Different responses of banana classical AGP genes and cell wall AGP components to low-temperature between chilling sensitive and tolerant cultivars

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Abstract

Key message Seventeen classical MaAGPs and 9 MbAGPs were identified and analyzed. MaAGP1/2/6/9/16/17, the antigens of JIM13 and LM2 antibodies are likely to be involved in banana chilling tolerance.

Classical arabinogalactan proteins (AGPs) belong to glycosylphosphatidylinositol-anchored proteins, which are proved to be involved in signaling and cell wall metabolism upon stresses. However, rare information is available on the roles of classical AGPs in low temperature (LT) tolerance. Cultivation of banana in tropical and subtropical region is seriously threatened by LT stress. In the present study, 17 classical MaAGPs and nine MbAGPs in banana A and B genome were identified and characterized, respectively. Great diversity was present among different classical MaAGP/MbAGP members while five members (AGP3/6/11/13/14) showed 100% identity between these two gene families. We further investigated different responses of classical AGPs to LT between a chilling sensitive (CS) and tolerant (CT) banana cultivars. In addition, different changes in the temporal and spatial distribution of cell wall AGP components under LTs between these two cultivars were compared using immunofluorescence labeling. Seven classical MbAGPs were upregulated by LT(s) in the CT cultivar. Classical MaAGP4/6 was induced by LT(s) in both cultivars while MaAGP1/2/9/16/17 only in the CT cultivar. Moreover, these genes showed significantly higher transcription abundance in the CT cultivar than the CS one under LT(s) except classical MaAGP4. Similar results were observed with the epitopes of JIM13 and LM2 antibodies. The antigens of these antibodies and classical MaAGP1/2/6/9/16/17 might be related to LT tolerance of banana. These results provide additional information about plant classical AGPs and their involvement in LT tolerance, as well as their potential as candidate genes to be targeted when breeding CT banana.

Keywords Banana (Musa spp.) · Classical arabinogalactan proteins · Genome-wide identification · Immunofluorescence labeling · Low temperature · Plant cell wall

Abbreviations

AGPs Arabinogalactan proteins
CS Chilling-sensitive
CT Chilling-tolerant
GPI Glycosylphosphatidylinositol
LT Low temperature
PASTT% The percentage of Pro, Ala, Ser, and Thr in whole protein sequence
qPCR Quantitative real-time PCR
MEME Multiple Em for Motif Elucidation
MW Molecular weight
NJ Neighbor-joining
UTR Untranslated region

Introduction

Low temperature (LT) is one of the most important abiotic stresses affecting plant growth and development, and thereafter seriously threatening crop production (Chinnusamy et al. 2007; Zhang et al. 2011a; Cui et al. 2018). Banana
Plant cell walls are the first physiological barriers when plants encounter stresses from the environment. Plants adopt many strategies to survive dynamic environmental changes, such as cell wall remodeling (Rui and Dinneny 2019), changes in cell wall structures and composition (Ma et al. 2013; Yan et al. 2015), modulating defense-related signaling (Van Holle and Van Damme 2018; Seifert 2021), protein modification (Gong et al. 2020), and gene expression (Sperotto et al. 2018; Meng et al. 2020; Yuan et al. 2021). Plant cell walls are complex and dynamic structures, which are composed mostly of polysaccharides, smaller proportions of highly glycosylated proteins and, in some specialized cell types, various noncarbohydrate substances such as lignin, suberin and cutin (Fry 2004). There are five cell wall glycoproteins classes, namely exensin, glycin-rich proteins, proline-rich proteins, arabinogalactan proteins (AGPs) and solanaceous lectins (Showalter 1993). AGPs are one of the most complex types of macromolecules found in plants and widely distributed in the plant kingdom (Showalter 2001; Ellis et al. 2010). Classical AGPs, one AGP subfamily, possess an N-terminal signal sequence, a core protein region rich in Pro, Ala, Ser, and Thr (PASTT%>50%), followed by a C-terminus glycosylphosphatidylinositol (GPI) anchor (Showalter et al. 2010). In 1998, five genes encoding the protein backbones of classical AGPs were firstly identified in Arabidopsis (Arabidopsis thaliana) (Schultz et al. 1998). From then on, classical AGP families have been identified in several other plant species, such as rice (Oryza sativa), Chinese cabbage (Brassica rapa) and eelgrass (Zostera marina) (Ma and Zhao 2010; Showalter et al. 2010; Han et al. 2017; Ma et al. 2017; Pfeifer et al. 2020).

