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Review

Arabinogalactan proteins: Distribution during the development of male and female gametophytes

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ABSTRACT

Arabinogalactan proteins (AGPs), i.e. a subfamily of hydroxyproline-rich proteins (HRGPs), are widely distributed in the plant kingdom. For many years, AGPs have been connected with the multiple phases of plant reproduction and developmental processes. Currently, extensive knowledge is available about their various functions, i.e. involvement in pollen grain formation, initiation of pollen grain germination, pollen tube guidance in the transmission tissue of pistil and ovule nucellus, and function as a signaling molecule during cell-cell communication. Although many studies have been performed, the mechanism of action, the heterogeneous molecule structure, and the connection with other extracellular matrix components have not been sufficiently explained. The aim of this work was to gather and describe the most important information on the distribution of AGPs in gametophyte development. The present review provides a summary of the first reports about AGPs and the most recent knowledge about their functions during male and female gametophyte formation.

1. Introduction

Arabinogalactan proteins (AGPs) are widely distributed in the plant kingdom. AGPs, i.e. a subfamily of hydroxyproline-rich proteins (HRGPs), are extracellular glycoproteins that form the amorphous component of the cell wall as structural proteins (Seifert and Roberts, 2007). Among other cell wall proteins, AGPs are characterized by high sugar content, up to 90% of the total molecular weight, heterogeneity of their protein backbone and carbohydrate chains, and the presence of a C-terminal glycosylphosphatidylinositol (GPI) sequence that allows anchoring the AGP molecule to the cell membrane. The sugar moiety is made up of a β-(1,3) galactan backbone to which oligosaccharide or polysaccharide side chains are substituted, which are rich in galactose and arabinose, as well in rhamnose, fucose, and galacturonic acid. The protein core is about 10% by weight of the entire AGP molecule, and is composed of hydroxyproline, proline, serine, alanine, and threonine (Knox, 1995; Cheung et al., 2000; Schultz et al., 2000; Showalter, 2001; Rumyantseva, 2005; Showalter and Basu, 2016; Ma et al., 2017; Su and Higashiyama, 2018).

The heterogeneous nature of arabinogalactan proteins is reflected in their functions. They are anchored in the cell membrane and may act as adhesion molecules connecting cell wall elements with plasma membrane (Ellis et al., 2010). The localization of AGPs has been described at the tissue, cellular and subcellular level. This allowed recognition of their huge multifunctionality (Showalter, 2001; Lamport et al., 2006; Seifert and Roberts, 2007; Nguema-Ona et al., 2012; Su and Higashiyama, 2018; Lamport et al., 2018b; Tucker et al., 2018). Numerous studies indicate the spatio-temporal occurrence of AGPs. In a single cell, the presence of different kinds of AGPs can be noted in particular developmental stages (Majewska-Sawka and Nothnagel, 2000; Pereira et al., 2015).

Additionally, the hypothetical ability to bind calcium ions is an AGP property that has a strong influence on their functions. It is likely that AGP molecules may constitute a carrier of calcium ions, which are released in specific stages of morphogenesis, germination, and elongation of the pollen tube as well as during early stages of embryogenesis. In addition, the accumulation of AGP-Ca^{2+} may be associated with the adaptation of the cell for changing conditions and its response to stress factors (Lamport and Varnai, 2012; Lamport et al., 2014, 2018a; 2018b; Mareri et al., 2018).

Moreover, the functions of AGPs are associated with the possibility of forming linkages with the other components of the cell wall, mainly hemicellulose and pectic polysaccharides. It was elucidated that the Rha residue in the AG domain in AGPs formed covalent bonds with rhamnogalacturonan-I and arabinoxylan. This proteoglycan structure called ARABINOXYLAN PECTIN ARABINOGALACTAN PROTEIN1 (APAP1) supports the existence of a permanent network, and, in consequence, influence the extracellular matrix integrity (Tan et al., 2012,

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Table 1
Commonly used AGPs antibodies, epitope structural characterization, and plant origin. According to Complex Carbohydrate Research Center at the University of Georgia - Athens, GA USA (CarboSource Services), and Paul Knox Cell Wall Lab at the University of Leeds – PlantProbes, Leeds, UK.

Antibody Name	Epitope structure for carbohydrate antigen	Immunogen	Plant Origin	Reference
JIM4	βGlcA(1 → 3)-αGalA(1 → 2)Rha	Protoplasts from suspension cultured cells	Carrot (*Daucus carota*)	Yates et al. (1996) Knox et al. (1991)
JIM8	epitope: unknown	Protoplasts from suspension cultured cells	Sugar beet (*Beta vulgaris*)	Pennell et al. (1991)
JIM13	βGlcA(1 → 3)-αGalA(1 → 2)Rha	Arabinogalactan protein (AGP2)	Carrot (*Daucus carota*)	Yates et al. (1996) Knox et al. (1991)
JIM14	epitope: unknown	Arabinogalactan protein (AGP2)	Carrot (*Daucus carota*)	Yates et al. (1996) Knox et al. (1991)
JIM15	D-GlcA; GlcA-β(1-*O*-Me)	Arabinogalactan protein (AGP1)	Carrot (*Daucus carota*)	Yates et al. (1996) Knox et al. (1991)
JIM16	epitope: unknown	Arabinogalactan protein (AGP1)	Carrot (*Daucus carota*)	Yates et al. (1996) Knox et al. (1991)
JIM101	epitope: unknown	Arabinogalactan protein	Liverwort (*Gymnocolea inflata*)	Pattathil et al. (2010)
MAC204	epitope: unknown	Peribacteroid membrane	Pea (*Pisum sativum*)	Pattathil et al. (2010)
MAC207	βGlcA(1 → 3)-αGalA(1 → 2)Rha	Peribacteroid membrane	Pea (*Pisum sativum*)	Pattathil et al. (2010)
LM2	β-D-GlcA	Cell wall material	Rice (*Oryza sativa*)	Yates et al. (1996)
LM14	AG type II arabinogalactan	–	–	Moller et al. (2008)
PN 16.4B4	uncharacterized epitope in carbohydrate part of the glycoprotein	Membranes from suspension-cultured cells	Tobacco (*Nicotiana glutinosa*)	Pattathil et al. (2010)

