer et al. 2006; Choi et al. 2018). Root infection by the fungus and development of arbuscules necessitate a substantial transcriptional reprogramming process, involving the exchange and perception of signals between the plant and fungus (Lanfranco et al. 2018). This reprogramming is orchestrated by plant transcription factors that play a crucial role in effecting root morphological and developmental changes essential for the accommodation of arbuscules (Gobbato et al. 2012; Wang et al. 2012; Volpe et al. 2013; Foo et al. 2013; Devers et al. 2013; Xue et al. 2015; Park et al. 2015; Heck et al. 2016; Floss et al. 2017; Russo et al. 2019; Choi et al. 2020; Seemann et al. 2022). Interestingly, there is evidence that rhizosphere signals from arbuscular mycorrhizal fungi influence root cortical patterning (Heck et al. 2016; Seemann et al. 2022). A better understanding of the interplay of rhizosphere and plant signals is directly relevant for improving plant hydro-mineral nutrition, and therefore plant growth and abiotic stress tolerance.

How may the interplay of mycorrhizal fungi arbuscule development and genetic control of root cortical traits be exploited for crop improvement?

Root growth depends on mechanisms balancing cellular axial and radial expansion in the elongation zone. Root cell axial expansion has been associated with gibberellin/DELLA signaling in *Arabidopsis* (Ubeda-Tomás et al. 2008). It was shown that the gibberellin-mediated destabilization of DELLA proteins of the GRAS family in the endodermis promoted anisotropic growth in the cortex (i.e., axial expansion) while disruption of this gibberellin response by expressing a stabilized DELLA protein slowed anisotropic cell growth causing radial expansion of cortical cells. SCARECROW-LIKE 3 (SCL3), another GRAS transcription factor, acts as a positive regulator of the gibberellin pathway and DELLA repressor, and works in conjunction with the SHORTROOT–SCARECROW (SHR-SCR) stem cell program to coordinate ground tissue elongation during root development (Zhang et al. 2011).

DELLA proteins also play essential roles in regulating the establishment of arbuscular mycorrhizal symbiosis. They are important in the initial stages of arbuscule development when the host cells increase their size to accommodate the fungal structure. In *Medicago*, *MYCORRHIZA INDUCED GRAS1* (*MIG1*) is induced in cortical cells colonized by the fungus and interacts with DELLA to promote radial cell expansion and allow arbuscule development (Heck et al. 2016). Recently, *MYCORRHIZA INDUCED GRAS2* (*MIG2*) was identified as another positive regulator of radial cortical cell expansion during arbuscule formation in *Medicago* roots

(Seemann et al. 2022). Conversely, *MYCORRHIZA INDUCED GRAS3* (*MIG3*) restrains cortical cell growth and is a negative regulator of arbuscule development (Seemann et al. 2022). Overexpression of *MIG1* and *MIG2* increased cortical cell size, cortical cell file layers and root diameter (Fig. 1) while over-expression of *MIG3* has opposite effects on cortical cell size and root diameter in the absence of mycorrhizal fungus (Seemann et al. 2022). In the presence of mycorrhizal fungus, overexpression of *MIG1* and *MIG2* have no impact on root fungus infection and arbuscule development (Seemann et al. 2022).

MIG1 and *MIG2*, and their homologues in crop species, represent opportunities for enhanced stress adaptation through both enhanced accommodation of the fungal structure and the genetic manipulation of root cortical cell size which may have additive or even synergistic effects on plant drought and nutrient stress tolerance. Roots that have a greater cortical cell size may enhance plant growth under drought and nutrient stress (Chimungu et al. 2014; Lopez-Valdivia et al. 2023). An increased volume of individual cortical parenchyma cells, or the size of cortical cells, can decrease the metabolic costs of root growth and maintenance, in terms of both carbon costs of root respiration and the nutrient content of cortical tissue. For example, contrasting maize lines exposed to drought in the field or simulated under suboptimal nutrient availability with functional-structural plant models, demonstrated that plants with a larger cortical cell size had reduced respiration, deeper rooting, greater water and nitrogen uptake, and hence greater growth and yield (Chimungu et al. 2014; Lopez-Valdivia et al. 2023). The benefits of mycorrhizal colonization for enhanced plant nutrient and water status combined with greater cortical cell sizes that enhance soil foraging and stress tolerance may have synergistic effects for stress adaptation and enhanced yield.