During the past decades, AGPs have been implicated in various processes associated with plant growth and development (Choi et al. 2010; Lamport et al. 2018; Lopez-Hernandez et al. 2020; Huang et al. 2021), and responses to various biotic and abiotic stresses (Mareri et al. 2018; Zhao et al. 2020; Huang et al. 2021), and various signaling (Van Holle and Van Damme 2018; Seifert 2021), protein modification (Gong et al. 2020), and gene expression (Sperotto et al. 2018; Meng et al. 2020; Yuan et al. 2021). Plant cell walls are complex and dynamic structures, which are composed mostly of polysaccharides, smaller proportions of highly glycosylated proteins and, in some specialized cell types, various noncarbohydrate substances such as lignin, suberin and cutin (Fry 2004). There are five cell wall glycoproteins classes, namely exensin, glycin-rich proteins, proline-rich proteins, arabinogalactan proteins (AGPs) and solanaceous lectins (Showalter 1993). AGPs are one of the most complex types of macromolecules found in plants and widely distributed in the plant kingdom (Showalter 2001; Ellis et al. 2010). Classical AGPs, one AGP subfamily, possess an N-terminal signal sequence, a core protein region rich in Pro, Ala, Ser, and Thr (PASTT%>50%), followed by a C-terminus glycosylphosphatidylinositol (GPI) anchor (Showalter et al. 2010). In 1998, five genes encoding the protein backbones of classical AGPs were firstly identified in Arabidopsis (Arabidopsis thaliana) (Schultz et al. 1998). From then on, classical AGP families have been identified in several other plant species, such as rice (Oryza sativa), Chinese cabbage (Brassica rapa) and eelgrass (Zostera marina) (Ma and Zhao 2010; Showalter et al. 2010; Han et al. 2017; Ma et al. 2017; Pfeifer et al. 2020).
to compare different changes in the abundance and distribution of their antigens in leaves between these two banana cultivars. The results not only can provide additional information about plant classical AGPs and their involvement in LT response, but also can help to screen candidate classical AGP genes potentially involved in chilling tolerance for banana breeding.

Materials and methods

Plant materials and natural LT conditions

Plant materials used in the present study and the LT conditions were described by Meng et al. (2020). In brief, samples were collected from two banana genotypes, *Musa* spp. AAA cv. Baxijiao (CS) and *Musa* spp. ABB cv. Dongguandajiao (CT), in the field when the average daily temperature was approximately 25 °C, 16 °C, 10 °C and 6 °C during a cold wave in winter. The changes in temperature and humidity are shown in Fig. S1. Three replicates were completed for each temperature point.

Identification of classical AGPs by calculating the biased amino acid composition and length

All banana proteins were downloaded from banana genome hub (http://banana-genome-hub.southgreen.fr/), banana A genome proteins from "Musacumminata_ssp.malaccensis_2.0" (updated on 14 October 2021), banana B genome proteins from "Musabalbisiana_BGI_1.1" (updated on 12 October 2021). The searching criteria for classical AGPs referred to the guidelines that are widely used by previous studies (Schultz et al. 2002, 2004; Tan et al. 2003; Ma and Zhao 2010). A Python script named Finding-AGP was obtained from Prof. Haoli Ma (Northwest A&F University, Yangling, China) to calculate the sequences characteristics of whole protein sequences and AGP-like sequences (part of whole protein sequences). The Finding-AGP script could screen for AGP candidates using seven variables parameters, including the length of whole protein sequence (LengthP)>90 amino acids, the percentage of Pro, Ala, Ser, and Thr in whole protein sequence (PASTT%)>50%, and the length of AGP-like sequence (Lengthp)>55%, the glycocomodule number of the whole protein sequence (GlycoNoP)>0, the number of Ala-Pro, Pro-Ala, Ser-Pro, Pro-Ser, Thr-Pro, and Pro-Thr in AGP-like sequence (GlycoNoP)>5, and the glycocomodule index of the AGP-like sequence (GlycoIndex) set to 0.15. In addition, the proteins were classified as classical AGPs if they contained predominantly Ala-Pro, Pro-Ala, Ser-Pro, or Thr-Pro throughout the protein with no more than 11 amino acid residues between consecutive Pro residues, but did not contain repeats associated with extensins or proline-rich proteins (e.g. Ser-Pro3/4, Pro-Pro-Val repeats or C-Xn-C-Xn-CC-Xn-CXC-Xn-C-Xn-C) (Schultz et al. 2002; Zhang et al. 2021).

Signal GPI and subcellular localization prediction

The N-terminal signal peptides were predicted using SignalP 4.1 Server (https://services.healthtech.dtu.dk/service.php?SignalP-4.1) (Nielsen 2017), the input files were in fasta format and the D-cutoff values (0.34) were set in the sensitive mode. The C-terminal GPI-anchored signals were determined on big-PI Predictor-GPI Modification Site Prediction (https://mendel.imp.ac.at/gpi/plant_server.html) (Eisenhaber et al. 2003). Proteins possessing both signal peptide and GPI anchor were considered as classical AGPs, and their subcellular localization was predicted by ProtComp 9.0 (http://linux1.softberry.com/).

