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Full Length Article

Bioinformatics Analysis of LSD Transcription Factor in Maize and its Role in Resistance to Stem Base Rot

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Abstract

The structural characteristics and tissue-specific expression of LSD (Lesion simulating disease 1) transcription factors containing a cysteine-2/cysteine-2-class zinc-finger domain in maize were identified and analyzed by bioinformatics methods. The early onset of stem rot was simulated by *Fusarium graminearum* infection in maize roots, and the expression of LSD transcription factor infected by stem rot was analyzed by real-time quantitative fluorescence PCR. Six LSD transcription factors (LSD-1-LSD-6) were screened from maize genome. In the prediction of subcellular localization, it was found that most of the LSD transcription factors in maize were located on the cell membrane, except for LSD-3 possibly located in the nucleus. The transcriptome sequencing results of 81 tissues/developmental stages showed that different genes in LSD family expressed differently in different tissues. The expression of LSD-4, LSD-3 and LSD-1 in most tissues was very low while of LSD-5 was not concentrated in most tissues. The expression of LSD-5 was higher in anthers, leaves and internodes, and roots and of LSD-6 in roots and anthers. The expression level of LSD-1, LSD-2, LSD-4 and LSD-5 increased with the infection of corn stem rot fungus, while LSD-3 decreased with the increase of infection time and of LSD-6 did not change significantly after infection. LSD transcription factors in maize were up-regulated or down-regulated by stem rot, suggesting that LSD gene family genes may be involved in maize response to stem rot.

Key words: Maize; LSD transcription factors; Bioinformatics analysis; Fungal infection; Response

Introduction

Maize is an important grain, forage and cash crop, and also the most widely planted and highest total yield crop in China. It occupies a pivotal position in the national economy (Zhao *et al*., 2016, 2018). However, the yield and quality of maize are often subjected to biological stress such as viruses, bacteria and fungi which seriously threatens the safety of maize production in China (Wang *et al*., 2010; Khokhar *et al*., 2014). Corn stalk base rot is a common and important disease affecting maize yield and quality. It is common in maize production areas all over the world. In recent years, many hybrids with low resistance have been widely spread in China, and the harm of maize stalk base rot has become more and more serious (Feng *et al*., 2018). There are many methods to control maize stem base rot, such as chemical control, biological control and so on (Yang *et al*., 2018). However, chemical reagents and pesticide residues used in chemical control have brought great harm to plants, animals, human beings and their surrounding environment (Su, 2011). It is the most economical and environmentally friendly method to breed maize resistant varieties by studying disease resistance genes.

LSD1 is a transcription factor of zinc finger protein that contains a special C2C2 zinc finger domain. These genes have been cloned for the first time in *Arabidopsis thaliana*. These transcription factors can regulate cell anaphylactic necrosis, plant broad-spectrum disease resistance and abiotic environmental stresses such as low temperature and long sunshine (Ye *et al*., 2011). Xu and He (2007) showed that *OsLOL2* encoded 163 amino acids and had two LSD1-like zinc finger domains related to rice growth and disease resistance. Bhatti *et al.* (2011) showed that over-expression of transgenic tobacco enhanced resistance to bacterial wilt and clove pseudomonas. In Arabidopsis, a new zinc finger protein is encoded by the LSD1 gene of Arabidopsis and acts as a negative regulator of plant cell death. Dietrich *et al*. (1997) suggested that LSD1 mutant of *Arabidopsis thaliana* regulates transcription by regulating transcriptional mode, inhibiting pre-death pathway or activating anti-death pathway in response to signals from cells receiving pathogen-induced hypersensitive cell death. At the same time, LSD1 zinc finger protein also exists in maize, which may play an important role in maize growth and disease resistance. Therefore, it is of great significance to identify new stem rot resistance genes and analyse their biological functions for cultivating new varieties of food crops with persistent resistance to stem rot.

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Materials and Methods

Plant Material

Nucleic acid and protein sequences of LSD transcription factor family genes in maize and LSD transcription factor family genes in *Arabidopsis thaliana* were downloaded from PlantTFDB (http://planttfdb.cbi.pku.edu.cn/) for correlation analysis in this study.