While mycorrhizal fungi can mobilize plant molecular actors to alter the size and number of root cortical cells, it remains unclear how localized these responses are in the root. For example, these responses have been observed to be localized to only colonized cortical cells (Balestrini et al. 2007), but also at distal sites of the root and in both colonized and uncolonized cortical cells (Maldonado-Mendoza et al. 2005). While *MIG1* and *MIG2*, and their homologues, may represent opportunities for enhanced stress adaptation, the benefit of altering cortical cell properties for enhanced stress tolerance will depend on the extent of these changes in cortical tissue within the entire root organ and if the magnitude of these benefits (or trade-offs) is enough to influence the metabolic cost of soil foraging and subsequently stress tolerance.
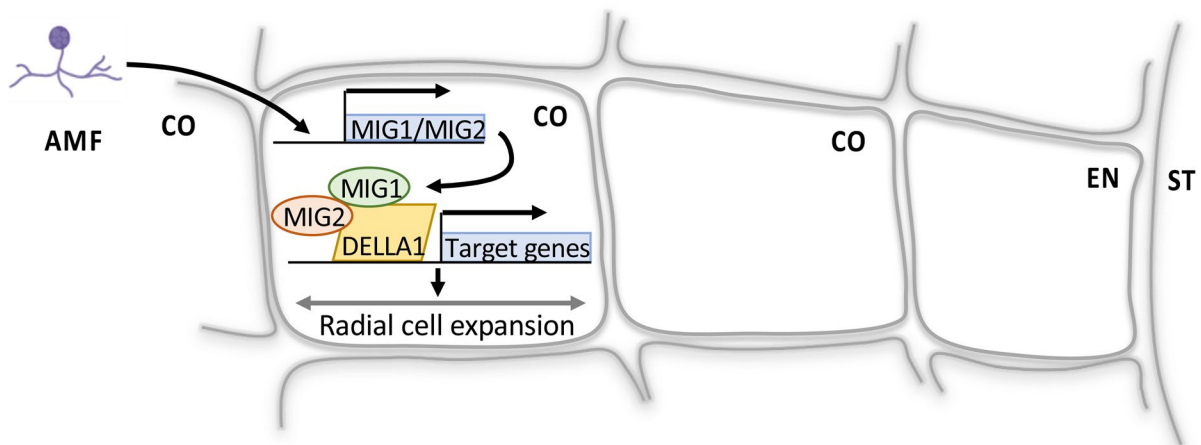

Fig. 1 Arbuscular mycorrhizal colonization effects on cortical cell size in *Medicago truncatula* and their impacts on tissue structure and plant nutrition. Arbuscular mycorrhizal fungi (AMF) induce cell radial expansion in the cortex through recruitment of GRAS transcription factors. AMF induces expression of MIG1 and MIG2 proteins that induce DELLA1 expression and inhibits its gibberellin acid-mediated destabilisation. The DELLA1 complex induces the expression of target genes promoting radial cell expansion. ST: stele; EN: endodermis; CO: cortex

A better understanding of the trade-offs between root cortical traits and mycorrhizal fungi colonization in the root cortex may be useful for crop improvement