2013). In addition, a *SALT-OVERLY SENSITIVE5* (*SOS5)* gene has been identified whose expression is connected with the interaction the GPI anchor of AGPs (glycophosphatidylinositol at the C-terminus) and rhamnogalacturonan-I. The presence of *SOS5* determines the formation of a network stiffening the cell wall, which may affect cellulose biosynthesis (Griffiths et al., 2014). Disorder in the interactions of AGP and other polysaccharides affects the cell wall-plasma membrane continuum, and the rheological properties of the cell wall (Hijazi et al., 2014).

Arabinogalactan proteins are regarded as a necessary element in the process of sexual reproduction of both angiosperms and gymnosperms. In studies aimed at their localization, changes in distribution, and determination of functions, it has been described that AGPs are a group of proteoglycans involved in many stages of this process, starting from the formation of male and female gametophyte structures, through pollen tube elongation, to the process of double fertilization. The most common technique for determination of the occurrence of arabinogalactan proteins is an immunocytochemical reaction, using specific antibodies directed against the carbohydrate epitopes of AGPs (Table 1.)

1.1. Distribution of arabinogalactan proteins in male gametophyte development

Arabinogalactan proteins are involve in the development of male plant reproductive organs, act in formation of gametophyte, pollen grains germination, and pollen tube movement along the transmission tissue during the progamic phase (Cheung and Wu, 1999; Nguema-Ona et al., 2012; Pereira et al., 2015). In all publications referred to in Table 2, the localization and role of AGPs during the development of the male gametophyte of several plant species is discussed.

In case of male gametophyte, epitopes recognized by JIM8, JIM13, JIM14, JIM15, MAC207 antibody were located during the formation of anther walls. The examined proteins are found in the epidermis, endothelium, and transitional layer. The involvement of AGP proteins at the early stages of anther development was observed in many species, including *Lolium perenne* (Wiśniewska and Majewska-Sawka, 2006), *Nicotiana tabacum* (Qin et al., 2007), *Bellis perennis* (Chudzik et al., 2014), and *Brassica napus* (Corral-Martínez et al., 2016).

Arabinogalactan proteins act as signal molecules during the development of pollen grains. There are many papers with a precise description of their appearance during microsporogenesis, in which they are treated as molecular markers of particular stages of microsporogenesis (Pereira et al., 2015). In the premeiotic stages of *Bellis perennis* (Chudzik et al., 2014), *Quercus suber* (Costa et al., 2015), *Brassica napus* (Corral-Martínez et al., 2016), and *Arabidopsis thaliana* (Li et al., 2017) significant amounts of their epitopes were observed in the tapetum layer. During later stages of development, AGPs also appeared in the forming walls surrounding individual microsporocytes (Qin et al., 2007; Coimbra and Pereira L.G. 2012). In studies on microsporogenesis of *Beta vulgaris* (Majewska-Sawka and Rodriguez-García, 2006) and *Bellis perennis* (Chudzik et al., 2014), AGPs were located in close area to the callose wall surrounding the tetrad of microspores.

During the development of pollen grains of *Brassica napus*, AGPs epitopes were noticeable in microspore cell walls. Examined epitopes were accumulated in the cytoplasm and in the walls of generative cells (El-Tantawy et al., 2013; Corral-Martínez et al., 2016). Similarly, AGP epitopes were located in the generative cells of pollen grains of *Nicotiana tabacum* (Li et al., 1995), *Olea europaea* (Castro et al., 2013), *Quercus suber* (Costa et al., 2015), *Mangifera indica* (Lora and Hormaza, 2018), and in male gametes of *Brassica napus* (Southworth and Kwiatkowski, 1996). Interestingly, AGP epitopes were abundant in extraprotoplasmic matrix around differentiating male gametes during spermatogenesis of *Ceratopteris richardii*, what underline critical role of AGPs in development of multiflagellated sperm cells (Lopez and Renzaglia, 2014).

The AGPs epitopes distribution was also analyzed during primexine and exine formation in *Arabidopsis* mutants with abnormal pollen exine structure. These studies demonstrate that defects in AGPs occurrence resulted in disturbance in pollen development and viability (Suzuki et al., 2017). Furthermore, AGPs epitopes were observed in mature pollen grains, especially in the intine layer. This was confirmed by studies of pollen grains of *Nicotiana tabacum* (Li et al., 1995), *Camellia japonica*, *Camellia sasanqua, Nicotiana alata, Lilium longiflorum, Petunia hybrida* (Hasegawa et al., 2000), *Actinidia deliciosa (*Abreu and Oliveira, 2004*), Trithuria submersa* (Costa et al., 2013a), and *Mangifera indica*

Table 2
Presence and roles of arabinogalactan proteins during microsporogenesis, development of male gametophyte, and in the progamic phase. Selected the most frequently analyzed species. Research methods: Immunocytochemistry (1), Staining with Yariv Reagent (2), Molecular biology techniques (3).

