


Development specifies, diversifies and empowers root immunity

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Abstract

Roots are a highly organised plant tissue consisting of different cell types with distinct developmental functions defined by cell identity networks. Roots are the target of some of the most devastating diseases and possess a highly effective immune system. The recognition of microbe- or plant-derived molecules released in response to microbial attack is highly important in the activation of complex immunity gene networks. Development and immunity are intertwined, and immunity activation can result in growth inhibition. In turn, by connecting immunity and cell identity regulators, cell types are able to launch a cell type-specific immunity based on the developmental function of each cell type. By this strategy, fundamental developmental processes of each cell type contribute their most basic functions to drive cost-effective but highly diverse and, thus, efficient immune responses. This review highlights the interdependence of root development and immunity and how the developmental age of root cells contributes to positive and negative outcomes of development-immunity cross-talk.

Keywords cell identity; pattern-triggered immunity; plant growth; root body plan; root development

Subject Categories Development; Immunology; Plant Biology

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Introduction

Healthy and efficient below-ground root systems are crucial for plant development and productivity. Plant roots anchor the plant in the ground and provide it with water and nutrients. Adverse conditions, especially those exacerbated by climate change, including extreme temperatures, flooding, drought, high salinity or pathogen infection, can impair root development and overall plant growth (Rivero *et al.*, 2022). Supported by new ways of automated and noninvasive root phenotyping, the optimisation of root system architecture is becoming more and more accessible as a breeding target for improved resilience of crop plants to biotic and abiotic stress factors (e.g. de Dorlodot *et al.*, 2007; Khan *et al.*, 2016; Atkinson *et al.*, 2019; Tracy *et al.*, 2020; Wasson *et al.*, 2020; Amtmann *et al.*, 2022;

Lynch, 2022). Those studies reveal that the root's unique multicellular organisation plays an essential role in plant stress resilience. Plant roots have a strict cell type-based organisation that determines the root body structure and allows the assignment of a specific task to each cell type. The multifunctionality of roots is thus the result of their multicellularity, where each cell type adds its specific function to the overall functionality of roots (Petricka *et al.*, 2012). Moreover, it equips roots with functional plasticity that essentially allows roots to operate under (often rapidly) changing environments (Hodge, 2004; Morris *et al.*, 2017; Walker *et al.*, 2017; Motte & Beekman, 2019; Karlova *et al.*, 2021). In this context, it is astonishing to see how microbes can affect root functionality and development. Importantly, roots serve as an interface for communication with a diverse set of soil-borne microbes (Fitzpatrick *et al.*, 2020; Eichmann *et al.*, 2021). The impact these organisms can have on plant development ranges from detrimental (pathogens), via neutral (commensals) to growth-promoting (mutualists) (Raaijmakers *et al.*, 2009; Yu *et al.*, 2019; Thoms *et al.*, 2021). Some plant-colonising microbes can uncover the potential of plants to cope with environmental stress. Beneficial microbes not only attenuate adverse conditions but have positive effects on root development to help plants to survive under environmental stress conditions (Lugtenberg & Kamilova, 2009; Vacheron *et al.*, 2013; Verbon & Liberman, 2016; Yadav *et al.*, 2017). In turn, plant immune responses, although generally protective against plant pathogens, can have adverse effects. The observation that (excessive) immune activation can lead to reduced growth of roots, leaves and shoots and even to yield reductions in the absence of pathogens suggests that some defence- and development-related signalling processes may be interconnected (Huot *et al.*, 2014; Reitz *et al.*, 2015). Importantly, immune responses can vary in quality and quantity in different root zones and even root cell types (Poncini *et al.*, 2017; Chuberre *et al.*, 2018; Rich-Griffin *et al.*, 2020; Zhou *et al.*, 2020; Fröschel *et al.*, 2021). Considering the fact that the genetic identity of a cell type specifies its individual functions to ascertain overall root development, the response of a cell type to stress can only be understood in the context of its developmental function. As the demand for food is tremendously increasing with a growing world population, it is crucial to understand the interconnections and interdependencies of regulatory processes of root development and immunity. While current studies mostly focus on younger root cells and tissue to uncover mechanisms underlying the regulation of growth under immunity, we just start to understand the immunity-

development interplay in differentiated cells in older root tissue. Here, we summarise, also in the context of cell age, how the developmental identity of root cell types regulates their individual contribution to establish a diverse and thus highly robust root immunity, while immunity activation can inhibit fundamental growth regulatory processes depending on the developmental age of cells.

Plant roots possess a highly effective immune system

Root diseases caused by soil-borne pathogens are highly devastating for plants (Raaijmakers *et al*, 2009; Bodah, 2017; Katan, 2017). Such pathogens are mostly fungi (e.g. *Rhizoctonia*, *Fusarium* and *Verticillium* spp.) or oomycetes (e.g. *Phytophthora* and *Pythium* spp.) that can persist in the soil as spores, hyphae or sclerotia (Lockwood, 1988; Raaijmakers *et al*, 2009). Only a few pathogenic bacteria (e.g. *Ralstonia solanacearum*, *Agrobacterium tumefaciens*, *Rhizobium rhizogenes* and *Streptomyces* spp.) can survive in bulk soil over longer periods before they infect plant roots mostly through wounds or natural openings (Raaijmakers *et al*, 2009; Mansfield *et al*, 2012). Due to their persistence, soil-borne pathogens are generally hard to control in the field. This is very critical as they often have a broad host range, a wide geographical distribution and a high destructive potential (Raaijmakers *et al*, 2009; Mansfield *et al*, 2012; Bodah, 2017; Katan, 2017). Most concerningly, their abundance is expected to increase with global warming (Delgado-Baquerizo *et al*, 2020). This growing future challenge requires the development of crops with improved root resistance traits.

Pattern-triggered immunity (PTI) is a critical line of plant defence against microbes (Jones & Dangl, 2006; Cook *et al*, 2015) and relies on the recognition of damage-associated molecular patterns (DAMPs) or conserved microbe-associated molecular patterns (MAMPs). Among the known MAMPs are proteins/peptides such as flagellin (active epitope flg22), elongation factor thermo unstable (EF-Tu, active epitope elf18), enigmatic MAMP of *Xanthomonas* (eMax), necrosis and ethylene-inducing peptide 1-like proteins (NLPs) or polygalacturonases, as well as peptidoglycan, chitin (active epitope chi7) or a medium-chain 3-hydroxy fatty acid metabolite (active epitope (R)-3-hydroxydecanoic acid), and there are likely many others (Gómez-Gómez & Boller, 2000; Kunze *et al*, 2004; Kaku *et al*, 2006; Gust *et al*, 2007; Yamaguchi *et al*, 2010; Bartels *et al*, 2013; Jehle *et al*, 2013; Albert *et al*, 2015; Kutschera *et al*, 2019; Lee *et al*, 2021). DAMPs such as plant elicitor peptide 1 (Pep1) from *Arabidopsis thaliana* are endogenous signals generated by plants in response to biotic and abiotic stress (Boller & Felix, 2009; Chuberre *et al*, 2018; Rzemieniewski & Stegmann, 2022). Any MAMP or DAMP is recognised by specific pattern recognition receptors (PRRs) at the plasma membrane, which are receptor-like kinases (RLKs) or receptor-like proteins (RLPs). As reported for leaves, the PRRs FLAGELLIN SENSING 2 (FLS2), and PEP1 RECEPTORS PEPR1 and PEPR2 are expressed in roots and recognise flg22 or Pep1, respectively (Robatzek *et al*, 2006; Millet *et al*, 2010; Yamaguchi *et al*, 2010; Jacobs *et al*, 2011; Bartels *et al*, 2013; Wu *et al*, 2016). Upon pattern recognition and independently of immune signals from the shoot, complex downstream signalling processes are activated in roots, including a reactive oxygen species (ROS) burst and MITOGEN-ACTIVATED PROTEIN KINASE (MAPK or MPK) phosphorylation, which initiate a diversity of immune

