Plant Omics Journal POJ

POJ 8(2):190-194 (2015) ISSN:1836-3644

Advances in research of fasciclin-like arabinogalactan proteins (FLAs) in plants

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Abstract

Fasciclin-like arabinogalactan proteins (FLAs) family, belonging to a subclass of arabinogalactan proteins (AGPs), contains AGP-like glycosylated domains and fasciclin-like domains. FLAs are widely distributed in various plants and are involved in plant growth and development. In this paper, recent advances in the structure, expression pattern, biological function and application prospect of plant FLAs are summarized.

Key words: FLA; Fasciclin-like domains; AGP-like domains; Gene function.
Abbreviations: AGP_arabinogalactan protein; FLA_fasciclin-like protein; GPI_glycosyl phosphatidylinositol; GUS_β-glucuronidase; SOS5_salt overly sensitive 5.

Introduction

As a type of highly glycosylated proteoglycans, arabinogalactan proteins (AGPs) exist in tissues and cells of almost all aquatic and terrestrial plants, containing O-glycosylated core protein backbone that accounts for 2-10% of the total molecular weight and more than 90% of type II arabinogalactan polysaccharide chains, with the molecular weight of 60-300 kD. The core chain is abundant in hydroxyproline, alanine, serine and threonine. The polysaccharide chains are mainly composed of arabinose and galactose (Majewska-Sawka and Nothnagel, 2000; Johnson et al., 2003). AGPs exist in the cell wall, plasma membrane and extracellular matrix, which are involved in all stages of plant growth and development such as cell proliferation, cell division, reproductive development, regeneration of somatic embryos, abiotic stress and hormonal signaling (Seifert and Roberts, 2007; Ellis et al., 2010; Majewska-Sawka and Nothnagel, 2000).

According to the differences in core protein backbone sequence, AGPs can be divided into six types: classical AGPs, lysine-rich AGPs, AG peptides, fasciclin-like proteins (FLAs), chimeric AGPs and nonclassical AGPs (Faik et al., 2006). To be specific, most of AGPs contain an N-terminal signal peptide, proline/hydroxyproline-rich domains, a hydrophobic C-terminus with glycosyl phosphatidylinositol (GPI) anchor signal.

The AGP family in *Arabidopsis* comprises of 85 members (Table 1): 22 classical AGPs that are composed of 87-739 amino acids, only 19 contain signal peptide, 14 GPI anchor signal; 3 lysine-rich AGPs that are composed of 185-247 amino acids, all contain signal peptide, 2 GPI anchor signal; 16 AG peptides that are composed of 58-87 amino acids, all contain signal peptide, 12 GPI anchor signal; 17 chimeric AGPs that are composed of 177-370 amino acids, all contain signal peptide, 16 GPI anchor signal; 21 FLAs that are composed of 247-462 amino acids, only 20 contain signal peptide, 11 GPI anchor signal; 6 nonclassical AGPs that are composed of 222-826 amino acids, only 5 contain signal peptide, 1 GPI anchor signal (Showalter et al., 2010). AGP proteins are extensively involved in plant growth and development in different periods and under different conditions. At present, a large number of plant FLA proteins have been isolated. In this paper, the classification, structure and function of *FLA* genes were analyzed, aiming at providing reference for subsequent studies.

Structure and classification of FLA genes in plants

Fasciclin-like arabinogalactan proteins (FLAs) are a subclass of arabinogalactan proteins (AGPs). FLAs belong to the nonclassical type, which all contain 1-2 AGP-like glycosylated domains and 1-2 fasciclin-like domains. Specifically, the fasciclin-like domain is composed of 110-150 amino acids with two highly conserved regions (H1 and H2) and each region comprises of 10 amino acids (Kawamoto et al., 1998; Johnson et al., 2003).

FLA genes have been identified in a variety of plants such as *Arabidopsis*, cabbage, rice, wheat, cotton, poplar, loblolly pine, and Zinnia (Dahiya et al., 2006; Faik et al., 2006; Johnson et al., 2003; Lafarguette et al., 2004; Loopstra et al., 2000; Yang et al., 2005; Huang et al., 2008). Current studies are mainly focused on the isolation, functional identification, expression analysis and bioinformatics analysis of *FLA* genes.