Species Name	Research method			Localization of AGPs * used antibody	Presumed function of AGPs	References
	1	2	3			
Actinidia deliciosa	+	+		-intine, exine -pollen tube wall *JIM8, MAC207	- maintenance of cell shape during pollen growth and development	Abreu and Oliveira (2004)
	+			- transmission tissue - exudate inside transmitting channel - stigmatic surface, papillae * *JIM8, JIM13, MAC207*	- involvement in the process of adhesion of pollen grain to the papillae - role in pollen-pistil interaction	Coimbra and Duarte (2003)
Amaranthus hypochondriacus	+			- transmission tissue of the style - stigma papillae cells - pollen tube pathway * *JIM8, JIM13, MAC207*	- directing the pollen tube growth until its final target, the embryo sac	Coimbra and Duarte (2003)
Annona cherimola	+			- papillae of the stigma * *JIM8, JIM13*	- supporting role in pollen tube growth - prevention of polytubey	Lora et al. (2018)
Arabidopsis thaliana	+	+	+	- pollen grain - pollen tube - transmission tissue * *JIM8, JIM13, MAC207, LM2*	- pollen tube guidance into the embryo sac (role as a signaling molecule) - involvement in avert untimely germination of pollen *(agp6, agp11)*	Coimbra et al., (2007); Coimbra et al., (2008); Coimbra et al., (2009); Coimbra et al., (2010);
		+	+	- pollen grain *(AGP23)* - pollen tube *(AGP23)* - stigma, style, transmitting track *(AGP1, AGP12)*	- candidates for male–female communication during reproduction - contribution in the different steps of pollen tube growth through the pistil	Pereira et al. (2014)
	+		+	- pollen tube wall * *MAC207, LM2*	- pollen tube guidance into the embryo sac - important signaling molecules at the pollen tube apex	Pereira L.G. et al., 2006; Pereira L.G. et al., 2013
	+		+	- pollen tube wall, the tip region * *JIM13, MAC207, LM2*	- involvement in pollen tube cell wall biosynthesis and growth dynamics	Dardelle et al. (2010)
	+		+	- microspore primexine (*kns4*) - tapetal walls and exine cavities * *JIM8, MAC204*	- critical impact in pollen grain development and pollen viability	Suzuki et al. (2017)
	+	+		- pollen grain - pollen tube - transmission tissue * *JIM13, JIM8, LM2*	- component of the septum epidermal ECM	Lennon et al. (1998)
			+	- tapetum cells	- pollen grain wall formation - responsible for tapetum cell wall degradation	Li et al. (2017)
Bellis perennis	+			- anther wall - pollen grain * *JIM13, JIM15, MAC207*	- detected in the protoplasts of tapetal cells, dividing microsporocytes, and microspores - involvement in anther development	Chudzik et al. (2014)
Beta vulgaris	+	+		- primexine and incipient exine - young microspore wall * *JIM13, JIM8, JIM4, LM2*	- localized within the callose wall surrounding post-telophase tetrads	Majewska-Sawka and Rodriguez-García (2006)
Brassica napus	+			- sperm cells - pollen tube * *JIM8, JIM13, MAC207*	- AGP antibodies as a useful marker for describing the overall shape of sperm cells and for identifying sperm among other cell types	Southworth and Kwiatkowski (1996)
	+			- tapetal anther layers - microspore cytoplasm - exine, intine of mature pollen grain * *JIM8, JIM13, JIM14*	- involvement in microspore differentiation and tapetal dismantling	Corral-Martínez et al. (2016)
	+		+	- generative cell wall - embryo cells - mature pollen grain (cytoplasm, wall of generative and sperm cells) - aperture regions * *JIM13, JIM14, MAC207, LM2, LM6*	- AGPs as potential regulating/signaling molecules in microspore reprogramming and embryogenesis - relation with pollen maturation	El-Tantawy et al. (2013)
Brassica campestris			+	- microspore	- contribution in intine development and aperture formation	Lin et al. (2018)
Camelia japonica, Camelia sasanqua, Camelia sinensis	+			- outer layer of pollen tube wall - callose plugs - intine of pollen grain wall * *JIM13*	- important role in pollen tube growth	Hasegawa et al. (2000)
Ceratopteris richardii	+	+		- extraprotoplasmic matrix during spermatid development * *JIM13, JIM8, LM6*	- role as a signaling molecules during cell shaping, cytoskeletal development, vesicle trafficking, cytoplasmic elimination	Lopez and Renzaglia (2014)
Lilium longiflorum	+	+	+	- pollen tube tip region - transmitting track in the style * *JIM13-JIM16, LM2, MAC207*	- roles in adhesion during pollination and pollen tube growth	Jauh and Lord (1996)
	+	+		- pollen tube tip * *JIM13*	- contribution to extension of the pollen tube cell wall, important in the initial polarization	Mollet et al. (2002)
Lolium perenne	+			- microspore * JIM13	- protection of developing microspores against mechanical injury or the harmful influence of environmental factors	Wiśniewska and Majewska-Sawka (2006)

(*continued on next page*)

Table 2 (*continued*)