Maize inbred line B73 provided by and Fusarium provided by Northeast Normal University (*Fusarium graminearum*) were used in present study.

LSD-like Transcription Factor Sequences

LSD sequences of *Arabidopsis thaliana* and maize were downloaded from plant TFDB (http://planttfdb.cbi.pku.edu.cn/), 12 and 20 amino acid sequences of LSD transcription factor family proteins were obtained, respectively. The LSD protein sequences of maize and Arabidopsis obtained from the above databases include proteins translated from multiple transcription isoforms with different LSD genes. In this study, three coding regions and their protein sequences of LSD gene in Arabidopsis and six maize were obtained by subsequent analysis of the longest-selected transcripts (and their encoded proteins) with multiple transcripts. The coding region of LSD gene and its protein sequence.

Construction of Phylogenetic Tree of Transcription Factor LSD Gene

Clustal W was used to align the amino acid sequences of six LSD transcription factor family proteins and three Arabidopsis LSD transcription factor family proteins. Nehbor Joining (NJ) method built in MEGA 5.05 was used to construct the adjacency tree. Bootstrap was repeated 1000 times, and other parameters were set by default.

Analysis of Conserved Domains of Amino Acid Sequences of LSD Transcription Factor Family Proteins

Conserved domains of amino acid sequences of LSD proteins in maize were predicted by using the Conserved Domain Database online program (https://www.ncbi.nlm.nih.gov/Structure/bwrpsb/bwrpsb.cgi) in NCBI.

Location of LSD Gene on Chromosome

Based on the published information of maize genome B73 RefGen_v3, the distribution of six LSD transcription factor family genes on 10 maize chromosomes was determined. The specific location of LSD gene on chromosome was found by BLSAT comparison on maize GDB database (https://www.maizegdb.org/).

Analysis of Protein Properties

On-line Protparam software (http://web.expasy.org/protparam/) provided by ExPaSy was used to analyze the number, molecular weight, theoretical isoelectric point, aliphatic amino acid number and protein hydrophobicity.

Expression Analysis of LSD Family Genes

Using published transcriptome data of maize at different developmental stages/tissues, the expression patterns of six LSD transcription factor family genes in different maize tissues and developmental stages were analyzed. The heatmap.2 software package in R language was used to draw the heat map of gene expression.

Subcellular Localization of LSD

Plant-m PLoc (http://www.csbio.sjtu.edu.cn/bioinf/plant-multi/) was used to predict the location of six LSD transcription factor family proteins in cells.

Infection of Corn Stem Base Rot

Preparation of pathogen inoculator: *F. graminearum* was cultured on PDA medium for 5 days. Five pieces of cake were beaten on the edge of the colony with a perforator. The cake was transplanted into mung bean Decoction liquid medium (mung bean 40 g, water 1000 mL, boiling for 10 min. It was appropriate to keep mung bean from cracking. The supernatant was filtered by gauze and sterilized at 121ºC for 20 min under high pressure (300 mL in 500 mL triangular bottle) and cultured oscillating at 25ºC (150 rpm ~ 200 rpm) for 5 days, the conidia were filtered and collected, and then the suspension with 2 x 10^6 spores/mL of sterile water was used for inoculation.

Gene expression analysis materials: Thirty B73 maize seeds were soaked in sodium hypochlorite for 20 min. The surface was disinfected and washed three times in sterile water. Maize seeds were germinated in seed bags of 30 cm*20 cm, with 15 seeds per bag. When the main roots of the seedlings were 8–10 cm long, the seedlings with the same growth potential were screened out and soaked in the prepared spore suspension of *F. graminearum*. The seedlings were shaken in a shaker with a rotating speed of 50 rpm for 1 h. Sterile water was used as control. The main roots were taken at 0, 6, 12 and 24 h after infection. Three plants were collected at each time point, wrapped in tinfoil paper and labeled. The roots were immediately put into liquid nitrogen and stored in refrigerator at -70ºC. The RNA was to be extracted. Three independent biological repeats were set.