Physicochemical properties and phylogenetic analysis of banana classical AGP genes

All the final presumed classical AGP protein sequences were submitted to Expasy online software4 (https://web.expasy.org/compute_pi/) to calculate molecular weight (MW) and theoretical isoelectric point. TBtools (Chen et al. 2020) was used to get the chromosomal positions of MaAGPs and MbAGPs. Multiple sequence alignment of the amino acid sequences of classical AGP proteins, including the reported classical AGP protein sequences of Arabidopsis from the Arabidopsis information resource (TAIR, https://www.arabidopsis.org/), and rice (Oryza sativa) from rice genome annotation project (RGAP, http://rice.uga.edu/) (Ma et al. 2010), were performed using MUSCLE in MEGA 7.0.26 software with default parameters. The phylogenetic tree of classical AGP was constructed by MEGA 7.0.26 software according to the neighbor-joining (NJ) method (Kumar et al. 2016), and the test parameter bootstrap was repeated 1000 times.

Analysis of gene structure and conserved motifs

The exon/intron structures of the genes were illustrated through Gene Structure Display Server (GSDS, http://gsds.gao-lab.org/). Multiple Em for Motif Elicitation (MEME, https://meme-suite.org/tools/meme) was employed to identify the conserved motifs with default settings except number of motifs where the number of motif was set as 10. The TBtools (Chen et al. 2020) was used to display the results.

qPCR detection of AGP expression in bananas

The differential responses of classical AGPs at transcript level between the CS and CT banana cultivars to natural LT
conditions was revealed by qPCR analysis. Total RNA was extracted from the samples using the RNAprep Pure Plant Kit (TIANGEN, Beijing) and converted to cDNA using HiScript III RT SuperMix for qPCR (+gDNA wiper) (Vazyme, Nanjing) following the manufacturer's guidelines. qPCR reactions were performed as reported by Chen et al. (2011) and the actin1 gene was selected as the calibration gene. The relative expression levels of target genes were calculated with formula 2-ΔΔCT method. The primers used in this study are illustrated in Supplementary Table S1.

**Immunofluorescence labeling analysis of AGPs and quantification of the signal intensity**

The fixation and immunolabeling fluorescence were performed according to the method described by Xu et al. (2011). Primary antibodies used in this study and their antigens are listed in Table S2. LM2 and LM14 were purchased from PlantProbes (Leeds, UK), while all the other antibodies from Complex Carbohydrate Research Center (Athens, USA). The secondary antibody was anti-rat IgG-FITC (F6258, Sigma). An Axio Imager D2 used to examine the fluorescence and ZEN software was employed to quantify the fluorescence. Three biological replicates were prepared for each treatment. The fluorescence signal was selected using appropriate threshold levels for individual sections. Equal threshold levels were applied for each replicate, treatment and genotype for certain epitopes to ensure an exact comparison of cultivars and treatments.

**Statistical analysis**

Statistical analyses were performed using ANOVA in the statistics program IBM SPSS Statistics for Windows, version 21.0 (IBM Corporation, Armonk, NY, USA). At least three replicates were used in the experiments. The data are expressed as the mean ± SE. Differences between two cultivars for each temperature were statistically evaluated using Student’s t test.

**Results**

**Identification of banana classical AGP genes from Musa acuminata and Musa balbisiana**

In total, 17 classical MaAGP proteins of Musa acuminata have been identified according to genome database version 2.0 of banana A genome, and nine MbAGP proteins of Musa balbisiana according to newly released B genome.

The basic physiological and biochemical information of these two gene families were presented in Table 1. The information corresponding to MaAGPs and MbAGPs are presented in Table S3. Seventeen classical MaAGPs are located in all 11 banana chromosomes except Chr7 and 11. Classical MbAGPs are located only in 7 chromosomes (Chr2-6, 8-9). There was no classical MbAGPs in Chr7 and 11 (Table 1, Fig. S2A-B). The amino acid number of classical MaAGPs varied from 113 (classical MaAGP12) to 530 (classical MaAGP5), and it was 130 (classical MbAGP17) to 380 (classical MbAGP3-2) for MbAGPs. The MW of classical MaAGPs was from 11.0-51.6 kD, and that of classical MbAGPs varied from 12.5 to 36.1 kD. The PASTel% of both gene families was from 50 to 73 (Table 1). Eleven out of 17 classical MaAGPs (64.71%) and 7 out of 9 MbAGPs (77.78%) are alkaline proteins. Subcellular localization analysis based on the AGP amino acid sequences suggested that most of them are secreted to extracellular space, while MaAGP1/3/6/8/9/11 and MbAGP11/13/14/17 were predicted to be located at plasma membranes (Table 1).

