Review

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Arabinogalactan proteins in root–microbe interactions

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Arabinogalactan proteins (AGPs) are among the most intriguing sets of macromolecules, specific to plants, structurally complex, and found abundantly in all plant organs including roots, as well as in root exudates. AGPs have been implicated in several fundamental plant processes such as development and reproduction. Recently, they have emerged as interesting actors of root–microbe interactions in the rhizosphere. Indeed, recent findings indicate that AGPs play key roles at various levels of interaction between roots and soil-borne microbes, either beneficial or pathogenic. Therefore, the focus of this review is the role of AGPs in the interactions between root cells and microbes. Understanding this facet of AGP function will undoubtedly improve plant health and crop protection.

Arabinogalactan proteins

Arabinogalactan proteins (AGPs) are highly glycosylated members of the hydroxyproline-rich glycoprotein (HRGP) superfamily of plant cell wall proteins. The members of this family share common features, including their typical, but variable arabinogalactosylated glycomodules, and many other features associated with their protein and nucleic sequences such as the presence of numerous hydroxyproline (HyP)-based sites of *O*-glycosylation, the existence of many functional domains (often putative), or the possibility to be anchored to the plasma membrane via a glycosylphosphatidylinositol (GPI) anchor (Figure 1) [1–3]. Occurrence of AGPs in almost all root cell types including root hairs, epidermal and cortical cells has been reported in most (if not all) species studied so far (Table 1). In addition, root tips release large amounts of AGP-rich rhizodeposits in the soil, including living root border cells/border-like cells (BCs/BLCs) and mucilage-rich exudates [4–8]. The use of various anti-AGP antibodies [9,10] and immunomicroscopy has established that AGPs are differentially distributed and developmentally regulated in root tissues (Table 1 and references therein). For example, JIM13-recognized epitopes have only been found in xylem and root cap cells/BLCs in developing *Arabidopsis* (*Arabidopsis thaliana*) roots [6,11], whereas JIM4 epitopes have been found associated with developing pericycle cells in carrot (*Daucus carota*) [10]. Examinations of AGP-associated glycans using analytical chemistry techniques have also highlighted the strong heterogeneity in the composition and structure of AGPs in roots (Table 1). The use of Yariv reagent, known to bind and selectively precipitate AGPs [12,13], has also facilitated many of these studies (Table 1). Finally, bioinformatics and molecular tools have confirmed heterogeneity of AGP expression in roots (Figure 2). Hence, the diversity of AGP structure and localization is likely to prelude the diversity of biological functions that AGPs play in root development and survival.

Indeed, the biological roles of AGPs in a wide range of physiological plant processes have attracted the attention of plant biologists for decades (see recent reviews in [14–17]) and are still the object of many exciting studies. Different possible modes of action of AGPs in general were proposed: AGPs were proposed to operate as soluble (and diffusible) signals which bind to a receptor. This mode of action is likely to occur during tracheary elements differentiation or during female gametogenesis [17–19]. The precise structural motif involved in such signaling is unknown but multiple studies suggest that whole AGPs or AGP-derived glycans are good candidates. Although not yet experimentally proven, receptor-like kinases (RLKs) and wall-associated kinases (WAKs) [17,20–22] were proposed to act as AGP receptors. Cleavage of GPI-anchored AGPs by phospholipases (C or D) also results in the release of the GPI anchor, which was also proposed to play a role in downstream signaling [23].

Comparatively, little, or discrete, attention has been given to the role of AGPs in plant–microbe interaction (PMI), particularly in roots, and between root cells and microbes. Root cell AGPs have recently emerged as interesting players of PMI. Indeed, many recent studies suggest that AGPs play a crucial role at several stages of PMI, including root colonization, repelling or attraction of soil microbes, and development of infection structures. Here, we review the role and some properties AGPs display in root cells and in root exudates which, directly or indirectly, may favor or inhibit root colonization by soil microbes and enhance the ability of plants to protect themselves against

