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Bioinformatic Analysis of Catalase Gene Family of *Arabidopsis* and Maize

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Abstract Catalase (CAT) is an antioxidant enzyme, which plays a key role in plant development and abiotic stress response. In this study, three maize *ZmCATs* and three Arabidopsis *AtCATs* genes were identified by screening NCBI and phytozome databases. The protein characteristics, evolutionary relationship, gene structure, protein secondary and tertiary structure, gene expression at different developmental stages or under abiotic stress treatment were analyzed. The results showed that there were some similarities between CAT families from the two species. The proteins encoded by ZmCATs and AtCATs genes were hydrophobic. According to phylogenetic tree analysis, CATs gene family was divided into two subfamilies. ZmCATs and AtCATs both contain two conserved domains, and the secondary structures of ZmCATs and AtCATs protein are mainly α-helix and random coils. The cluster analysis of ZmCATs expression in different growth and development stages showed that *ZmCAT1*, *ZmCAT2* and *ZmCAT3* were highly expressed in maize growth and development stage. Under abiotic stress, the expression of *ZmCATs* gene was significantly affected by temperature stress. The results of this study provide a theoretical basis for exploring the function of CAT in maize and other crops.
Keywords Maize (*Zea mays* L.); *Arabidopsis* (*Arabidopsis thaliana*); Catalase (CAT); Gene Family; Gene Expression; Abiotic stress

Catalase (CAT), which converts H_2O_2 to H_2O and O_2, is a common antioxidant enzyme in almost all organisms and plays an important role in the protection of plants against abiotic stresses and oxidative stresses (Zhou et al., 2018). CAT mainly scavenges hydrogen peroxide in free radicals and non-radical reactive oxygen species, thus maintaining a certain balance between the production and scavenging of ROS and maintaining the stability in plants (Sofo et al., 2015). The appropriate amount of H_2O_2 in an organism can act as a second messenger involved in cellular signaling pathways, causing activation of immune cells, cell proliferation, cellular senescence and apoptosis (Dash et al., 2012). On the contrary, excess ROS is capable of damaging various components in biological cells, such as proteins, lipids, DNA, etc. (Umeno et al., 2017). Therefore, CAT as a scavenger plays an extremely vital role in plants. The *CATs* gene family that encodes catalase in plants is a small family, which has been reported in different species. Barley (*Hordeum vulgare* L.) (Kendall et al., 1983) has 2 *CATs* genes, whereas there are three *CATs* genes in *Arabidopsis* (*Arabidopsis thaliana*) (Du et al., 2008), tobacco (*Nicotiana* L.) (Willekens et al., 1994) and rice (*Oryza sativa* L.) (Willekens et al., 2014), and four CATs genes in cucumbers (*Cucumis sativus* L.) (Hu et al., 2016) and Cotton (*Gossypium spp.*) (Wang et al., 2019). In cotton, the CAT proteins of two different varieties both contained a catalase core domain and a catalase immune response domain (Wang et al., 2019).

In ginseng, various expression profiles of *PgCat1* was found in the leaves, stems and roots of the seedlings (Purev et al., 2010). Different stresses such as heavy metals, plant hormones, osmotic agents, high light, and abiotic stress can all induce the expression of *PgCAT1* (Purev et al., 2010). The mRNA transcripts of *CAT1* and *CAT2* were only detected in non-senescent leaves of tobacco, but the expression of CAT3 was detected in both non-senescent leaves and senescent leaves (Niewiadomska et al., 2009). Overexpression of *ScCAT1* enhanced the growth of recombinant E. coli under the stress of $CuCl_2$, $CdCl_2$ and NaCl, indicating that ScCAT1 could improve the tolerance of recombinant E. coli (Su et al., 2014). In rice seedlings, *CATA*, *CATB* and *CATC* genes are highly

expressed in leaf sheaths, roots and leaves, respectively (Iwamoto et al., 2013). In *Arabidopsis*, the expression of *CAT* genes have obvious tissue specificity. *CAT1* and *CAT2* are mainly expressed in leaves and siliques, while *CAT3* is mainly expressed in stems and roots. The expression of *CAT2* and *CAT3* was found to be controlled by circadian rhythms; *CAT2* can be activated by drought stress, while *CAT3* can be activated by abscisic acid, oxidative treatments and senescence (Du et al., 2008).

