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Review

Tansley insight

The endodermal passage cell – just another brick in the wall?

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Summary

The endodermis surrounds and protects the vasculature partly by depositing hydrophobic suberin in the cell walls. Yet, some cells remain unsuberised. These historically termed 'passage cells' are assumed to provide a low-resistance pathway to the xylem. Only recently have we started to gain molecular insights into these cells, which allow us to probe how roots coordinate communication with the environment across barriers with single-cell precision. Increased understanding of root physiology at a high-resolution is intriguing, as it is likely to provide us with new tools to improve overall plant health. With this in mind, we here provide a brief overview of passage cells, their presence across plant species, as well as a molecular update and future directions for passage cell-related research.

I. Introduction

The aboveground parts of plants constitute food and feed through energy harvested from photosynthesis. It is therefore not surprising that most historical and currently used agricultural traits are associated with these tissues (seed yield, biomass, plant height, etc.). Yet, plants live in two opposite environments and, despite an increased focus on root–microbiome interactions, the root system is still somewhat overlooked when it comes to agricultural qualities. While we do have simplistic models for specific individual traits of the root system, we are only beginning to understand how they are integrated into root developmental plasticity at a cellular level.

In roots, the vasculature is surrounded by a barrier-containing cell layer termed the endodermis. Only within the recent years have we gained molecular insight into the formation and function of the barriers established in the endodermis (Barberon *et al.*, 2016; Li *et al.*, 2017) coordinating root association and communication with the environment (Durr *et al.*, 2019; Holbein *et al.*, 2019; Liu *et al.*, 2019). Dependent on the stage of root development, the endodermis deploys different barrier systems to protect and isolate the vasculature and its long-distance transport capacity. Between endodermal cells close to the root tip, lignin depositions known as the Casparian strip (CS) constitute an apoplastic barrier that serves to block diffusion between cell walls and forces solutes across the plasma membrane. This is analogous to tight junctions in the mammalian gut system (Barberon & Geldner, 2014). As the endodermal cells get older, they deposit hydrophobic suberin lamellae across the entire cell surface, which completely inhibit their ability to facilitate cross-membrane transport (reviewed in Doblas *et al.*, 2017). Intriguingly, certain xylem pole (XP)-

associated endodermal cells do not undergo suberisation. These cells are termed 'passage cells' (PCs) as they are historically believed to provide a low resistance radial path for flow of solutes directly into the xylem (Kroemer, 1903).

PCs occur across a wide range of species, yet their function and formation are still enigmatic (Peterson & Enstone, 1996). Although first observed more than a century ago (Kroemer, 1903), PCs have until recently lacked any framework to study their molecular development and function. It was recently found that these cells are determined very early in the meristem, but do not manifest until much later in development (Andersen *et al.*, 2018). Thus, they provide an intriguing model to study the interplay between root developmental and physiological processes at single-cell level. With basis on this, we here present an overview of current knowledge on PCs, speculations on their function(s) and directions of future research.

II. Exo- and endodermal passage cells – us and them

In certain plant species, the second outermost cell layer of the root functions as a protective layer (termed the exodermis), which in many ways is similar to the endodermis (reviewed in Geldner, 2013). The exodermis is a specialised hypodermis, which is also equipped with CSs and often with suberin depositions (Peterson & Perumalla, 1990; Damus *et al.*, 1997). PCs occur in both layers and were, interestingly, discovered almost simultaneously with the anatomical description of the endodermis and exodermis as barrier-containing cell layers. According to records, exodermal passage cells were first identified and described as stoma-like openings in aerial roots of epiphytic orchids in the 19th century (Kroemer, 1903; von Guttenberg, 1940). By then they were referred to as transfer cells, thin-walled endodermis cells or simply short cells (Schwendener, 1882; Kroemer, 1903; Wilson & Robards, 1980). 'Passage cell' (from the original German term: 'Durchlaßzelle') did not become widely accepted until publishing of the comprehensive work *Handbook of Plant Anatomy* (*Handbuch der Pflanzenanatomie*) by Hermann von Guttenberg in 1940.