While a larger cortical cell size may promote the accommodation of arbuscular mycorrhizal fungi in cortical cells, other anatomical traits also influence the ability of colonization and hyphae growth and spread in the cortex. For example, root cortical aerenchyma can facilitate mycorrhizal spread as intercellular hyphae may benefit from a low-resistance path (i.e., air-filled lacunae) to grow through young roots (Brundrett et al. 1985; Brundrett and Kendrick 1987; Smith and Smith 1997). In maize inbred lines, increased arbuscular mycorrhizal colonization was associated with decreased aerenchyma formation (Galindo-Castañeda et al. 2019). However, in maize hybrid lines mycorrhizal colonization increased with larger aerenchyma lacunae, which coincided with larger root diameters (Galindo-Castañeda et al. 2019). Generally, mycorrhizal colonization occurs in living regions of the cortex not occupied by aerenchyma tissue with large, air-filled lacunae (Figs. 2 and 3) (Strock et al. 2019). In addition to its potential role in influencing mycorrhizal spread and spatial colonization, root cortical aerenchyma can improve abiotic stress tolerance. Aerenchyma can reduce the nutrient and respiratory demands of root tissues, reducing root metabolic costs that can translate into increased carbon allocation for deeper root growth and improved yield under suboptimal nutrient and water conditions (reviewed in Lynch et al. 2021). The interaction between root cortical aerenchyma formation and root mycorrhizal colonization, and their respective effect on plant hydromineral nutrient, remains to be further explored.

Similar to aerenchyma formation, the development of the anatomical trait, multiseriate cortical sclerenchyma, may also be an adaptation to improve soil foraging in edaphic stress. Multiseriate cortical sclerenchyma are characterized by small cell with thick cell walls encrusted with lignin in the outer cortex which enable plants to penetrate hard, dry soil and enhance soil foraging in deeper soil domains by increasing the tensile strength of the root (Schneider et al. 2021). However, mature palm root tissue with extensive cortical aerenchyma formation and sclerenchyma in the outer cortex showed reduced mycorrhizal colonization (Fig. 2) (Dreyer et al. 2010). Suberized and
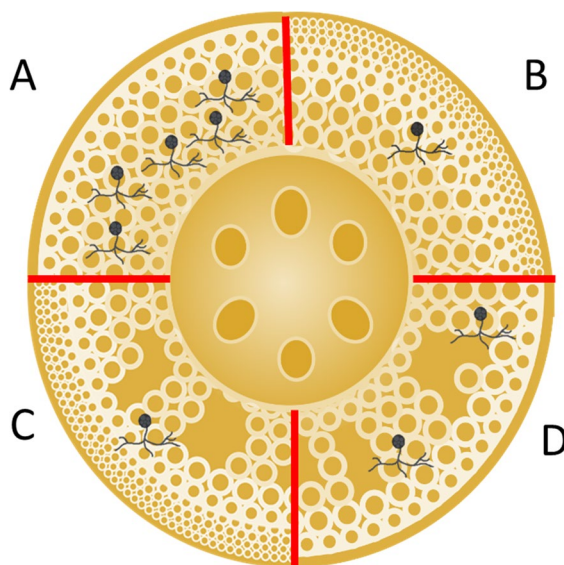

Fig. 2 Potential trade-offs effect of root aerenchyma and multiseriate cortical sclerenchyma on arbuscular mycorrhizal infection. The patterning and development of root anatomical traits can have direct physical interactions with the ability of soil microorganisms to interact and colonize the root spatially and temporally. In different panels, four root-cross sections are depicted with different cortical traits. Several cortical traits may enhance or reduce mycorrhizal colonization in roots. **A** simple cortex with large cortical parenchyma cells may enhance colonization, **B** lignified multiseriate cortical sclerenchyma in outer cortical tissue may reduce colonization, **C** multiseriate cortical sclerenchyma and root cortical aerenchyma formation reduce colonization, and (**D**) the formation of cortical aerenchyma tissue may reduce colonization. These traits alter the cortical habitat for colonization and paths for initial penetration and subsequent growth through cortical tissue. However, the impact of anatomical traits on arbuscular mycorrhizal colonization appears species specific and may also largely depend on the environment

lignified apoplastic barriers in outer cortical tissue may reduce initial penetration of mycorrhiza into the root tissue and therefore reduce mycorrhizal colonization of the cortex (Sharda and Koide 2010). Further studies are required to understand the dynamics of these complex interactions between root anatomical traits and mycorrhizal colonization to unravel the benefits and trade-offs of these interactions for stress adaptation and enhanced yield.