Species Name	Research method			Localization of AGPs * used antibody	Presumed function of AGPs	References
	1	2	3			
Malus x *domestica*	+	+		- transmission tissue - stigmatic cells * *JIM13, JIM8*	- contribution to the acceleration of heterotrophic pollen tube growth - active contribution of female tissues to prezygotic male–female crosstalk	Losada and Herrero (2012); Losada and Herrero (2014) Losada and Herrero (2017)
Mangifera indica	+			- microspore mother cell - aperture of the microspore * *JIM13, JIM8*	- communication between the male germline and the surrounding somatic cells - contribution in intine layer formation	Lora and Hormaza (2018)
Nicotiana alata		+	+	- stigma - style cells	- involvement in the expression of self-incompatibility - generation of conditions important for adhesion and germination of the pollen tube	Gell et al. (1986)
		+	+	- stigma exudate	- source of nutrition for growing pollen tube	Gane et al. (1995)
Nicotiana tabacum	+			- exine, intine - inside vesicles and cytoplasmic compartments in generative cell and vegetative cell - aperture region of pollen grain - pollen tube wall * *JIM8, MAC207*	- important stabilizing factor for the cell wall architecture of the pollen grain - involvement in 'the mechanism of generative cell movement within the vegetative cell and the new wall formation during its division' - association with cell-cell interaction during pollen tube growth and development	Li et al. (1995)
	+		+	- anther at the pollen mother cell stage (epidermal cells) - microspore - intine, cytoplasm in mature pollen grains - wall of generative cell - pollen tube wall and cytoplasm * *JIM4, JIM13, LM2*	- participation in male gametogenesis, pollen tube growth - act as surface molecules in generative and sperm cells	Qin et al. (2007)
Olea europaea	+		+	- wall of generative cell - outer exine layer * *JIM13, JIM14*	- 'recognition and adhesion of the pollen tube and the stylar transmitting cells, as well as the egg and sperm cells'	Castro et al. (2013)
	+		+	- stigma exudate - cytoplasm of papillae - transmission track in the style * *JIM13*	- component of stigmatic exudate - implications for pollen-pistil interaction, pistil development	Suárez et al. (2013)
Quercus suber	+		+	- anther wall layers - tapetum, pollen mother cell wall - intine wall near the pollen apertures - intine of the vegetative cell and the generative cell wall * *JIM8, JIM13, MAC207, LM6*	- involvement in micro-gametogenesis	Costa et al. (2015) Costa et al. (2017)
Taraxacum officinale	+			- transmitting tissue cell cytoplasm compartments * *JIM8, JIM13, JIM16*	- relationship between the AGPs presence and pathway of pollen tube growth	Gawecki et al. (2017)
Tourenia fournieri			+	- surface cell layer of the placenta	- intercellular communication	Mizukami et al., (2016) Jiao et al., (2017)
Trithuria submersa	+			- intine wall of pollen grain * *JIM8, JIM13, MAC207*	- acting as signaling molecules, located in pollen grain apertures, associated with future pollen tube emergence	Costa et al. (2013a)

(Lora and Hormaza, 2018). In pollen grains of *Olea europaea* (Castro et al., 2013) and *Quercus suber* (Costa et al., 2015, 2017), an intensive immunocytochemical reaction was also observed in the aperture region, i.e. at the site of future pollen tube growth.

1.2. Distribution of arabinogalactan proteins during the progamic phase

The progamic phase begins with pollination, which is correlated with directed transport of pollen grains to the stigma of the pistil (Lord and Sanders, 1992; Cassab, 1998). Studies have been conducted to describe the biochemical structure of the stigma cell in *Nicotiana alata* (Gell et al., 1986; Gane et al., 1995; Du et al., 1996), *Actinidia deliciosa, Amaranthus hypochondriacus* (Coimbra and Duarte, 2003), *Malus* x *domestica* (Losada and Herrero, 2012), *Olea europaea* (Suárez et al., 2013), and *Trithuria submersa* (Costa et al., 2013a), in which substantial amounts of AGPs were found outside the epidermal cells. As part of the stigma exudate, AGPs are connected with acquisition of receptivity by the stigma (Losada and Herrero, 2012).

The next stage of the progamic phase is hydration, germination of pollen grains, and pollen tube growth in the transmission pathway to reach the micropylar part of the embryo sac. Genetic research carried out has demonstrated that arabinogalactan proteins may determine the beginning of the germination of pollen grains. The expression of *agp6* and *agp11* genes is related to the development of pollen grains and the start of the germination process (Pereira L.G. et al., 2006; Coimbra and Pereira L.G. 2012). It is possible that their role is to stop the formation of the pollen tube and its growth in the anther. Prevention of premature germination in the pollen tube is caused by interference of *agp6* and *agp11* in the process of pollen grain hydration (Coimbra et al., 2008; Coimbra et al. 2009; Coimbra et al. 2010; Pereira L.G. et al., 2013).

The localization of arabinogalactan proteins is closely related to the pathway of pollen tube growth in the pistil. Immunocytochemical reactions in pistils of *Actinidia deliciosa, Amaranthus hypochondriacus* (Coimbra and Duarte, 2003), *Arabidopsis thaliana* (Coimbra et al., 2007), and *Malus* x *domestica* (Losada and Herrero, 2014) revealed that AGPs were abundant in the matrix of the extracellular transmission

tissue. This was confirmed by the examination of the transmission tissue in the pistils of *Lilium longiflorum* (Jauh and Lord, 1996*), Arabidopsis thaliana* (Lennon et al., 1998), and *Olea europaea* (Suárez et al., 2013) using a transmission electron microscope. Arabinogalactan proteins accumulating in the cells of the transmission pathway constitute a source of nutrients supplied to the growing pollen tube (Gane et al., 1995; Lennon et al., 1998). Also, Lora and coworkers (2018) suggested supporting role of AGPs in preventing multiple tube entrance (polytubey) into micropyle.

Many studies have confirmed the occurrence of arabinogalactan proteins in the pollen tube walls, mainly at its apex. The pollen tube is the fastest growing plant cell. A fast rate of growth requires a continuous supply of structural elements needed to enlarge the surface of the membrane and cell wall (Mollet et al., 2002; Abreu and Oliveira, 2004; Pereira L.G. et al., 2006; Qin et al., 2007; Losada and Herrero, 2014). Analysis of the ultrastructure of its apex demonstrated numerous vesicles containing pectin and AGPs (Li et al., 1995; Jauh and Lord, 1996; Lennon et al., 1998; Dardelle et al., 2010; Castro et al., 2013). In addition, AGPs are a factors acting as a chemoattractant for growing tubes. This is related to the next function of AGPs, i.e. the involvement in the direction of the pollen tube towards the micropyle (Nguema-Onaet al. 2012; Costa et al., 2013b; Pereira et al., 2015; Pereira et al., 2016a; Noyszewski et al., 2017; Mizuta and Higashiyama, 2018). Moreover, AGPs as a Ca^{2+} capacitors, and pollen tube guides are implicated in osmosensing or gravisensing as well other plant tropisms (Lamport et al., 2018a).