**Molecular features of classical MaAGPs and MbAGPs**

As shown in Fig. 1a, classical MaAGPs could be classified into six clades (Class I, II, III, IV, V and VI). But there are only four clades (Class I, II III and IV) in MbAGP family (Fig. 1a). The intron/exon arrangements and conserved motifs of classical MaAGPs and MbAGPs are shown in Figs. 1b, 2b, respectively. The result indicated that most banana classical AGPs (11 classical MaAGPs and 6 classical MbAGPs) have no introns, while the others contain 1–2 introns. The conserved motifs of these two gene families were predicted by MEME and ten individual motifs were isolated. The results revealed that all classical MaAGPs possess motif 2 except MaAGP14 and all MbAGPs possess motif 1. There were great differences among the other classical AGPs (Figs. 1c, 2c).

**Phylogenetic analysis of the putative classical MaAGPs and MbAGPs**

For better understanding the evolutionary history of banana classical AGP proteins, a NJ phylogenetic tree was constructed from plant classical AGP domains from banana A and B genome. As shown Fig. 3, banana classical AGPs could be divided into six classes (Class I, II, III, IV, V and VI). Class II is the biggest class, containing 10 member while Class V is the smallest one, with only one member (MaAGP12). Classical AGP3/6/11/13/14 showed the 100% identity between A and B genome.

As mentioned above, phylogenetic analysis can reveal the evolutionary history of plant genes/proteins and therefore predict their physiological function. In the present study, a NJ phylogenetic tree was constructed from banana classical AGP domains from banana A (MaAGPs)/B...
Table 1  Putative classical arabinogalactan protein genes in *Musa acuminata* and *balbisiana*