According to the number and location of fasciclin-like and AGP-like domains and the presence or absence of glycosyl phosphatidylinositol (GPI) anchor signal, *Arabidopsis* FLAs

have been divided into four groups (Fig. 1): group A harbors one fasciclin-like domain with AGP-like domains at both ends and GPI anchor signal at the C-terminus, which is composed of six members, FLA6/7/9/11/12/13, with the amino acid similarity of 43%-85%; Group B harbors AGP-like domains between two fasciclin-like domains, which is composed of four members, FLA15/16/17/18, with the amino acid similarity of 81%-88%. In addition, FLA16 possesses a small AGP-like domain near the C-terminus without GPI anchor signal; Group C harbors 1-2 fasciclin-like domains and 1-2 AGP-like domains with one GPI anchor site at the C-terminus, which is composed of seven members, FLA1/2/3/5/8/10/14, with the amino acid similarity of 46%-62%; Fasciclin-like domains of FLA3/5/14 are similar to the first fasciclin-like domain of other members in group C. Therefore, these three members are not classified into group A. Group D is composed of four members, FLA4/19/20/21, which share low similarities (33%-48%) with other members in group D or with other FLAs (Gaspar et al., 2001; Johnson et al., 2003; MacMillan et al., 2010). Moreover, the classification of 19 cotton FLAs and 33 cabbage FLAs is similar to that in *Arabidopsis*.

Expression patterns of FLAs genes in plants

In *Arabidopsis*, expression patterns of *AtFLA1/3/4/11/12* were investigated with qRT-PCR, Northern blot and GUS staining. However, no studies have been reported on the expression patterns of other dozens of *FLA* genes, which may be due to the insignificant phenotype of *Arabidopsis fla* mutants. To be specific, *AtFLA11* and *AtFLA12* exhibit extremely high expression abundance in stems and extremely low expression abundance in roots, leaves, flowers and silique (MacMillan et al., 2010). *AtFLA1* and *AtFLA4* possess low expression level in stems and extremely high expression level in root vascular tissues, indicating that these two genes have functional redundancy and respective expression characteristics. In addition, *AtFLA1* is highly expressed in petioles, stomata and trichomes, while *AtFLA4* tends to be expressed in guard cells and root tips (Johnson et al., 2011; Li et al., 2010). In general, sequences with high similarities exhibit similar expression levels and characteristics. However, the similarity between these two sequences is lower than 50%. According to the classification results of *Arabidopsis* FLAs, genes with similar functions have consistent domain characteristics, which may result in their similar expression characteristics. Detection of GUS activity shows that *AtFLA3* is highly expressed in anthers, indicating that function of *AtFLA3* may be related with pollen development (Li et al., 2010). In recent years, a number of studies have been carried out on the expression patterns of *FLA* genes in rice, cotton and cabbage by qRT-PCR. Results show that *FLA* genes are expressed throughout the life cycle and exhibit high expression levels in stems, roots and reproductive organs (Huang et al., 2008; Li and Wang, 2012; Ma and Zhao, 2010).

Biological functions of FLA genes in plants

Compared with other members in the AGPs family, little information is available on FLAs in plants. At present, it has been confirmed that FLAs mainly affect plant growth and development.

FLA and pollen development

AtFLA3 plays an important role in the development of male reproductive organs and pollen grains of *Arabidopsis*, and directly confirmed the function of *AtFLA3* by overexpression and RNAi interference technology. RNAi transgenic plants with reduced expression of *AtFLA3* have shorter stamen filaments and mature silique, with developmental defects in the inner wall of pollen grains, resulting in a pollen abortion percentage of 50%, indicating that *AtFLA3* can maintain the integrity of the inner wall of pollen grains and provide a safe internal environment for the development of microspore. At the flowering stage, anthers of *AtFLA3*-overexpressing transgenic plants cannot reach the stigma, and the ratio of stamen filament length to pistil length is significantly lower than that in wild-type plants; thereby, leading to significant increase in sterility rate. Thus, it is inferred that *AtFLA3* plays an important role in the reproductive development of plants (Li et al., 2010).