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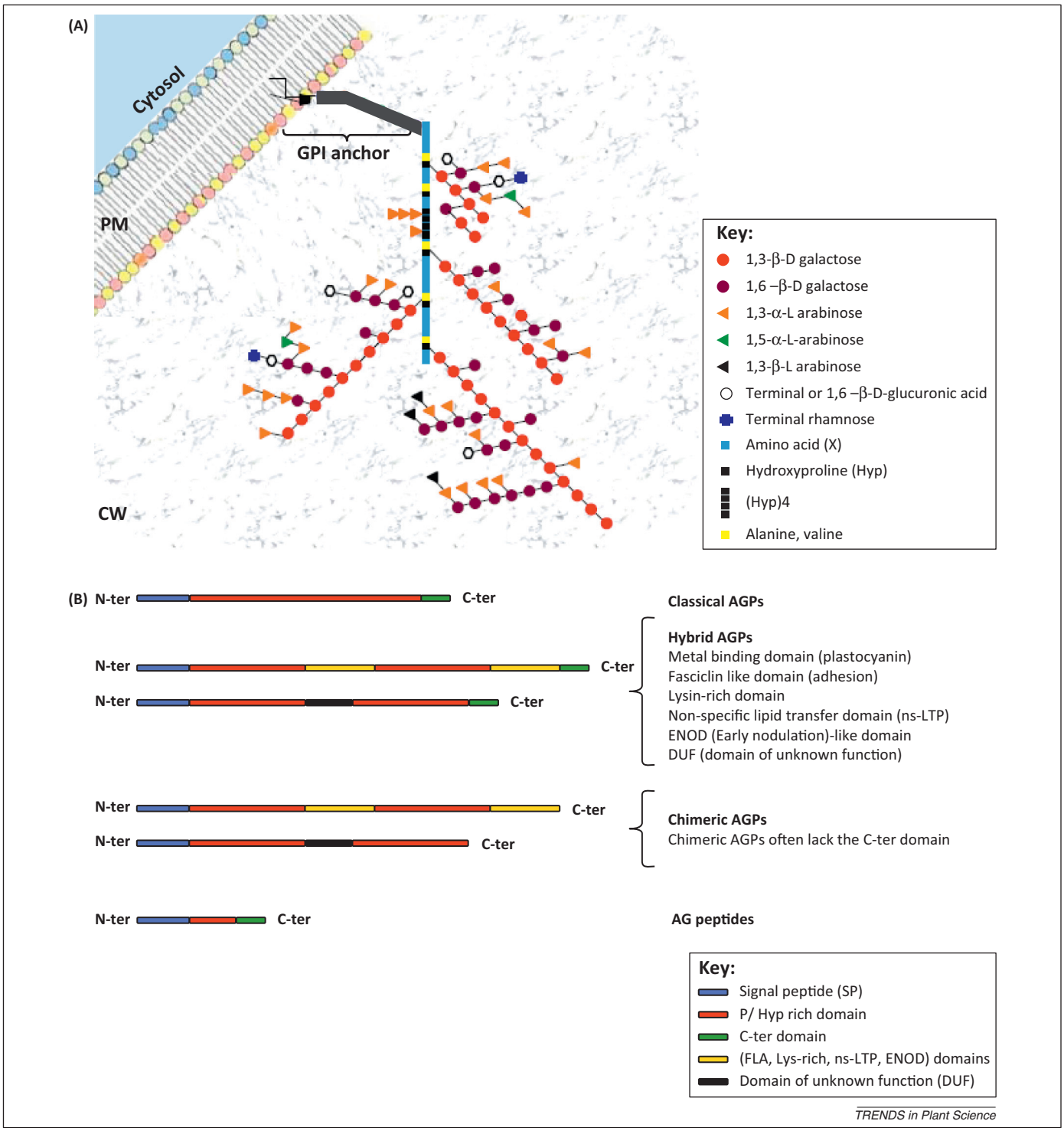

Figure 1. Structure of arabinogalactan proteins (AGPs). **(A)** AGPs are heavily glycosylated cell wall proteins and their glycans predominantly consist of arabinose and galactose. Minor sugars, such as glucuronic acid or rhamnose, are also present. The backbone of the protein is enriched in hydroxyproline residues. AGPs can be anchored to the plasma membrane via a glycosylphosphatidylinositol (GPI) anchor. AGP glycan structures were adapted from [95–97]. Note the high heterogeneity in the structure of the glycan chains. **(B)** AGP backbones are synthesized by members of a large multigene family and are classified into classical AGPs, hybrid AGPs, chimeric AGPs, and AG peptides (short classical AGPs) [2,3]. Classical AGPs are characterized by a signal peptide domain, a P/Hyp-rich domain, and a C-ter domain. Hybrid AGPs often consist of classical AGPs which may contain FLA, Lys-rich, nonspecific lipid transfer protein (ns-LTP), ENOD domains, or domains of unknown functions (DUFs) within their sequence. These domains can be interspersed within the sequence. Chimeric AGPs often lack the C-ter domain responsible for GPI anchorage. For recent reviews describing the chemistry of AGPs in general, see [14,16].

their enemies. Together, these findings suggest that AGPs can be a target of strategies aimed at improving plant health and controlling interaction of plants with the soil microbial community, particularly soil-borne pathogens.