In both the endodermis and exodermis, PCs carry the same name, but display distinct features. The minority of plant species develop an exodermis and PCs were only reported in certain exodermis-containing species (Peterson & Perumalla, 1990; Damus *et al.*, 1997; Enstone *et al.*, 2002). Moreover, the endodermal PCs appear to co-localise significantly with XPs and this strong correlation was not shown for exodermal PCs except for a study on clones of *Salix* spp. (Fig. 1a) (Peterson & Enstone, 1996; Hose *et al.*, 2001; Enstone *et al.*, 2002; Lux *et al.*, 2004).

With few exceptions, vascular plants form an endodermis layer equipped with CSs and suberin barriers. Despite the fact that relatively few species have been investigated for PC occurrence, they have been observed in a number of angiosperm orders (18 out of the total 64 angiosperm orders), including the basal angiosperm *Amborella trichopoda* as well as in certain gymnosperms, such as *Picea* and *Pinus* (Table 1). In the model plant *Arabidopsis thaliana* (Arabidopsis) suberin patterning is dynamic and dependent on abiotic stress factors (Barberon *et al.*, 2016; Andersen *et al.*, 2021). The definition of PCs as unsuberised XP-associated endodermal cells emphasises the situation that we technically do not know what defines these cells. Based on this loose definition they are hard to distinguish in the maturing endodermis. This is especially true close to emergence sites for lateral roots in which unsuberised emergence points can be hard to distinguish from PCs (Andersen *et al.*, 2018). Thus, while this still needs to be empirically determined, it suggests that exodermal and endodermal PCs might serve distinct, yet possibly overlapping, roles. Moreover, endodermal PCs occur in a noteworthy wide evolutionary span of plants, which suggests a common, and most likely important, function.

III. Endodermis differentiation – poles apart

Only recently did we start to gain insights into how endodermal PCs are formed. Although solely based on analysis in Arabidopsis, recent evidence suggests that they represent a distinct endodermal cell type with a developmental programme overlapping with xylem formation (Andersen *et al.*, 2018). The currently earliest insight on definition of this cell type is that it depends on noncell autonomous functions of the cytokinin signal-repressive Arabidopsis Histidine Phosphotransfer Protein 6 (AHP6) in the early endodermis. While the underlying mechanism remains to be investigated in detail, one outcome of AHP6 diffusion to the early XP-associated endodermis is that cell division/elongation rates in the XP- and phloem pole (PP)-associated endodermis are measurably different (cells are shorter in the XP) (Lavrekha *et al.*, 2017; Andersen *et al.*, 2018). Therefore, this might represent a prepatterning event in which PC formation is an end-point developmental feature of the XP-associated endodermis. Such bifurcation of endodermal development is supported by recent single-cell RNA experiments on the root meristem, which reveal distinct populations of early endodermal cells (Ryu *et al.*, 2019; Zhang *et al.*, 2019; Shahan *et al.*, 2020; Wendrich *et al.*, 2020). Further endodermis-focussed single cell characterisation might therefore reveal the distinct identities and regulators of the XP- and PP-associated endodermal cell linages.

IV. Passage cell function – just another brick in the wall?

From the perspective of the whole root, solutes absorbed from the soil are transported radially into the vasculature to be allocated elsewhere via the xylem. Despite this rather simplistic function, this is an incredibly complex task when considering the required underlying coordination. Three distinct mechanisms can theoretically facilitate this multicellular journey: (1) apoplastic diffusion in which solutes diffuse freely in the apoplastic space within cells; (2) plasmodesmata-dependent symplastic flow between cells; and (3) consecutive influx and efflux steps through transcellular-expressed polar plasma membrane localised transporter proteins (Peterson & Enstone, 1996; reviewed in Ramakrishna & Barberon, 2019). In older suberised root parts, the hydrophobic impregnation of the cell walls is most likely to represses transcellular transport, suggesting that, in this area, this mechanism can only occur in PCs. Therefore, it is not unreasonable to assume that certain transporter proteins would show expression in PCs.

