Genome-wide Analysis of the Rice Mate Gene Family: Identification, Genomic Organization and Expression Profiles in Response to Abiotic Stresses

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Abstract

Background: Multidrug and toxic compound extrusion (MATE) proteins are involved in many physiological functions of plant growth and development. Although an increasing number of MATE proteins have been identified, the understanding of MATE proteins is still very limited in rice.

Results: In this study, 46 MATE proteins were identified from the rice (*Oryza sativa*) genome by homology searches and domain prediction. In addition, physical and chemical properties of the encoded proteins, subcellular localization, chromosome localization, stress-related cis-elements in abiotic stresses were determined, and a phylogenetic analysis and conserved motif analysis were performed. The rice MATE family can be divided into four subfamilies. It is speculated that members of the rice MATE family have many potential functions, such as the transport and accumulation of flavonoids and alkaloids, the extrusion of plant or exogenous compounds, the regulation of disease resistance and the response to abiotic stress, based on the proteins and cis-acting elements with known functions in the same subfamily. Analysis of gene expression showed that most of the genes were constitutively expressed. Furthermore, eight *MATE* genes were chosen for qRT-PCR-based analysis and showed differential expression patterns in response to salt and drought stress.

Conclusions: Phylogenetic analysis, element prediction, expression data and homology with other species provided strong evidence for functional homology of MATE gene in rice. The analysis results of this study provide comprehensive information on the *MATE* gene family in rice and will aid in understanding the functional divergence of *MATE* genes.

Background

Multidrug and toxic compound extrusion (MATE) transporters constitute a class of secondary active transporters widely present in archaea, bacteria, prokaryotic and eukaryotic cells, and rely on the electrochemical potential of sodium or hydrogen ions to excrete compounds for transport activity as part of a secondary active transport mode [1]. All MATE proteins have approximately 40% sequence similarity [2]. Currently, three-dimensional crystal structure data are available only for the bacterial NorM protein (a norfloxacin efflux protein). The NorM protein has twelve transmembrane domains, which are double-layered along the lipid plane and arranged into two bundles of six transmembrane helices (TM1-TM6 and TM7-TM12) to form a large open cavity exposed to the extracellular space [3-5].

The first MATE transporter (NorM) was identified from *Vibrio paralyticus*; this protein expels norfloxacin and ciprofloxacin out of cells in an energy-dependent manner [6, 7]. Mammalian MATE proteins were first identified in humans and mice (MATE1 and MATE2) [8]. Human MATE1 and MATE2 proteins are encoded by the SLC47A1 and SLC47A2 genes, respectively[9], which are mainly expressed in the kidney and liver[10]. Mammalian MATE protein can be used as multispecific and electron-neutral transporters of organic cations, mediating the discharge of various organic cations and cationic drugs [11, 12].

In plants, members of the MATE protein family are extremely abundant and participate in regulating plant growth and development processes. These processes include transporting secondary metabolites, toxic compounds and heavy metals; regulating disease resistance; and participating in plant hormone regulation. An *Arabidopsis thaliana* seed coat color mutant (*tt12*) has been identified. This phenotype is caused by the mutation of the *TT12* gene, which is a member of the MATE family [13], and is responsible for regulating the transport and accumulation of proanthocyanidin in the seed coat cells to the vacuole [14]. The protein encoded by the barley *MATE* family gene *HvAAVT1* is located on the cell membrane and is mainly distributed in barley root tip epidermal cells; its substrate is citrate, which can increase resistance to aluminum [15]. *The AltSB gene, which is involved in similar physiological mechanisms as those of aluminum tolerance, is also found in sorghum* [16]. The tobacco gene *Nt-JAT1* (*Nicotiana tabacum* jasmonate-inducible alkaloid transporter 1) encodes a protein located on the vacuolar membrane that can regulate the synthesis and transportation of nicotine and other alkaloids, effectively avoiding the toxicity of alkaloids to tobacco [17]. Overexpression of the *ADP1-D* gene inhibited the synthesis of auxin in Arabidopsis, resulting in a phenotype consisting of an abnormal plant height, an increased number of lateral branches and rosette leaves and no significant apical dominance [18]. The Arabidopsis *MATE* gene overexpression mutant *ads1-D* (Activated Disease Susceptibility 1) has a reduced salicylic acid content, and is a sensitive to multiple pathogens [19]. Moreover, expression of the *BIGE1* (BIG EMBRYO 1) gene in maize accelerates leaf and root development and causes an enlarged embryo scutellum [20].

In rice, there are few studies on *MATE* genes, and their functions are poorly understood. The *MATE* gene *OsFRDL1* (Ferric Reductase Defective 3) encodes a citric acid transporter that is necessary for the efficient transport of iron to the stem in the form of an iron-citric acid complex in rice [21]. Similarly, *OsFRDL4* (Os01g0919100) encodes an aluminum-induced citric acid transporter located in the plasma membrane of rice root cells and is one of the components of rice high aluminum tolerance [22]. In addition, *MATE* genes also mediates the defense response of rice, and *OsMATE1* and *OsMATE2* regulate the growth and development of plants and negatively affect disease resistance [23]. Transcriptomic data also show that these genes may be related to the stress response.

Members of the MATE family participate in important regulation and control of the growth and development of organisms, but related functional studies of the rice MATE family members are still lacking, and no systematic analysis has been carried out. This study used bioinformatic methods to systematically analyze the chromosome distribution, subcellular localization, physical properties, conservation, evolution and expression patterns of rice MATE family members, providing an important theoretical basis for the functional identification of MATE family members.