pathways that synergistically or autonomously activate transcriptional regulators to prompt a broad range of immune responses (Boudsocq *et al*, 2010; Jeworutzki *et al*, 2010; Jacobs *et al*, 2011; Beck *et al*, 2014; Wyrsh *et al*, 2015; Birkenbihl *et al*, 2017; Poncini *et al*, 2017; Yu *et al*, 2017; Rich-Griffin *et al*, 2020; Zhou & Zhang, 2020). Wounding, as observed at lateral root initiation sites or upon pathogen attack, can further boost PTI to protect those root cells from pathogen colonisation (Zhou *et al*, 2020). In the process of microbe recognition, the root immune system equally responds to pathogenic and beneficial microbes and triggers immune responses that limit or prevent their colonisation success (Jacobs *et al*, 2011; Pel & Pieterse, 2013; Gourion *et al*, 2015; Stringlis *et al*, 2018; Fröschel *et al*, 2021). Importantly, recent studies indicated cell type-specificity of root PTI. The ability of each root cell to activate a PTI response that is specific for each cell type might add to the robustness and thus effectiveness of root immunity (Rich-Griffin *et al*, 2020). This concept of cell type-specific PTI responses is based on a strict organisation of the root body plan that essentially determines the diversity of root functions.

Root body plan is driven by cell identity

Plant roots are structurally and functionally complex organs. We mainly refer to the roots of the model plant *Arabidopsis*, whose development and structure have been well described but may not always reflect the even higher complexity of the ones in other plant species. In longitudinal direction, the primary root is organised in root apical meristem (RAM), elongation zone (EZ) and differentiation zone (DZ) (Fig 1; Brady *et al*, 2007; Salvi *et al*, 2020). At the very tip of the root (apical meristem), the root cap facilitates soil penetration and guides the direction of growth through the perception of gravity. The root cap also functions as an environmental sensor and protects the meristematic stem cell niche from damage (Kumpf & Nowack, 2015). The stem cell niche, a group of undifferentiated mitotically active stem cells (or initials), which is arranged around rarely dividing quiescent centre (QC) cells at the base of the RAM, is the root organising centre from which all root tissues derive (Clowes, 1953; Dolan *et al*, 1993; van den Berg *et al*, 1997; Aichinger *et al*, 2012; de Luis Balaguer *et al*, 2017; Pardal & Heidstra, 2021). Cells that emerge from the stem cell niche subsequently divide in the RAM and then increase in length while passing through the EZ. Subsequently, cells differentiate and obtain specific genetically predestined functions. Emerging root hairs, for example, mark the beginning of the DZ (Datta *et al*, 2011; Topp & Benfey, 2012). The basis for the formation of lateral roots is also already being established when cells pass the RAM and EZ before they eventually emerge in the DZ (Laskowski & ten Tusscher, 2017; Banda *et al*, 2019). Based on their specific transcriptional signatures, 15 different cell types with presumably different biological functions can be distinguished in *Arabidopsis* roots (Birnbaum *et al*, 2003; Brady *et al*, 2007). Epidermis, cortex, endodermis and the pericycle around the vascular tissue (stele) are major cell types, which emerge from the stem cell niche and form cell files that appear as concentric rings in root cross-sections (Benfey & Scheres, 2000). Together with the root cap they form the core root body (Dolan *et al*, 1993; Birnbaum, 2016) (Fig 1). The stem cell niche determines this pattern of cell types as concentric files (Dolan *et al*, 1993; van den Berg

et al., 1997; Pardal & Heidstra, 2021). In addition to root patterning, the stem cell niche functions in cell identity determination (Dinneny & Benfey, 2008). Stem cell divisions produce one cell with stem cell identity and a daughter cell that obtains cell type-specific identity depending on the position in the stem cell niche: Stem cells proximal to the QC found the stele in the centre of the root, which consists of the primary vascular tissues, procambium and pericycle (Brady *et al.*, 2007; Tomescu, 2021). The ground tissue initials next to the stele initials generate two tissues, namely cortex and endodermis, following asymmetric cell divisions (Cruz-Ramírez *et al.*, 2012; Pardal & Heidstra, 2021). Casparian strip cell wall impregnations and suberin depositions are hallmarks of apoplastic diffusion barrier formation during endodermis differentiation (Geldner, 2013; Barberon & Geldner, 2014). In Arabidopsis and other plant species, epidermis and lateral root cap cells also emerge from the same initials surrounding the QC through an asymmetric periclinal division followed by anticlinal divisions (Pardal & Heidstra, 2021). Lateral root cap cells differentiate into secretory cells (Arnaud *et al.*, 2010; Kumpf & Nowack, 2015). The differentiated epidermis of Arabidopsis roots consists of alternating files of root hair and non-hair cells. This pattern of alternating cell types depends upon their position relative to the underlying cortex cells: Root hair-forming trichoblasts sit on the gap between two adjacent cortex cells, while non-hair-forming atrichoblasts develop over a single cortical cell (Datta *et al.*, 2011). Finally, columella cells derive from asymmetric anticlinal divisions of columella initials, which are located distally of the QC. Differentiating columella cells start to accumulate starch in amyloplasts immediately after the division of the columella stem cells and later undergo significant cytological changes when they transition into secretory cells (Arnaud *et al.*, 2010; Kumpf & Nowack, 2015).

The formation, maintenance and consequently the specific function of each cell type are determined by cell identity regulators that, in general, are transcription factors (TFs) (Dolan *et al.*, 1993; Moreno-Risueno *et al.*, 2015; Shahan *et al.*, 2021). Most of what is known about root patterning comes from studies in Arabidopsis. Recent comparative analyses of root cell type atlases in tomato, rice and Arabidopsis have revealed functional conservation (especially in the root meristem) but also considerable divergence of transcriptional regulation in cell type-specific development, indicating limitations of translatability of single species analyses (Kajala *et al.*, 2021). Cell identity TFs implement the root body plan that provides an organisational frame in which each root cell type fulfils a defined function, which is the basis for the multifunctionality and functional plasticity of roots. The root cap facilitates and guides gravitropic root growth into the soil. At the same time, it protects the stem cell niche and meristem from physical damage and infection by potentially pathogenic microbes (Iijima *et al.*, 2008; Arnaud *et al.*, 2010; Kumpf & Nowack, 2015; Kumar & Iyer-Pascuzzi, 2020; Driouich *et al.*, 2021). Directional growth through the soil requires the perception and processing of various environmental cues such as gravity, physical obstacles, water and nutrient availability (Arnaud *et al.*, 2010; Kumar & Iyer-Pascuzzi, 2020). Cells in the columella sense gravity with the help of sedimentation of starch-filled amyloplasts and then trigger an auxin-related growth response in the EZ (Su *et al.*, 2017). The root cap may also sense touch stimulation and moisture gradients (Massa & Gilroy, 2003; Dietrich *et al.*, 2017; Dietrich, 2018). Besides the epidermis, root cap cells take up a considerable amount of phosphate (Kanno *et al.*, 2016).