Extraction of total RNA and synthesis of the first chain of DNA: Trizol method was used to extract the total RNA of the samples from different periods after infection. The D260

nm and D280 nm of RNA were detected by NanoDorp spectrophotometer (NanoDorp 2000C). D260 nm and D260 nm of the samples were determined. The concentration and purity of the tablets were determined, and the integrity of the samples was detected by agarose gel electrophoresis with a volume fraction of 12.5% formaldehyde. Using total RNA as template, the first-strand synthesis kit of the cDNA was used to retrieve the DNA. The reverse transcription kit TransScript TM One-Step DNA Removal and cDNA Synthesis SuperMix (AT311-01) were purchased from Beijing Full-style Gold Biotechnology Co., Ltd.

Real-time fluorescence quantitative PCR: Primer 5.0 was used to design primers according to the sequence of LSD family genes. The length of products was 50–300 bp, and the optimal primers were selected as shown with primer sequence in Table 1. The cDNA was diluted 20 times and used for real-time quantitative fluorescence PCR. The reaction system consisted of Syber Green (2x) 10 μL, upstream and downstream primers 1 μL, template 2 μL, and ddH_2O to 20 μL. Real-Time PCR reaction procedure was 95 pre-denaturation for 5 min; denaturation at 95ºC for 15s, annealing at 60ºC for 30 s, 40 cycles; dissolution curve reaction procedure: 95ºC for 15 s, 60ºC for 30 s, 60ºC for 15 s. Each sample was repeated three times. All samples were normalized with *Actin1* gene as internal reference primer. The formula for calculating relative expression was as follows.

Rel Exp = $2^{-\Delta\Delta Ct}$, in which Ct = Ct (LSD gene)-Ct (actin1), $\Delta\Delta Ct = \Delta Ct$ under stress-untreated ΔCt. According to the change of relative expression, the column diagram is drawn.

Results

Identification of LSD Transcription Factors

LSD proteins identified in plant TFDB were analyzed. For proteins translated from different transcripts with the same LSD gene, the protein with the longest amino acid sequence was selected for the following analysis. Three LSD proteins of *Arabidopsis thaliana* were screened: AT1G32540, AT4G20380 and AT4G21610. Six LSD proteins of maize were obtained: GRMZM2G002606, GRMZM2G055135, GRMZM2G060057, GRMZM2G089106, GRMZM2G114613 and GRMZM2G173425. The six LDD genes of maize were named LSD-1, LSD-2, LSD-3, LSD-4, LSD-5 and LSD-6, respectively.

Phylogenetic Analysis of LSD Gene in Maize and Arabidopsis

Three LSD genes from *Arabidopsis thaliana* and six LSD genes from maize were sequenced by ClustalW (Fig. 1). The LSD transcription factors of maize and Arabidopsis can be divided into three groups (GroupI, GroupII, GroupIII). In subfamilies I, II and III, LSD proteins exist in both maize and *Arabidopsis*, but the number of LSD proteins is different, suggesting that these subfamilies of LSD proteins in maize and Arabidopsis may be functionally differentiated, and after the evolution of monocotyledons and dicotyledons separated, new LSD genes have been evolved in maize in GroupI and GroupII.

Table 1: List of primers for RT-PCR analysis

Primer name	Primer sequence (5'→3')
LSD-1-F	GCCTGTGGTCTGTGGAAGTG
LSD-1-R	TGCTCGTCCCCAACAAATAC
LSD-2-F	AACCTGGCTATGGAAGCAAAT
LSD-2-R	CCAACCGATGTCACAAAACTG
LSD-3-F	CGGTCAGGGATGCTCGG
LSD-3-R	GCGGGAAGGAGGGGTCT
LSD-4-F	AGTTCCAACCAGGGATGCTC
LSD-4-R	GCGTCTTAGGATTCTCCACCA
LSD-5-F	CTTCCTACGGGTCGTCCTCA
LSD-5-R	ACGGGTGGTTATTCGGTCA
LSD-6-F	CCAATCCGAAATCATCTCCC
LSD-6-R	CACGGCACATTTTACTGAAGG