Results

Identification of the MATE genes in the rice genome

Via homology searches and domain (Pfam: PF01554) prediction, 46 genes encoding specific MATE proteins were ultimately identified in the rice genome. The genes were named *OsMATE1-OsMATE46* according to their physical location on the chromosome. The length of the proteins encoded by these genes is between 370 and 598 aa, the molecular weight ranges from 39.41 to 61.65 kD, and the predicted isoelectric point ranges from 5.01 to 11.98. Most of the proteins are neutral or partially alkaline. The protein subcellular localization prediction results indicate that rice MATE proteins are distributed on the endoplasmic reticulum (Table1).

Chromosome distribution and replication pattern of the *OsMATE* genes

The results of the *OsMATE* gene chromosome mapping show that 46 *MATE* genes are distributed across the 12 chromosomes of rice, but the distribution is uneven. Among them, chromosome 3 contains the largest number of *MATE* genes—a total of 10, and only one of the *MATE* genes is on chromosome 5 (Figure 1A). There are 3 pairs of tandem repeat *OsMATE* genes (*OsMATE21* and *OsMATE22*, *OsMATE39* and *OsMATE40*, and *OsMATE41* and *OsMATE42*) in rice, which are located on chromosomes 6, 10 and 11, respectively, and there is a high similarity between the protein sequences within each gene cluster. In addition, 6 pairs of fragment repeat genes were detected (Figure 1B). Taken together, these results indicate that tandem repeats and fragment replication contribute to the expansion of the rice MATE gene family.

Phylogenetic analysis of the MATE family

To study the phylogenetic relationship of rice MATE proteins, a phylogenetic tree was constructed using the MATE protein sequences of four different species (rice, corn, cotton and soybean) (Figure 2). According to the topology of the evolutionary tree, 46 rice MATE proteins could be grouped into four groups. The first group contains the largest number of MATE proteins, a total of 18, followed by the second group, which contains 13 MATE proteins. According to the phylogenetic relationship of the protein sequences, the functions of plant MATE proteins with known functions can be used to predict the functions of rice MATE proteins.

The first group contains 18 rice MATE proteins and several known genes, including *AT3G59030* (*AtTT12*), *AT4G25640* (*AtFFT*) and others. The function of the known MATE transporters in this branch suggests that members of the MATE subfamily I may be involved in the transport and accumulation of plant flavonoids, anthocyanins or alkaloids. The second group contains 13 rice MATE proteins. According to genes with known functions, the members of MATE subfamily II mainly transport multiple complexes. The third group includes nine MATE proteins. The members of this group of known MATE proteins has many different functions, including disease resistance, organogenesis, iron ion homeostasis regulation, and leaf senescence. The fourth group contains 6 MATE proteins. *OsMATE4* and *OsMATE9* have been found to participate in the secretion of citric acid in the root tips or in the transport of metal ions, indicating that these proteins are likely to participate in the physiological process of metal ion detoxification.

Gene structure and conserved motifs of the *OsMATE* gene family

The evolution of a family is mainly manifested as the diversity of gene structures and changes in conserved motifs. To better understand the structure of the rice *MATE* genes, the exon-intron structure of the *OsMATE* genes was analyzed using the annotation information of the rice reference genome (Figure 3B). The *OsMATE* genes were found to contain 1 to 14 exons, which is similar to the clustering results of the evolutionary tree. Genes in the same group often have similar structures but vary in their length of introns. Most genes in group I contain 7 or 8 exons, but *OsMATE30* and *OsMATE31* contain only 3 exons; moreover, the intron length of the genes in this group varies greatly. The genes in group II have 6-8 exons, but the length of their introns is shorter than that of many genes in group I. The group III genes have the fewest number of exons, with only 1 or 2, and the length of the exons is longer than that of the members in the other three subgroups. The group IV genes have the largest number of exons—7~13. The MEME online prediction tool was used to identify the conserved motifs in the rice MATE proteins (Figure 3C). A total of 10 conserved sequences (motifs 1~10) were identified. The results showed that all the rice MATE proteins contained at least 2 conserved motifs, and most MATE proteins (54%) contained all the conserved motifs. Most proteins in subfamilies I, II, and III contain similar types and numbers of conserved motifs, but there are significant differences from the proteins in the fourth group. The MATE proteins in the fourth group contained only 2 to 3 conserved motifs, and the number of motifs was significantly lower than the number of proteins in the first three groups (Figure 3C). These findings are similar to the prediction results of the conserved motifs of the MATE proteins in soybean [29], which may indicate that the function of the protein in the fourth group is more differentiated than that of the other three groups of members.

Characterization of putative cis-regulatory elements in the promoter regions of *OsMATE* genes

Cis-acting regulatory elements in the promoter regions play important roles in the plant response to stress. Using the PlantCARE database, we identified 11 putative stress-responsive cis-acting elements 1500 bp upstream of these OsMATE genes, including ABREs (ABA-responsive elements), TGACG motifs, CGTCA motifs (which are involved in the MeJA response), LTRs (low-temperature-responsive elements), MYBs, MBSs (MYB-binding sites), TCA elements (which are involved in salicylic acid responsiveness), TC-rich repeats (defense- and stress-responsive elements), WUN motifs (wound-responsive elements), GARE motifs (gibberellin-responsive elements) and AREs (anaerobic-responsive elements). The elements associated with the highest number of stress response elements within the *OsMATE* gene family are abscisic acid stress-related regulatory elements (ABREs) and drought-related elements (MYBs, MBSs) (Figure 4). ABA is synthesized mainly in response to drought and high salinity stress. Among the elements, the number of defense- and stress-related response elements (TC-rich repeats) is the smallest. In addition, there are regulatory elements related to anaerobic stress (AREs), low-temperature response elements (LTRs), and hormone response elements (TGACG motifs, CGTCA motifs, GARE motifs and TCA elements, etc). These results showed that the rice MATE genes and stress-related response elements are relatively complete, but the type and number of stress-related elements contained in each MATE gene

promoter differ, indicating that members of the rice MATE gene family can respond differently to different stresses.