Since both cortical traits and mycorrhizal fungi have the potential to improve plant hydro-mineral nutrition, the interplay of rhizosphere signals altering root cortical traits have the potential to have synergistic or potentially antagonistic interactions for soil

Fig. 3 Maize root cross-sections with root cortical aerenchyma and arbuscular mycorrhizal colonization. Maize root cross-sectional images of non-inoculated (left panels) and inoculated (right panels). Arbuscular mycorrhizal colonization is segmented in red (**b**, **e**) and root cortical aerenchyma is segmented in green (**c**, **f**). Segmentation was performed based on RGB spectra from cross-sectional images (**a**, **d**). Reprinted from Strock et al. 2019 by permission of Oxford University Press
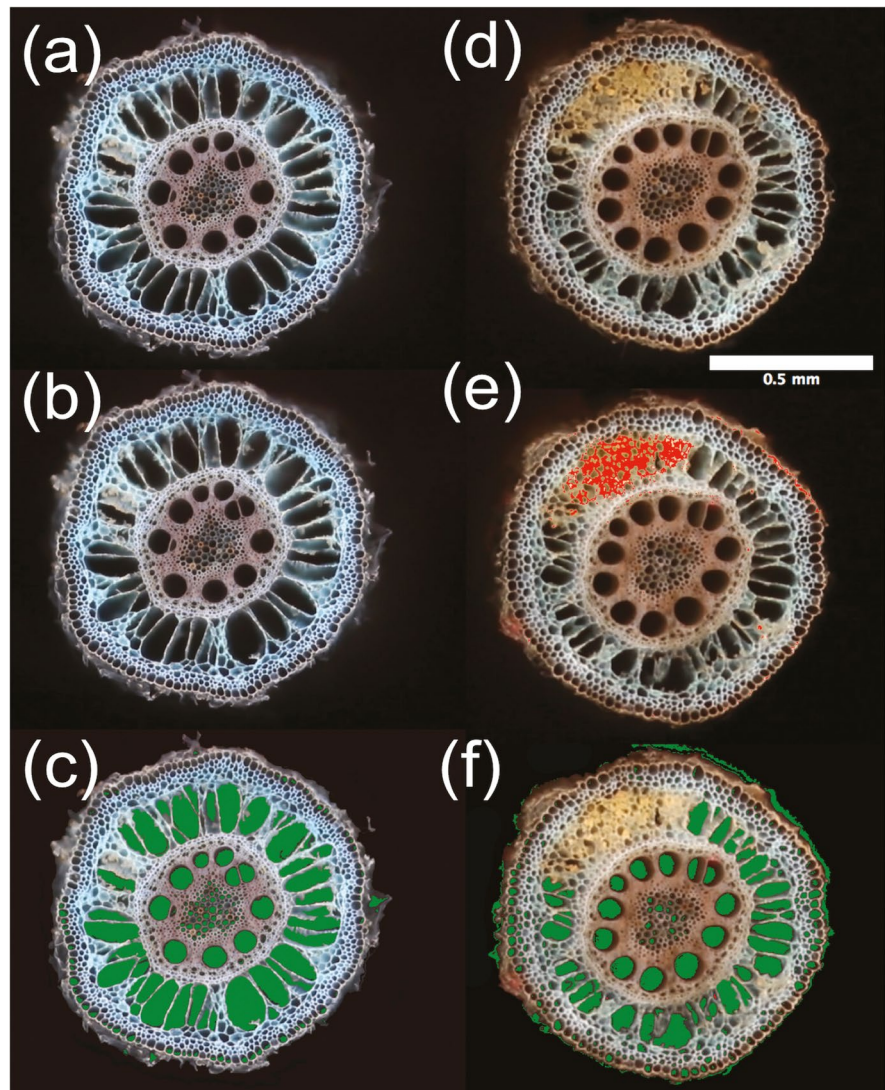
resource acquisition and plant growth, particularly under drought and nutrient stress. We advocate for a comprehensive understanding of the benefits and trade-offs of root anatomical traits and root-rhizosphere interactions for plant growth in specific environments. The benefits of several anatomical traits for soil foraging and water and nutrient capture have been documented (as reviewed in Lynch et al. 2021), however the benefits and trade-offs of many of these traits on rhizosphere interactions in diverse environments remain to be explored. A cost-benefit optimization (i.e., applying microeconomic principles to plant resource allocation) may be used to determine the most beneficial plant (and rhizosphere) phenotypes