In most examples of nutrient transporter characterisation, their localisation and expression patterns have been determined using

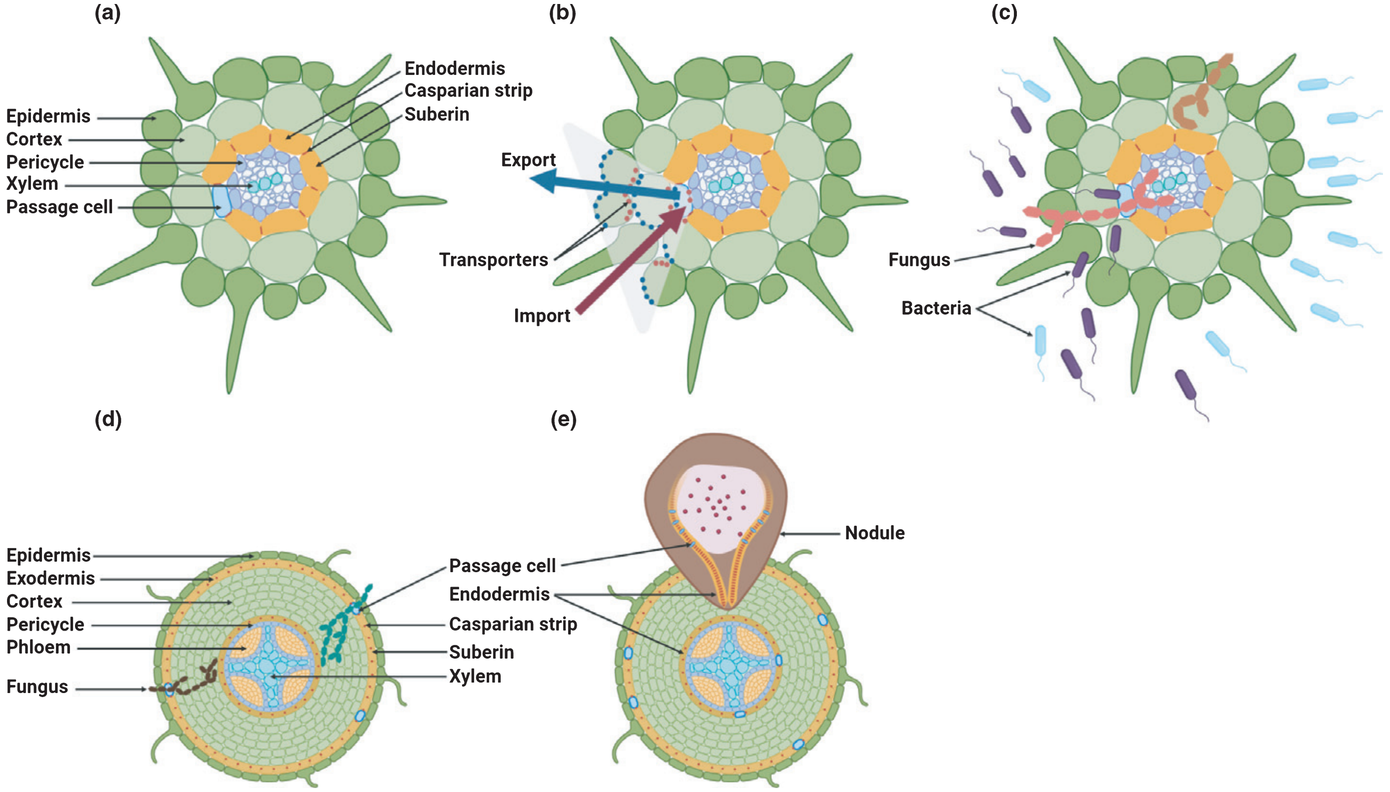

Fig. 1 Schematic cross-sections illustrating the occurrence and putative functions of endodermal passage cells (PCs). (a) PCs occur as 'open' cells adjacent to the xylem pole in the fully differentiated root parts where the endodermis has both Casparian strips and hydrophobic suberin depositions that block apoplastic and transcellular transport. (b) Certain transporter genes show expression in PC-associated cortex and epidermal cells (Andersen *et al*., 2018), which suggest that the PCs might coordinate a 'funnel-like' pattern of influx and efflux carriers in cortical and epidermal cells associated to passage cells. This patterning in the outer tissues might form a basis for import and export of nutrients and/or signals from the surrounding rhizosphere. (c) Interactions as well as xylem pole-localised infection with fungi and bacteria (d). Schematic view of typical dicot root cross-sections with arbuscular mycorrhizal fungi entering root tissue through exodermal PCs and remaining in the cortex. It is unknown if this occurs in xylem pole-adjacent cells or distinct passage cell-associated cells. (e) Schematic view of a cortex-initiated nodule organ (at the xylem pole) that accommodates nitrogen-fixing *Rhizobium* bacteria and the nodule vasculatures are connected to the root vasculature for long-distance transport of solutes through the xylem pole. It remains to be investigated if the xylem pole localisation is correlated to passage cell occurrence. Created with BioRender.com.

classical methods such as GUS (β-glucuronidase) staining, immunolocalisation and/or *in situ* transcript analysis. However, obtaining high-resolution insights into distinct cells such as PCs is notoriously difficult due to the necessity of sectioning, as well as the diffusive nature of GUS crystals (Jefferson *et al*., 1987). Despite this, genes coding for *IRON REGULATED