Expression patterns of *OsMATE* genes in different tissues

Via RNA-seq data, heat maps of 43 mate genes represented by FPKM values in different tissues and organs were constructed. A heatmap of gene expression was generated from a representative sample of 10 different organs (Figure 5). All *OsMATE* genes were expressed, while a few (*MATE4*, *MATE32*, *MATE38* and *MATE45*) were expressed only in one tissue or organ. The number of gene families with members expressed in the leaves is the largest. Eleven genes, *MATE1*, *MATE5*, *MATE14*, *MATE20*, *MATE24*, *MATE25*, *MATE26*, *MATE31*, *MATE34*, *MATE37* and *MATE40*, were expressed in all of the tissues and showed constitutive expression. Some *OsMATE* genes showed similar expression patterns in various tissues. *MATE41*, *MATE42* and *MATE44*, which were placed in the first group in the phylogenetic analysis, showed relatively high expression levels in the shoots. *MATE2* and *MATE39* of the second gene family in the phylogenetic analysis were highly expressed in embryos, and *MATE19* and *MATE45* exhibited high expression levels in the pistil. The expression in different plants parts is closely related to the functions of genes.

Expression analysis of the rice MATE genes in response to abiotic stress

Crop production and yield quality in most farmlands are severely affected by salt and drought stresses. To further explore the expression changes in *MATE* genes in response to various abiotic stresses, including salt and drought, we randomly used eight *OsMATE* genes from the four phylogenetic groups. qRT-PCR was used to measure the transcript levels of the OsMATE genes. The expression levels of the MATE genes under salt and drought stresses varied among the eight members (Figure 6). *MATE42* and *MATE46* were downregulated after treatment. The remaining *OsMATE* genes were upregulated under salt stress, but the changes were not as extreme as those under drought stress. The expression of four genes (*MATE4*, *34*, *16* and *45*) reached the highest level for 24 h after salt stress, but the expression of two genes increased sharply for 3-6 hours after salt stress. The *OsMATE* genes were sensitive to drought stress, with none being downregulated. Notably, all genes presented their highest expression levels for six hours after drought treatment. There were different responses and regulatory mechanisms of the MATE family members under various abiotic stress conditions.

Discussion

The MATE gene family comprises one of the largest family of genes that encode transporters in plants, and the members are involved in many physiological processes during plant growth and development. At present, the structure and function of the members of the MATE transporter family have been analyzed in many plant species, such as Arabidopsis [24, 25], soybean [26], tomato [27], and sesame [28]; however, this information has not been reported in rice.

The MATE family of genes has a large number of stress response elements, including elements that respond to low temperature, drought [29], mechanical damage and hormones, and it has been shown that stress-related elements in the promoter regions of plants under adverse conditions can improve gene transcription and enhance the resistance of plants to adverse conditions [30-32].

Many functional gene families evolve and expand during gene replication. The MATE gene family has expanded mainly through tandem and segmental duplication events [33, 34]. In contrast to the amplification pattern of the *MATE* gene family in tomato, tandem replication in the *OsMATE* gene family is less abundant. In rice, there was more fragment replication of the *MATE* gene, which is similar to that which has occurred in diploid cotton and soybean. Fragment replication was the main driving force for the amplification of the *MATE* gene family, which may be related to the multiple genome-wide replication events experienced by the genome during the evolutionary process.

In previous studies, *MATE* genes were classified into four subfamilies [26]. Some of the genes in the first group were highly expressed in the roots. The proteins in group I are mostly involved in the transport and accumulation of various plant secondary metabolites. For example, *AtTT12* (*At3g59030*) encodes a protein that is localized on the vacuolar membrane and is involved in the transport of proanthocyanidin precursors into the vacuole, and the seed coat color of the mutant is lighter than that of the wild type [13]. The AtFFT protein is a flavonoid transporter that affects the level of flavonoids in Arabidopsis [35]. In other species, MATEs have similar functions. *MtMATE1* is the key gene whose encoded protein is involved in transmembrane transport of original anthocyanins [36], and the protein encoded by *MtMATE2* mediates vacuolar sequestration of flavonoid glycosides and glycoside malonates in *Medicago truncatula* [37]. *Nt-mate1* and *NT-MATe2* in tobacco mediate the transport and isolation of nicotine in the vacuole [38], and *MdMATE1* and *MdMATE2* of apple were grouped with *AtTT12* in the phylogenetic tree. Both genes were transferred into *tt12* mutants of Arabidopsis to rescue the mutant phenotype to that of the wild type, indicating that *MdMATE1* and *MdMATE2* are the key genes involved in proanthocyanidin transport in apple [39]. Similarly, in grape, *VvMATE1* and *VvMATE2* regulate the transport of procyanidins during berry development [40].

Proteins in the second group mediate the transport and efflux of multiple complexes and toxins. For example, *AtALF5* (*At3g23560*) is associated with plant resistance to toxins in Arabidopsis. *Alf5* mutants are unable to form lateral roots, and their roots are more sensitive to multiple complexes than are wild-type roots [41]. *AtDTX1*(*At2g04040*), the first cloned plant *MATE* gene, has been identified as encoding a detoxifying efflux carrier for plant-derived antibiotics and other toxic compounds, including Cd^{2+}[42]. *OsMATE2* in rice is upregulated in response to arsenic stress and predominately in developing seeds, regulating the transport and accumulation of arsenic in grains [43]. Tobacco *NT-JAT1* has been shown to encode a nicotine transporter that is involved in the deposition of alkaloids in the vacuole [17]. Some genes in the second group are highly expressed in embryos and may be involved in the regulation of seed development.