in specific environments. Only after understanding the interplay between the root and rhizosphere can we identify optimal anatomical traits and root-rhizosphere interactions for improved plant performance in specific environments.

Perspectives and conclusions

Many opportunities remain to understand how developmental root and rhizosphere signals combine in the patterning of root cortical anatomy. For example, cortical cells colonized by arbuscular mycorrhizal fungi are not only typically larger in size, but also have

thicker cell walls with altered cell wall characteristics including increased cellulose and hemicellulose content (Balestrini et al. 2005; Basyal and Emery 2021). While many of the molecular mechanisms of cell wall remodeling upon mycorrhizal signaling and colonization are unknown, several plant cell wall related genes have been shown to respond to symbiosis of mycorrhizal fungi (Balestrini and Bonfante 2014; Gutjahr et al. 2015). Thicker cell walls in cortical cells colonized by mycorrhizae may also be beneficial in edaphic stress. An increased proportion of volume occupied by energy-efficient compartments including vacuoles and cell walls can potentially reduce root metabolic cost and thereby plant fitness under conditions of drought, suboptimal nutrient availability, and soil mechanical impedance (Sidhu and Lynch 2024). We propose that arbuscular mycorrhizal fungi and plant developmental signals can frequently and extensively combine to alter root anatomy with potential synergistic interactions for enhanced nutrient efficiency.

A challenge to understanding root anatomy and rhizosphere interactions is the complexity of these interactions in time and space. Root exudation and nutrient, water, and oxygen concentration in the rhizosphere, and many other factors vary spatially and temporally on the root system. In addition, root anatomy depends on many factors including root class, tissue age, and root-microbe interactions (Canarini et al. 2019; Lynch et al. 2021; Salas-González et al. 2021). For example, the soil microbiome has been demonstrated to influence aerenchyma formation and endodermal suberization (Kawa et al. 2022). The integration of multiple root anatomical and architectural traits and rhizosphere characteristics may have synergistic or antagonistic effects for nutrient and water acquisition, pathogen resistance, and ultimately plant performance. In addition, consideration of dependency between anatomical and rhizosphere traits is important as the utility of specific traits can be masked by the integrated effects of multiple root and rhizosphere traits.

The influence of root anatomical and rhizosphere interactions on plant growth, health, and productivity are multifaceted and we must embrace this complexity to better define optimal phenotypes for specific environments. Because of these intricate complexities, it will be essential to study root anatomy and rhizosphere interactions on the same plant, rather than integrating information from distinct plants and systems. Due to the vast diversity of plant species and traits, microbiota, and growth environments a holistic approach is needed to study these interactions, emphasizing the importance of interdisciplinary collaboration among geneticists, microbiologists, agronomists, and computational biologists.

There is evidence that signals from the rhizosphere can mobilize plant molecular actors to modify the patterning and development of root anatomy. We highlight an example of this interplay describing how mycorrhizal fungi from the rhizosphere mobilize plant molecular actors controlling root anatomical traits including cortical cell size to facilitate their establishment and accommodation within the cortex. In addition, root anatomy and mycorrhizal fungi can have physical interactions in the cortex to promote or inhibit colonization. Research and breeding efforts targeting root anatomy to improve soil resource capture should consider microbial tradeoffs and microbial-root feedback that have the potential to modify or be modified by the root-rhizosphere environment. Understanding how roots and the rhizosphere interact is critical in mitigating impacts of abiotic and biotic stress on plant productivity.