Maize (*Zea mays* L.) is a widely grown food crop and an important energy crop and fodder that plays an important role in the national economy. Abiotic stresses such as salt (Iwamoto et al., 2013), drought (Du et al., 2008), low temperature (Hackenberg et al., 2013*)* and high temperature (Li et al., 2013) are the main factors affecting its yield. For example, abiotic stress and other osmotic stress will cause ROS accumulation, which will affect plant growth and yield (Zou et al., 2015). In this study, the *ZmCATs* and *AtCATs* gene families were identified and bioinformatics analysis was performed. The protein characteristics, evolutionary relationships, structural domains, secondary and tertiary structures of the *ZmCATs* and *AtCATs* gene families and the expression levels at different developmental stages were predicted and analyzed. This study will provide a theoretical basis and lay a solid foundation for the further cloning and identification of the biological functions of *ZmCATs* and *AtCATs*.

1 Results and Analysis

1.1 Genome-wide identification of the ZmCATs and AtCATs gene families

In order to retrieve catalase (*CAT*) genes from the maize genome, the *Arabidopsis* accession numbers in published articles were used to query the CATs protein sequence, and three maize *CATs* genes were retrieved in the NCBI database and the maize genome database. The characteristics of *ZmCATs* and *AtCATs* are shown in Table 1. The three *ZmCATs* gene family members are named ZmCAT1~3 according to their chromosomal distribution. The coding region of *ZmCATs* is between 1628~2500 bp, the number of amino acids of the protein is between 492~704 aa, the molecular weight is between 56~80 kDa, and the isoelectric point is between 6.45~9.33. The coding region of AtCATs ranged from 1900 to 2023 bp, the amino acid number of the protein was 492 aa, the molecular weight was 56.69 to 56.93 kDa, and the predicted isoelectric points were 6.63 to 7.31, respectively. The proteins encoded by both *ZmCATs* and *AtCATs* genes are hydrophobic proteins. Chromosome mapping indicated that the three *ZmCATs* genes were located on three of the ten chromosomes of maize, while the three *AtCAT* genes are located on two of the five chromosomes of Arabidopsis (Figure 1). The prediction of subcellular localization showed that 3 ZmCATs and 3 AtCATs proteins were localized in different subcellular localizations, which may play different functions in different positions.

Table 1 Protein characterization of AtCATs and ZmCATs

Gene	Gene ID	ORF Length (bp)	Length (aa)	Molecular formula	Molecular weigth (kDa)	Isoelectric point	Hydrophilic relationship	Subcellular localization
AtCAT1	AT1G20630.1	2023	492	$C_{2557}H_{3858}N_{722}O_{723}S_{15}$	56.762	6.95	-0.559	cytoplasm; nucleus; mitochondria
AtCAT2	AT4G35090.1	1930	492	$C_{2566}H_{3873}N_{715}O_{730}S_{16}$	56.931	6.63	-0.574	chloroplast; cytoplasm; mitochondria
AtCAT3	AT1G20620.1	1901	492	$C_{2563}H_{3897}N_{707}O_{725}S_{15}$	56.695	7.31	-0.482	cytoplasm; mitochondria
ZmCAT1	GRMZM2G090568	1628	531	$C_{2719}H_{4128}N_{778}O_{782}S_{17}$	60.7	6.45	-0.506	chloroplast; mitochondria
ZmCAT2	GRMZM2G079348	2469	704	$C_{3564}H_{5463}N_{1043}O_{980}S_{27}$	79.467	9.33	-0.454	nucleus; mitochondri; cytoplasm
ZmCAT3	GRMZM2G088212	2178	492	$C_{2552}H_{3860}N_{720}O_{718}S_{20}$	56.7563	6.96	-0.515	chloroplast; mitochondria