AGPs at the interface of root cells and microbes

Many studies have shown that AGPs play an important role at the root surface during different steps leading to the colonization of roots by pathogenic and symbiotic microbes

Table 1. Distribution of arabinogalactan proteins in roots of a range of plant species[a]

Species	Root cell type	Use of antibodies/lectins	Use of	Analytical chemistry	Molecular genetic (mutant)	Refs
		Immunohistochemistry/ blotting	Yariv reagent			
Arabidopsis thaliana	Root cap and BLCs	JIM13, JIM14, MAC207	Root treatment			[6]
A. thaliana	Root cap and BLCs	JIM13				[7]
A. thaliana	Epidermal cells	JIM13, JIM14	Root treatment			[98]
A. thaliana	Epidermal cells	LM2, JIM14				[99]
A. thaliana	Epidermal cells		Root treatment		*AtAGP17*	[24]
A. thaliana	Epidermal cells		Root treatment and electrophoresis techniques			[100]
A. thaliana	Differentiating cells	Eel anti-H agglutinin	Electrophoresis techniques	Sugar composition		[101]
A. thaliana	Elongating cells	JIM8, MAC207, JIM16		Sugar composition	*AtAGP30*	[21]
A. thaliana	Epidermal, cortical and endodermal cells				*AtFLA4/SOS5*	[102]
A. thaliana	Young xylem cells	JIM13, JIM14				[11]
Pisum sativum	Root cap and BCs	JIM13, JIM14, JIM8	Electrophoresis techniques	Sugar composition and glycosidic linkage analyses		[8]
P. sativum	Root mucilage	JIM13		Sugar composition		[25]
P. sativum	Root cells[b] and root infection structure	JIM8, MAC207, MAC265				[31]
P. sativum	Root mucilage			Sugar composition and glycosidic l inkage analyses		[68]
Zea mays	Root mucilage			Sugar composition and glycosidic linkage analyses		[66]
Z. mays	Root mucilage			Proteomic analysis		[49]
Z. mays	Root epidermal cells and mucilage	LM2				[103]
Daucus carota	Root pericycle cells	MAC207, JIM4				[10]
D. carota	Root pericycle cells	JIM4				[104]
D. carota	Root apical meristem	MAC207, JIM4, JIM15, JIM8, JIM14, JIM16				[105]
Raphanus sativus	Root tip/cap cells and BLCs	Gal4-BSA				[106]
R. sativus	Primary/mature roots[b]			Sugar composition and glycosidic linkage analyses		[107]
Brassica napus	Root cap and BLCs	JIM13, JIM14, JIM8	Electrophoresis techniques	Sugar composition and glycosidic linkage analyses		[8]
Benincasa hispida	Epidermal cells	LM2, JIM14, JIM16, JIM15, JIM17, JIM101, MAC265, MAC266				[108]
Triticum spp.	Root mucilage			Sugar composition and glycosidic l inkage analyses		[67]
Vigna unguiculata	Root mucilage			Sugar composition and glycosidic linkage analyses		[67]
Alnus spp.	Cortical cells and root infection structure	JIM13, JIM4				[26]
Oryza sativa	Root apex[b]	JIM8				[109]

[a]Different approaches have been used to study AGP distribution, including analytical chemistry, immuno-based methods, electrophoretic techniques, bioinformatics, and molecular tools.

[b]Indicates that the root cell type investigated in the study is not explicitly mentioned.

[6,24–35]. These steps include the recognition between root cells and the microbe, the colonization, and later on the formation of infectious structures [36,37].

First, at the initiation of the dialog, or recognition, between root cells and microbes, and subsequent colonization, the presence of AGPs was found to be essential. An *Arabidopsis* mutant with a mutation in the *AGP17* gene was shown to be resistant to transformation by *Agrobacterium tumefaciens* (the *rat1* mutant) [24]. A pretreatment of wild type roots with Yariv reagent reduced the frequency of root