In addition, molecular biology techniques have identified the distinct expression of individual genes from the class of 'classical AGPs' during progamic phrase. Due to the high content of sugar residues, AGPs contribute to the formation of a convenient environment for germinating pollen grains. In addition, they are involved in the process of identifying pollen grains and their adhesion with the stigmoid tissue. Expression of *AGP1* and *AGP15* in the stigma, style, transmission tissue, and *AGP9* in pistil transmitting track, the septum, funiculus showing involvement of AGPs in pollen tube growth until it reaches the embryo sac. Moreover, strong *AGP1* and *AGP12* genes expression in stigmatic cells may suggested AGPs role in pollen – stigma interactions, as well as initiation of pollen tube growth (Pereira et al., 2014).

1.3. Distribution of arabinogalactan proteins in female gametophyte development

While the role of AGPs during the development of the male gametophyte is well documented, studies aimed at determining the localization of arabinogalactan proteins in ovary have been carried out in few species. Investigations have been focused on the presence of AGPs in the stigma, exudate, and the transmission tissue of the pistil, but less frequently in ovaries and ovules (Table 3.).

As demonstrated by authors of publications on plant embryogenesis, such processes as megasporogenesis, megagametophytogenesis, and double fertilization are successive stages in the continuity of processes related to a highly important period in plant reproduction. Therefore, we describe the distribution of AGPs taking into account the order of the individual processes bearing in mind their continuity and key importance in the reproduction processes. The first report on the role of arabinogalactan proteins during megasporogenesis was presented in the early 90's. Its author described AGP epitopes as markers signaling the initiation of the development of the female gametophyte (Pennell and Roberts, 1990). In all publications referred to in Table 3, the role of arabinogalactan proteins during the development of the female gametophyte of several plant species is discussed. The presented research shows that AGPs are a source of nutrients for the developing embryo sacs, are involved in the direction of the pollen tube in the ovule nucellus, and signal the presence of a fertile female gametophyte (Pereira et al., 2015). A significant contribution to the explanation of this issue was offered by molecular and genetic studies carried out by Pereira and coworkers (2014, 2016a, 2016b, 2016c). Studies on the expression of specific AGP genes in individual ovule cell compartments allow determination of the precise role of the examined proteins in each single part of the ovule. These genes include *AGP1* showing the clearest expression in funiculus cells and in the integument near the micropyle, *AGP12* in the chalazal region of the ovule, or *AGP19* in the ovary wall. Their interaction influences the functioning of AGPs as signal molecules, which give a possibility of cell-cell contact (Pereira et al., 2014). Also, strong expression of mentioned above genes from the top of the chalazal tissues along nucellus to developing embryo may indicate AGPs involvement in nutritionally supporting of ovule growth (Pereira et al., 2014).

As reported by Rafińska and Bednarska (2011), in the ovule of the *Larix decidua* gymnosperm, AGPs appear in nucellus cells with the megasporocyte. The authors suggest that the examined proteins may determine changes in the ovule cells during megasporogenesis and the presence of AGPs allows their participation in the subsequent initiation of the development of the female gametophyte (Rafińska and Bednarska, 2011). Also, in *Boechera stricta* ovules, AGP epitope recognized by JIM13 was initially localized at the surface of chalazal cell of dyad and in region surrounding the chalazal megaspore at the end of megasporogenesis, what give possibility to form the hypothesis about AGPs function as a universal marker for initial cells, destined to undergo next stages of development (Rojek et al., 2018). Similarly, the results of studies published by Acosta-García and Vielle-Calzada (2004) confirm the important function of AGPs during megasporogenesis in *Arabidopsis thaliana* ovules. Their research focuses on the analysis of the *AGP18* gene. Its expression was noted in the functional megaspore and adjacent cells of the nucellus. It was found that the *AGP18* gene is required for the initiation of megagametogenesis, as a necessary element during the interaction between somatic cells and female gametophyte cells (Acosta-García and Vielle-Calzada, 2004). Nearly 10 years later, the information on this gene was supplemented. It has been proved that it is associated with selection of a megaspore that will become a functional megaspore. It was found that AGPs have an impact on determining the functional megaspore by clearly supporting its development. Their function in determining the megaspore undergoing further development was confirmed by the determination of the expression of the *AGP18* gene only in the wall of the functional megaspore. The expression of the examined gene was observed from the stage of somatic cells to the cell wall of the functional megaspore, which is another proof confirming the hypothesis from 2004 (Demesa-Arè;valo and Vielle-Calzada, 2013).

The studies of Tucker and Koltunow refer to the above-mentioned function of arabinogalactan proteins (2014). Being elements of extracellular matrix regulated during development, they appear as markers of specific cells of the nucellus and influence their future reproductive function. Molecular studies of AGPs as components of the cell wall of generative cells prove that their properties (detachment of the GPI anchor and movement inside the extracellular matrix) give a possibility of contact between cells of various types, both somatic and generative. As shown by the authors, information on signaling molecules provides knowledge of the complexity of megagametogenesis processes and their role in the mechanism of differentiation (Tucker and Koltunow, 2014).