References

Balestrini R, Bonfante P (2014) Cell wall remodeling in mycorrhizal symbiosis: a way towards biotrophism. Front Plant Sci 5:1–10

Balestrini R, Cosgrove DJ, Bonfante P (2005) Differential location of α-expansin proteins during the accommodation of root cells to an arbuscular mycorrhizal fungus. Planta 220:889–899. https://doi.org/10.1007/s00425-004-1431-2

Balestrini R, Gómez-Ariza J, Lanfranco L, Bonfante P (2007) Laser microdissection reveals that transcripts for five plant and one fungal phosphate transporter genes are contemporaneously present in arbusculated cells. Mol Plant Microbe Interact 20(9):1055–1062. https://doi.org/10.1094/MPMI-20-9-1055

Basyal B, Emery SM (2021)An arbuscular mycorrhizal fungus alters switchgrass growth, root architecture, and cell wall chemistry across a soil moisture gradient. Mycorrhiza 31:251–258. https://doi.org/10.1007/s00572-020-00992-6

Besserer A, Puech-Pagès V, Kiefer P et al (2006) Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. PLoS Biol 4:1239–1247. https://doi.org/10.1371/journal.pbio.0040226

Brundrett MC, Kendrick B (1987) The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. Can J Bot 66:1153–1173. https://doi.org/10.1139/b88-166

Brundrett MC, Piche Y, Peterson RL (1985) A developmental study of the early stages in vesicular-arbuscular mycorrhiza formation. Can J Bot 63:184194. https://doi.org/10.1139/b85-021

Canarini A, Kaiser C, Merchant A et al (2019) Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front Plant Sci 10:157. https://doi.org/10.3389/fpls.2019.00157

Chimungu JG, Brown KM, Lynch JP (2014) Large root cortical cell size improves drought tolerance in maize. Plant Physiol 166:2166–2178. https://doi.org/10.1104/pp.114.250449

Choi J, Summers W, Paszkowski U (2018) Mechanisms underlying establishment of arbuscular mycorrhizal symbioses. Annu Rev Phytopathol 56:135–160. https://doi.org/10.1146/annurev-phyto-080516-035521

Choi J, Lee T, Cho J et al (2020) The negative regulator SMAX1 controls mycorrhizal symbiosis and strigolactone biosynthesis in rice. Nat Commun 11:2114. https://doi.org/10.1038/s41467-020-16021-1

Devers EA, Teply J, Reinert A et al (2013) An endogenous artificial microRNA system for unraveling the function of root endosymbioses related genes in Medicago truncatula. BMC Plant Biol 13:1–10. https://doi.org/10.1186/1471-2229-13-82

Dreyer B, Morte A, López JÁ, Honrubia M (2010) Comparative study of mycorrhizal susceptibility and anatomy of four palm species. Mycorrhiza 20:103–115. https://doi.org/10.1007/s00572-009-0266-x

Enstone DE, Peterson CA, Ma F (2003) Root endodermis and exodermis: structure, function, and responses to the environment. J Plant Growth Regul 21:335–351. https://doi.org/10.1007/s00344-003-0002-2

Floss DS, Gomez SK, Park HJ et al (2017) A transcriptional program for Arbuscule degeneration during AM Symbiosis is regulated by MYB1. Curr Biol 27:1206–1212. https://doi.org/10.1016/j.cub.2017.03.003

Foo E, Ross JJ, Jones WT, Reid JB (2013) Plant hormones in arbuscular mycorrhizal symbioses: an emerging role for gibberellins. Ann Bot 111:769–779. https://doi.org/10.1093/aob/mct041