| Gene name | Gene ID       | AP/PA/SP/TP Repeats | PASTT% | Chr       | Start     | End       | Strand | Amino Acid | pl    | MW (kD)   | Predicted localization     |
|-----------|---------------|---------------------|--------|-----------|-----------|-----------|--------|------------|-------|-----------|-----------------------------|
| MaAGP1    | Ma01_g14820   | 9/14/5/6            | 72.44  | chr01     | 10805841  | 10806506  | −      | 156        | 10.29 | 14472.75 | Plasma membrane              |
| MaAGP2    | Ma02_g14530   | 3/7/3/3             | 53.66  | chr02     | 22570063  | 22571119  | +      | 205        | 8.95  | 20132.08 | Extracellular (Secreted)    |
| MaAGP3    | Ma02_g15320   | 7/12/13/7           | 72.77  | chr02     | 23079946  | 23081656  | −      | 213        | 9.30  | 19850.59 | Plasma membrane              |
| MaAGP4    | Ma02_g19230   | 3/9/3/6             | 52.22  | chr02     | 25477670  | 25478577  | +      | 180        | 8.95  | 17707.39 | Extracellular (Secreted)    |
| MaAGP5    | Ma03_g04920   | 37/15/7/9           | 54.91  | chr03     | 3250482   | 3252123   | −      | 530        | 5.15  | 51608.99 | Extracellular (Secreted)    |
| MaAGP6    | Ma03_g06570   | 20/15/6/7           | 72.30  | chr03     | 4534189   | 4534632   | +      | 148        | 4.65  | 13836.80 | Plasma membrane              |
| MaAGP7    | Ma04_g07630   | 0/2/3/2             | 50.29  | chr04     | 5522974   | 5523946   | −      | 171        | 4.78  | 16578.81 | Extracellular (Secreted)    |
| MaAGP8    | Ma04_g09680   | 10/11/8/1           | 65.70  | chr04     | 6871321   | 6871836   | +      | 172        | 3.92  | 15911.49 | Plasma membrane              |
| MaAGP9    | Ma04_g24210   | 7/6/11/7            | 72.09  | chr04     | 26271570  | 26272085  | −      | 172        | 8.02  | 16103.36 | Plasma membrane              |
| MaAGP10   | Ma04_g27880   | 2/3/2/9             | 53.62  | chr04     | 29037531  | 29038659  | −      | 207        | 9.10  | 20198.27 | Extracellular (Secreted)    |
| MaAGP11   | Ma05_g20100   | 6/9/5/3             | 69.40  | chr05     | 31277384  | 31278011  | −      | 134        | 9.52  | 12651.52 | Plasma membrane              |
| MaAGP12   | Ma05_g31510   | 4/3/8/0             | 59.29  | chr05     | 41393235  | 41393573  | +      | 113        | 9.43  | 11040.71 | Extracellular (Secreted)    |
| MaAGP13   | Ma06_g11780   | 7/10/8/7            | 73.05  | chr06     | 8213575   | 8214292   | −      | 141        | 9.50  | 13231.25 | Extracellular (Secreted)    |
| MaAGP14   | Ma06_g20320   | 3/2/4/2             | 53.14  | chr06     | 14396474  | 14416261  | +      | 175        | 9.39  | 17382.97 | Extracellular (Secreted)    |
| MaAGP15   | Ma08_g25260   | 9/11/10/1           | 65.90  | chr08     | 38191442  | 38191960  | −      | 173        | 3.96  | 16212.70 | Extracellular (Secreted)    |
| MaAGP16   | Ma09_g17930   | 12/14/12/4          | 67.50  | chr09     | 13770323  | 13771042  | +      | 240        | 3.67  | 21716.56 | Extracellular (Secreted)    |
| MaAGP17   | Ma10_g19190   | 10/9/5/4            | 69.01  | chr10     | 29839596  | 29840429  | +      | 142        | 9.70  | 13368.63 | Extracellular (Secreted)    |
| MbAGP3    | Mba02_g14340  | 5/11/13/8           | 72.95  | Bch02     | 25984350  | 25986136  | −      | 207        | 9.30  | 19338.96 | Extracellular (Secreted)    |
| MbAGP3-2  | Mba04_g39150  | 28/23/20/3          | 70.79  | Bch04     | 41814577  | 41816674  | −      | 380        | 11.67 | 36145.38 | Extracellular (Secreted)    |
| MbAGP6    | Mba03_g06560  | 16/11/7/8           | 70.95  | Bch03     | 4663954   | 4664397   | +      | 148        | 4.48  | 13960.93 | Extracellular (Secreted)    |
| MbAGP6-2  | Mba09_g13660  | 22/14/6/4           | 71.07  | Bch09     | 10039785  | 10042621  | +      | 159        | 7.94  | 14875.04 | Extracellular (Secreted)    |
| MbAGP11   | Mba05_g16950  | 7/9/5/4             | 71.43  | Bch05     | 20887270  | 20887668  | −      | 133        | 8.25  | 12487.27 | Plasma membrane             |
| MbAGP13   | Mba06_g10960  | 5/10/7/7            | 71.53  | Bch06     | 8656635   | 8657045   | −      | 137        | 9.50  | 12846.78 | Plasma membrane             |
| MbAGP14   | Mba06_g19140  | 2/26/4              | 50.00  | Bch06     | 14708339  | 14709640  | +      | 200        | 8.78  | 19758.50 | Plasma membrane             |
| MbAGP16   | Mba03_g10130  | 3/5/7/6             | 64.60  | Bch03     | 8169068   | 8169550   | +      | 161        | 3.99  | 14973.33 | Extracellular (Secreted)    |
| MbAGP17   | Mba08_g18280  | 6/6/6/2             | 65.38  | Bch08     | 31327062  | 31327451  | −      | 130        | 9.98  | 12519.37 | Plasma membrane             |

$kD$ kilodaltons, $MW$ molecular weight, PASTT\% the percentage of Pro, Ala, Ser, and Thr in whole protein sequence, $pI$ isoelectric point
(MbAGPs) genome, rice, as well as Arabidopsis, respectively. As shown in Fig. S3, several groups of classical AGPs from one plant species were separate from the others, such as MaAGP2/4/7/10, MaAGP11/13/17, AtAGP2/3/4/5/7/10 and AtAGP9/51/54/56/57/58. There are only two pairs of orthologous classical AGPs between banana and Arabidopsis (MaAGP9-AtAGP6/11, MaAGP12-AtAGP25/27), all showing identity of less than 30% (Fig. S3A). Two pairs of orthologous classical AGPs between banana and rice was less than 50% (MaAGP6-OsAGP4/5, MaAGP16-OsAGP3). Similar result was observed with the phylogenetic tree of classical AGPs from Musa balbisiana and Arabidopsis (Fig. S3B). These results suggest a great diversity in AGPs is present among different plant species, especially between monocotyledon and dicotyledon.