The third group contained many known genes involved in a variety of physiological processes, including disease resistance, organogenesis, ion transport and leaf senescence. For example, *AT4G29140* encodes activated disease susceptibility 1 (*ADS1*), a putative MATE transport protein that negatively regulates plant disease resistance and the elongation of hypocotyl cells [44]. *ZF14* encodes a plant MATE transporter that is localized to the Golgi complex and other small organelles and is involved in determining the rate of organ initiation; this gene is also involved in iron homeostasis when plants are under osmotic stress [45]. *ELS1* is related to the senescence of *Arabidopsis thaliana* leaves [46]. *Bige1*(*Zm00001d012883*) encodes a trans-Golgi apparatus-related transporter that is involved in regulating organ structure and size. Loss of Bige1 function leads to increased embryo size and accelerated production of lateral organs, including both leaves and roots, as well as early flowering [47]. RNA sequencing also showed that some of the genes in the third group were highly expressed in the pistil and are involved in Fe nutrition during organ initiation and development.

In the fourth group, the MATE proteins are known to be involved in metal ion transport. Arabidopsis EDS5(enhanced disease susceptibility 5), which is a chloroplast- localized salicylic acid transporter, is an essential component of salicylic acid-dependent signaling needed for disease resistance and expression induced by salicylic acid [48, 49]. MATE transporters transport iron by transporting citric acid and protocatechuic acid, which can chelate Fe ions and increase their solubility. OsFRDL1 (Os03g0216700) is a citric acid transporter localized in pericycle cells and is necessary for the effective transport of iron to the stem in the form of iron-citric acid complexes [50]. FRD3 is likely to function in root xylem loading of iron chelators or other factors necessary for efficient iron uptake from the xylem or apoplastic space and into leaf cells [51, 52]. OsFRDL4 (Os01g0919100) is an aluminum-induced citric acid transporter localized in the plasma membrane of rice root cells and is one of the components involved in the high aluminum tolerance of rice [53]. Two MATE proteins, OsPEZ1 and OsPEZ2, were identified in rice as being essential to achieve Fe ion exudation by transporting phenolic compounds and protocatechuic acid [54, 55].

The gene structure analysis showed that the members of each group had similar exon-intron structures, but the gene structure of the members in the different groups were quite different, indicating that the members of the rice *MATE* gene family had differentiated into groups with different functions during the evolutionary process. The conserved base sequence prediction results also showed that rice MATE proteins in the different groups have different types and numbers of conserved motifs. In the first, second and fourth groups, MATE proteins contain a relative abundance of conserved motifs, which explains why the role of these transporter variations is relatively large. Substrate proteins may exert a variety of different functions and were present in the three groups of known plants; these proteins include MATE proteins involved in secondary metabolite transport and accumulation of a variety of external complexes, ion transport and organs, and a variety of physiological functions. The third group had relatively few exons. In some studies, to respond to stress in a timely manner, genes must be activated quickly, aided by a compact structure with relatively few introns [58, 59] ; these properties were the same as those of the *MATE* genes in both cotton and maize [65, 66]. QRT-PCR clearly indicated that *OsMATE* genes play a significant role in avoiding the effects of salt and drought stress in rice. The response pattern is different, which shows that MATE genes have different regulatory pathways in response to abiotic stress.

Conclusions

Overall, our genome-wide analysis of 46 *MATE* genes identified in the rice genome and the comparison with homologous genes of other species revealed the potential function of these genes in transport. Given their important role in plant physiology, MATE transporters may be ideal targets for breeding programs to improve agricultural-related traits such as aluminum tolerance, iron nutrition and accumulation of secondary metabolites (such as increasing anthocyanin contents or eliminating toxic alkaloids).

Methods

Identification of MATE transporters in the rice genome

Rice genomic data were downloaded from the Ensemble database (http://asia.ensembl.org/index.html). The sequence of the conserved domain of the MATE proteins was determined via a hidden Markov model (HMM) (PF01554). We downloaded the HMM profile of MATEs from the Pfam protein family database [60], and used it as the query ($P < 0.001$) to search the rice protein sequence data. After removing the redundant sequences, a total of 46 MATE family genes were identified. The NCBI CDD (https://www.ncbi.nlm.nih.gov/Structure/bwrpsb/bwrpsb.cgi), Pfam database and SMART database [61] (http://smart.embl-heidelberg.de/) were used to confirm the conserved domain. The theoretical isoelectric point (pI), the number of amino acids and the molecular weight (MW) of the MATE proteins were computed by ExPASy (http://web.expasy.org/protparam/)[62]. The subcellular localizations of the MATE proteins were subsequently predicted using WoLF PSORT (http://www.genscript.com/wolf-psort.html).

Chromosomal locations and gene duplication analysis

The chromosomal locations of the *OsMATE* genes were illustrated by MapChart software 2.2 [63]. Segmental and tandem duplication events of the MATE family were identified using the Multiple Collinearity Scan tool kit (MCScan)[64] from the Plant Genome Duplication Database. Homologous genes (E<1e-40, similarity>50%) within 3 gene loci were considered tandem replication genes, and TBtools software was used to draw a schematic diagram of the positional relationship of the collinear genes.

Phylogenetic analysis of MATE proteins

Phylogenetic analysis was performed using the full-length sequence of MATE amino acids from Arabidopsis, maize and cotton combined with the sequence of the newly identified OsMATE proteins. Multiple sequences were aligned by ClustalX software, with the default parameters. MEGA 6 software with 1000 bootstrap tests was used to construct an unrooted neighbor-joining phylogenetic tree.