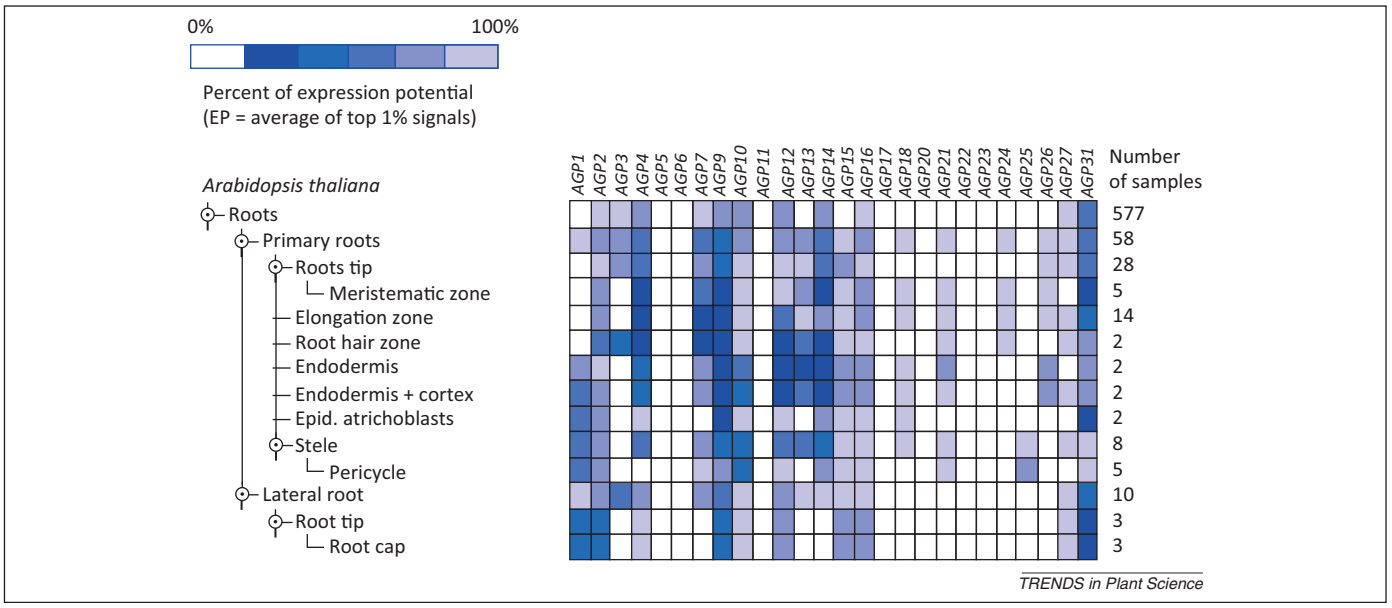

Figure 2. Relative level of expression of arabinogalactan protein (AGP) genes in different root tissues of *Arabidopsis thaliana* (modified from [14]). The figure was generated using Genevestigator [110]. Reproduced, with permission, from *Annals of Botany* © Oxford Press.

transformation events, thus suggesting that AGPs are involved in the recognition and initial attachment of rhizobia to the root [24]. The complementation of *rat1* mutants with the wild type *AtAGP17* gene restored the wild type phenotype [24]. The role of AGPs in recognition and attachment of rhizobia to root surface was also proven with *Rhizobium* species: it has been shown that AGPs secreted by *Arabidopsis* root cap cells and BLCs influence attraction and/or attachment of *Rhizobium* sp. [6]. Pretreatment of *Arabidopsis* roots with Yariv reagent significantly reduced the ability of *Rhizobium* sp. to colonize root tip cells [6]. Taking this finding further, the authors showed that inhibiting AGP *O*-glycosylation with a chemical analog of proline (3,4-dehydroprolin), also altered the ability of *Rhizobium* sp. to attach to the root cap cells and BLCs [6]. More recently, it has been elegantly demonstrated that a novel molecular mechanism involving AGPs of pea (*Pisum sativum*) root mucilage and an unknown *Rhizobium leguminosarum* factor were responsible for the polar attachment of *R. leguminosarum* to the root surface [25]. Interestingly, *R. leguminosarum* mutants lacking plasmidic nodulation genes or extracellular glucomannan were still able to show this polar attachment [25,38,39], supporting the idea of a novel molecular mechanism. Together, these studies show that an AGP-based recognition system is required and complementary to other modes of recognition of host roots by beneficial microbes and contribute to the success of root colonization by symbiotic bacteria. By contrast, it is not known if secreted AGPs play a role during early phases (recognition, attraction) of root colonization by symbiotic fungi forming mycorrhizae. It has been shown that an agglutinin isolated from stinging nettle (*Urtica dioica* agglutinin, UDA [40,41]), and shown to display antifungal properties, inhibits the development of a symbiotic fungi forming vesicular arbuscular mycorrhizae, *Glomus mosseae*. However, whether UDA interacts with plant AGPs is not known.

Finally, AGPs have also been frequently found at the interface of microbe infectious structures and root cells. Microbial infection is often mediated by the formation of infectious structures where microbes and root cells meet. Examples of such structures are infection threads [36], actinorhizal nodules [26], arbuscular mycorrhizae [27,28], and cyanobacterial stem gland symbioses [29]. A chimeric population of AGPs (called arabinogalactan protein extensins, AGPEs), shown to be enriched in arabinose and galactose [30], and recognized by the monoclonal antibody (mAb) MAC265 [42,43], has been identified as the major component of infection thread lumen of the rhizobium–pea symbiosis [31–33]. It has been hypothesized that physical and biochemical properties of AGPEs may have an important influence on the progress of tissue and cell colonization by *Rhizobium*, probably by surrounding the bacteria in the infection thread or by regulating the growth of the infection thread itself [31]. Interestingly, AGPE epitopes recognized by the mAb MAC265 have also been detected in a pathogenesis context. Indeed, these epitopes were shown to be more abundantly present in the cell wall of a pearl millet (*Pennisetum glaucum*) cultivar resistant to infection by the pathogenic oomycete *Sclerospora graminicola*, when compared to a susceptible cultivar [34]. The authors proposed that these AGPEs may crosslink to each other and form a network which might provide anchorage for lignification and create a barrier impermeable to fungal hyphae. Interestingly, they also observed an increase in peroxidase and H_2O_2 contents required for crosslinking (see also [35] for oxidative crosslinking of AGPs).