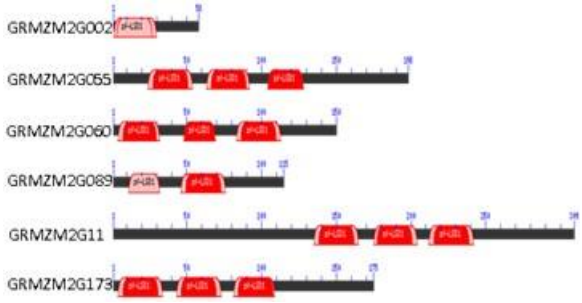

Fig. 1: Systematic evolution of the LSD genes in maize and *Arabidopsis*

Analysis of Conserved Domain of LSD Transcription Factor Family Protein Sequence

Conservative domains are highly conservative in the process of biological evolution (Chen *et al.*, 2009). The analysis of conserved domains of amino acid sequence of LSD protein in maize showed that all six LSD transcription factors in maize contained zf-LSD1 domain (Fig. 2). It is noteworthy that GRMZM2G002606 contains a zf-LSD1 domain. GRMZM2G089106 contains two zf-LSD1 domains. GRMZM2G055135, GRMZM2G060057, GRMZM2G114613 and GRMZM2G173425 contain three zf-LSD1 domains, respectively. The typical LSD1 protein contains three zinc finger domains, namely CxxCxRxxLMYxxGASxVxCxxC. Therefore, it was speculated that GRMZM2G055135, GRMZM2G060057, GRMZM2G114613 and GRMZM2G173425 may have transcription factor activity.

Location of LSD Gene on Chromosome

Based on the information of maize genome B73_ref_v2, the length of six LSD transcription factor family genes (Table 2) and their distribution on 10 maize chromosomes were determined (Fig. 3). LSD-1 and LSD-5 were located on chromosome 3, at about 225 Mb and 122 Mb, respectively.

While LSD-2 and LSD-4 on chromosome 4, at about 31 Mb and 36 Mb, respectively, and LSD-3 on chromosome 6 at about 8 Mb, LSD-6 is on chromosome 1 at about 252 Mb. Six LSD transcription factors in maize were most distributed on chromosomes 3 and 4 with two LSD genes, while only one LSD gene was found on chromosomes 1 and 6.

Physicochemical Properties of LSD Transcription Factor Family Proteins

The amino acid composition and physico-chemical properties of different LSD transcription factor family proteins are different. The number, molecular weight, theoretical isoelectric point, fat coefficient and hydrophobic average coefficient of amino acid composition are different among different LSD transcription factors. As a whole, LSD transcription factor family proteins in maize are rich in basic amino acids, most of the isoelectric points are in the alkaline range, only GRMZM2G002606 isoelectric points are in the acidic range (Table 3). The average hydrophobicity coefficients of LSD transcription factor family proteins in maize were both negative and positive, indicating that both hydrophilic and hydrophobic proteins existed in LSD transcription factor family proteins. Fat coefficient can be used as an index of protein stability with the higher fat coefficient, the higher the protein stability. And the fat coefficient of LSD transcription factors in maize ranged from 60 to 80. Overall, the stability of LSD transcription factor family proteins was strong.

Analysis of LSD Expression in Maize

Using transcriptome sequencing data published by Stelpflug *et al.* (2016), the tissue-specific expression of six LSD families in maize was analyzed, and the heat map (heatmap) was drawn based on FPKM values of each gene (Fig. 4). The tissues analyzed included germinated seeds, different regions of roots, seedlings, stems at different locations, apical meristem of stems, leaves, internodes, spikes, anthers and maize whiskers at different stages of development. It shows that expression patterns of LSD transcription factor family genes are different in different tissues and developmental stages of maize (Fig. 4).

GRMZM2G002606 (LSD-1), GRMZM2G060057 (LSD-3) and GRMZM2G089106 (LSD-4) did not express significantly at all stages of the analysis, while GRMZM2G114613 (LSD-5) and GRMZM2G173425 (LSD-6) showed moderate expression levels at all stages and tissues, while GRMZM2G055135 (LSD-2) gene expression patterns were different in each tissue. The relative expression of GRMZM2G055135 (LSD-2) was higher in leaves, especially in top leaves; the expression of GRMZM2G055135 (LSD-2) was higher in seeds sown for 2–8 days; the expression of GRMZM2G173425 (LSD-6) was higher in primary root zone 4 (primary Z4) at 7 days of sowing; and the expression of GRMZM2G114613 (LSD-5) was higher in internodes and internodes at 6 days of pollination. It is highly expressed in internode and anther.