In studies of *Amaranthus hypochondriacus*, the authors regarded arabinogalactan proteins as embryo sac markers (Coimbra and Salema, 1997). Similar conclusions were formulated in the investigations of ovules of *Actinidia deliciosa* (Coimbra and Duarte, 2003), *Galanthus nivalis, Sinapis alba* (Chudzik et al., 2005), *Arabidopsis thaliana* (Coimbra et al., 2007), *Sida hermaphrodita* (Chudzik et al., 2010), *Olea europaea* (Suárez et al., 2013) and *Fragaria* x *ananassa* (Leszczuk and Szczuka, 2018). The authors of these studies attribute the role of signaling molecules involved in the process of formation of the female gametophyte to arabinogalactan proteins. At the same time, they emphasize the role of AGPs in the pollen tube guidance, and through their presence in the wall of the embryo sac, they may act as a long-distance factor affecting

Table 3
Occurrence of arabinogalactan proteins during megasporogenesis, in the development of female gametophyte, and in the double fertilization process. Selected the most frequently analyzed species. Research methods: Immunocytochemistry (1), Molecular biology techniques (2).

Species Name	Research method		Localization of AGPs * used antibody	Presumed role of AGPs	References
	1	2			
Actinidia deliciosa	+		- obturator - embryo sac * *JIM8, JIM13, MAC207*	- acting as a signaling molecule indicating the entrance to the ovule	Coimbra and Duarte (2003)
Amaranthus hypochondriacus	+		- micropylar pole of nucellus - embryo sac - egg apparatus * *JIM8, JIM13, MAC207*	- providing directional guides for tube growth inside the ovule	Coimbra and Salema (1997) Coimbra and Duarte (2003)
Annona cherimola	+		- egg apparatus - chalazal pole of nucellus - inner integument * *JIM8, JIM13*	- supporting the role of the inner integument in preventing multiple tube entrance (polytubey)	Lora et al. (2018)
Arabidopsis thaliana	+		- integuments - embryo sac wall - egg apparatus * *JIM8, JIM13, MAC207, LM2*	- working as markers for gametophyte cell differentiation - involvement in the programmed cell death (PCD)	Coimbra et al. (2007)
		+	- chalazal and funiculus cells of the ovule *(AGP12)*	- signaling the presence of a mature female gametophyte	Pereira et al. (2014)
	+	+	- stigma surface - ovary wall - embryo sac wall - the filiform apparatus - micropylar integuments * *JIM8, JIM13, MAC207, LM2*	- involvement in *Arabidopsis* developmental processes	Follet-Gueye et al. (2012)
		+	- functional megaspore	- acting as signaling molecules at the beginning of female gametophyte development - selection of a single megaspore for development into a functional megaspore	Tucker and Koltunow (2014)
	+	+	- integumentary cells in the abaxial region of the ovule - functional megaspore - mature female gametophyte (in the central cell, the synergids, and the egg cell) * *JIM13*	- active regulation of selection and survival of megaspores - 'promotion of viable megaspores' *(AGP18)*	Demesa-Arè;valo and Vielle-Calzada (2013) Acosta-Garciá and Vielle-Calzada (2004)
		+	- synergid	- involvement in the signaling 'pathway that leads to a blockage of pollen tube attraction' *(JAGGER – AGP4)*	Pereira et al. (2016b) Pereira et al. (2016c)
Boechera stricta	+		- chalazal cell of dyad - functional megaspore - integument cells * *JIM13*	- universal marker for initial cell, which are destined to undergo female gametophyte formation	Rojek et al. (2018)
Brassica napus	+		- egg cell - synergid - suspensor - first cell of the embryo - nucellar epidermis * *JIM8, MAC207*	- JIM8 as a marker for cell-cell interactions - role for plasma membrane AGPs in gametic recognition	Pennell et al. (1991)
Ceratopteris richardii	+		- matrix around egg cell * *JIM13, JIM8, LM2*	- important in egg maturation and gamete fusion - protection of the egg apparatus	Lopez and Renzaglia (2016)
Fragaria x ananassa	+		- micropylar pole of nucellus - embryo sac wall - egg apparatus - suspensor - embryo at globular stage * *JIM13, JIM15, MAC207*	- signaling the presence of mature female gametophyte - acting as nutrition for a growing embryo sac - participation in double fertilization	Leszczuk and Szczuka (2018)
Galanthus nivalis	+		- micropylar canal - embryo sac * *JIM8, JIM13*	- pollen tube guidance in the ovule nucellus	Chudzik et al. (2005)
Larix decidua	+		- nucellus cells - megasporocyte - megaspore after meiosis - functional megaspore - mature archegonium * *JIM4, JIM8, JIM13, LM2*	- involvement in initiation of female gametogenesis - acting as 'biochemical support or directional clues for the pollen tube to reach its target'	Rafińska and Bednarska (2011)
Lolium perenne	+		- ovule integuments * *JIM13*	- contribution in differentiation processes	Wiśniewska and Majewska-Sawka (2006)
Malus x domestica	+		- obturator * *JIM13, JIM8*	- role in regulating pollen tube access to the ovule	Losada and Herrero (2017)
Nicotiana tabacum		+	- pre- and post-fertilized egg cells - two-celled proembryos	- involvement in fertilization, zygotic division, and proembryo development	Qin and Zhao (2006)

(*continued on next page*)

Table 3 (*continued*)

Species Name	Research method		Localization of AGPs * used antibody	Presumed role of AGPs	References
	1	2			
Oenothera hookeri	+		- embryo sac * *JIM8, JIM13*	- signal molecules participating in cell-cell interaction and cellular signaling during morphogenetic processes	Chudzik et al. (2005)
Pisum sativum	+		- progenitors of the germ cell * *MAC207*	- impact on the gametes, zygote and globular-stage embryo.	Pennell and Roberts (1990)
Sida hermaphrodita	+		- nucellus - embryo sac * *JIM13, MAC207*	- signaling the pathway for the pollen tube in the nucellus and the presence of a mature embryo sac	Chudzik et al. (2010)
Quercus suber	+		- inner wall of the integument - newly formed endosperm cell walls * *JIM8, JIM13*	- acting as signaling molecule during female gametogenesis	Lopes et al. (2016)
Taraxacum officinale	+		- integument cells surrounding the micropylar canal - apex of the synergids - borders between cells of the egg apparatus and the central cell * *JIM8, JIM13, JIM16*	- useful marker for the borders between egg apparatus and the central cell	Gawecki et al. (2017)
Trithuria submersa	+		- ovary wall - outer integuments - stigmatic hairs * *JIM8, JIM13, MAC207*	- acting as essential structural components and probably important signaling molecules	Costa et al. (2013a)

the germinating pollen tube (Cheung and Wu, 1999).