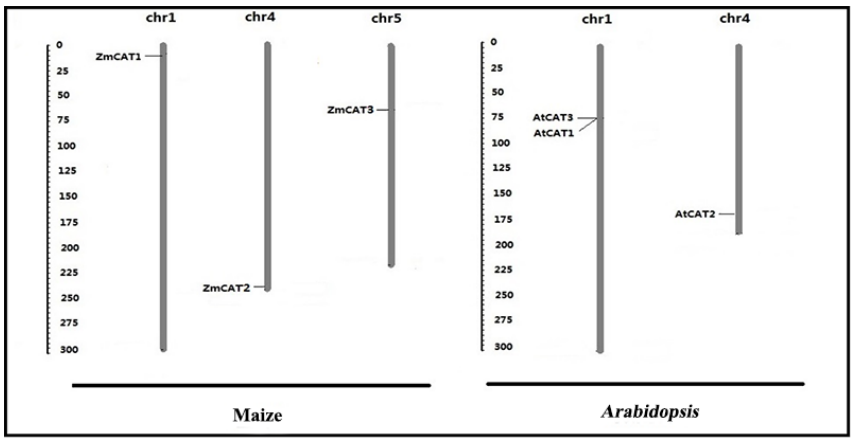

Figure 1 Chromosome mapping of *ZmCATs* and *AtCATs*

1.2 Phylogenetic tree of ZmCATs and AtCATs gene families

The CAT protein sequences of *Arabidopsis thaliana*, wheat, rice, *Sorghum*, and upland cotton were retrieved from online databases and compared with ZmCATs. The phylogenetic tree was constructed using MEGA 7.0 software. The results show that subfamily I contains all members of the maize CAT family and one member of the *Arabidopsis* family (AtCAT3) as well as SbCATs, OsCATs, and TaCATs. Subfamily II is composed of two members of the *Arabidopsis* family (AtCAT1, AtCAT2) and members of the GhCAT family (Figure 2). In Figure 2, the CATs of monocotyledonous plants and dicotyledonous plants converge into different branches, and the relationship between *Arabidopsis* AtCAT3 and monocotyledonous CAT is closer than that of dicotyledonous plants. Most *Arabidopsis* CAT and its upland cotton homologues form phylogenetic branches with higher values, which indicates that they have a high degree of sequence homology. Similarly, maize CATs have a high degree of sequence homology with *Sorghum*, indicating their close kinship.

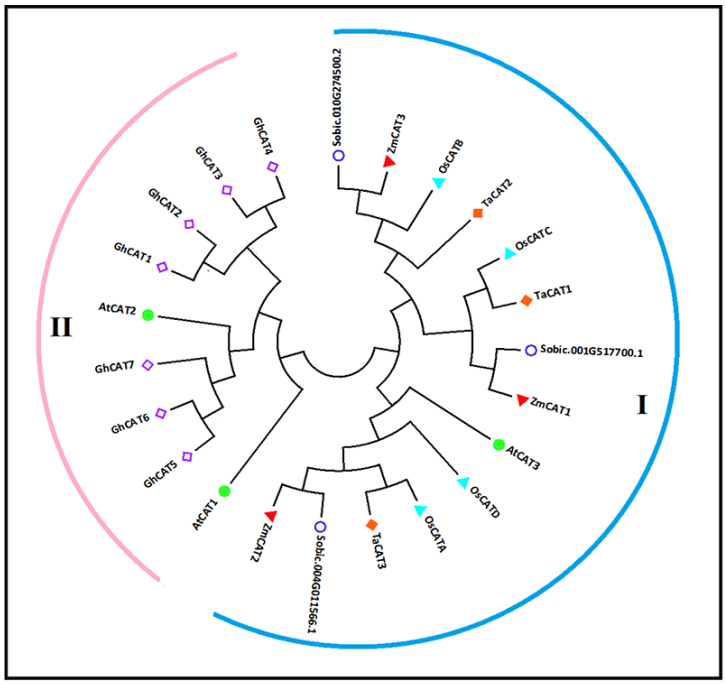

Figure 2 Phylogenetic relationships of CAT proteins from rice, maize, *Arabidopsis*, soybean, sorghum, wheat and upland cotton

Note: Zm: *Zea mays* L. At: *Arabidopsis thaliala*. Os: *Oryza sativa* L., Ta: *Triticum aestivum* L., Sobic: *Sorghum bicolor*, Gh: *Gossypium hirsutum Linn*

1.3 Structure and functional domain analysis of ZmCATs and AtCATs

The online analysis software GSDS was used to analyze the structure of maize and *Arabidopsis* CAT family genes. The number of exons in *ZmCATs* is between 4 to 8, whereas the number of exons in *AtCATs* is between 6 and 7,

respectively (Figure 3A). In order to further verify the characteristics of the CATs family of maize and *Arabidopsis*, a conserved domain analysis was conducted. The results showed that the two species have a high degree of similarity in the domains, and they both contain a catalase core, the structural domain (Catalase, Pfam: PF00199) and the catalase-related immune response domain (Catalase-rel, Pfam: PF06628) (Figure 3B). It shows that these two domains are necessary for CAT protein to function.