Table 2: GeneBank ID and length of LSDs

Gene	Locus	Gene location
LSD-1	GRMZM2G002606	Chr3: 225173856..225181043
LSD-2	GRMZM2G055135	Chr4: 31604407..31607471
LSD-3	GRMZM2G060057	Chr6: 8682402..8684083
LSD-4	GRMZM2G089106	Chr4: 36350301..36351182
LSD-5	GRMZM2G114613	Chr3:122121701..122125249
LSD-6	GRMZM2G173425	Chr1:252316945..252321358

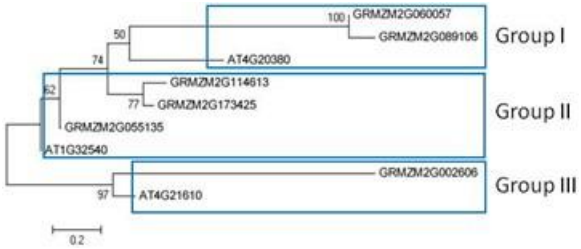

Fig. 2: Conserved domain of LSD in maize

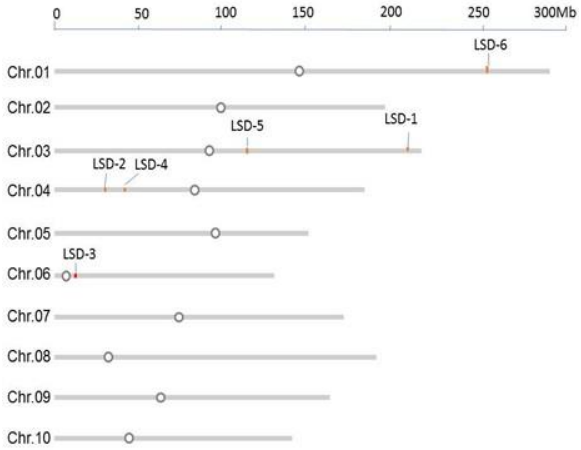

Fig. 3: Location of *LSD* genes on chromosomes of maize

Subcellular Localization

Subcellular localization was predicted by online tools (http://www.csbio.sjtu.edu.cn/bioinf/plant-multi/). The results showed that LSD-like transcription factor family was mainly located on the cell membrane, while LSD-3 was located not only on the cell membrane, but also in the cell wall and nucleus, and LSD-5 on the cell membrane and cell wall (Table 3).

Infection Experiment of Corn Stem Base Rot

The expression level of LSD family genes was analyzed by real-time fluorescence quantitative PCR at 6 h, 12 h and 24 h in normal maize (S0) after infection by *Fusarium* (Fig. 5). It showed that the expression of LSD-1, LSD-2, LSD-4 and LSD-5 increased with the infection time, while the expression of LSD-3 decreased with the infection time (Fig.

Table 3: Physical and chemical properties and subcellular localizations of LSDs

Gene	Locus	Amino acid number	Molecular weight	Theoretical isoelectric point	Fat coefficient	Average coefficient of hydrophobicity	Predicted location
LSD-1	GRMZM2G002606	58	5970.82	4.5	83.97	0.388	Cell membrane
LSD-2	GRMZM2G055135	198	21531.2	8.84	74.34	0.168	Cell membrane
LSD-3	GRMZM2G060057	150	15809.16	9.42	63.73	-0.235	Cell membrane/ Cell wall/Nucleus
LSD-4	GRMZM2G089106	115	12216.16	9.45	66	-0.209	Cell membrane
LSD-5	GRMZM2G114613	309	33165.91	9.06	86.67	0.278	Cell membrane Cell wall
LSD-6	GRMZM2G173425	175	18288.11	8.68	77.31	0.116	Cell membrane

5). The expression level of LSD-6 did not change significantly after infection (less than 2 times). It is noteworthy that the expression of LSD-2 increased to more than 350 times of the control after 6 h inoculation. These results suggest that LSD gene family may be involved in the immune response induced under biotic stress.