Soil penetration is facilitated by the production of polysaccharide-containing mucilage by secretory cells in the lateral root cap and the continuous shedding of border cells from the outermost layer of the root cap (Iijima *et al.*, 2008; Arnaud *et al.*, 2010; Kumar & Iyer-Pascuzzi, 2020; Driouich *et al.*, 2021). Besides this, root cap exudates promote nutrient availability (Iijima *et al.*, 2008). Epidermis and especially root hair cells provide an extended surface, which is crucial for water and selective nutrient uptake (Gilroy & Jones, 2000; Datta *et al.*, 2011; Geldner, 2013; Barberon & Geldner, 2014; Salazar-Henao *et al.*, 2016). Cortex cells participate in the symplastic transport of water and nutrients towards the vasculature (Geldner, 2013; Barberon & Geldner, 2014). A function of cortex cells in sensing water potential gradients in the soil has been proposed recently (Dietrich *et al.*, 2017). Due to the presence of the primary wall-impregnating Casparian strip, the endodermis functions as an apoplastic diffusion barrier, which ensures selective nutrient uptake into the vasculature (Geldner, 2013; Robbins *et al.*, 2014). Pericycle cells encompass the vascular tissue and can be subdivided into xylem pole and phloem pole pericycle cells. Some pericycle cells maintain mitotic competence for lateral root initiation. Pericycle cells also function in xylem loading and phloem unloading (Beckman & De Smet, 2014; Tegeder & Hammes, 2018). The xylem functions in the root-to-shoot transport of water and nutrients but also of long-distance signalling molecules such as hormones, small peptides and proteins. By contrast, the phloem mediates the transport of photosynthates and nitrogen compounds (e.g. amino acids) from source to sink tissues (Notaguchi & Okamoto, 2015; Shabala *et al.*, 2016; Augstein & Carlsbecker, 2018; Koenig & Hoffmann-Benning, 2020; Sakakibara, 2021). The strict organisation of the root is a prerequisite to accurately fulfill its multiple functions. However, root morphology displays a certain degree of plasticity based on the interference with cell identity TFs and networks.

Microbes alter fundamental root development processes for accommodation

The phenotypic and functional plasticity helps roots to adjust their morphology as part of the adaptation to changing environments (Hodge, 2004; de Jong & Leyser, 2012; Gifford *et al.*, 2013; Gaillochet & Lohmann, 2015). This plasticity can further be exploited by microbes. Some members of the root microbiota can alter root morphology and/or function considerably, which may further impinge on root system architecture (Verbon & Liberman, 2016). Such morphological changes are based on microbial reprogramming of fundamental plant developmental pathways and indicate the potential for phenotypic plasticity even of older, differentiated root cells and tissue (e.g. see nodule organogenesis below). They are often associated with altered plant TF activities and involve cell cycle genes, suggesting that reprogramming of fundamental transcriptional networks is highly essential (Crespi & Frugier, 2008; Ichihashi *et al.*, 2020; Kawa & Brady, 2022; Yang *et al.*, 2022). However, with a few exceptions, underlying mechanisms are still poorly understood. Only recently, plant-associated microbes have been shown to be able to alter endodermal suberin depositions likely by repressing an abscisic acid (ABA)-dependent transcriptional network controlling root barrier functions (Salas-González *et al.*, 2021). A well-studied system to show morphological changes in roots involves the

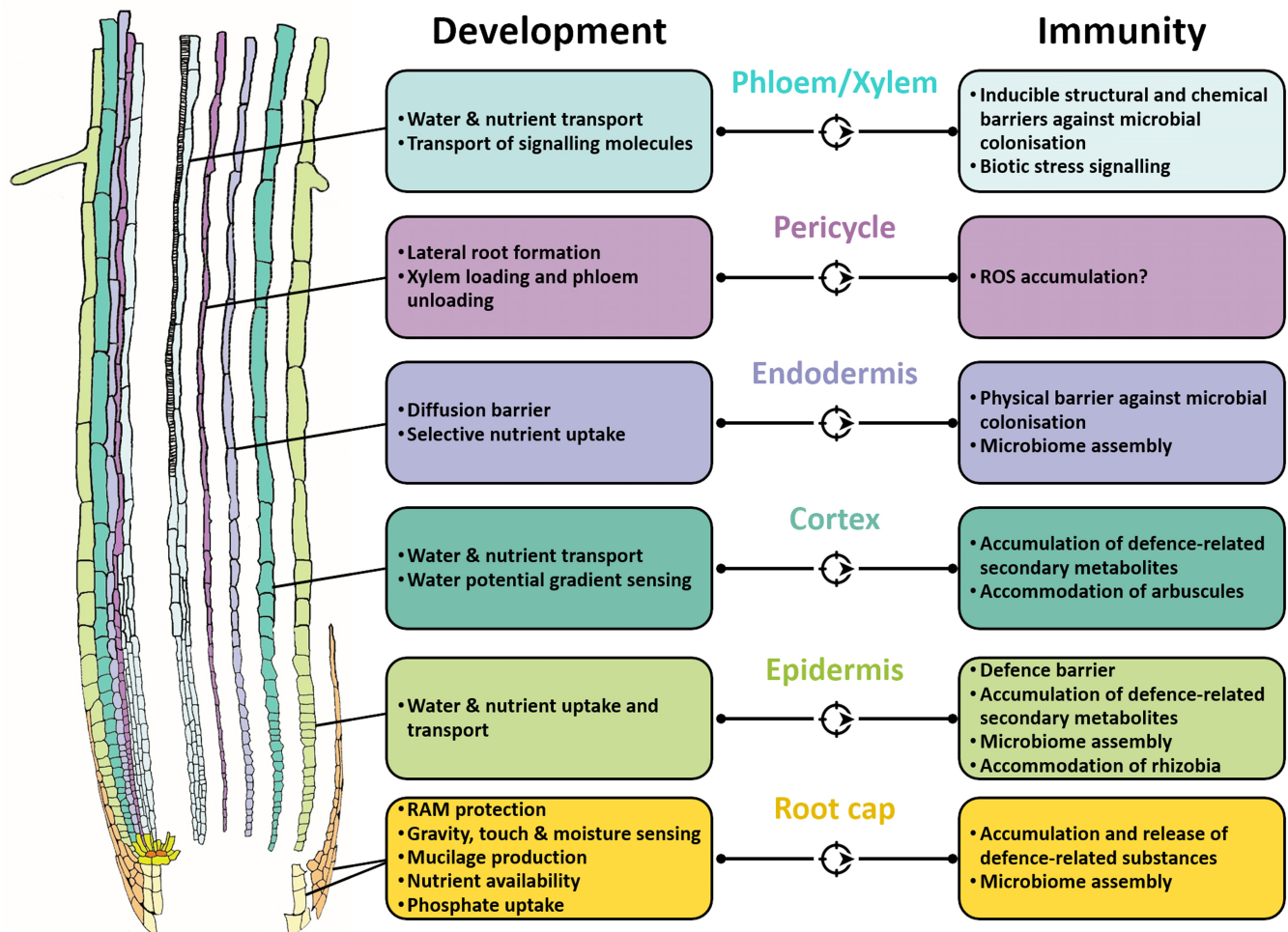


Figure 1. Functions of specific root cell types in plant development and immune responses to (pathogenic) microbes.