AGPs were also found to play an active role during the formation of root actinorhizal nodules in alder (*Alnus glutinosa*)–*Frankia* symbiosis [26]. Using immunocytochemistry coupled to electron microscopy, Berry *et al.* [26] showed that AGP-associated epitopes were abundantly present in nodule-infected tissues. AGP epitopes recognized by the mAb JIM4 were found associated with pectic polysaccharides in the cell walls, whereas those recognized by JIM13 were abundantly found at the membrane–cell wall border along the symbiotic interface at the early

infection stage [26]. The authors proposed that the JIM13 antigen may function in directing *Frankia* growth during early infection, or that the antigen could participate in the formation of new plant cell walls at the interface that accompany the colonization of the host cells by *Frankia*. Interestingly, in mature-infected cells, JIM13-associated epitopes were found in the host cytoplasm and vacuole [26]. Here, it was suggested that this location may indicate a turnover of this epitope after cell wall synthesis has ceased.

In symbiotic fungi–root associations between *Medicago truncatula* roots and symbiotic fungi of the genera *Glomus*, two independent studies have shown that the transcript of an AGP was particularly abundant in cells containing arbuscular mycorrhizae [27,28]. The authors speculated that this AGP may be a structural component of the interface compartment or, alternatively, it might be involved in mediating the interaction between the plant cortical cells and fungal hypha during arbuscule development [27]. It is also noteworthy that AGP-like proteins from *Glomus intraradices* were shown to be expressed during root colonization where they are believed to facilitate the formation of arbuscular mycorrhizae [28]. Interestingly, *Nostoc* spp., cyanobacteria species which also develop symbioses with plants, have been shown to contain several consensus domains defining AGP genes and to exhibit glycan epitopes associated with higher plant AGPs [29]. The role of these AGP-like proteins in symbiosis remains to be clearly established.

Apart from microbe–plant infection, it was also shown that AGPs were required for a successful infection of plant tissues, by plant parasites. For example, the holoparasite plant *Cuscuta reflexa* was shown to induce a localized (restricted to the infection sites) synthesis of an AGP, termed 'attachment AGP: attAGP' by the host, required for parasite attachment [44]. Using the RNA interference approach, a correlation between the level of expression of the attAGP and the force of attachment of the parasite to its host was observed: the lower the level of attAGP, the lower was the force of attachment of the parasite to its host [44].

Together, these studies link AGPs to the formation of infectious structures of either beneficial or pathogenic microbes, and of plant parasites. They also suggest that AGPs could be possible targets for strategies aiming at controlling root infections.

In addition to the above-mentioned roles at the interface of plants and microbes, it was proposed that AGPs may contribute to a signaling cascade responsible for the modulation of plant immune response [24]. Such a modulation of the plant immune system upon infection by soil microbes is well documented and contributes to the success or the failure of root infection and disease establishment [45]. In a study on the *rat1 Arabidopsis* mutant, it was shown that, prior and after root infection by *A. tumefaciens*, the content of salicylic acid (SA) and pathogenesis-related proteins1 (PR-1) remains unchanged in the mutant roots [24]. By contrast, SA and PR-1 contents are reduced in the wild type roots upon infection and this reduction is likely to favor successful infections by *A. tumefaciens*. The authors proposed that AGPs were required for the modulation of the content of SA and PR1, thus allowing colonization of roots by *A. tumefaciens*. They have also suggested that certain structural features (likely to be glycans) of *At*AGP17 may be responsible for such modulation [24]. The presence of a GPI anchor would allow *At*AGP17 to interact with wall kinases such as WAKs located in the plasma membrane [20], or to be cleaved by specific phospholipases and released as a soluble-signaling molecule [23]. The role of AGPs as soluble-signaling molecules has previously been demonstrated in several studies: xylogen, for example, is a diffusible, high molecular weight AGP, able to induce differentiation of Zinnia (*Zinnia elegans* L.) mesophyll cells into tracheary elements [18].

AGPs secreted by root cap cells and BCs/BLCs: a role in plant protection

AGPs are also synthesized by root cap cells and root cap-derived BCs and BLCs. BCs and BLCs are released within the rhizosphere and are required for the survival and protection of the root in the soil [4–6,46–48]. AGPs are highly expressed at the cell surface of BCs and BLCs [6–8], but are also abundantly secreted into the rhizosphere by the same cells, as components of the polysaccharide-rich mucilage [6,7,25,49]. An interesting study has shown that an *Arabidopsis* mutant unable to form root BLCs released BCs [7]. Surprisingly, this unexpected release of BCs, instead of BLCs, was accompanied by a secretion of a thick layer of mucilage termed 'BC biofilm' [50], mostly consisting of AGPs and pectic xylogalacturonan (XGA). Secreted XGA and AGPs were both proposed to contribute to root cap protection: XGA is described as highly resistant to degradation by microbial pectin-hydrolyzing enzymes [51], whereas AGPs would help hold the cells together like a 'glue', thus allowing them to remain close to the root tip to ensure its protection [7,46,50].