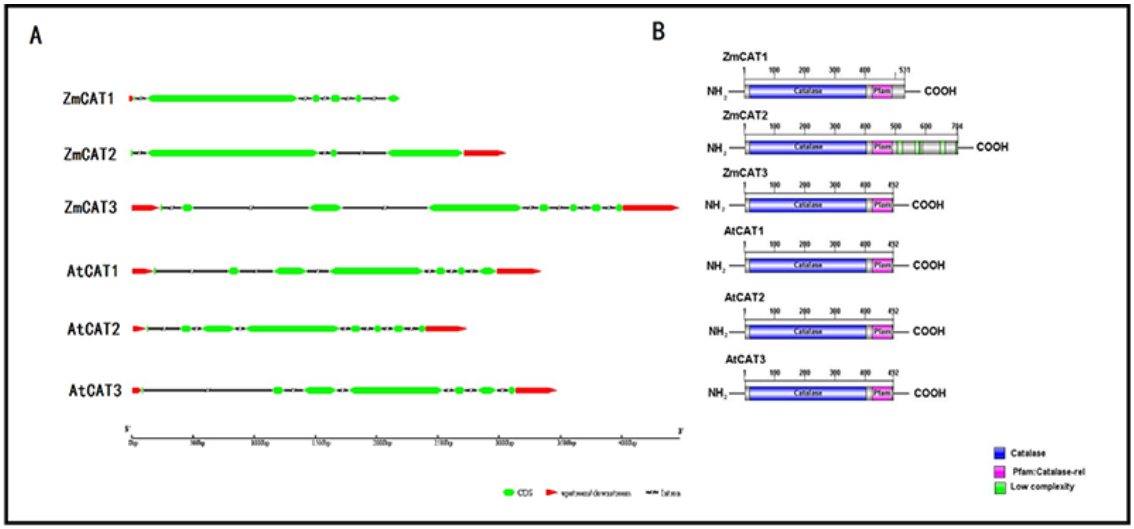

Figure 3 Structural analysis and domain analysis of ZmCATs and AtCATs families

1.4 Analysis of the secondary and tertiary structure of ZmCATs and AtCATs

The prediction of the secondary structure of ZmCATs and AtCATs family proteins shows that the proportion of α-helical amino acids in ZmCATs is between 26.42% and 27.87%, the proportion of extended chain amino acids is between 14.43% and 15.34%, the proportion of β-sheet amino acids is generally between 5.40% and 5.65%, and the proportion of random curly amino acids in ZmCATs is generally between 51.41% and 53.66%, respectively. The proportion of α-helical amino acids in AtCATs is between 26.02% and 26.42%, the proportion of extended chain amino acids is between 15.45% and 15.65%, the proportion of β-sheet amino acids is between 4.885 and 5.49%, the random coil amino acids of AtCATs, and the quantity ratio is between 52.44% and 53.25%, respectively. It can be seen that both ZmCATs and AtCATs proteins have α-helices and random coils as their main structures (Table 2; Figure 4A). Predictive analysis of the tertiary structure of ZmCATs and AtCATs protein showed that the tertiary structure of ZmCAT3 and AtCAT1 protein is similar, and the tertiary structure of ZmCAT1, ZmCAT2, AtCAT2, AtCAT3 protein is similar (Figure 4B).

Table 2 The amino acid number and percentage of the secondary structure of ZmCATs and AtCATs proteins

Protein	α-helix		Extension chain		β-sheet		Random coil	
	Amount	Proportion	Amount	Proportion	Amount	Proportion	Amount	Proportion
AtCAT1	128	26.02	76	15.45	26	5.28	262	53.25
AtCAT2	131	26.63	77	15.65	24	4.88	260	52.85
AtCAT3	130	26.42	77	15.65	27	5.49	258	52.44
ZmCAT1	148	27.87	80	15.07	30	5.65	273	51.41
ZmCAT2	199	27.41	108	15.34	38	5.4	365	51.85
ZmCAT3	130	26.42	71	14.43	27	5.49	264	53.66

1.5 Expression analysis of ZmCATs and AtCATs genes in different tissues and developmental stages

In order to determine the expression profiles of *CAT* genes in maize and *Arabidopsis* in different tissues and developmental stages, the maize GDB database was searched and expression analysis was performed. As shown in Figure 5, *ZmCATs* genes are expressed in different tissues, and the expression levels of *ZmCATs* are different in each developmental stage of vegetative growth and reproductive growth. The expression levels of the same *ZmCAT* in different developmental stages are also different. Compared with *ZmCAT1* and *ZmCAT2*, *ZmCAT3* has

a higher expression level in various tissues in the reproductive and vegetative growth phases. The expression level of *ZmCAT2* in various tissues during the reproductive growth stage and the vegetative growth stage is higher. Compared with *ZmCAT2* and *ZmCAT3*, the expression level of *ZmCAT1* in various tissues during the reproductive growth period is lower. *AtCATs* genes are expressed in different tissues. The expression level of *AtCAT1* in mature pollen is higher than that in other growth and developmental stages, and the expression level of *AtCAT1* in the developmental stages other than mature pollen is lower than that of other *AtCATs* genes. Compared with *AtCAT3* and *AtCAT2*, *AtCAT1* has a higher expression level in the growth and development stage of Arabidopsis.