FLA and shoot regeneration

FLA plays a significant role in the formation of new shoot and root meristems. Shoot regeneration will go through three stages in tissue culture: (a) responds to the hormone signal, (b) directional induced organogenesis, and (c) shoots emerged. The proportions of hormone are different in each phase (Christianson and Warnick, 1985). Wild-type maturation zone of root explants were incubated on callus medium for 4d, and then transferred to differentiation medium for 14d. The northern blot showed that mRNA level of *AtFLA1* and *AtFLA2* in root were significantly up-regulated on callus medium. The *AtFLA2* mRNA level of root was noticeably increased on differentiation medium, which indicates although these two genes involved in the same developmental pathways, but play a role in different phases. *AtFLA1* positively participated in the first two stages of shoot regeneration and perhaps *AtFLA2* involved in shoot induction process (Johnson, 2011). If we could carry out research on *fla1* and *fla2* mutants, it might help us to better understand how *FLA* gene plays in shoot regeneration. Maybe we could discover several new functions.

Recent researches indicate that there is no significant difference between the phenotypes of *fla1-1* mutants and wild-type *Arabidopsis*. GUS staining shows that *AtFLA1* is highly expressed in the primary root tips and lateral root base. The maturation zone of primary roots of *fla1-1* and *Col* were collected for callus induction. Subsequently, shoot induction showed that shoot regeneration rate of *fla1-1* was far lower than that of *Col*, and the root development rate was only 15%, suggesting that *AtFLA1* may be closely related with shoot regeneration. Compared with *Col*, lateral root number and root length of *fla1* mutants increased slightly (Johnson et al., 2011). However, the specific mechanism of the influences of *AtFLA1* on lateral root development requires further investigation.

FLA and cell adhesion

Proteoglycan deficiency will seriously affect plant growth and development. As one of the important members encoding cell surface adhesion proteins, *SOS5* exists in organs and tissues of all plants. Researchers used a transmission electron microscope to observe the root tips of *Col* and found that the epidermal cells and cortical cells are separated by high-electron

Table 1. Classification of AGPs in *Arabidopsis thaliana.*

Name	Genes	Amino acids	Signal peptide	GPI anchor
Classical AGPs	22	87-739	19	14
Lysine-rich AGPs	3	185-247	3	2
AG peptide	16	58-87	16	12
Chimeric AGPs	17	177-370	17	16
Fasciclin-like proteins FLAs	21	247-462	20	11
nonclassical AGPs	6	222-826	5	1

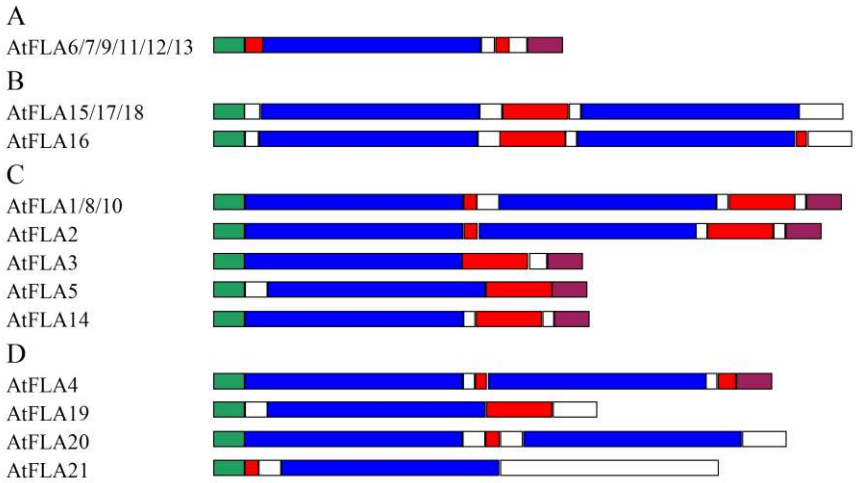

Fig 1. Schematic representation of *Arabidopsis* FLAs deduced from DNA sequences (Modified from Johnson et al., 2003).
The AtFLAs are classified into four groups (A–D) based on the numbers of AGP-like regions and fasciclin-like domains. The colored regions indicate the N-terminal secretion signal (green), fasciclin-like domain (blue), AGP-like region (red), and C-GPI addition signal (purple).