The role of AGPs in pollen tube guidance has been investigated more closely in an *Actinidia deliciosa* ovule (Coimbra and Duarte, 2003) and *Malus* x *domestica* (Losada and Herrero, 2017), in which the presence of AGPs was noted in the obturator cells and the pistil. It was found that AGPs are involved in the regulation of the gradient responsible for the direction of the pollen tube on the way through the ovary and nucellus, to the embryo sac. Similar results were discussed on the example of *Arabidopsis thaliana*, in which the presence of AGPs was associated with biochemical support and preparation for contact with the pollen tube (Follett-Gueye et al., 2012). The phenomenon of targeting pollen tubes by ovules containing a properly developed embryo sac with simultaneous lack of tropism of the pollen tubes has been published by Rodrigo and Herrero (1998). Using an example of *Prunus armeniaca*, the authors describe the interaction of gametophytes in one ovule. They conclude that there is only one well-developed ovule containing an embryo sac that is attractive for pollen tubes. Similarly, this was observed during the progamic phase of *Galanthus nivalis*, in which the pollen tubes never grow into ovules without an embryo sac (Chudzik et al., 2005). Moreover, methyl-glucuronosyl arabinogalactans are involved in intercellular communication, and make pollen tubes competent to respond to attractant peptides, which are abundant in the ovary. Interestingly, the occurrence of AGPs and arabinogalactan polysaccharides is responsible for *AMOR* activity. In turn, *AMOR* activates the attractant peptide, named *LURE*, signaling cascade in pollen tube (Mizukami et al., 2016; Higashiyama and Yang, 2017; Jiao et al., 2017; Tekleyohan et al., 2017).

Correlation of ovule receptivity and growth of pollen tubes is described by an example of *Arabidopsis thaliana* (Hülskamp et al., 1995). The research was carried out using ovules with impaired development. In the case of ovaries with improperly developed ovules - abnormal cells of the nucellus and without embryo sacs, random and imprecise growth of pollen tubes on the placenta and along the ovary walls was observed. Likewise, pollen tubes did not penetrate ovules without an embryo sac. Only in the ovules characterized by a correct, typical structure with the embryo sac, no interference penetration of the pollen tube was seen in the nucellus (Hülskamp et al., 1995). The distribution of arabinogalactan proteins in the female gametophyte cell wall may be related to indication of the pollen tube direction, creation of an appropriate environment for its growth, and providing a source of nutrients and structural materials for the developing embryo sac, which is an active partner signaling readiness for fertilization (Chudzik et al., 2005).

In many studies, the occurrence of AGPs in the last phase of pollen tube migration in the egg apparatus is explained by their role in intercellular signaling. Similar results were obtained in ovules of *Brassica napus* (Pennell et al., 1991), *Amaranthus hypochondriacus* (Coimbra and Salema, 1997), *Galanthus nivalis, Galtonia candicans, Sinapis alba* (Chudzik et al., 2005), *Arabidopsis thaliana* (Coimbra et al., 2007), *Sida hermaphrodita* (Chudzik et al., 2010), *Larix decidua* (Rafińska and Bednarska, 2011), *Olea europaea* (Suárez et al., 2013), *Ceratopteris richardii* (Lopez and Renzaglia, 2016), *Taraxacum officinale* (Gawecki et al., 2017), and *Annona cherimola* (Lora et al., 2018). Additionally, Qin and Zhao (2006) showed that the level of AGPs is much higher in an unfertilized egg cell, which confirms the participation in the recognition of an egg cell and sperm cell. Already in 1999, Cheung and Wu described the presumed role of AGPs in the biochemical support of the gamete fusion process during double fertilization. Also, in the ovule of *Larix decidua*, epitopes of AGPs recognized by the JIM13 monoclonal antibody during the fusion of the sperm cell and the egg cell occur. This provided evidence for the participation of the AGPs in the recognition of released gametes (Rafińska and Bednarska, 2011). Similarly, in the case of the *Fragaria* x *ananassa* ovule, abundance of AGPs was observed in egg apparatus, mainly in close to egg cell during the double fertilization (Leszczuk and Szczuka, 2018). Also, it was found that, as a reservoir of calcium ions, AGPs were able to regulate its availability in individual stages of ovule development. After using the LM2 and JIM8 antibodies, the authors noticed a fluorescence signal in the layer surrounding the egg cell. The layer containing AGPs appeared just prior to fertilization. Additionally, AGPs role in the release of calcium ions during fertilization was discussed. The authors attributed the first source of calcium to AGPs, a key to the start of gamete fusions, also involved in early embryogenesis by providing favorable conditions for the transforming pre-embryo (Lopez and Renzaglia, 2016).