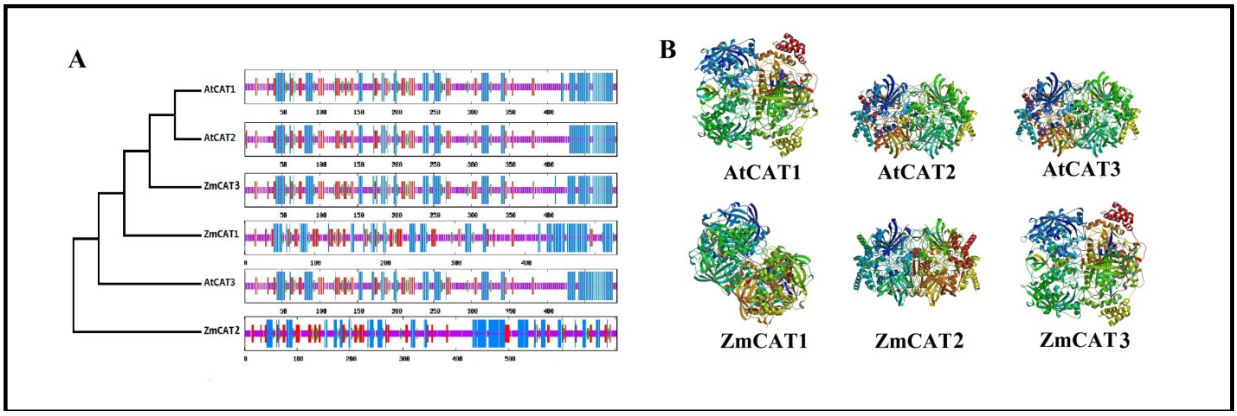

Figure 4 Predicted results of secondary (A) and tertiary structure (B) of ZmCATs and AtCATs protein