Gene structure and motif analyses

Gene structure analysis was performed using the Gene Structure Display Server[65] (GSDS, http://gsds.cbi.-pku.edu.cn/) program, with the default settings. Motifs within the MATE proteins were

identified using MEME [66] (http://meme-suite.org/), with the default settings (motif width: between 6~50 (inclusive)). The maximum number of motifs was 10.

Analysis of cis-elements in the promoter regions of OsMATE genes

The 1.5 kb upstream sequence of the *MATE* gene translation initiation codon was downloaded from the Phytozome database. Using the PlantCare database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/), cis-elements in the 1500 bp upstream region were subsequently predicted.

Analysis of RNA sequencing (RNA-seq) data from the MATE family

RNA-seq data were downloaded from the Rice eFP Browser (http://www.bar.utoronto.ca/efprice/cgi-bin/efpWeb.cgi) to study the expression in various tissues and at various stages of reproductive development of rice. To render the data suitable for cluster display, the absolute FPKM value was divided by the average of all the values and then log2 transformed. Origin software was used to generate a heatmap.

Plant materials and abiotic stress treatments

For salt stress, rice seedlings were cultivated in an artificial growth chamber under a of 14-h day/10-h night photoperiod and a 26/24 °C (day/night) temperature cycle to the three-leaf stage. Yoshida nutrient solution with a final NaCl concentration of 120 mmol/L was used for stress treatment. For drought stress, the plants were treated with PEG6000 at 29 days after rice germination. Under these different stress conditions, the aboveground parts of whole plants were collected at 0, 3, 6, 9, 12 and 24 h after treatment.

RNA extraction and expression analyses of MATE genes

Total RNA was extracted using an RNA Simple Total RNA Kit (Takara, Japan). Primer Premier 5 was used to design primers specific to the MATE genes. First-strand cDNAs were synthesized using a PrimeScript First Strand cDNA Synthesis Kit (Takara) in a total of 20 μl reaction volume consisting of 1 μg of total RNA, 4 μl of 5X Prime Script RT Master Mix, and RNAase-free ddH2O. The PCR program was as follows: 95 °C for 2 min followed by 40 cycles of 95 °C for 5 s and 60 °C for 30 s.

Quantitative real-time PCR was performed on an ABI 7500 quantitative real-time PCR system following the manufacturer's instructions. QRT-PCR was performed in a final volume of 20 μl, consisting of 2 μl of cDNA, 10 μl of 2X SYBR Green Master Mix (Takara), and 1 μl of forward and reverse primers. The amplification program was as follows: initial denaturation at 95 °C for 5 min; 40 cycles of denaturation at 95 °C for 10 s and annealing at 60 °C for 20 s; and a final extension at 72 °C for 20 s.

Declarations

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Authors' contributions

ZXD, QTS, ZW, and ZH carried out the data mining, bioinformatics, gene expression analysis, and drafted the manuscript. JZB, JBL, HT and JL performed the data analyses, stress treatment and RNA isolation. JRF and HHH carried out the revising process. All authors read and approved the final article.

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Availability of data and materials

All data generated or analysed during this study are included in this published article.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

All of the authors declare no competing interests.

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W208.

Tables

Table 1 Details of the 67 MATE proteins in rice

ensemble ID	Gene name	Chromosome	protein Length (aa)	Molecular weight (Da)	Isoelectric point	Subcellular Location
Os01t0504500	OsMATE1	1	502	53543.6	5.41	endoplasmic reticulum
Os01t0684900	OsMATE2	1	491	52984.2	7.15	endoplasmic reticulum
Os01t0766000	OsMATE3	1	546	58346.1	9.83	endoplasmic reticulum
Os01t0919100	OsMATE4	1	598	61652.2	9.05	endoplasmic reticulum
Os02t0122200	OsMATE5	2	477	50490.4	8.54	endoplasmic reticulum
Os02t0676400	OsMATE6	2	549	57831.5	7.35	endoplasmic reticulum
Os02t0821600	OsMATE7	2	491	52508.1	5.21	endoplasmic reticulum
Os03t0188100	OsMATE8	3	489	52964.1	7.32	endoplasmic reticulum
Os03t0216700	OsMATE9	3	571	59963.9	8.36	endoplasmic reticulum
Os03t0229500	OsMATE10	3	602	61512.9	7.47	endoplasmic reticulum
Os03t0570800	OsMATE11	3	500	53838.9	7.35	endoplasmic reticulum
Os03t0571700	OsMATE12	3	370	39408.6	5.66	endoplasmic reticulum
Os03t0571900	OsMATE13	3	520	55795.1	5.01	endoplasmic reticulum
Os03t0572900	OsMATE14	3	500	53622.7	6.96	endoplasmic reticulum
Os03t0626700	OsMATE15	3	477	51833.8	8.92	endoplasmic reticulum
Os03t0839200	OsMATE16	3	516	53507.3	7.28	endoplasmic reticulum
Os03t0858800	OsMATE17	3	479	50620.2	10.07	endoplasmic reticulum
Os04t0373400	OsMATE18	4	483	50960.8	7.58	endoplasmic reticulum
Os04t0571600	OsMATE19	4	560	59186.8	6.74	endoplasmic reticulum
Os05t0554000	OsMATE20	5	500	53486.3	7.38	endoplasmic reticulum
Os06t0494400	OsMATE21	6	490	52046.9	6.51	endoplasmic reticulum
Os06t0495500	OsMATE22	6	479	51117.8	7.93	endoplasmic reticulum
Os06t0558300	OsMATE23	6	568	58865.9	7.19	endoplasmic reticulum
Os06t0707100	OsMATE24	6	483	51956.8	6.74	endoplasmic reticulum
Os07t0108200	OsMATE25	7	486	52845.4	6.98	endoplasmic reticulum
Os07t0502200	OsMATE26	7	482	51372.7	8.04	endoplasmic reticulum
Os07t0516600	OsMATE27	7	493	51871.5	8.46	endoplasmic reticulum
Os08t0480000	OsMATE28	8	489	52549.5	6.51	endoplasmic reticulum
Os08t0545900	OsMATE29	8	536	55666.9	8.35	endoplasmic reticulum
Os08t0550200	OsMATE30	8	522	56172.4	7.22	endoplasmic reticulum
Os08t0562800	OsMATE31	8	451	47495.5	5.57	endoplasmic reticulum
Os09t0468000	OsMATE32	9	482	51985.9	8.97	endoplasmic reticulum
Os09t0524300	OsMATE33	9	541	56434.6	7.55	endoplasmic reticulum
Os09t0548300	OsMATE34	9	577	60065.4	9.64	endoplasmic reticulum
Os10t0190900	OsMATE35	10	417	46361.6	11.98	endoplasmic reticulum
Os10t0195000	OsMATE36	10	464	50215.8	8.73	endoplasmic reticulum
Os10t0206800	OsMATE37	10	537	57722.7	6.92	endoplasmic reticulum
Os10t0344500	OsMATE38	10	519	54761.9	8.32	endoplasmic reticulum
Os10t0344900	OsMATE39	10	477	50734.7	8.55	endoplasmic reticulum
Os10t0345100	OsMATE40	10	479	50790.6	8.31	endoplasmic reticulum
Os11t0126100	OsMATE41	11	497	54675.9	6.75	endoplasmic reticulum
Os11t0129000	OsMATE42	11	470	51570.6	8.64	endoplasmic reticulum
Os12t0106600	OsMATE43	12	550	58374.2	5.14	endoplasmic reticulum
Os12t0126000	OsMATE44	12	507	55443.7	6.39	endoplasmic reticulum
Os12t0552600	OsMATE45	12	472	49684.5	8.12	endoplasmic reticulum
Os12t0615700	OsMATE46	12	500	54101.2	6.75	endoplasmic reticulum