TRANSPORTER 3* (*AtIRT3*), *YELLOW STRIPE-LIKE 2* (*AtYSL2*), *HIGH AFFINITY POTASSIUM TRANSPORTER 1* (*OsHAK21*), STELAR K + OUTWARDS RECTIFIER (SKOR) and the phosphate exporter *PHOSPHATE 1* (*AtPHO1*) have indeed been observed in PCs (Gaymard *et al*., 1998; Hamburger *et al*., 2002; Schaaf *et al*., 2005; Lin *et al*., 2009; Shen *et al*., 2015). While these patterns remain to be investigated in detail, this situation suggests that PCs are involved in metal-ion and potassium/phosphate homeostasis or signalling. Fascinatingly, through the use of sensitive fluorescent transciptional reporters in combination with histochemical staining (Ursache *et al*., 2018), genes of the *PHO1* family (11 members in total) were shown to not only have PC-associated expression, but several members were expressed in individual cortex cells associated with the PCs, which in 3D would occur as a 'funnel-like' pattern (Andersen *et al*., 2018) (Fig. 1b). This observation not only suggests that individual (anatomically identical) cells in root tissues can obtain distinct genetic profiles, but it further emphasises that PCs might work as 'hubs', coordinating radial expression patterns that might relay information from the root surroundings to the vasculature. Future analysis employing tissue-specific promoters for untargeted mRNA analysis such as Translating Ribosome Affinity Purification (TRAP) (Mustroph *et al*., 2013) or fluorescence-associated cell sorting (FACS) coupled with single-cell RNA-seq analysis will provide insights into the role of these intriguing and overlooked aspects of root organisation.

V. Cross-barrier communication – is there anybody out there?

Roots do not work alone. Most root systems establish mutualistic associations with microbes to improve nutrient acquisition and stress tolerances. Arguably, the most widespread examples of such a connection are phosphate acquisition through arbuscular mycorrhiza (AM) symbiosis and nitrogen fixation via nodule formation

Table 1 A summary of passage cell occurrence in plants.