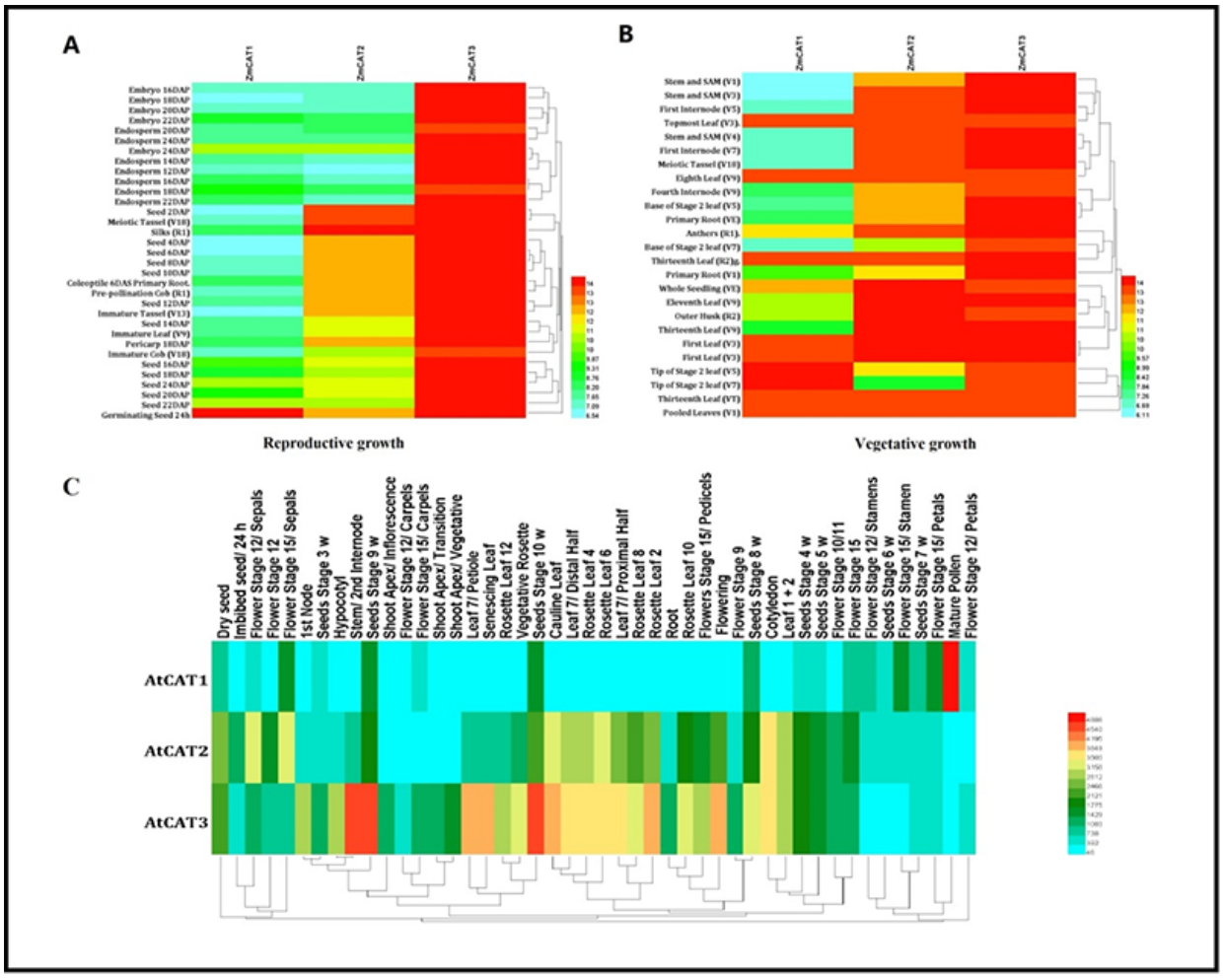

Figure 5 The expression profiles of *ZmCATs and AtCATs* gene in different developmental stages and tissues

Note: FPKM: Fragments per kilobase per million reads, same below

1.6 Expression analysis of ZmCATs gene under abiotic stress

Under high temperature stress, the expression of *ZmCAT1* and *ZmCAT3* genes in the *ZmCATs* family shows an up-regulated expression pattern, and the *ZmCAT2* gene shows a down-regulated expression pattern. Under cold stress, the up-regulated expression of *ZmCAT2* gene is greater than the down-regulated expression of *ZmCAT1* and *ZmCAT3* genes. Under salt and ultraviolet irradiation stress, *ZmCAT3* gene is up-regulated, but the magnitude of up-regulation is not obvious (Figure 6).