The importance of root cap cells and BCs/BLCs in recognition and attraction of beneficial soil microbes has been described previously [6,24,25]. These studies suggest that AGPs secreted by root cap cells and BCs/BLCs are required for successful infection of roots by beneficial microbes. By contrast, attraction of pathogenic microbes by AGPs seems to be a strategy of entrapment of the pathogen, followed by their subsequent neutralization [8]. Using an *in vitro* assay, it has been shown that AGPs synthesized by pea root cap cells and BCs were able to inhibit the development of the pathogenic oomycete *Aphanomyces euteiches*, thus providing, to the best of our knowledge, the first report of antimicrobial properties of AGPs [8]. Infection by oomycetes involves zoospore attraction by chemotaxis, followed by encystment, and subsequent cyst germination [52]. A purified AGP fraction extracted from pea root cap cells and BCs has been found effective in attracting, by chemotaxis, *A. euteiches* zoospores [8]. Interestingly, the purified AGP fraction also provoked zoospore encystment (immobilization of deflagellated zoospores or cysts). Therefore, it is probable that AGPs may contribute to protection against root infection by immobilizing zoospores at the periphery of the tip or in the surrounding environment. It has been reported that many antimicrobial compounds and extracellular DNA are secreted by root cap cells and BCs into the so-called 'extracellular traps' that neutralize the immobilized pathogen much like the

ones formed by human neutrophil cells [5,47]. AGPs have been proposed to be part of the trap complex [46]. Finally, the purified AGP fraction was shown to significantly reduce cyst germination and hyphal proliferation [8]. The precise mode of action of AGPs on *A. euteiches* development is unknown. However, it is noteworthy that certain AGPs harbor a nonspecific lipid transfer protein domain (ns-LTP-like AGPs) [53], which may physically target microbe membranes and inhibit microbe development. It has been shown that ns-LTP proteins, which are classified as pathogenesis-related proteins 13 [54], were able to exhibit cytotoxic and membrane permeabilization properties towards bacterial and fungal plant pathogens [55–57]. That ns-LTP-like AGPs have the same effects on *A. euteiches* as pea root AGPs remains to be proven. Similarly, it is not known whether the Yariv-precipitated AGPs in the pea root cap study [8] contain LTP-like proteins.

AGPs secreted into the rhizosphere: role in communication with soil microbes?

Along with organic acids, secondary metabolites, and proteins, AGP-containing mucilages are abundantly secreted into the rhizosphere by root tips. Organic acids [58], secondary metabolites [59], and proteins [60,61] are known to play a role in microbial cooperation in the rhizosphere [62–65], but how AGPs affect the rhizosphere microbiome has been neglected. Evidence for AGP occurrence in root exudates was initially provided by two studies [66,67], when chemical structures typical of AGPs were found in maize (*Zea mays*), wheat (*Triticum aestivum*), and cowpea (*Vigna unguiculata*) mucilage. AGP occurrence in root exudates was later reported in several other species including pea [25,68], soybean (*Glycine max* L.) [69], *Arabidopsis* [6,7], and maize [49]. AGP-containing root exudates were frequently proposed to serve as lubricants protecting the root tip as it pushes through the soil [70–72], to stabilize soil aggregates [72,73], and protect root tips against toxicity of aluminum and other heavy metals [72,74]. AGP-rich mucilage also facilitates water retention in the rhizosphere [75] and may indirectly contribute to the attraction of living soil microbes towards a water-rich and carbon-rich microenvironment. Chemotaxis, for example, is a phenomenon that is impacted by AGPs [8].

In the rhizosphere, the microbiome consists of commensal, pathogenic, and beneficial microbes [62,65]. To colonize a given rhizosphere, microbes have to, among other things, be able to use available nutrients. Interestingly, it was shown that many soil microbes including the biocontrol agents *Trichoderma viride* [76] and *Streptomyces avermitilis* [77–79], the soil-borne pathogenic fungus *Fusarium oxysporum* [80], as well as many other microbes (*Aspergillus niger* [81] and *Neurospora crassa* [82]) all produce AGP glycan-degrading enzymes (e.g., β-1,3-galactanases, β-1,6-galactanases, arabinofuranosidases, β-glucuronidases). Furthermore, a set of experiments showed that rhizobacteria were able to grow on an AGP-rich mucilage, suggesting their ability to hydrolyze and metabolize AGP-derived sugars for their growth in the rhizosphere [68]. In support of this is a study [83] that showed that maize root mucilage (particularly enriched in AGPs) [49,66] was able to influence the composition of bacterial communities in soil. Consequently, root AGPs seem to significantly contribute to the shaping of the rhizosphere microbiome. It is possible that AGPs would select for specific antagonist microbes to help the root prosper within the rhizosphere. Microbial interactions occurring in such a microenvironment have been extensively reviewed [62,64,65,84]. Different types of antagonism behavior including mycoparasitism, antibiosis, and competition can develop between inhabitants and lead to soil suppressiveness towards a disease caused by a specific soil-borne plant pathogen [85]. How root-secreted AGPs of a given plant species would affect the establishment of beneficial microbes (e.g., plant growth promoting bacteria/fungi) within a rhizosphere is an interesting issue to unravel.