The plant root body plan follows a strict cell type-based organisation that determines the root's structure and equips it with functional plasticity to respond to changing environments. Consequently, each cell type fulfils specific tasks during plant development and in interaction with beneficial or pathogenic microbes. The outermost cell types, i.e. epidermis and root cap, promote nutrient availability and uptake in and from the soil. All cell types participate in the transport of water and/or nutrients towards the vasculature. Some root cell types have additional specific functions, e.g. in sensing physical stimuli during growth (root cap cells), lateral root formation (pericycle) or shootward transport of signalling molecules (phloem). Cell types such as the root cap, epidermis, cortex, endodermis and xylem produce various defence-related substances or establish physical barriers to fend off or prevent the spread of potentially harmful microbial intruders. Besides this, root cap, epidermis and endodermis can affect the assembly of the root microbiome, e.g. by altering the nutrient composition in the rhizosphere. In addition, root hair and cortex cells can accommodate beneficial rhizobia, endophytes or mycorrhizal fungi, respectively. See text for references.

bacterial pathogen *Rhizobium rhizogenes* (formerly *Agrobacterium rhizogenes*). *R. rhizogenes* changes plant organ morphology (Veena & Taylor, 2007; Bourras et al, 2015), known as hairy root disease, by integrating a part of a root-inducing plasmid containing so-called *root oncogenic loci* genes into the host cell genome. The expression of *root oncogenic loci* genes leads to the formation of new roots as a disease phenotype (Veena & Taylor, 2007; Hooykaas & Hooykaas, 2021), which involves induced expression of *KNOTTED1-LIKE HOMEBOX (KNOX)* TFs and cell cycle regulator genes in the host plant (Stieger et al, 2004). KNOX TFs are known to participate in meristem maintenance and organ patterning (Hake et al, 2004). Hairy root formation may thus employ regulatory mechanisms of host cell dedifferentiation and propagation (Stieger et al, 2004). Beneficial plant growth-promoting bacteria (e.g. *Bacillus* spp.,

Pseudomonas spp.) or fungi (e.g. *Trichoderma* spp.) can increase primary and/or lateral root length, or promote the formation of lateral roots or root hairs, thus rendering root systems more efficient and supporting shoot growth especially under unfavourable conditions (Lugtenberg & Kamilova, 2009; Glick, 2012; Vacheron et al, 2013; Yadav et al, 2017). In addition to rewiring transcriptional networks, altering root system architecture often involves changes in endogenous levels of growth-related plant hormones, microbial production of phytohormones or hormone mimic strategies (Sukumar et al, 2013; Ludwig-Müller, 2020; Eichmann et al, 2021). The cellular reprogramming during root nodule organogenesis in legumes by N-fixing rhizobia under nitrogen limitation involves host cell manipulations at different levels. Besides plant hormones (particularly cytokinins and auxin), the process employs

transcriptional networks and regulatory components of the plant's endogenous developmental programme (Crespi & Frugier, 2008; de Zélicourt et al, 2012; Ichihashi et al, 2020; Lin et al, 2020; Yang et al, 2022). Upon bacterial attachment to the root and perception of bacteria-derived Nod factors through Nod factor receptors, colonised young root hairs curl, cortical cells start to divide to form a nodule primordium, and a plant-derived infection thread is established, which allows the bacteria to invade the developing nodule (Oldroyd et al, 2011). In certain legumes (e.g. *Medicago truncatula*), the growing primordia establish and retain an apical meristem that ensures indeterminate growth. Following division in the meristematic zone of such indeterminate nodules, cells redifferentiate and obtain new identities and functions to support bacterial accommodation and nitrogen fixation (Crespi & Frugier, 2008; de Zélicourt et al, 2012). Accumulating evidence suggests that nodule organogenesis shows some overlap with regulatory processes and transcriptional networks in (lateral) root formation (Bishopp & Bennett, 2019; Ichihashi et al, 2020; Soyano et al, 2021; Yang et al, 2022). Interestingly, the TFs *WUSCHEL-RELATED HOMEBOX 5 (WOX5)* and *PLETHORA (PLT) 1–4*, which function as cell identity regulators and determine fundamental processes in root patterning (Aida et al, 2004; Sarkar et al, 2007; Burkart et al, 2022), are expressed in nodule primordia and/or meristems and are required for nodule meristem maintenance in *M. truncatula* (Franssen et al, 2015). In addition, the TF *LATERAL ORGAN BOUNDARIES DOMAIN 16 (LBD16)*, which promotes pericycle cell divisions during lateral root development, is also a key regulator of cortical cell divisions during nodule organogenesis (Schiessl et al, 2019; Soyano et al, 2019). While LBD16 is usually expressed in lateral root primordia in the pericycle, the TF *NODULE INCEPTION 1 (NIN1)* cytokinin-dependently induces expression of LBD16 also in cortical nodule primordia, where it regulates cell divisions in collaboration with the NIN1 target *NUCLEAR FACTOR-Y (NF-Y)*. Conversely, ectopic expression of the nodulation genes *NIN1* or *NF-Y* can induce cell divisions in lateral root primordia in the pericycle (Soyano et al, 2013, 2019). In a similar way, NIN1 may control a *SCARECROW (SCR)-SHORTROOT (SHR)* module that, unlike the one in *Arabidopsis* (see below), is present in cortex cells of legume plants (Dong et al, 2021; Yang et al, 2022). In response to rhizobial signals, this SCR-SHR module can initiate cortical cell divisions during nodule primordia formation and is required for nodule organogenesis (Dong et al, 2021). These studies show that changes in spatial regulation of development-related transcriptional networks may be critical to initiate de novo organ development (Bishopp & Bennett, 2019). This indicates the ability of microbes to rearrange fundamental processes of plant development as a prerequisite for successful plant colonisation. In addition, it visualises root developmental processes and morphological traits that support root resilience under unfavourable or even harmful environments.

Concept of cell identity in the regulation of immunity

While microbes are able to interfere with central root cell identity regulators, cell identity networks have been shown to be connected with stress-adaptive plant signalling (Dinneny et al, 2008; Iyer-Pascuzzi et al, 2011; Rich-Griffin et al, 2020). In terms of immunity, it is important to distinguish between preformed and inducible

mechanisms. The former ranges from structural (e.g. cell walls) to metabolic mechanisms (e.g. phytoanticipins) and can greatly vary in different root cell types. The cell wall of the endodermis, for instance, is an unbreachable barrier for a number of pathogens because of its fortification with suberin and lignin (Robbins et al, 2014; Fröschel et al, 2021). Inducible mechanisms, in turn, encompass what is generally defined as PTI. For roots, it is worth noting that PTI perception and initial core immune signalling cascades are present and functional in different root cell types, and that the intensity of the cell type-specific immune responses does not depend on the level of PRR expression (Wyrsh et al, 2015; Poncini et al, 2017). However, the downstream transcriptionally regulated immunity gene networks significantly differ between cell types resulting in cell type-specific immunity (Rich-Griffin et al, 2020; Fröschel et al, 2021). This cell type-specificity of immunity enables each cell type to ultimately launch different immune responses. While fundamental developmental processes apparently take a key role in cell type-specific immunity, it remains unclear at which stage in the signalling cascade PTI diversifies between cell types and which regulatory principles determine cell type-specific immunity (Box 1).

Studies over the last decade have revised models that separate PTI and developmental signalling. Instead, by connecting with development, PTI can immediately recruit developmental metabolism and incorporate metabolic dynamics in order to install a diverse and, thus, highly effective immune momentum (Rich-Griffin et al, 2020). Cell identity TFs might be of central importance as they control cell identity networks that specify the root body plan and root functionality. Consistent with this, cell type-specific immunity networks were found to be tightly connected with cell identity networks (Fig 2A; Rich-Griffin et al, 2020). By determining cell (type) identities and cell differentiation (Brady et al, 2007; Drapek et al, 2017; Pardal & Heidstra, 2021; Shahan et al, 2022), cell identity TFs mastermind root development by regulating and coordinating cell type-specific functions (Sozzani et al, 2010; Cruz-Ramírez et al, 2012; Long et al, 2015). Plants lacking respective cell identity TFs show an irregular root body with cell types missing, supernumerous or altered in their function (Di Laurenzio et al, 1996; Helariutta et al, 2000; Drapek et al, 2018). In addition to the formation and fate specification of cell types at the stem cell niche, a second important function of cell identity TFs is the maintenance of cell

Box 1. In need of answers

- Which regulatory principles determine cell type-specific immunity?
- To what extent do the developmental cell age and differentiation affect cell type-specific immunity signalling?
- Which cell identity transcription factors participate in cell type-specific immune responses?
- How conserved is the regulation of cell type-specific immune responses in different plant species?
- Does the type and/or composition of pattern recognition receptor complexes affect growth-immunity trade-offs?
- How does immune signalling interfere with the cell cycle or other fundamental growth regulatory processes?
- Can growth-immunity trade-offs be genetically uncoupled?