Classification	Order	Family	Species	PCs in endodermis	PCs in exodermis/ hypodermis	References*
Gymnosperms	Pinales	Pinaceae	*Picea sitchensis*	✓		MacKenzie (1983)
			Pinus banksiana	✓		McKenzie & Peterson (1995)
		Cupressaceae	*Chamaecyparis obtusa*	✓	✓	Hishi *et al.* (2006)
			Chamaecyparis obtusa	✓		Hishi & Takeda (2005)
Basal Angiosperm	Amborellales	Amborellaceae	*Amborella trichopoda*	✓		Seago & Fernando (2013)
Magnoliids	Magnoliales	Magnoliaceae	*Magnolia soulangeana*	✓		Seago & Fernando (2013)
			Liriodendron tulipifera		✓	Zadworny & Eissenstat (2011)
Monocots	Alismatales	Araceae	*Calla palustris*	✓		Kroemer (1903)
			Caladium hybridum	✓		Kroemer (1903)
			Hydrosme rivieri	✓		Kroemer (1903)
		Tofieldiaceae	*Tofieldia calyculata*	✓		Schwendener (1882)
	Arecales	Arecaceae	*Serenoa repens*	✓		Fisher & Jayachandran (1999)
	Asparagales	Asparagaceae	*Agave deserti*	✓		North & Nobel (1991)
		Orchidaceae	*Habenaria rhodocheila*		✓	Stern (1997)
			Laelia anceps	✓		Napp-Zinn (1953)
			Stanhopea tigrina		✓	Esnault *et al.* (1994)
			Vanda suavis	✓		Napp-Zinn (1953)
		Amaryllidaceae	*Agapanthus praecox*	✓		Kroemer (1903)
			Allium ascalonicum	✓		Haberlandt (1884)
			Allium cepa	✓	✓	Wilson & Robards (1980), Shishkoff (1989), Stasovski & Peterson (1993), Peterson & Enstone (1996), Sharda & Koide (2008, 2010)
			Leucojum aestivum		✓	Seago & Fernando (2013)
		Asparagaceae	*Asparagus officinalis*		✓	Kamula *et al.* (1994), Peterson & Enstone (1996), Sharda & Koide (2008)
			Asparagus sprengeri	✓		Kroemer (1903)
			Aspidistra elatior	✓		Kroemer (1903)
			Yucca schidigera	✓		North & Baker (2007)
			Aloe vera		✓	Shishkoff (1987)
		Iridaceae	*Iris germanica*	✓		Schwendener (1882), Kroemer (1903)
		Orchidaceae	*Dendrobium kingianum*		✓	Esnault *et al.* (1994)
			Dendrobium nobile		✓	Hou & Guo (2009)
			Dendrobium spp.	✓		Seago & Fernando (2013)
			Dendrophylax lindenii	✓	✓	Chomicki *et al.* (2014)
			Epidendrum radicans		✓	Esnault *et al.* (1994)
			Phalaenopsis spp.	✓	✓	Peterson & Enstone (1996)
			Renanthera coccinea	✓		Schwendener (1882)
			Vanilla planifolia		✓	Koyyappurath *et al.* (2015)
	Laurales	Lauraceae	*Persea gratissima*	✓		Schwendener (1882)
	Liliales	Smilacaceae	*Smilax* spp.		✓	Peterson & Enstone (1996)
	Poales	Poaceae	*Echinochloa crus-galli* var. *praticola*		✓	Ejiri & Shiono (2020)
			Hordeum vulgare	✓		Clarkson *et al.* (1971), Kreszies *et al.* (2018)
			Oryza sativa	✓		Momayezi *et al.* (2012), Shen *et al.* (2015)
			Poa nemoralis	✓		Napp-Zinn (1953)
			Triticum aestivum	✓		Wu *et al.* (2011)
			Zea mays	✓		Kroemer (1903), Ma & Peterson (2003), Niu *et al.* (2011), Tylová *et al.* (2017)
	Zingiberales	Musaceae	*Ensete ventricosum*	✓		Kroemer (1903)
		Zingiberaceae	*Hedychium gardnerianum*	✓		Kroemer (1903)
Eudicots	Asterales	Asteraceae	*Coreopsis grandiflora*		✓	Sharda & Koide (2008, 2010)
			Rudbeckia fulgida		✓	Sharda & Koide (2008, 2010)
			Bellis perennis		✓	Shishkoff (1987)
	Brassicales	Brassicaceae	*Arabidopsis thaliana*	✓		Andersen *et al.* (2018)
	Fabales	Fabaceae	*Glycine max*	✓		Thomas *et al.* (2007)

Table 1 (Continued)