**Change in transcriptional expression of banana classical AGPs under LT**

qPCR was used to reveal the systemic responses of MbAGPs in the CT cultivar to LT stress. As shown in Fig. 4, seven out of nine MbAGP gene family members were upregulated by LT(s). MbAGP6-2 and MbAGP13 showed higher expression level only at 6°C (Fig. 4a–b), MbAGP3-2, MbAGP16 and MbAGP17 only at 16°C (Fig. 4c–e), MbAGP14 at 10°C (Fig. 4f), and it was both 16°C and 6°C for MbAGP3 (Fig. 4g). No significant change was observed with the expression of MbAGP11 after exposure to LTs (Fig. 4h). MbAGP6 was inhibited by LT stress (Fig. 4i). The responses of classical MaAGPs in the CS cultivar to LTs were quite different from those in the CT one. MaAGP1,
MaAGP9, MaAGP16, MaAGP17, MaAGP2, MaAGP12 and MaAGP15 were induced by LT only in the CT cultivar (Fig. 4j-p), and the former four classical MaAGPs showed significant higher expression levels in the CT cultivar than the CS one under LTs (Fig. 4j-m). On the contrary, MaAGP11 and MaAGP13 were only induced by LT(s) in the CS cultivar. However, the CT cultivar still showed significantly higher expression level than the CS one at 25°C, and also under LT of 16°C or 6°C, the expression level in the control CT plants cultivar was 85.56–94.86% higher than the CS one, respectively (Fig. 4q-r). MaAGP5 was inhibited by LTs in the CS cultivar but it kept stable in the CT one (Fig. 4s). MaAGP14 showed a decreased expression level in the CT cultivar under LTs (Fig. 4t). Only MaAGP4, MaAGP6-7 and MaAGP3 showed similar responses to LT stress in both cultivars, the former three were induced by LTs while it was on the opposite for MaAGP3 (Fig. 4u-x). Among them, the expression level of MaAGP3 and MaAGP6 in the CT cultivar was higher than the CS one at two temperature points, respectively.

**Subcellular distribution of AGPs in banana leaves and their responses to natural LT stress**

**Antigens of JIM4, JIM16 and JIM14 antibodies**

As shown in Fig. 7a, very weak JIM13 signal was observed mainly in the bundle sheath and epidermis in the CS cultivar. Differently, this antibody showed much stronger signal in the sclerenchyma cells and the epidermis (including the guard cells) in the CT cultivar (Fig. 7b). Natural LT stress resulted in a significant increase in antibody intensity in both cultivars. The signal intensity in the CT cultivar was higher than the CS one at 25 °C and 10 °C (Fig. 7c). Very strong signal of the JIM15 antibody was present in the bundle sheath, the sclerenchyma cells and the guard cells of the CS cultivar. A weak signal could be observed in the epidermal cells (Fig. 7d). When compared to the CS cultivar, the signal in the epidermis and hypodermis cells of the CT cultivar was slightly stronger, while that in the bundle sheath was nearly undetectable (Fig. 7e). Upon LT stress, an increase in the antibody intensity was observed only in the CS cultivar, which showed higher antibody intensity than the CT one at 25 °C and 16 °C (Fig. 7f).
Antigens of LM2, LM14, and MAC207 antibodies

In the CS cultivar, a moderate fluorescent signal of LM2 antibody was observed in the mesophyll cells whereas in the phloem and the xylem, the fluorescent intensity was much stronger (Fig. 8a). When compared to the CS cultivar, the CT cultivar showed much stronger signals in the bundle sheath and mesophyll cells (Fig. 8b). Natural LT stress resulted in an accumulation of the antigen in both cultivars, and the antigen level in the CT cultivar was significantly (24.66% to 49.46%) higher than that in the CS cultivar at all tested temperatures (Fig. 8c).

Middle signal of LM14 antibody could be observed across the leaf section of banana, with relatively weaker one in the leaf vein. The image from the CS cultivar was selected as the representative (Fig. 8d). The LM14 antibody antigen did not response to LT stress, and no difference in antigen level was present between the CS and CT cultivars except at 6 °C (Fig. 8f). The labelling pattern of MAC207 antibody was similar to that of LM14 in both cultivars (Fig. 8e) but this was not the case for its response to LT. An increase in MAC207 intensity was observed in the CT cultivar when the temperature dropped to 16 °C. The CT cultivar showed higher antibody intensity than the CS one at this temperature points while it was on the contrary at 25 °C and 10 °C (Fig. 8g).

In the present study, the distribution of eight AGP components in 6-month-old CS and CT banana cultivars was calculated using one-way ANOVA followed by a Duncan’s multiple range tests. Values marked with a star were considered significant at \( P < 0.05 \), while values marked with two stars were considered significant at \( P < 0.01 \) when evaluated using Student’s t test.

![Fig. 4 qPCR analysis of classical arabinogalactan protein gene expression in banana (Musa spp.) under natural low-temperature. BX ‘Baxijiao’, chilling sensitive; DJ ‘Dongguandajiao’, chilling tolerant. Data are the average of three replicates ± standard error. Different letters above the bars indicate significantly different values (\( P < 0.05 \))](image-url)
investigated, and they were compared to each other using an immunofluorescence labeling method. An overview of the immunolabeling results of AGPs in the two banana cultivars is provided in Table S4. Six antibodies showed different labeling patterns between these two cultivars. The CT cultivar showed higher antigen levels of JIM4, JIM14 and LM2 antibodies in the bundle sheath, higher antigen levels of LM2, JIM13, JIM15 and JIM16 in the epidermis and hypodermis cells, higher antigen levels of LM2 in the mesophyll, and a higher antigen level of JIM13 in the sclerenchyma cells when compared to the CS cultivar.