(type) identities throughout their life (Moreno-Risueno *et al*, 2015; Drapek *et al*, 2018). This means that the stem cell-defined identity needs to be maintained to preserve the root body plan. For instance, the formation of cortex and endodermis cells requires the GRAS family TFs SCR and SHR in close interaction with the BIRD/INDETERMINATE DOMAIN (IDD) C2H2 TF family (Long *et al*, 2017). In cortex cells, SCR is the master regulator of gene networks that maintain identity, which is supported by its interaction with the BIRDS IDD4/IMPERIAL EAGLE (IME), IDD8/NUTCRACKER and IDD10/JACKDAW (Moreno-Risueno *et al*, 2015). SHR, in turn, activates SCR and the TF MYB DOMAIN PROTEIN 36 (MYB36) to maintain the identity of endodermis cells (Lieberman *et al*, 2015; Drapek *et al*, 2018). Consistently, ectopic expression of SHR in the Arabidopsis root epidermis results in an additional subepidermal cell layer with endodermis identity (Drapek *et al*, 2018). Atrichoblast differentiation is regulated by a complex consisting of the MYB TFs WEREWOLF (WER) and MYB23, the basic helix–loop–helix (bHLH) TFs GLABRA3 (GL3), EGL3 and MYC1, and the WD40-repeat TF TRANSPARENT TESTA GLABRA 1 (TTG1). The WER-bHLH-TTG complex directly regulates the homeodomain-leucine zipper TF GL2 to suppress the bHLH TF ROOT HAIR DEFECTIVE 6 (RHD6) and to induce MYB23, CAPRICE (CPC), TRYPTICHON (TRY) and ENHANCER OF TRY AND CPC (ETC1). CPC, TRY and ETC1 move to trichoblasts to regulate their differentiation with RHD6 as key TF acting upstream of RHD6-LIKE 4 (bHLH54), bHLH66 and bHLH82 (Bruex *et al*, 2012; Schiefelbein *et al*, 2014).

By overseeing the concerted regulation of cell type-specific gene networks, the functional concept of cell identity TFs is to form, maintain and differentiate cell types (Brady *et al*, 2007). This concept further supports the functional plasticity of roots. It enables roots to effectively adapt to changing environments, e.g. microbial challenge, based on the differential contribution of each cell type (Dinneny *et al*, 2008; Iyer-Pascuzzi *et al*, 2011). For almost all major root cell types, a function in root–microbe interactions and/or root immunity can be assigned (Fig 1). Root cap cells exude organic substances such as carbohydrates, amino and organic acids (Iijima *et al*, 2008). Such root exudates may shape the composition of the rhizosphere microbiome (Vives-Peris *et al*, 2020). The root cap and border cells, in particular, are thought to contribute to plant defence by releasing extracellular DNA, as well as antimicrobial peptides and metabolites into the soil (De Coninck *et al*, 2015; Hawes *et al*, 2016; Kumar & Iyer-Pascuzzi, 2020; Driouich *et al*, 2021). This is supported by the finding that columella cells accumulate defence-related indole glucosinolates (in *Brassica* species) and flavonoids (Hassan & Mathesius, 2012; Moussaieff *et al*, 2013). The epidermis as the outermost cell file serves as an important interface for the regulation of interactions with microbes in the rhizosphere. It constitutes a defence barrier against potential pathogens but is also important for the bilateral communication with beneficial microbes, e.g. nodule-forming rhizobia (Dolan *et al*, 1993; Datta *et al*, 2011; Hassan & Mathesius, 2012; Salazar-Henao *et al*, 2016). Interestingly, the cell type-specific analysis of defence-related gene expression in Arabidopsis trichoblasts versus atrichoblasts suggests a more important role for trichoblasts in immunity activation, at least in response to the beneficial rhizobacterium *Pseudomonas simiae* WCS417 (preprint: Verbon *et al*, 2022). Epidermis cells accumulate secondary metabolites such as dipeptides and flavonoids and regulate soil nutrient availability and microbiome composition through the exudation of organic

compounds (Saslowky & Winkel-Shirley, 2001; Badri & Vivanco, 2009; Datta *et al*, 2011; Hassan & Mathesius, 2012; Moussaieff *et al*, 2013). Cortex cells also accumulate defence- and abiotic stress-related secondary metabolites such as aliphatic glucosinolates (in *Brassica* species), flavonoids and other phenylpropanoids and are involved in biotic and abiotic stress responses (Saslowky & Winkel-Shirley, 2001; Hassan & Mathesius, 2012; Moussaieff *et al*, 2013). In addition, cortex cells of certain plant species allow for the accommodation of arbuscules and subsequent nutrient exchange in the mutualistic interaction with arbuscular mycorrhizal fungi (Lanfranco *et al*, 2018). The suberin-containing endodermis cell layer can physically prevent pathogens from entering into the vascular stele and even limit root colonisation by beneficial microbes (Geldner, 2013; Robbins *et al*, 2014; Fröschel *et al*, 2021; preprint: Verbon *et al*, 2022). Recent findings indicate the endodermis-specific synthesis of certain phenylpropanoid metabolites required for Casparian strip formation and suberin deposition in this cell type. This compartmentalised metabolite production might support fast adjustments to barrier formation when required (Andersen *et al*, 2021). It is conceivable that compartmentalised production of specific phenylpropanoid metabolites might support the generation of defence-related compounds as part of a cell type-specific immune responses as well. Interestingly, alterations in endodermal diffusion barrier functions affect plant microbiome compositions, and, vice versa, microbes can change Casparian strip and suberin depositions and thus plant mineral nutrient homeostasis. This renders the endodermis a potential regulatory hub for microbiome assembly in connection with the nutrient acquisition (Salas-González *et al*, 2021; preprint: Verbon *et al*, 2022). It has to be noted, that Casparian strip formation and suberin deposition in the endodermis occur in distinct developmental root zones (e.g. Andersen *et al*, 2021), adding spatiotemporal complexity to immunity regulation in this specific cell type, which has not yet been addressed experimentally, especially in the context of immunity. Pericycle cells can accumulate high levels of ROS, e.g. during lateral root development or salt stress (Jiang *et al*, 2012; Manzano *et al*, 2014). If ROS accumulation in the pericycle plays a role in root–microbe interactions remains to be shown. In xylem vessels, inducible structural and chemical barriers such as tyloses, or depositions of gels, lignins, suberins and callose can prevent both, vertical and horizontal spread of vascular pathogens (Kashyap *et al*, 2021). The phloem mediates the transport of molecules for long-distance signalling during development or biotic and abiotic stress responses, e.g. hormones, lipids, peptides and nucleic acids (Notaguchi & Okamoto, 2015; Shabala *et al*, 2016; Augstein & Carlsbecker, 2018; Koenig & Hoffmann-Benning, 2020; Sakakibara, 2021).