Discussion

Transcription factors play an important regulatory role in plant growth and development and response to environmental changes. These are the key links in regulating various physiological activities (Bai *et al.*, 2010; Zheng, 2013). In recent years, many transcription factors related to drought, high salinity, low temperature, hormones, pathogenic response and development have been isolated from plants. Over expression of some transcription factors can enhance the resistance and adaptability of plants to stress (Zhuang *et al.*, 2009). LSD1-Like gene is a family of multi-resistance, as plant growth and development are affected by biotic and abiotic stress factors, including diseases, pests, low temperature, drought, high salinity and injury. In order to grow and develop under the interference of adversity, plants have formed a variety of complex signal transduction and regulation mechanisms in long-term evolutionary adaptation (Hsieh *et al*., 2002).

Six LSD sequences, named LSD-1, LSD-2, LSD-3, LSD-4, LSD-5 and LSD-6, were screened out from maize LSD transcription factor family by bioinformatics analysis. The number of LSD sequences was more than *Arabidopsis thaliana* (3), suggesting that the expansion of LSD gene number may be an evolutionary feature for better adaptation of maize to environment. Six LSD transcription factors in maize all have 1–3 zinc finger domains. Dietrich *et al*. (1997) argued that LSD1 defines zinc finger protein subclasses, and signals from cells that die from allergic cells induced by pathogens can activate LSD1 expression. LSD1 regulates transcription by inhibiting apoptotic pathways or activating anti-death pathways.

Comparing the physico-chemical properties of LSD transcription factor family proteins, it was found that most of the LSD transcription factor family proteins are rich in basic amino acids, most of the isoelectric points are in the alkaline range, only the isoelectric points of LSD-1 are in the acidic range. The hydrophobicity of LSD transcription factor family proteins is different, including hydrophilic and

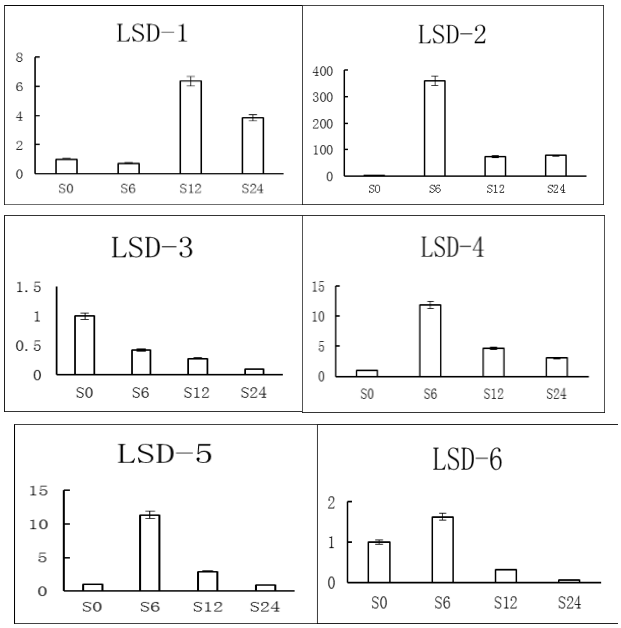

Fig. 5: Expression level of *LSD* after *F. graminearum* infecting

hydrophobic proteins, which indicates that LSD transcription factor family proteins are relatively rich and complex.

In subcellular localization, LSD transcription factors are basically located on the cell membrane. LSD-3 is located not only on the cell membrane, but also in the cell wall and nucleus. LSD-5 is located on the cell membrane and cell wall. It is speculated that LSD transcription factors may interact more with membrane in their function (Li *et al.*, 2013).