**Fig. 5** The distribution and the response of AGPs recognized by JIM4 antibody in banana (*Musa* spp.) leaves. BS bundle sheath, Ph phloem, Xy xylem vessel. Bars represent 50 µm. a Distribution in BX ('Baxijiao', chilling sensitive), b Distribution in DJ ('Dongguandajiao', chilling tolerant), c Changes in fluorescence signal optical density. Data are the average of three replicates ± standard error. Different letters above the bars indicate significantly different values (*P*<0.05) calculated using one-way ANOVA followed by a Duncan’s multiple range tests. Values marked with a star were considered significant at *P*<0.05, while values marked with two stars were considered significant at *P*<0.01 when evaluated using Student’s *t* test.

**Fig. 6** The distribution and the response of AGPs recognized by JIM16 and JIM14 antibodies in banana (*Musa* spp.) leaves. BS bundle sheath, Hy hypodermis, LE lower epidermis, Me mesophyll, Ph phloem, Sc sclerenchyma cells, UE upper epidermis, Xy xylem vessel. Bars represent 50 µm. a, d Distribution in BX ('Baxijiao', chilling sensitive), b, e Distribution in DJ ('Dongguandajiao', chilling tolerant). c, f Changes in fluorescence signal optical density. Data are the average of three replicates ± standard error. Different letters above the bars indicate significantly different values (*P*<0.05) calculated using one-way ANOVA followed by a Duncan’s multiple range tests. Values marked with a star were considered significant at *P*<0.05, while values marked with two stars were considered significant at *P*<0.01 when evaluated using Student’s *t* test.
the other hand, the CS cultivar showed stronger signals of JIM13, JIM15 and JIM16 in the bundle sheath.

Discussion

The classical MaAGP and MbAGP gene families

The AGP family are probably one of the most heterogeneous and complex families of macromolecules in the plant kingdom due to their structure, high glycosylation, and high similarity in carbohydrate moieties. The identification of gene families and their feature analysis can give people help in understanding their structure, function, and evolution. Till today, though classical AGP gene families have been identified in several types of plants, most of them have been identified not according to the present criteria (with 100% of N-terminal signal and GPI) (Han et al. 2017; Ma et al. 2017). The number of identified classical AGP genes varies among plant species, ranging from 2 in *Solanum lycopersicum* (Fragkostefanakis et al. 2012) to 36 in *Brassica rapa* (Ma et al. 2017) (Table S5). In this study, 17 and 9 genes were identified to be putative classical MaAGPs and MbAGPs, respectively.

Interestingly, there are no introns in most banana classical AGPs. Similar result was observed in Arabidopsis (Schultz et al. 2002). In agreement with previous studies (Ma and Zhao 2010; Han et al. 2017; Ma et al. 2017), great differences in the molecular and physiological natures (e.g. MW, isoelectric point, PASTT%, UTRs, the number of intron and exons) were present among different members in classical MaAGP or MbAGP gene family. Moreover, great variation is also present between MaAGPs and MbAGPs, including the size of gene family. However, there are five banana classical AGP genes (AGP3/6/11/13/14) showing 100% identity between A and B genome, suggesting conservation feature of plant classical AGPs in some way.

Involvement of banana classical AGPs in LT stress

As mentioned above, LT stress is one of most important factors that limit banana growth and productivity. Change in gene expression is one of the responses of plants when encountered biotic and abiotic stresses. In the present study, qPCR was employed to compare the response of classical MaAGP and MbAGP gene families in the CT and CS banana cultivars to natural LT conditions. The results revealed that the members from these two gene families responded to

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Fig. 7 The distribution and the response of AGPs recognized by JIM13 and JIM15 antibodies in banana (*Musa* spp.) leaves. BS bundle sheath, GC guard cells, Hy hypodermis, Ep epidermis, Sc sclerenchyma cells, Xy xylem vessel. Bars represent 50 µm. a, d Distribution in BX (‘Baxijiao’, chilling sensitive), b, e Distribution in DJ (‘Dongguandajiao’, chilling tolerant). c, f Changes in fluorescence signal optical density. Data are the average of three replicates ± standard error. Different letters above the bars indicate significantly different values (*P*<0.05) calculated using one-way ANOVA followed by a Duncan’s multiple range tests. Values marked with a star were considered significant at *P*<0.05, while values marked with two stars were considered significant at *P*<0.01 when evaluated using Student’s *t* test.
the natural LT stress differentially, among different family members and between the CS and CT cultivars. Similarly, our previous study indicated that another AGP subfamily, MaFLAs, was also differentially regulated by LT in banana (Meng et al. 2020). Fluctuation of AGP levels under LT stress occurs also in other plant species (Faik et al. 2006; Ma and Zhao 2010).