By connecting cell type identity networks with PTI (Fig 2A), each cell type can access and incorporate developmental processes to launch PTI responses according to its functional identity (Fig 2B; Rich-Griffin *et al*, 2020; Kawa & Brady, 2022). Based on our recent findings, developmental/cell identity TFs and immunity-associated TFs form pairs to bind to promoters of immunity genes and to regulate them in a cell type-specific manner (Fig 3; Rich-Griffin *et al*, 2020). This cell identity-coupled regulatory system, which diversifies and invigorates overall root immunity, allows cell types to respond with high plasticity and to act jointly to adjust immune responses to attacking pathogens (Rich-Griffin *et al*, 2020; Fröschel *et al*, 2021). This might further explain why the intensity of PTI

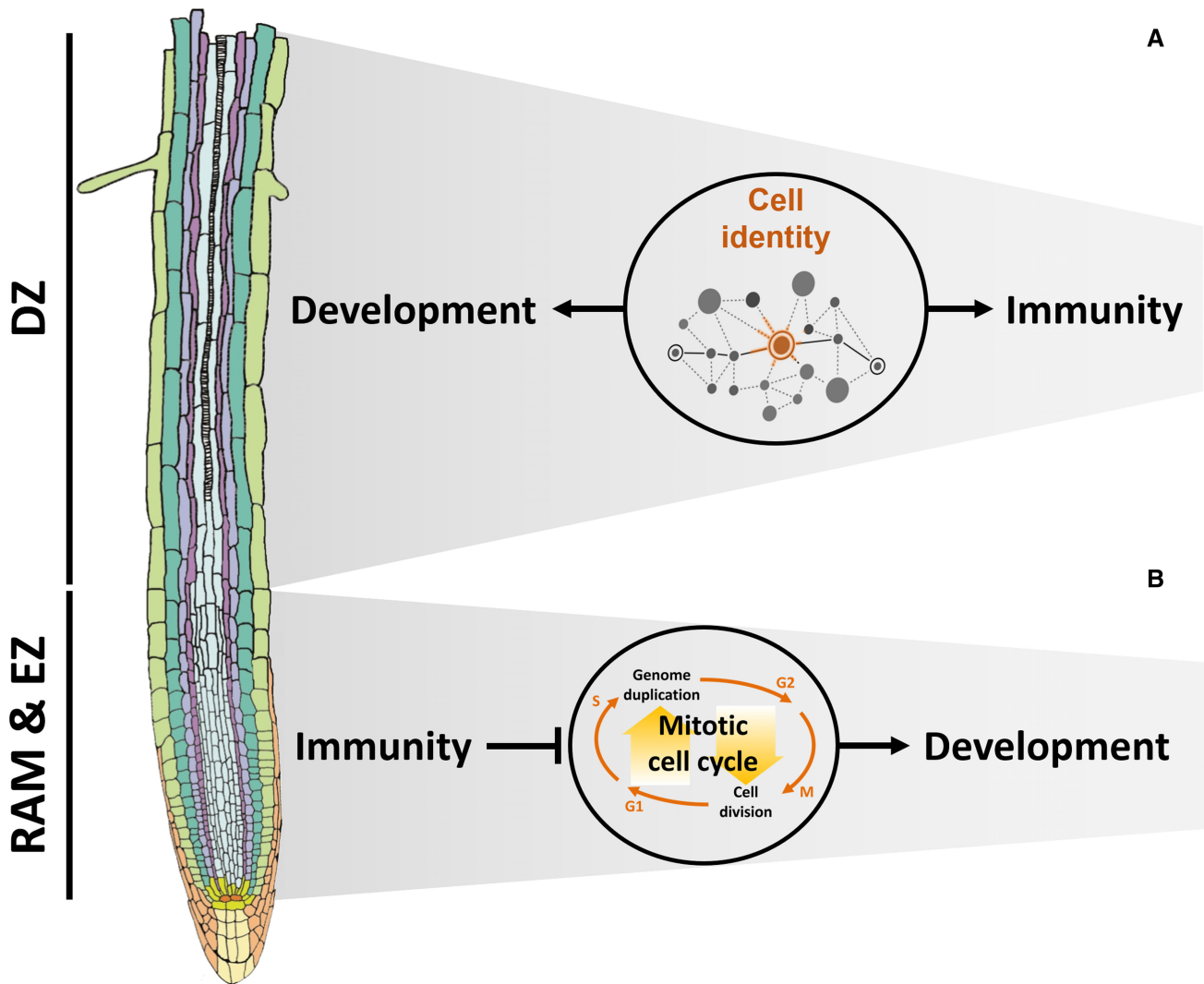


Figure 2. Development- and immunity-related signalling processes are interconnected.

(A) In mature cells in the differentiation zone (DZ), cell identity TFs (in orange) regulate gene networks that determine cell type-specific functions in root development and immune responses to (pathogenic) microbes. This cell type-specific interconnection of development with immune responses results in a highly versatile, and thus robust, overall root immunity. (B) Immunity interferes with developmental signalling and inhibits growth in younger, mitotically active cells of the root apical meristem (RAM) and elongation zone (EZ), e.g. via negatively regulating the activity of the cell cycle.

responses is highly cell type-dependent (Wyrsh *et al*, 2015; Emonet *et al*, 2021). The importance of cell identity TFs in immunity was shown for IDD4/IME, which coordinates the formation of cortex and endodermis cells from stem cells (Long *et al*, 2015; Moreno-Risueno *et al*, 2015). Upon flg22 treatment, IDD4/IME phosphorylation by MPK6 results in transcriptional reprogramming of gene networks. The respective phosphosite is conserved among IDD proteins and found to be phosphorylated under different conditions (Völz *et al*, 2019). In addition, the shoot stem cell regulator WUSCHEL (WUS) activates immunity upon viral attack to protect stem and nascent daughter cells from viral infection (Wu *et al*, 2020). Importantly, WUS belongs to the WOX TF family, which strongly suggests that this immune strategy is conserved in roots. This indicates that cell identity TFs, and thus fundamental

developmental networks, participate in and even sustain plant immunity against root diseases. Incorporating cell type-specific housekeeping functions via cell identity TFs would further represent a very cost-effective strategy to operate a highly diverse and robust immune system, where any given MAMP/DAMP activates divergent immune responses in different cell types. It would not be surprising that plants have evolved such a sophisticated (rather than static and uniform) immune system in roots, considering that the rhizosphere hosts many diverse beneficial microbes that roots depend on (e.g. for nutrient supply or defence priming), while roots are at the same time attractive sites for pathogen entry (Chuberre *et al*, 2018). It will be interesting to learn which (other) cell identity TFs participate in cell type-specific immune responses, and, given the potential species-specific divergence in cell type-specific transcriptional

regulation (Kajala *et al*, 2021), whether these findings can be translated to other plant species (Box 1). In addition, it is currently unclear whether the cell identity-immunity cross-talk takes place in cells of any developmental age or whether it is specific for differentiated cells (Box 1).

Effect of immunity on plant growth

As effective as it is to link development with immunity to stop pathogens, PTI itself can significantly impair plant growth, which can further influence reproductive processes and translate into crop