There is a close relationship between gene expression pattern and function. Different genes in LSD family express differently in different tissues. Among them, LSD-2 has a higher expression level in leaves at different developmental stages. With the increase of days after pollination, the expression of LSD-2 tends to decrease in the same internodes, suggesting that LSD-2 plays an important role in plant leaf growth. LSD-6 is highly expressed in roots and anthers, suggesting that LSD-6 may be involved in the growth and pollination of plant roots. LSD-5 is highly expressed in anthers and in leaves, internodes and roots, suggesting its role in the development of related organs. The expression of LSD-4,

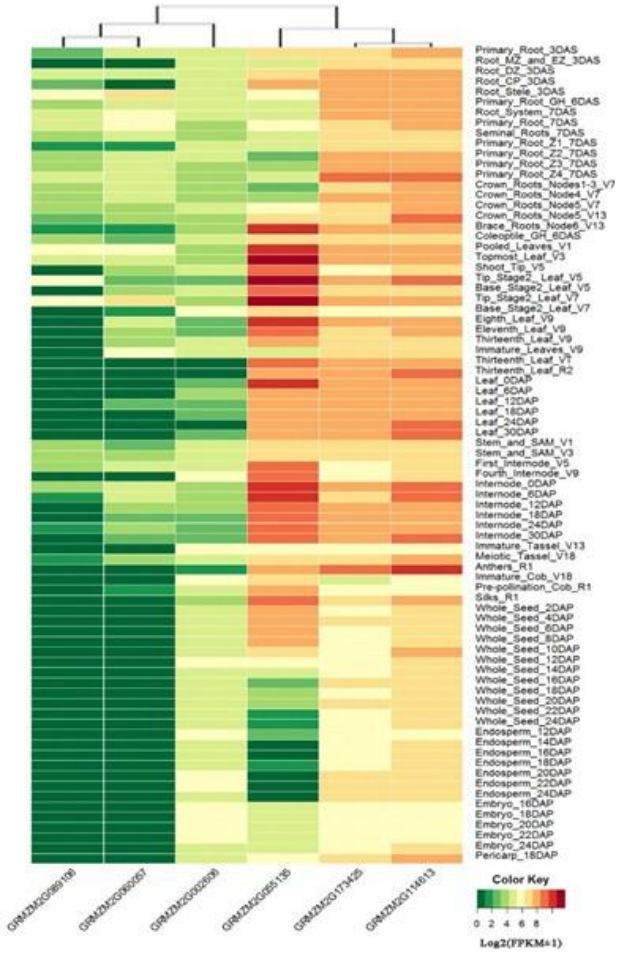

Fig. 4: Expression pattern of *LSD* in maize

LSD-3 and LSD-1 is very low in most tissues. The difference of LSD gene expression in maize indicates the complexity of maize growth and development, which might be a consequence of the interaction of natural selection and artificial directed selection (Hufford *et al*., 2007; Olsen and Wendel, 2013).

It was found that the expression of LSD-1, LSD-2, LSD-4 and LSD-5 increased with the increase of infection time. The expression of LSD-3 decreased with the increase of infection time. The expression of LSD-6 increased to 1.5 times before infection at 6 h. The results showed that the LSD gene family was induced by biological stress of stem-based rot fungi and transcribed. The up-regulated and down-regulated gene transcription induced by biological stress of stem rot fungi may be related to the immune process induced by biological stress of pathogenic fungi (Li *et al.*, 2013; Roberts *et al.*, 2013).

LSD transcription factor family genes are involved in the process of biological immunity and hypersensitivity. In this study, the structural characteristics and gene function expression of LSD transcription factor in maize by bioinformatics method were analyzed and found that there are six LSD genes in maize, more than three LSD genes in *Arabidopsis thaliana*. The transcriptomic sequencing results revealed diverse patterns of LSD genes in 81 tissues/developmental stages. It was found that the expression of LSD-1, LSD-2, LSD-4 and LSD-5 increased with the increase of infection time, while the expression of LSD-3 decreased with the increase of infection time. LSD-6 did not change significantly after infection. In this study, we found that the expression of LSD transcription factors in maize was significantly changed after infected by the pathogen of stem-based rot. Therefore, it was speculated that LSD gene might be involved in the immune response to stem-based rot.

Conclusion

In this study, the expression of LSD transcription factors in maize was significantly changed after infected by pathogen of stem base rot. LSD transcription factors in maize were up-regulated or down-regulated by stem-based rot, suggesting that LSD gene family genes may be involved in maize response to stem-based rot. This study plays an important role in guiding the breeding of new stress-resistant maize varieties and improving yield.

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