More importantly, the responses of MaAGP to LT stress were cultivar dependent. Under natural LT stress, most MaAGPs (10 out of 15 tested ones) in the CT cultivar were upregulated. However, there was only five MaAGPs in the CS showing an increased expression level under LT stress. Furthermore, six out of the ten upregulated MaAGPs (1/2/6/9/16/17) showed significant higher expression level in the CT cultivar than the CS one under LT(s) (at least at one LT point), and most of these genes belong to Class II and III. Among these six genes, MaAGP1/2/9/16/17 were upregulated by LT(s) in the CT cultivar but downregulated or kept stable in the CS one, while MaAGP6 were induced by LT(s) in both cultivars, suggesting their potential involvement of banana chilling tolerance.

Upregulation of these classical MaAGPs (MaAGP1/2/6/9/16/17) under LT stress might continuously release them as soluble monomers into the cytoplasm through cleavage of the anchor (Yeats et al. 2018), which could protect banana cell from damage resulted by LTs. Second, they might contact specific receptors located in the plasma membrane (e.g. wall-associated kinase) to form...
complexes, and/or interact with other plant cell components (e.g. pectin), and thereafter modulate LT stress signalling pathway (Tan et al. 2003; Yeats et al. 2018; Zhou 2019), leading to the activation of specific genes directly involved in low-temperature tolerance (Takahashi et al. 2016; Mareri et al. 2018). Third, these AGPs might accumulate between membranes and cell wall matrix and form a “buffer zone” that could prevent the direct interaction between them and thereby keep membrane stabilization under LT stress (Mareri et al. 2018). Further work should reveal the biological functions of these classical MaAGPs when subjected to LT stresses.

Different responses of cell wall AGP components to LT stress between the CS and CT cultivars

Structural modifications in cell wall are one of the most important tactics of plants in adaptation to the new environmental conditions rapidly (Xie et al. 2011; Pinski et al. 2019; Basińska-Barczak et al. 2020; Wolny et al. 2021). In the present study, eight antibodies that recognize different cell wall AGP components were employed to study their temporal and spatial distribution in banana leaves and the different responses (changes in the temporal and spatial distribution and abundance) of their antigens between CS and CT cultivars after encountered natural LT stress. First, we found that the distribution of AGPs was cultivar-specific, as six antibodies showed different distribution pattern between the CT and CS banana cultivars. For instance, higher levels of LM2 antigens were observed in the mesophyll in the CT cultivar when compared to the CS one. Cultivar-specific distribution of cell wall AGP components were observed in some other plant species (Xie et al. 2011). Whether the different labelling pattern between the CT and CS cultivar is related to the stress adaptation need further experimental investigation.

Second, the responses of AGP components to LT stress were both antibody- and cultivar-specific. For example, the epitopes of JIM15 and JIM16 in the CT cultivar kept stable under natural LT conditions, whereas in the CS cultivar, they were induced by LT stress. The epitope abundance of JIM13 and LM2 antibodies increased in both cultivars after exposure to LT stress, but this was not the case for the other six antibodies. This was good agreement with our previous study on younger banana plants upon artificial LT treatment (Yan et al. 2015). These results suggested that their epitopes might be involved in the chilling tolerance of banana to LTs. It was presumed that the JIM13 recognizing AGPs might be related to strengthening of the cell wall and providing better conditions for the transport of nutrients and water through leaf veins, while the AGP recognized by LM2 antibody might help banana maintain a relatively higher photosynthesis efficiency under LT stress. Differently, immunohisto-chemical analyses using antibodies bind to AGPs (JIM13, JIM16, LM2 and MAC207) were employed to investigate the responses of these AGPs to a LT (0 °C) and a high temperature (40 °C) in the leaves of Brachypodium distachyon. The authors found that the JIM16 epitopes decreased under LT stress, no changes were observed for AGP epitopes recognized by MAC207, LM2 and JIM13 antibodies. But the LM2 epitope was more abundant in leaves that had been subjected to the high temperature (Pinski et al. 2019). These findings suggest that the response of AGPs to LT stress is also plant species-dependent.

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Author contributions CX, XL, HC and CC conceived and designed research. JL, JM, TN, ZH, LD and ZS conducted experiments and/or prepared the materials. CX and JL analyzed the data and wrote the manuscript. All authors read and approved the manuscript.

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Declarations Conflict of interest The authors declare that they have no conflict of interest.

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