Figures

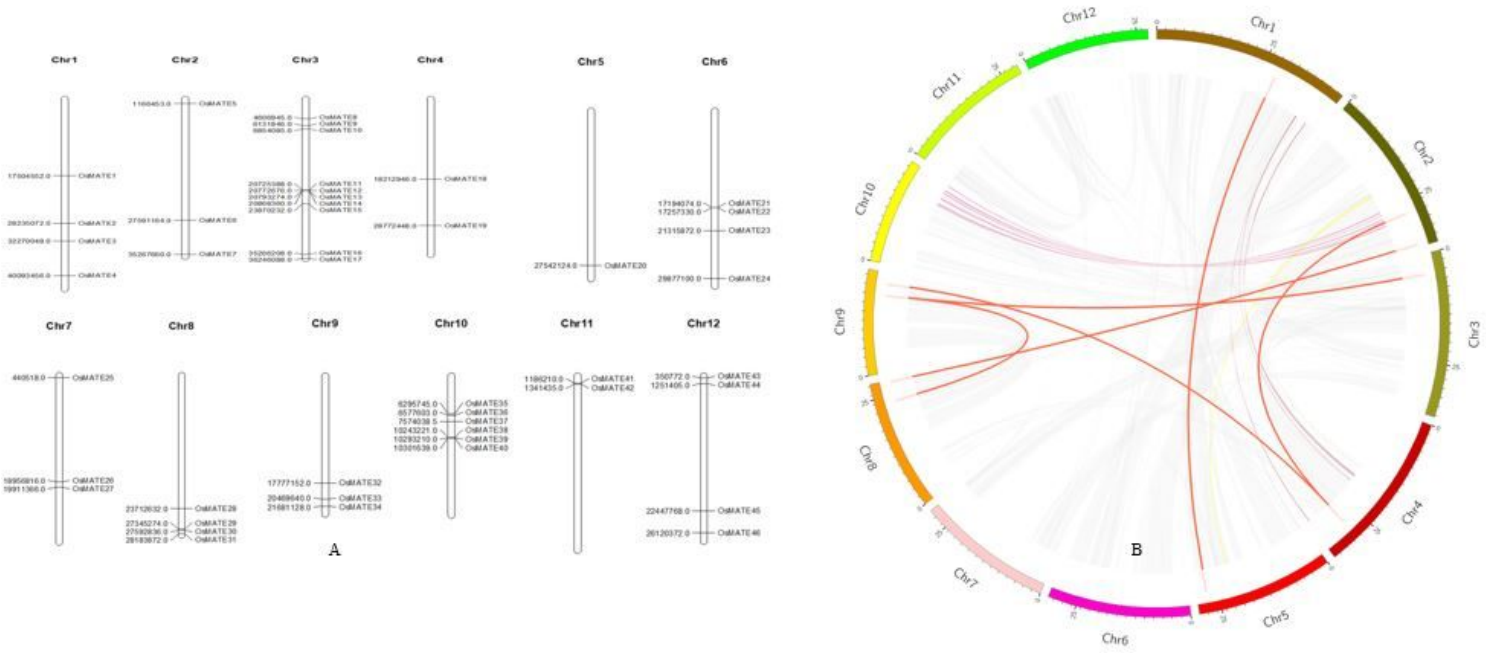

Figure 1

Chromosomal location and gene segmental duplication of OsMATE.