Classification	Order	Family	Species	PCs in endodermis	PCs in exodermis/ hypodermis	References*
		Juglandaceae	*Juglans nigra*		✓	Zadworny & Eissenstat (2011)
	Gentianales	Apocynaceae	*Asclepias syriaca*		✓	Francke (1927)
			Asclepias tuberosa		✓	Sharda & Koide (2008, 2010)
			Ceropegia bulbosa		✓	Francke (1927)
			Dischidia collyris		✓	Francke (1927)
			Dischidia rafflesiana		✓	Francke (1927)
			Hoya carnosa		✓	Francke (1927), Shishkoff (1987)
			Huernia macrocarpa		✓	Francke (1927)
			Marsdenia condurango		✓	Francke (1927)
			Stapelia trifida		✓	Francke (1927)
			Vinca minor		✓	Sharda & Koide (2008, 2010)
			Vincetoxicum officinale	✓		Kroemer (1903)
	Lamiales	Lamiaceae	*Ocimum basilicum*		✓	Sharda & Koide (2008, 2010)
		Linderniaceae	*Chamaegigas intrepidus*		✓	Hose *et al.* (2001)
		Scrophulariaceae	*Verbascum thapsus*		✓	Shishkoff (1987)
	Malpighiales	Euphorbiaceae	*Ricinus communis*	✓		Kroemer (1903)
		Salicaceae	*Populus tremuloides*		✓	Zadworny & Eissenstat (2011)
			Salix spp.	✓		Lux *et al.* (2004)
	Malvales	Malvaceae	*Gossypium hirsutum*	✓		Reinhardt & Rost (1995)
	Myrtales	Myrtaceae	*Eucalyptus pilularis*	✓		McKenzie & Peterson (1995)
	Proteales	Nelumbonaceae	*Nelumbo lutea*	✓		Seago & Fernando (2013)
	Ranunculales	Ranunculaceae	*Ranunculus acris*	✓		Scott & Peterson (1979)
			Ranunculus repens	✓		Seago & Fernando (2013)
	Sapindales	Rutaceae	*Citrus aurantium*		✓	Eissenstat & Achor (1999)
			Citrus jambhiri		✓	Eissenstat & Achor (1999)
			Citrus medica		✓	Storey & Walker (1987)
			Citrus reticulata var. *austera* hybrid	✓	✓	Walker *et al.* (1984); Storey & Walker (1987)
			Citrus volkameriana Tan. & Pasq.		✓	Eissenstat & Achor (1999)
			Poncirus trifoliata		✓	Eissenstat & Achor (1999)
		Sapindaceae	*Acer negundo*		✓	Zadworny & Eissenstat (2011)
			Acer saccharum		✓	Zadworny & Eissenstat (2011)
	Solanales	Convolvulaceae	*Ipomoea purpurea*		✓	Sharda & Koide (2010)
		Solanaceae	*Nicotiana tabacum*	✓		Banasiak *et al.* (2020)
			Petunia axillaris		✓	Kretzschmar *et al.* (2012), Sasse *et al.* (2015)

✓, Present.
*See full reference list in Supporting Information Notes S1.

and association with *Rhizobium* bacteria. Based on the anatomical and genetic knowledge of PCs, it is intriguing to speculate about their function in relation to communication with the biotic environment surrounding the roots.

For AM symbiosis a tight plant–fungal association improves transport and acquisition of, for example, phosphate in exchange for sugars and fatty acids (Keymer *et al.*, 2017). In several plant species AM fungi enter root tissue through exodermal PCs (Esnault *et al.*, 1994; Matsubara *et al.*, 1999; Sharda & Koide, 2010). However, it is not fully understood why AM fungi remain in the cortex as well as how they obtain nutrients from the vasculature across the endodermis (Peterson & Enstone, 1996). As detailed high-resolution analyses of the initial plant–fungi association are scarce, it is possible that the fungi select XP-adjacent cells or distinct PC-associated cortex cells (Fig. 1d).