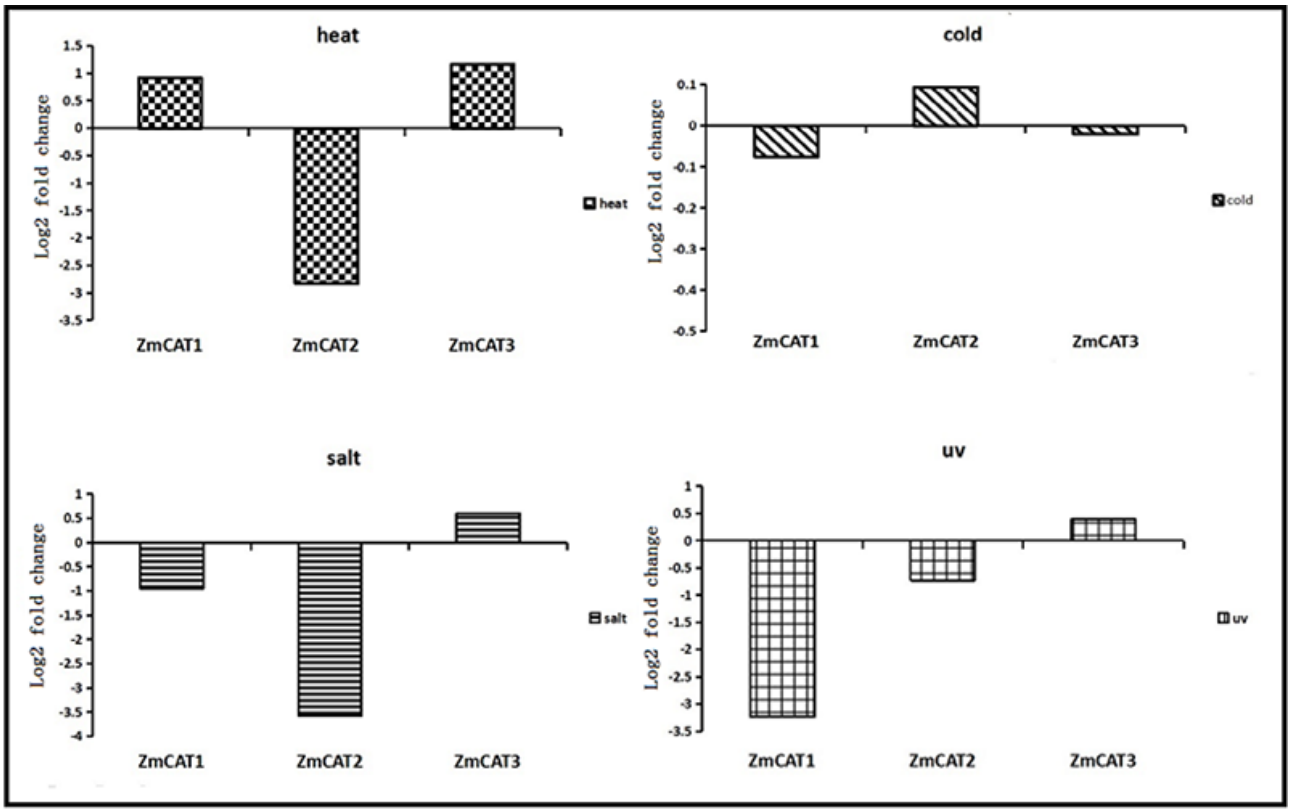

Figure 6 Expression of *ZmCATs* genes under abiotic stress

2 Discussion

Catalase (CAT) plays an important role in plant growth and development, adversity stress response, oxidative senescence and other physiological processes. Its activity is affected by various biological and abiotic factors, such as light, temperature, high salt, drought, and plant hormones and pathogenic microorganisms (Gondim et al., 2012; Luna et al., 2005). Catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) are effective scavengers of ROS, which can prevent cell damage (He et al., 2005).

In this study, the chromosome location map showed that AtCAT1 and AtCAT3 are localized on the same chromosome, but they are distributed in different subfamilies in the evolutionary tree. The reason why AtCAT1 and AtCAT2 are in the same subfamily may be that their sequences at the nucleotide and amino acid levels are more similar to each other than AtCAT3. Although they are not on the same chromosome, they remain tightly linked to promote co-regulation (Frugoli et al., 1996). In Hu L's study of cucumber CATs genes, the phylogenetic tree analysis of cucumber CATs revealed that *Arabidopsis* CATs were divided into three subfamilies, AtCAT1-3 were in different subfamilies, and the relationship between *Arabidopsis* and cucumber CAT families is relatively close (Hu et al., 2015). This study is based on the classification of CATs from monocotyledonous plants and divided them into two subfamilies. The reason for the obvious difference in this study may be related to the different members of the evolutionary tree and the different ways of classification.

In recent years, researchers have successively cloned related CAT genes from a variety of plants, and studied the functions and expression characteristics of these genes (Li et al., 2015). Chen Shanshan predicted and analyzed

the secondary structure of sugarcane S-CAT protein, and found that in the secondary structure of the protein, random coils accounted for the highest proportion of 60.77%, and the proportions of α-helix and extended strands were relatively small, accounting for 17.07% and 22.15%, respectively (Chen et al., 2012). It is consistent with the results of this study on the secondary structure prediction and analysis of *Arabidopsis* and maize CAT protein. It is speculated that random coils are the largest structural element in the secondary structure of CAT proteins, and α-helices and extended chains are dispersed throughout the protein.

DuYanyan's research showed that different stresses may trigger different signal transduction pathways and activate the transcription of different *CAT* genes (Du et al., 2008). Plant catalase plays a variety of roles in germination, photorespiration, resistance to oxidative stress, and may mediate signal transduction involving H_2O_2 as a second messenger (McClung, 1997; Yang et al., 1997). This conclusion is reflected in the expression patterns of maize *CAT* genes under different abiotic stresses in this study. In Frugoli's research, *Arabidopsis CAT2* and *CAT3* showed high expression patterns in leaves (Joo et al., 2014). In this study, the FPKM expression level of the *CAT* genes screened in the phyzome database showed that only *Arabidopsis CAT3* showed high expression levels in the leaves. In rice, *OsCATA*, *OsCATB* and *OsCATC* participate in the environmental stress response, the regulation of root growth regulation and photorespiration ROS level or dynamic balance, and the overexpression of *OsCATA* and *OsCATC* could enhance rice drought-tolerance (Leung et al., 2018).