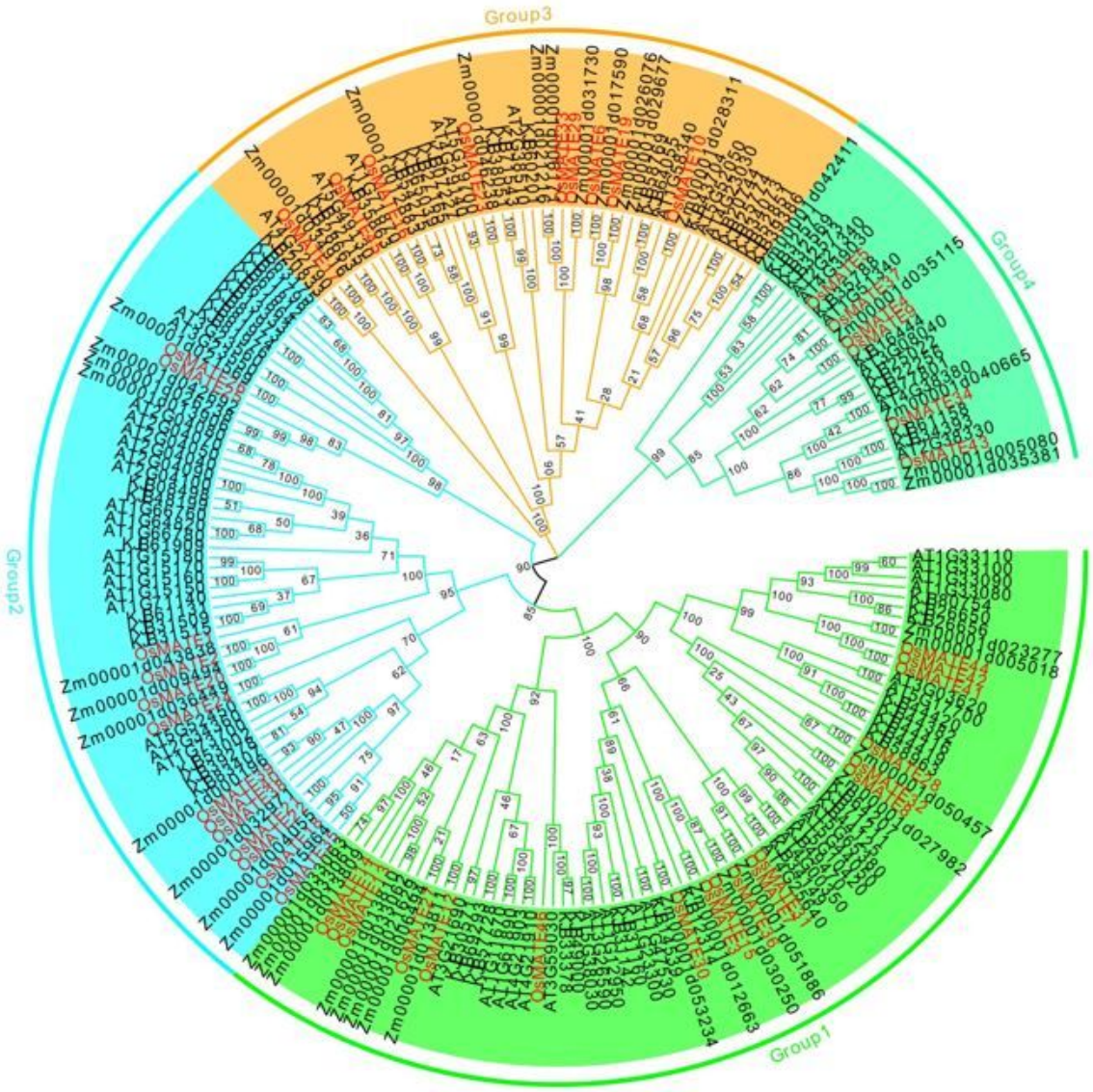

Figure 2

The phylogenetic tree of MATE family. The phylogenetic tree was constructed by MEGA 6.0 using the Maximum Likelihood (ML) method. Bootstrap values in percentage (1000 replicates) are indicated on the nodes. Different subfamilies are highlighted using different colors. Zm is Zea maize, At is arabidopsis, KJB is cotton.