Galindo-Castañeda T, Brown KM, Kuldau GA et al (2019) Root cortical anatomy is associated with differential pathogenic and symbiotic fungal colonization in maize. Plant Cell Environ 42:1–16. https://doi.org/10.1111/pce.13615

Galindo-Castañeda T, Lynch JP, Six J, Hartmann M (2022) Improving soil resource uptake by plants through capitalizing on synergies between root architecture and anatomy and root-associated microorganisms. Front Plant Sci 13:1–15. https://doi.org/10.3389/fpls.2022.827369

Gobbato E, Marsh JF, Vernié T et al (2012) A GRAS-type transcription factor with a specific function in mycorrhizal signaling. Curr Biol 22:2236–2241. https://doi.org/10.1016/j.cub.2012.09.044

Gutjahr C, Sawers RJ, Marti G, Andrés-Hernández L, Yang SY, Casieri L, Angliker H, Oakeley EJ, Wolfender JL, Abreu-Goodger C, Paszkowski U (2015) Transcriptome diversity among rice root types during asymbiosis and interaction with arbuscular mycorrhizal fungi. Proc Natl Acad Sci 112(21):6754–6759. https://doi.org/10.1073/pnas.1504142112

Heck C, Kuhn H, Heidt S et al (2016) Symbiotic fungi control plant root cortex development through the novel GRAS transcription factor MIG1. Curr Biol 26:2770–2778. https://doi.org/10.1016/j.cub.2016.07.059

Hunter MC, Smith RG, Schipanski ME et al (2017) Agriculture in 2050: recalibrating targets for sustainable intensification. Bioscience 67:386–391. https://doi.org/10.1093/biosci/bix010

IPCC (2021) Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. In: Masson-Delmotte V, Zhai P, Pirani A et al (eds) Cambridge University Press, Cambridge, 2391 pp. https://doi.org/10.1017/9781009157896

Kawa D, Thiombiano B, Shimels M (2022) The soil microbiome reduces Striga infection of sorghum by modulation of host-derived signaling molecules and root development. Cell Rep 62. https://papers.ssrn.com/sol3/papers.cfm?abstract_id=4350137

Kosuta S, Chabaud M, Lougnon G et al (2003) A diffusible factor from arbuscular mycorrhizal fungi induces symbiosis-specific MtENOD11 expression in roots of Medicago truncatula. Plant Physiol 131:952–962. https://doi.org/10.1104/pp.011882

Kotula L, Ranathunge K, Steudle E (2009) Apoplastic barriers effectively block oxygen permeability across outer cell layers of rice roots under deoxygenated conditions: roles of apoplastic pores and of respiration. New Phytol 184:909–917. https://doi.org/10.1111/j.1469-8137.2009.03021.x

Lanfranco L, Fiorilli V, Gutjahr C (2018) Partner communication and role of nutrients in the arbuscular

mycorrhizal symbiosis. New Phytol 220:1031–1046. https://doi.org/10.1111/nph.15230

Lopez-Valdivia I, Yang X, Lynch JP (2023) Large root cortical cells and reduced cortical cell files improve growth under suboptimal nitrogen in silico. Plant Physiol 192:2261–2275. https://doi.org/10.1093/plphys/kiad214

Lynch JP, Strock CF, Schneider HM et al (2021) Root anatomy and soil resource capture. Plant Soil 466:21–63. https://doi.org/10.1007/s11104-021-05010-y

Maldonado-Mendoza IE, Dewbre GR, Blaylock L, Harrison MJ (2005) Expression of a xyloglucan endotransglucosylase/hydrolase gene, Mt-XTH1, from Medicago truncatula is induced systemically in mycorrhizal roots. Gene 345:191–197. https://doi.org/10.1016/j.gene.2004.10.028

Park HJ, Floss DS, Levesque-Tremblay V et al (2015) Hyphal branching during arbuscule development requires reduced arbuscular mycorrhiza. Plant Physiol 169:2774–2788. https://doi.org/10.1104/pp.15.01155