opaque intercellular layers, but the intercellular layers in *sos5* mutants are not obvious. Further high-magnification observation showed that the intercellular layers may be composed of polysaccharides. However, due to the lack of polysaccharides in the intercellular layers, *sos5* mutants had thinner cell wall and exhibited abnormal cell expansion. Previous studies have shown that *AtAGP8* encodes cell adhesion proteins. The sequences of *AtSOS5* and *AtAGP8* are similar, suggesting that *AtSOS5* may be also involved in the synthesis of intercellular adhesion proteins to maintain normal cell expansion (Shi et al., 2003). The immunofluorescence labeling found that AtSOS5 has the property of highly glycosylation, which exists in the outer surface of the plasma membranes. This is the important theory for structure of the cell wall and cell expansion. GPI anchor signal may be involved in gene location.

In addition to the above functions, SOS5 also plays an important role in the synthesis of seed coat mucilage. In the process of seed development, seed coat mucilage-secreting cells continuously produce and release mucilage to the seed surface. Seeds maintain moisture balance and provide moisture for seed germination via self-absorption. The microscopic studies of *Arabidopsis* seed surface show that the inner-layer mucilage in *sos5* mutant seeds was reduced with structural change, but the outer-layer mucilage exhibited no changes (Harpaz-Saad et al., 2011).

FLA and cell wall formation

Researchers have found that *FLA* genes can be specifically and efficiently expressed in the stems of most angiosperms. The study found that the tensile intensity and stiffness declined, the structure and composition of the cell wall changed, contents of cellulose, arabinose and galactose decreased, lignin content and microfibril angle increased in *fla11/12* mutants (MacMillan et al., 2010). These indicate that *AtFLA11* and *AtFLA12* genes are involved in the synthesis of secondary cell wall. In addition, Ze*FLA11* gene can only be expressed in differentiating xylem vessels and adjacent parenchyma cells, resulting in thickening of secondary cell wall. This also shows that lots of glycoprotein deposited in differentiation of metaxylem tissue with reticulate vessels of secondary wall (Dahiya et al., 2006). *LuFLA1* can be expressed in phloem fiber and shows extremely high activity and specificity, which indicates that *LuFLA1* plays a key role in the formation of phloem fiber secondary cell wall. According to the above studies, *FLA* genes are important for the formation of secondary cell wall and wood (Hobson and Deyholos, 2013).

Currently, a large number of AGPs involved in the formation and elongation of fibers and the synthesis of secondary cell wall have been identified. They play an important regulatory role in fiber development. As a member of the AGP family, FLA also has similar function. Cotton *GhFLA* gene is related with the synthesis of primary cell wall. *GhFLA*-overexpressing transgenic plants exhibit significantly longer fibers, higher pectin level and lower contents of cellulose and hemicellulose, which is contrary to that in the inhibition of expression of *GhFLA*. Compared with non-transgenic cotton, the content of glucose, arabinose and galactose in the primary cell wall of transgenic cotton exhibited certain variations, which indicates that *GhFLA1* is not only related with the development of fibers, but also associated with the synthesis of primary cell wall (Huang et al., 2013). *GbFLA5* isolated from *Gossypium barbadense* affects fiber development and improves fiber strength by encoding important secondary cell wall specific proteins. As an important secondary cell wall specific proteins, *GbFLA5*

can affect the synthesis of cellulose on secondary cell wall and the angle of cellulose microfibrils. As the major cell wall-associated protein, AGP is widely distributed in plants. FLAs belong to chimeric AGPs and also plays a quite important role (Liu et al., 2013).