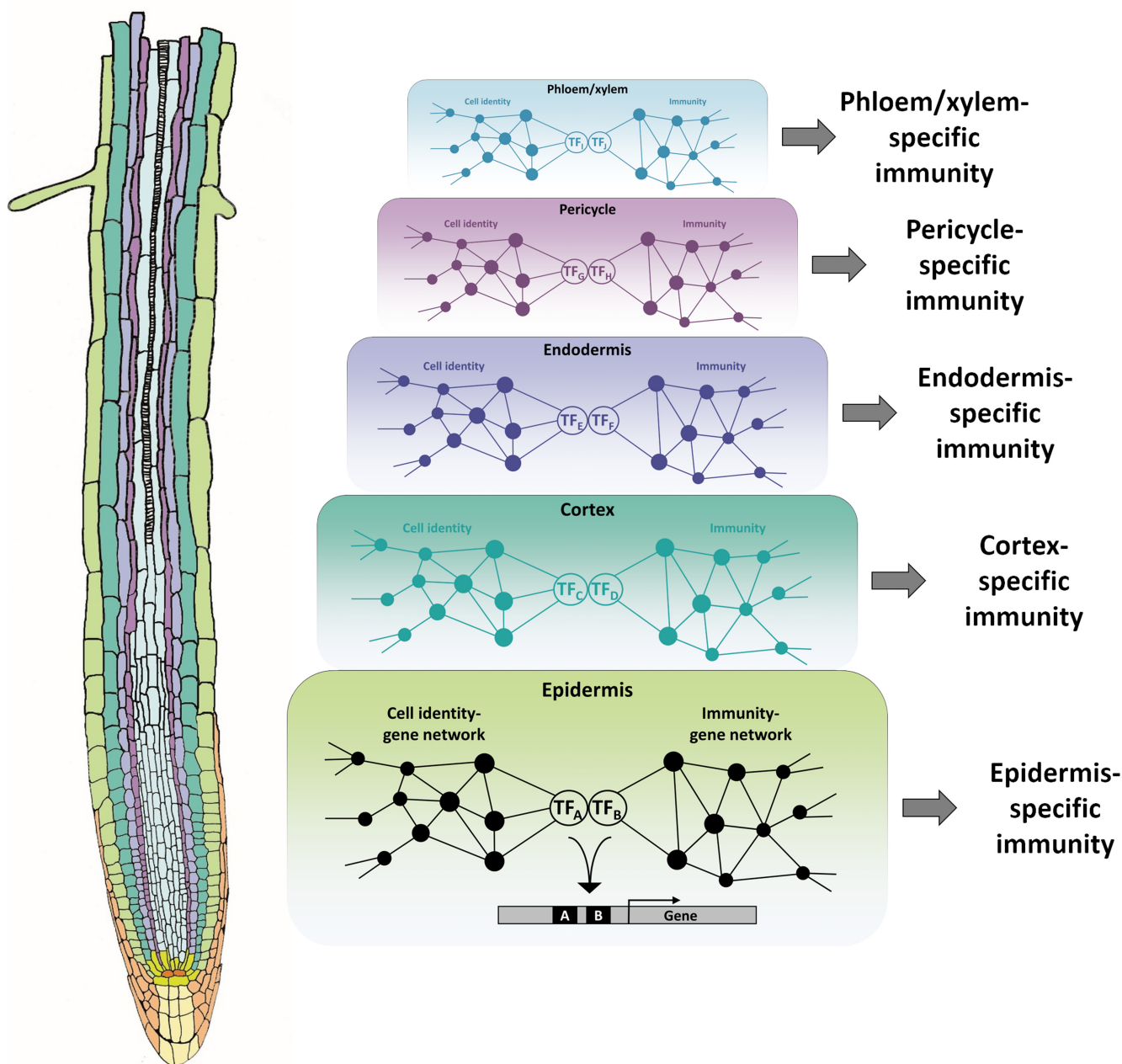


Figure 3. TFs connect cell identity and immunity gene networks to confer robust, cell type-specific immunity.

In the epidermis and other cell types, respective cell identity TFs pair up with immunity-associated TFs to regulate cell type-specific expression of immunity genes by binding to their promoters. This strategy allows the launch of cell type-specific immune responses according to the specific developmental functions of each cell type. The interconnection of development/cell identity with cell type-specific immunity gene networks diversifies the overall root immunity and may add to the robustness and adaptive plasticity of root responses to microbes under varying environments (compare Rich-Griffin *et al*, 2020).

yield decline (Huot *et al.*, 2014; Ning *et al.*, 2017). Growth-immunity trade-offs are best studied in Arabidopsis but occur in crops as well (Smedegaard-Petersen & Tolstrup, 1985). Since immunity and growth require a high amount of energy and other resources, it was hypothesised that growth-immunity trade-offs are the consequence of resource limitations and/or their imperfect reallocation. In such a model, plants would prioritise immunity over growth as cells and tissues may not be able to allocate sufficient resources to serve both processes at the same time (Herms & Mattson, 1992; Brown, 2003; Huot *et al.*, 2014; Monson *et al.*, 2022). Though resources might be limited under certain circumstances, the reallocation model might not be suitable to explain the phenomenon in general. While a range of MAMPs/DAMPs that are detected by RLK PRRs inhibit growth (e.g. flg22, elf18, Pep1), others such as chi7 or NLP (e.g. NLP20), which are ligands of RLP PRRs, do not (Böhm *et al.*, 2014; Poncini *et al.*, 2017; Pruitt *et al.*, 2021). It will be interesting to see whether the type of PRR or rather the composition of receptor complexes are determinants of growth-immunity trade-offs (Box 1).

The interactions of immunity and growth pathways are manifold. Only recently, it has been shown that the pathogen-responsively regulated long noncoding RNA salicylic acid (SA) biogenesis controller 1 (SABC1) balances plant immunity and growth by modifying the expression of a single TF, NAC DOMAIN CONTAINING PROTEIN 3 (Liu *et al.*, 2022). In addition, plant peptides with growth regulatory functions were shown to control immune responses. GOLVEN2, a member of a family of peptides also known as ROOT MERISTEM GROWTH FACTOR (RGFs) and, for example, perceived by the RGF1 INSENSITIVE 3 receptor, can increase PRR abundance and act as a positive regulator of PTI and antibacterial resistance in Arabidopsis leaves (Stegmann *et al.*, 2022). In a similar way, FERONIA (FER) and its RAPID ALKALINIZATION FACTOR (RALF) ligands are known to regulate plant growth, development and immune signalling pathways (Haruta *et al.*, 2014; Stegmann *et al.*, 2017; Xiao *et al.*, 2019; Zhang *et al.*, 2020).

Proteins long thought to have a principal function in immunity were later found to be important for growth and vice versa. Hence, the growth-immunity boundaries are fluent and an interdependency apparently exists, which is based on components shared by PTI and development-associated receptor complexes and signalling cascades. That growth penalties are dependent on the detection of specific MAMPs/DAMPs by PTI receptors, and the onset of respective PTI core signalling processes has been shown in Arabidopsis. For instance, flg22 or elf18-triggered growth inhibition in Arabidopsis was not detected in the PRR mutants *fls2* and *EF-Tu receptor (efr-1)*, respectively (Gómez-Gómez & Boller, 2000; Zipfel *et al.*, 2006; Jacobs *et al.*, 2011). BRASSINOSTEROID (BR) INSENSITIVE 1 (BRI1)-ASSOCIATED RECEPTOR KINASE (BAK1)/SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE 3 (SERK3) was among the first proteins shown to function as co-receptor of many PRRs, as well as of the growth-regulating BR receptor BRI1 (Li *et al.*, 2002; Chinchilla *et al.*, 2007). Later, downstream signalling components such as SUPPRESSOR OF BAK1-INTERACTING RECEPTOR-LIKE KINASE 1 1 (SOBIR1), RPM1-INDUCED PROTEIN KINASE (RIPK) or various MAPK family members were identified to contribute to growth-immunity trade-offs (Gao *et al.*, 2009; Du *et al.*, 2016; Li *et al.*, 2021; Sun & Zhang, 2022). Interestingly, BR pathway members are some sort of bi-functional constants in the PTI-development cross-talk. Besides BAK1, a number of other BR signalling proteins,

including BR-SIGNALLING KINASE 1 or BOTRYTIS-INDUCED KINASE 1, were found to be part of PTI signalling (Lin *et al.*, 2013; Shi *et al.*, 2013; Choi *et al.*, 2021), indicating a major role of BR in the regulation of PTI and growth-immunity trade-offs (Belkhadir *et al.*, 2012; Lozano-Durán & Zipfel, 2015; Ortiz-Morea *et al.*, 2020). Consistent with this, the TF HOMOLOGUE OF BEE2 INTERACTING WITH IBH 1 (HBI1) and BRASSINAZOLE RESISTANT 1 (BZR1) are activated downstream in the BR pathway to induce growth-related genes and suppress PTI genes, while flg22 inhibits HBI1 transcription (Lozano-Durán *et al.*, 2013; Fan *et al.*, 2014). HBI1 is a direct target of BZR1, and overexpression of HBI1 or constitutively active BZR1 impairs various PTI responses and PTI-induced growth inhibition, revealing a role of the BZR1-HBI1 module in the mediation of growth-immunity trade-offs. HBI1 also controls ROS homeostasis by differentially regulating the expression of genes involved in ROS production and detoxification (Neuser *et al.*, 2019). This and the observation that the ROS-responsive TF MYB30 regulates gene networks involved in both root growth and plant immunity (Mabuchi *et al.*, 2018), supports the notion that ROS might be one of the links in the growth-immunity cross-talk (Camejo *et al.*, 2016; Dwivedi *et al.*, 2021; Mase & Tsukagoshi, 2021).