Colletotrichum tofieldiae (*Ct*) is an endemic root endophyte in natural Arabidopsis populations (Hiruma *et al.*, 2016). *Ct* is allowed to enter the root, where it promotes plant growth, specifically under low phosphate conditions. This mutualistic behaviour is dependent on tryptophan-derived specialised metabolites and in a manner controlled by the phosphate starvation response (Hiruma *et al.*, 2016). Intriguingly, penetration of root tissue appears to be interrupted by suberin lamellae in the endodermis. In fact, fungal hyphae were detected only in unsuberised endodermal cells, hinting that entrance to the vasculature might occur through coordination of chemical defence employment and physical barriers such as suberin (Hiruma *et al.*, 2016). Intriguingly, this suggests that PCs might, despite lacking the protective suberin, provide a high concentration of defence compounds situated in the putative entry points, which could allow for selective, specialised microbial associations or host-preference in microbiome composition under certain conditions (Fig. 1c). This hypothesis is particularly intriguing to investigate with regards to opportunistic pathogens such as the bacterium *Ralstonia solanacearum,* of which progress is highly directed towards the XP (Digonnet *et al.*, 2012).

While phosphate exchange via AM symbiosis is a widespread phenomenon across the plant kingdom, only certain plant families form the tight and highly specific nodule organs that accommodate nitrogen (N)-fixing *Rhizobium* bacteria (reviewed in Oldroyd *et al.*, 2011). Nodules require a connection to the root vasculature for long-distance transport of solutes to and from the N-fixing bacteria and, fascinatingly, these lateral root-like structures can be derived from cortex cells facing the XP (Heidstra *et al.*, 1997; Xiao *et al.*, 2014). In depth analysis using live cell markers or clearing histochemical procedures (Ursache *et al.*, 2018) will reveal if cortex-initiated nodules correlate with PC occurrence or their associated cortex cells and might reveal new insights into nodule cross-barrier communication with the vasculature (Fig. 1e).

Communication from plants to the rhizosphere occurs, at least in part, through transporter-dependent exudation of bioactive specialised compounds (reviewed in Sasse *et al.*, 2018). While spatially restricted phytohormone production such as cytokinin is involved in nodule formation (Reid *et al.*, 2017), it is evident that secretion of signals helps to attract beneficial microbes (Sasse *et al.*, 2018; Harbort *et al.*, 2020). Interestingly, exodermal PCs were identified to exudate strigolactones through the ABC (ATP Binding Cassette)-type transporters termed PLEIOTRPOIC DRUG RESISTANCE (PDR (Kretzschmar *et al.*, 2012; Sasse *et al.*, 2015; Xie *et al.*, 2015; Liu *et al.*, 2019). It remains to be investigated if this is also the case for endodermal PCs and if any distinct funnel-like expression PC-associated cortex and epidermis might serve a similar function (Fig. 1c).

VI. Passage cells as an agricultural tool – high hopes

At present, we have only a few examples of how nutrient uptake is facilitated into the vasculature of roots at the single-cell level. PCs and their associated development represent a very intriguing model to study the communication between the vasculature and the surrounding tissues/rhizosphere. Endodermal PCs might be developmentally controlled nutrient responsive windows into the vasculature, possibly in combination with their brothers in the exodermis. They could provide a combination of entry points for beneficial microbes and floodgates for nutrient acquisition, which is in tight coordination with the xylem underlying endodermal PCs, thus an intriguing model for plant–environmental regulation with huge implications for agriculture (Fig. 1b,c). Nonrenewable resources and their extraction are becoming increasingly costly (Cordell *et al.*, 2009). Moreover, inefficient usage due to leaching and other environmental factors (reviewed in Sharma *et al.*, 2013) increases the urgency of new tools for agricultural development. Genetic tools that allow manipulation of PC occurrence have been established in Arabidopsis and further characterisation of these as well as translational efforts might provide a much-needed toolbox for further agricultural optimisation and investigation of underground traits for crop quality. Moreover, identification and application of microbial strains that induce PC patterning might additionally provide an ecological strategy towards the growth of healthier and more nutritious crops.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 References included in Table 1.