FLA and high-salinity stress

In recent years, a large number of studies have shown that ABA can improve the ability of drought resistance and salt tolerance in plants by lowering the stomatal movement. Under abiotic stress conditions, large amounts of ABA are accumulated in plants; however, applying exogenous ABA will improve the resistance in plants. *AtFLA4* gene is involved in the response of plants to high-salinity stress and can be induced by ABA. Under 100 mM NaCl stress, the root of *fla4* mutants exhibited shortened and swollen phenotype as a self-preservation response in plants. Applying an appropriate concentration of ABA can completely inhibit the phenotype produced by *fla4* mutants under high-salinity stress. Cell expansion is strictly controlled during cell growth and development. The plant show high levels of organization and regularity even under high salt stress. However, under high-salinity stress, applying ABA to roots of wild-type individuals poses no significant influences. Therefore, *AtFLA4* is conducive to the response of roots to high-salinity stress and can improve the salt tolerance in plants (Shi et al., 2003; Seifert et al., 2014).

It is interesting to note that *PtX14A9* of loblolly pine is *AtFLA11* homologous gene and preferentially expressed in xylem, which did not respond to ABA but decreased under drought stress. This shows that *FLA* induces distinct responses to plant hormones, which widely participates in plant biotic stress responses. Cotton fibers at 10d post-flowering were subjected to 200 mM NaCl and found that, except *GhFLA1*, other *GhFLA* genes were all down-regulated, indicating that *FLA* genes play an important role in response to high-salinity stress (Huang et al., 2013). In addition, wheat *TaFLA* gene expression abundance all have varying degrees of decline in heat, cold, salt, and drought treatment. It can be seen that the *FLA* genes can response to multiple stresses (Faik et al., 2006)

Other functions

It is an interesting phenomenon that the expression level of *SOS5* gene in guard cells is very high. It is presumed that guard cells are powerful entities with frequent and rapid swelling and contraction during stomatal opening and closing. The *SOS5* can produce proteoglycan and highly expressed in the specific types of cells which help guard cells to complete this special physical behavior (Shi et al., 2003).

Researchers have identified 15 *PopFLA* genes from Poplars. *PopFLA1-10* are expressed in tension wood, differentiating xylem and tension wood mature xylem. The rocket electrophoresis and immunocytochemistry method were also confirmed this conclusion. There is a high expression for the rest of *PopFLA* genes in differentiating xylem. The main function of *PopFLA* is to build secondary cell wall and stem biomechanics. What causes high specificity of poplar *PopFLA* is not known and studies are needed to find out the mechanism of action (Lafarguette et al., 2004).

Conclusion and outlook

As a member in the AGPs family, *FLA* genes are widely distributed in various tissues, organs and cells of higher plants. However, *Arabidopsis fla* mutants have not attracted much attention due to the lack of significant differences in the phenotype. At present, only a small number of *FLA* genes in *Arabidopsis*, cotton, wheat and other model plants have been identified and analyzed. Existing studies have shown that *FLA* may be related with plant cell wall formation, lateral root development and cell adhesion. This demonstrates that *FLA* plays certain roles in plant growth and development, but the depth and width of studies are still insufficient. There are still many important and challenging issues to be resolved. For instance, how do *FLA* genes with similar or the same functions play the role? In case of functional redundancy, what factor determines which gene to play a role primarily? Will knocking out a single or multiple redundant genes affect the growth and development of plants? What are the functions and mechanism in guard cells? By changing the plant growth environment and the development of the process, will stimulus help to reveal the *FLA* function? In short, with the rapid development of modern molecular genetics, cell biology and biochemistry techniques, *FLA* genes can be analyzed in-depth *via* sense and antisense expression, gene knock-out and other approaches; thus contributing to investigating the biological functions.

Besides the theoretical research value, *FLA* genes also possess certain practical values. For instance, proteins encoded by *FLA* genes are important components of acacia. In ancient Egypt, acacia was used as a type of adhesion agent to produce hieroglyphics. In modern times, acacia has been used as a novel food additive instead of perfumes and pigments (Showalter, 2001). Acacia can also be used in the sugar industry, seal industry, printing industry, cosmetics industry and pharmaceutical industry. In addition, acacia is also an ideal emulsifying agent with low viscosity and good adhesive function to prevent sugar crystallization. Therefore, acacia is very suitable to be used as an emulsion stabilizer such as citrus oil emulsion which is commonly used in soft drinks. In summary, the investigation and development of *FLA* genes have broad applied prospects (Majewska-Sawka and Nothnagel, 2000).

Acknowledgements

This work was supported by Twelfth Five National Key Technology R&D program (2012BAD01B03).

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