In addition to BR, various other plant hormones participate in the regulation of growth-immunity trade-offs. A number of excellent publications exist on this highly complex field (Kazan & Manners, 2009; Denancé *et al.*, 2013; Huot *et al.*, 2014; Lozano-Durán & Zipfel, 2015; Smakowska *et al.*, 2016; Guo *et al.*, 2018), and therefore, we address this topic only briefly here. In terms of growth-immunity trade-offs, hormone signalling might merge at some focal points. For instance, HBI1 regulation is further affected by gibberellic acid (GA) and auxin (Fan *et al.*, 2014). If there is a pathogen threat, plant hormones might mediate a switch from a “growth mode” to a “defence mode” (Reitz *et al.*, 2015) as reported for plants facing salt stress (Geng *et al.*, 2013). For instance, the crucial defence hormone SA antagonises activities of the plant growth hormone auxin by suppressing auxin signalling genes (e.g. auxin receptors) and by interfering with auxin transporter protein activities in Arabidopsis (Wang *et al.*, 2007; Kazan & Manners, 2009; Tan *et al.*, 2020; Ke *et al.*, 2021). A cross-talk between GA-mediated growth and JA-mediated defence signalling pathways is thought to participate in balancing growth-immunity trade-offs (Yang *et al.*, 2012; Huot *et al.*, 2014; Smakowska *et al.*, 2016). DELLA proteins repress growth-related TFs unless they become degraded in the presence of growth-promoting GA. flg22 treatment suppresses GA-mediated DELLA degradation, which may cause the observed flg22-induced root growth inhibition (Navarro *et al.*, 2008; Huot *et al.*, 2014). Furthermore, infection with a bacterial pathogen can stabilise DELLA proteins in an SA-dependent manner. DELLA accumulation suppresses immune responses and a resulting negative feedback loop may fine-tune the growth-immunity balance (Li *et al.*, 2019). While these studies have identified genes and pathways involved in the regulation of growth-immunity trade-offs, it remains unclear which growth regulatory processes and respective proteins are targeted by PTI and hormone signalling, and how.

Root growth is based on mitotic cell division and cell elongation regulated by the mitotic cell cycle and the endocycle, respectively (Breuer *et al.*, 2014; Edgar *et al.*, 2014; Sablowski & Carnier Dor-nelas, 2014; Sablowski & Gutierrez, 2022). Therefore, growth-immunity trade-offs are likely related to immunity effects on

meristematic and thus developmentally young and undifferentiated cells and tissues. As in all eukaryotes, the plant cell cycle is composed of specific phases: the DNA synthesis phase, in which DNA is duplicated, and the mitotic phase, where the mitosis takes place. These phases are separated by gap phases (Dewitte & Murray, 2003). In order to protect genome integrity and its transmission to the next generations during cell division, the transition between the phases is tightly controlled by cell cycle regulators such as CYCLIN-DEPENDENT KINASES (CDKs) and CYCLINS (CYCs) (Blomme et al, 2014; Polyn et al, 2015). According to endogenous and exogenous changes, plants can regulate their cell cycle machinery (Rymen & Sugimoto, 2012; Pedroza-Garcia et al, 2022). This allows them to survive nonfavourable conditions. CDKs and CYCs are thought to play a role in regulating cell division rates in response to environmental stress (Carneiro et al, 2021). It is known that abiotic stress, for instance, may lead to growth inhibition in plants by direct or indirect interference with the cell cycle. Salt treatment leads to root growth inhibition in an ABA-dependent manner (Geng et al, 2013). Recently it was shown that salt stress reduces the accumulation of CDKs (e.g. CYCB1;1) and some CYCs (e.g. CYCA2;1) in Arabidopsis roots (West et al, 2004; Qi & Zhang, 2020; Carneiro et al, 2021). In a similar way, biotic stress might affect cell cycle regulators and thus cell division. For instance, infection of Arabidopsis with geminiviruses changes the expression of cell cycle regulators, and overexpressing *CYCD3;1* or the cell cycle-promoting *E2F TRANSCRIPTION FACTOR 3* strongly increases plant resistance against geminivirus attack (Ascencio-Ibáñez et al, 2008). Little is known about biotic stress and cell cycle cross-talk. Hormones certainly take part directly or indirectly in underlying regulatory mechanisms. DELLA proteins, for instance, promote CDKA- and CDKB-inhibitors (Achard et al, 2009; Reitz et al, 2015), which may indicate a role of the defence hormone JA by its known function in growth inhibition based on its ability to downregulate CDKA1 and CYCB1;1 (Chen et al, 2011; Qi & Zhang, 2020). Taken together, while we have a better understanding about upstream processes involved in the growth-immunity cross-talk, further studies are needed to understand why or how immune signalling is connected to the mitotic cell cycle and/or endocycle as fundamental growth regulatory processes (Box 1).

Conclusions

The versatility of root immunity results in robustness that is greatly dependent on its interconnection with developmental networks and regulators. Cell identity regulators, as masterminds of the functional identity of each cell type, might play the most critical role here. Intriguingly, these cell identity regulators are TFs, and by teaming up with immunity TFs, they connect developmental and immunity gene networks to translate a rather uniform, since cell type-unspecific, PTI signalling into the activation of cell type-specific immunity gene networks (Rich-Griffin et al, 2020). As a result, each cell type contributes its specific immune responses based on its developmentally determined functional capability (Fig 1). In this way, roots might be able to fine-tune their versatile interactions with a highly complex rhizosphere microbiome. The high level of polymorphism in MAMPs observed in microbes may indicate evolutionary paths to evade or even manipulate PTI signalling to facilitate

host susceptibility (Colaiani et al, 2021; Ma et al, 2021). Most importantly, the outcome of growth/development-immunity cross-talks differs depending on the developmental cell age. While the interconnection with development results in a highly versatile immunity in cell types of the root DZ, immunity most likely interferes with developmental signalling and inhibits growth in young cells of the RAM (Fig 2). In addition to MAMPs, a diversity of inducible DAMPs (also called phytochemicals) with a strong growth inhibitory activity have been identified in recent years (Hou et al, 2021; Rzemieniewski & Stegmann, 2022). Interestingly, not all MAMPs interfere with growth, raising the question of whether immunity-induced growth inhibition represents an evolutionary artefact or indicates cell cycle checkpoint activation as part of DNA damage control. It is, however, likely that immunity has to interfere with the cell cycle machinery as the principal regulator of root growth. With regard to breeding efforts towards highly resistant crop plants with unimpaired growth, it will be interesting to see, whether these growth-immunity trade-offs can eventually be uncoupled (Box 1).

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Author contributions

Ruth Eichmann: Conceptualization; visualization; writing – original draft; writing – review and editing. **Sim Üstüner:** Conceptualization; writing – original draft; writing – review and editing. **Patrick Schäfer:** Conceptualization; visualization; writing – original draft; writing – review and editing.

Disclosure and competing interests statement

The authors declare that they have no conflict of interest.

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