2. Conclusion

Our review is a concise summary of the research on distribution of arabinogalactan proteins in female and male gametophytes, and functions performed by AGPs in the plant reproduction processes. The mentioned information allows a conclusion that AGPs are an important element in the strategic phases of plant development. To emphasize the spatio-temporal distribution of AGPs, the schematic representation of their specific presence and its changes during development has been

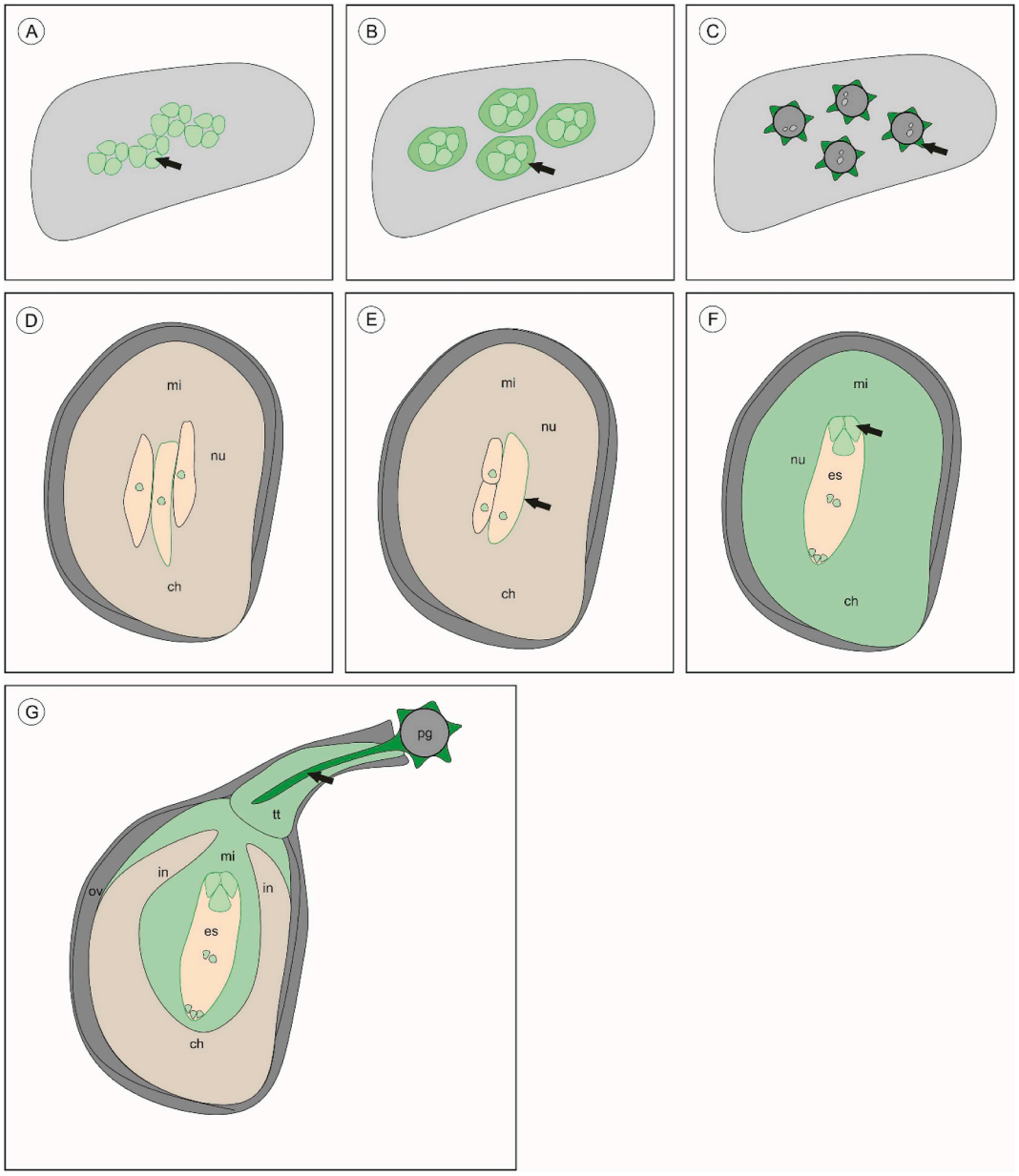

Fig. 1. The schematic representation of the AGPs distribution during development of the male and female gametophytes of *Fragaria* x *ananassa*. (Green colour shows presence of AGPs. The stronger shade of green colour of lines and surfaces indicates the higher level of AGPs.) Anther with differentiated microsporocytes (arrow) at early prophase stage. AGPs in the cell wall of microsporocyte (A). Tetrads of microspores. AGPs in the layer surrounding tetrad (arrow, B). Mature pollen grains. AGPs in the exine layer (arrow, C). Ovule with megasporocytes. AGPs present in megasporocyte continuing development (D). Ovule with functional megaspore. AGPs in the wall of functional megaspore (arrow, E). Ovule with mature embryo sac. Egg apparatus (arrow) consisted with egg cell and two synergids. AGPs in ovule nucellus, as well in the wall of female mature gametophyte, and in egg apparatus (F). The progamic phase - growing pollen tube (arrow) in transmission tissue. AGPs distributed in the pathway of pollen tube, from stigmatic tissue, transmission track to micropyle and egg apparatus (G). Abbreviations: ch – chalaza, es – embryo sac, in – integument, mi – micropyle, nu – nucellus, ov – ovary, pg – pollen grain, tt – transmission track (a reproduced and modified with permission from Leszczuk et al., 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

prepared (on example of well-known commercially plant, apomictic *Fragaria x ananassa*) (Fig. 1). However, many inaccuracies about AGPs indicate the necessity for further research to fill gaps in the knowledge, including elucidation of the mechanism of AGP activity, possible processes of remodeling and degradation of the carbohydrate chains, formation of bonds with other cell wall components, route of intracellular transport, and determinants of changes in their arrangement in the plant cell.

Authors contribution statement

AL compiled the literature, prepared tables, scheme and wrote the manuscript; ES, and AZ helped in manuscript preparation. All authors read and approved the manuscript.

Conflicts of interest

The authors have no conflicts of interest to declare.

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