Also the susceptibility of AGPs to degradation by microbial depolymerases may result in the production of AGP-derived oligosaccharides. Given the diversity of AGP glycans in plants, a high diversity of AGP-derived oligosaccharide structures can be generated from secreted AGPs, and may have interesting biological functions. The ability of cell wall-derived oligosaccharides to modulate or activate plant defense mechanisms has been studied for decades and was demonstrated for plant-derived as well as for fungal-derived cell wall degradation products (the oligosaccharin theory) [86,87]. It was shown, for example, that upon plant infection by pathogenic microbes, endopolygalacturonase-mediated degradation of pectin homogalacturonans yielded oligogalacturonans, which were found to activate plant defense mechanisms [88,89]. Recently, a hybrid kinase consisting of the extracellular domain of *WALL-ASSOCIATED KINASE1* and the intracellular domain of the Elongation Factor Tu-receptor kinase was shown to bind oligogalacturonans and activate defense responses [90]. It is therefore tempting to speculate on the ability of AGP-derived oligosaccharides to act as elicitors [17]. Plant cell wall-degrading enzymes of unknown functions, including β-galactosidases, were found to be released into the rhizosphere by BCs/BLCs [91,92]. That such AGP-derived fragments would act as damage-associated molecular patterns (DAMPs) [93] with the ability to modulate the plant immune system is plausible but remains to be demonstrated.

Concluding remarks and future outlook

It is clear that AGPs are abundantly synthesized by root cells and secreted into the rhizosphere. However, current understanding of AGP function in PMI is limited. Studies discussed in this review have clearly shown that AGPs play important roles in mediating many root cell–microbe interactions. First, AGPs are involved in attracting and initiating root tip colonization by beneficial microbes. They were also found expressed at the interface of infectious structures that are formed between various beneficial microbes and root cells, and which allow the exchange of nutrients between the root and its symbiont. At these physical interfaces, they are likely to be important as structural components and/or signaling molecules. Interestingly, in a pathogenesis context, they are also likely to set the scene for mounting an efficient and localized defense response. Based on recent finding of their