This study explored the evolutionary relationship of CAT genes in monocotyledonous and dicotyledonous plants, and found that it is relatively conservative in the evolution of different species. The distribution patterns of CAT gene structures, exons/introns and conserved motifs are relatively similar in maize and *Arabidopsis*. The gene expression profile showed that the CAT genes of the two species were specifically expressed in different tissues. At the same time, it was found that the expression patterns of the maize CAT genes were different under different abiotic stresses. Particularly, the expression of the CAT genes was obviously induced by temperature stress, which indicated that the CAT genes may play important roles in the regulation of response to temperature stress, while the specific regulation mechanism needs further study.

3 Materials and Methods

3.1 Identification of CATs gene family members

Arabidopsis was searched from the Plant Genome Database (https://phytozome.jgi.doe.gov) and NCBI database (https://www. ncbi. nlm.nih.gov) based on the previous study (Alam et al., 2018). Protein sequences of AtCATs were retrieved from the Plant Genome Database (https://phytozome.jgi.doe.gov), Maize Genome Database (https://www.maizegdb.org/) and NCBI database (https://www.ncbi.nlm.nih. gov). Blastp screening was performed, and the initial screening was followed by sequence comparison with DNAMAN to remove redundancy and obtain the maize (*Zea mays L.*) CAT gene family members. Non-redundant proteins were validated using the NCBI, SMART (http://smart.embl-heidelberg.de/) and Pfam (http://pfam.xfam.org/) databases.

3.2 Basic characteristics of CATs in maize and *Arabidopsis*

The accession numbers, coding lengths and amino acid numbers of *ZmCATs* genes were obtained from the Maize Sequence database (https://www.maizegdb.org/). The molecular formula, molecular weight, isoelectric point and hydrophilicity of *AtCATs* and *ZmCATs* were obtained using the Expasy website (https://web.expasy.org/protparam/). Subcellular localization analysis was performed using WolF PSORT Prediction (https://wolfpsort.hgc.jp/).

3.3 Protein evolutionary analysis of CATs

The CATs protein of *Sorghum*, *Arabidopsis*, rice, corn, wheat and upland cotton were analyzed by MEGA6.0 software. The Neighbor-Joining (NJ) method was used to construct a phylogenetic tree, and Bootstrap was set to 1000 for testing. In order to analyze the genetic relationship and phylogenetic relationship between the CATs of different species.

3.4 Analysis of gene structure and protein domains of CATs in maize and *Arabidopsis*

GSDS (http://gsds.cbi.pku.edu.cn/) was used to analyze the gene structure of ZmCATs and AtCATs. The conserved domains were analyzed through the SMART website (http://smart.embl-heidelberg.de/) and IBS 1.0.2 software.

3.5 Advanced structural prediction of CATs protein in maize and *Arabidopsis*

The protein secondary structure of ZmCATs and AtCATs was predicted through the online website (https://npsa-prabi.ibcp.fr/cgi-bin/npsa_automat.pl?page=/NPSA/npsa_server.html). The tertiary structure of ZmCATs and AtCATs was predicted using the swiss website (https://swissmodel.expasy.org/). The predicted protein secondary structures were combined with the phylogenetic tree constructed by MEGA6.0 into a graph.

3.6 Expression analysis of CATs genes in maize and *Arabidopsis* at different tissues and development stages

Expression analysis of annotated *ZmCATs* was performed using the maize GDB (https://www.maizegdb.org/) database, and expression analysis of annotated *AtCATs* was performed *via* the Plant Genome Database (https://phytozome.jgi.doe.gov), and HemI software was used for clustering the heat map.

3.7 Expression analysis of maize CATs under abiotic stresses

The transcriptome database of maize under various abiotic stresses was downloaded from NCBI (https://www.ncbi.nlm.nih.gov/sra), including hot (the SAR number: SRR1238715, SRR1819196 and SRR1819198), cold (SRR1238717, SRR1819204 and SRR1819205), salt (SRR1238719) and UV (SRR1238720) treatment conditions (Makarevitch et al., 2015). Maize seedlings was treated under 24 natural light conditions until two leaves and one heart stage, and the treatment for cold was set at 5°C for 16 h, heat treatment at 50°C for 4 h, salt treatment at 300 mmol for 20 h and UV treatment for 2 h. The differentially expressed maize *CAT* genes were screened and the data were compiled and plotted using Excel software.

Authors' contributions

GSN is the experiment designer and executor of the experiment, completing data analysis and writing the first draft of the paper; ZJJ and WYL participated in the experimental design and analysis of the experimental results; SWJ and LJX participated in the revision of the paper; DD and LM participated in the inspection and revision of the paper format; XJY is the creator and person in charge of the project, directing experimental design, data analysis, thesis writing and revision. All authors read and approved the final manuscript.

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