Ramírez-Flores MR, Perez-Limon S, Li M et al (2020) The genetic architecture of host response reveals the importance of arbuscular mycorrhizae to maize cultivation. Elife 9:1–18. https://doi.org/10.7554/eLife.61701

Russo G, Carotenuto G, Fiorilli V et al (2019) Ectopic activation of cortical cell division during the accommodation of arbuscular mycorrhizal fungi. New Phytol 221:1036–1048. https://doi.org/10.1111/nph.15398

Salas-González I, Reyt G, Flis P et al (2021) Coordination between microbiota and root endodermis supports plant mineral nutrient homeostasis. Science (1979) 371:eabd0695. https://doi.org/10.1126/science.abd0695

Schneider HM, Strock CF, Hanlon MT et al (2021) Multiseriate cortical sclerenchyma enhance root penetration in compacted soils. Proc Natl Acad Sci 118:e2012087118. https://doi.org/10.1073/pnas.2012087118

Seemann C, Heck C, Voß S et al (2022) Root cortex development is fine-tuned by the interplay of MIGs, SCL3 and DELLAs during arbuscular mycorrhizal symbiosis. New Phytol 233:948–965. https://doi.org/10.1111/nph.17823

Sharda JN, Koide RT (2010) Exploring the role of root anatomy in P-mediated control of colonization by arbuscular mycorrhizal fungi. Botany 88:165–173. https://doi.org/10.1139/B09-105

Sidhu JS, Lynch JP (2024) Cortical cell size regulates root metabolic cost. Plant J. https://doi.org/10.1111/tpj.16672

Smith FAA, Smith SE (1997) Tansley structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. New Phytol 137:373–388. https://doi.org/10.1046/j.1469-8137.1997.00848.x

Strock CF, Schneider HM, Galindo-Castañeda T, Hall BT, Van Gansbeke B, Mather DE, Roth MG, Chilvers MI, Guo X, Brown K, Lynch JP (2019) Laser ablation tomography for visualization of root colonization by edaphic organisms. J Exp Bot 70(19):5327–5342. https://doi.org/10.1093/jxb/erz271

Ubeda-Tomás S, Swarup R, Coates J et al (2008) Root growth in Arabidopsis requires gibberellin/DELLA signalling in the endodermis. Nat Cell Biol 10:625–628. https://doi.org/10.1038/ncb1726

Volpe V, Dell'Aglio E, Giovannetti M et al (2013) An AM-induced, MYB-family gene of Lotus japonicus (LjMAMI) affects root growth in an AM-independent manner. Plant J 73:442–455. https://doi.org/10.1111/tpj.12045

Wang E, Schornack S, Marsh JF et al (2012) A common signaling process that promotes mycorrhizal and oomycete colonization of plants. Curr Biol 22:2242–2246. https://doi.org/10.1016/j.cub.2012.09.043

Wang Y, Bao X, Li S (2021) Effects of arbuscular mycorrhizal Fungi on Rice growth under different flooding and shading regimes. Front Microbiol 12:756752. https://doi.org/10.3389/fmicb.2021.756752

Xue L, Cui H, Buer B et al (2015) Network of GRAS transcription factors involved in the control of arbuscule development in Lotus japonicus. Plant Physiol 167:854–871. https://doi.org/10.1104/pp.114.255430

Yang SY, Grønlund M, Jakobsen I et al (2012) Nonredundant regulation of rice arbuscular mycorrhizal symbiosis by two members of the PHOSPHATE TRANSPORTER1 gene family. Plant Cell 24:4236–4251. https://doi.org/10.1105/tpc.112.104901

Zhang ZL, Ogawa M, Fleet CM et al (2011) SCARECROW-LIKE 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in Arabidopsis. Proc Natl Acad Sci USA 108:2160–2165. https://doi.org/10.1073/pnas.1012232108