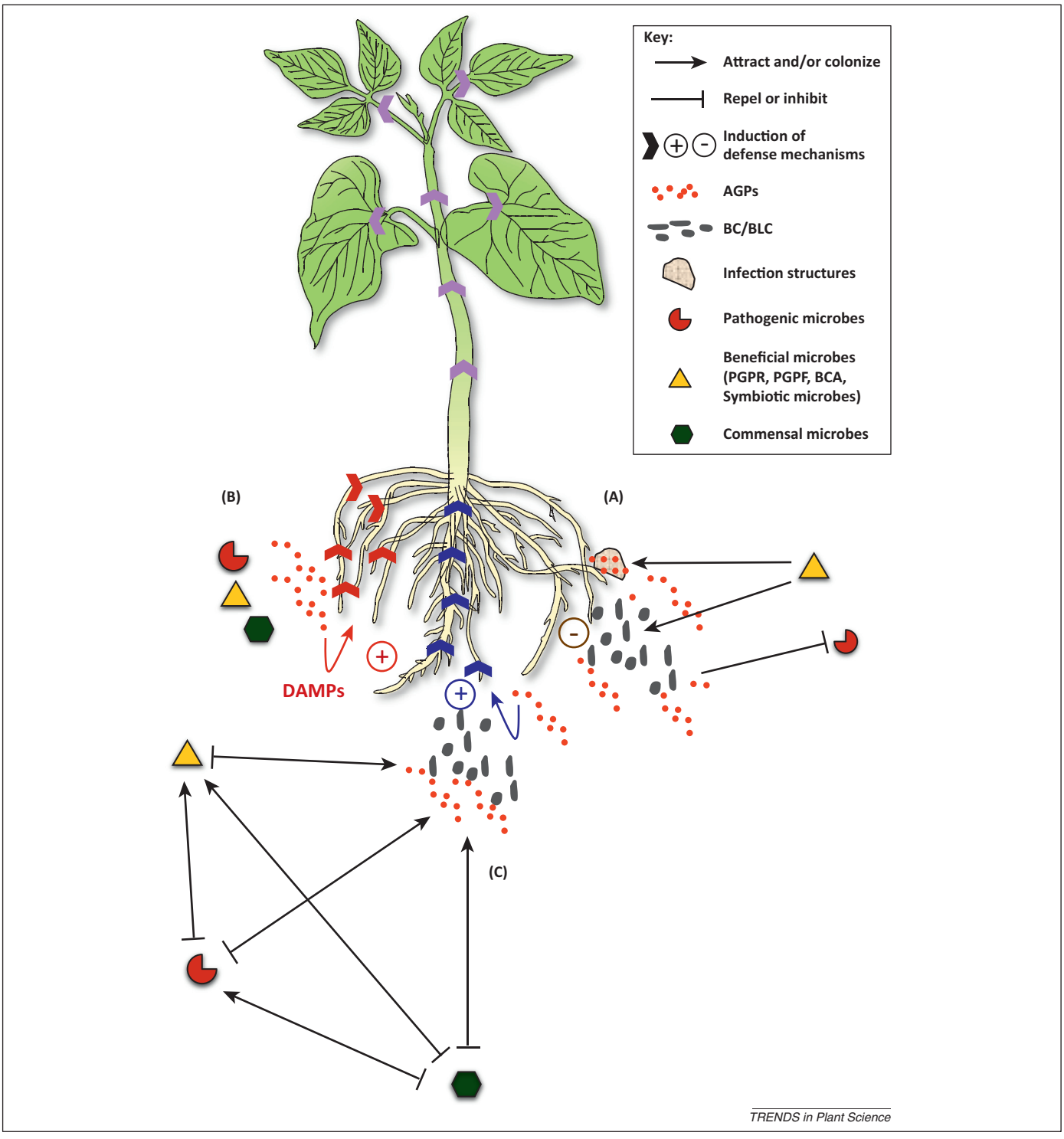

Figure 3. Model summarizing possible roles for arabinogalactan proteins (AGPs) during root cell interaction with microbes. **(A)** AGPs are able to attract symbiotic microbes (bacteria and fungi) that will later infect roots and develop infection structures. They are abundantly found at the physical interface of root cells and microbe infectious structures where they might control the formation of these structures and promote microbe adherence and progression into the root. AGPs are also able to repel root pathogens or to inhibit their development. **(B)** Soil microbes are able to degrade root AGPs, potentially releasing oligosaccharides and/or glycopeptides as damage-associated molecular patterns (DAMPs) that would activate plant defense mechanisms (red arrows). **(C)** Secreted AGPs may also favor the colonization of the rhizosphere by beneficial microbes (i.e., plant growth promoting rhizobia/fungi, PGPR/PGPF; biocontrol agent, BCA) which are able either to activate plant defense responses such as induced systemic resistance (ISR, [45]; blue arrows) or to antagonize pathogenic microbes and suppress a disease. Different microbes inhabiting the rhizosphere (i.e., symbiotic, commensal, and pathogenic microbes) may interact with each other. AGPs can also modulate the plant immune system to favor root colonization by soil microbes. Purple arrows indicate possible induction and/or modulation of defense mechanisms in the aerial parts of the plant, as a consequence of either the activation of defense mechanisms by AGP degradation products (B) or by beneficial microbes (PGPF, PGPR, or BCA) (C). (−) repression of plant immune system (A); (+) activation of plant immune system (B, C).

antimicrobial properties, AGPs are directly involved in controlling some pathogenic microbes. Purified AGPs from pea root cap cells and BCs were shown to effectively inhibit the development of a devastative pea pathogenic microbe [8]. However, many questions remain to be answered: what are the mechanisms involved? Can root AGPs perform in a similar manner with other soil-borne pathogens? Are AGPs from a given species (e.g., pea root AGPs) only effective on their, or some of their, natural microbial enemies (*A. euteiches* for pea)? A more general point to unravel is the promising role AGPs may play in the dialog between roots and soil microbes. Evidence points towards their involvement in this dialog as supporting players, or facilitators, of colonization of the rhizosphere by specific groups of microbes [6,8,68,83]. Additional research is needed to further understand how AGPs precisely inhibit or stimulate members of the microbial community. A recent review has proposed a model summarizing the many interactions occurring between roots and microbes in the rhizosphere [62], and it is tempting to include AGPs, or AGP-derived oligosaccharides and/or glycopeptides, in such a model. Here, we highlight in Figure 3 the possible roles played by AGPs in such processes. However, the precise modes of action of AGPs in some of these possible scenarios remain to be investigated, as these glycoproteins harbor complex chemical structures, and for most of the possible scenarios mentioned above it is unknown whether all AGP populations, specific families, or specific sequences (oligosaccharides or glycopeptides) are responsible for biological activity. An interesting study [94] showed that a given AGP can contain in its structure (the chitinase-sensitive motif) the ability to inhibit carrot somatic embryogenesis, whereas other motifs (i.e., glycopeptides remaining after endochitinase treatment and repurified using Yariv reagent) yielded the opposite result (reviewed in [17]). This supports that AGPs are able to play dual roles in different processes including interactions of roots with microbes.

Clearly, interactions between roots and microbes are crucial for plant health and AGPs play a significant role in such interactions. Basic and strategic studies, as well as the development of novel tools, should help not only to further understand the function of AGPs within the rhizosphere but also to facilitate their use, or the use of molecules derived from them (or modeled on them), as natural compounds for crop protection in a sustainable manner.

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