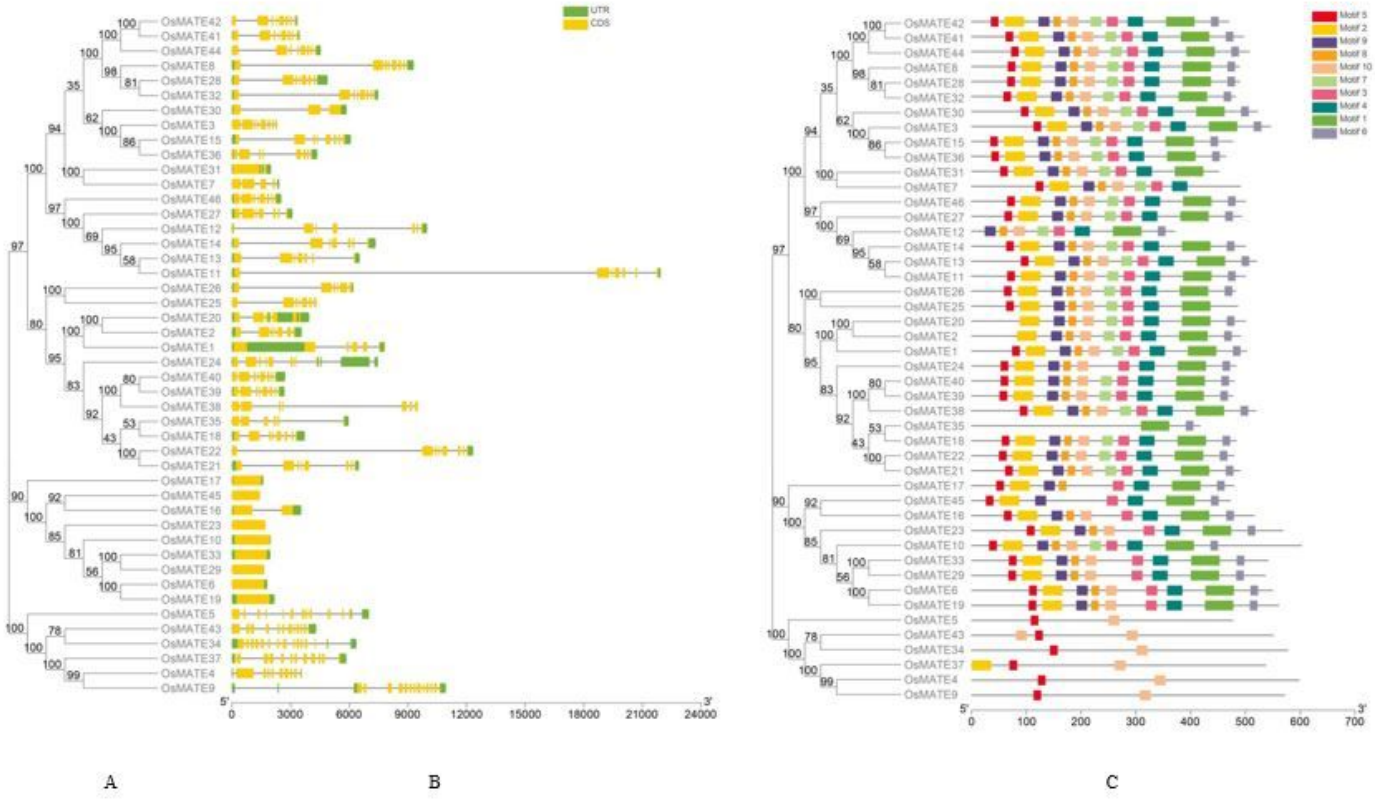

Figure 3

Phylogenetic relationship, gene structure and conserved motif analysis of OsMATE genes. A Phylogenetic tree of 46 OsMATE proteins. B Exon/intron organization of OsMATE genes. Yellow boxes represent exons and black lines with same length represent introns. The upstream/downstream region of OsMATE genes are indicated in green boxes. The length of exons can be inferred by the scale at the bottom. C Distributions of conserved motifs in OsMATE genes. Ten putative motifs are indicated in different colored boxes.

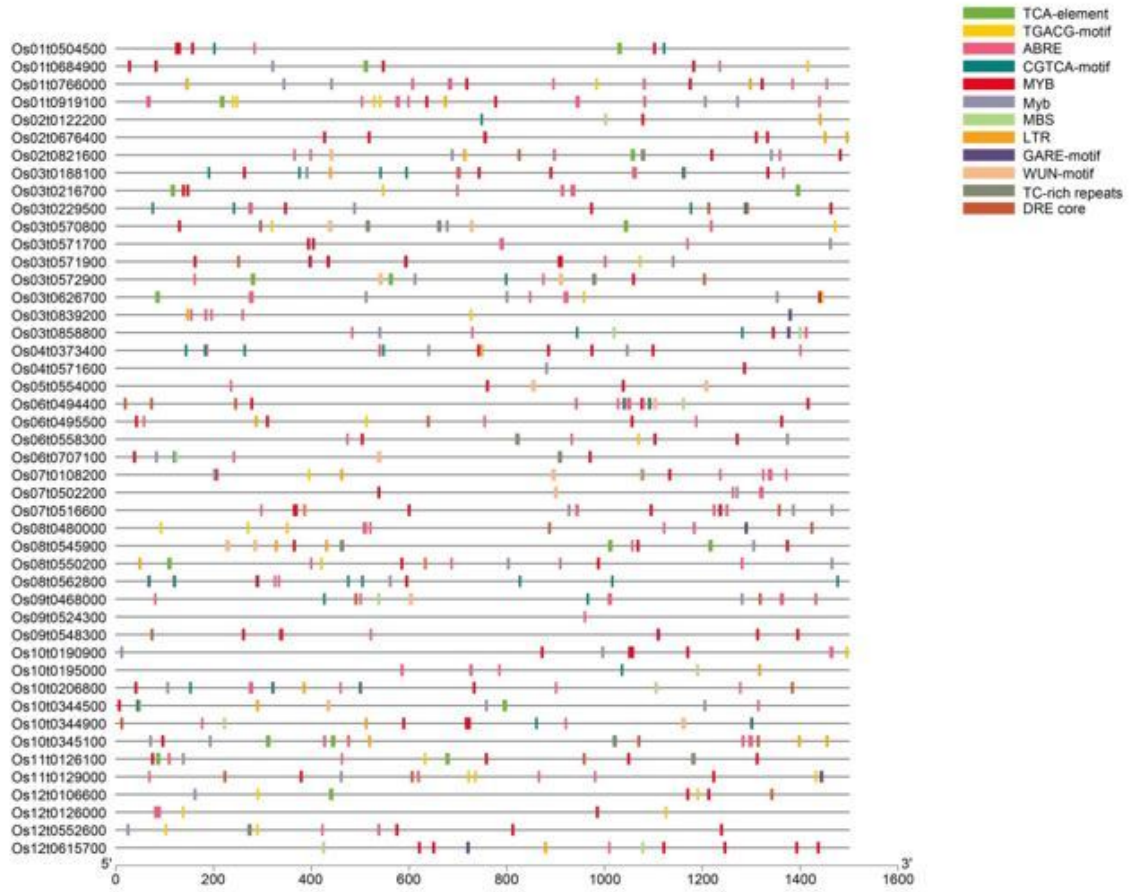

Figure 4

Predicted cis-elements in OsMATE promoters.

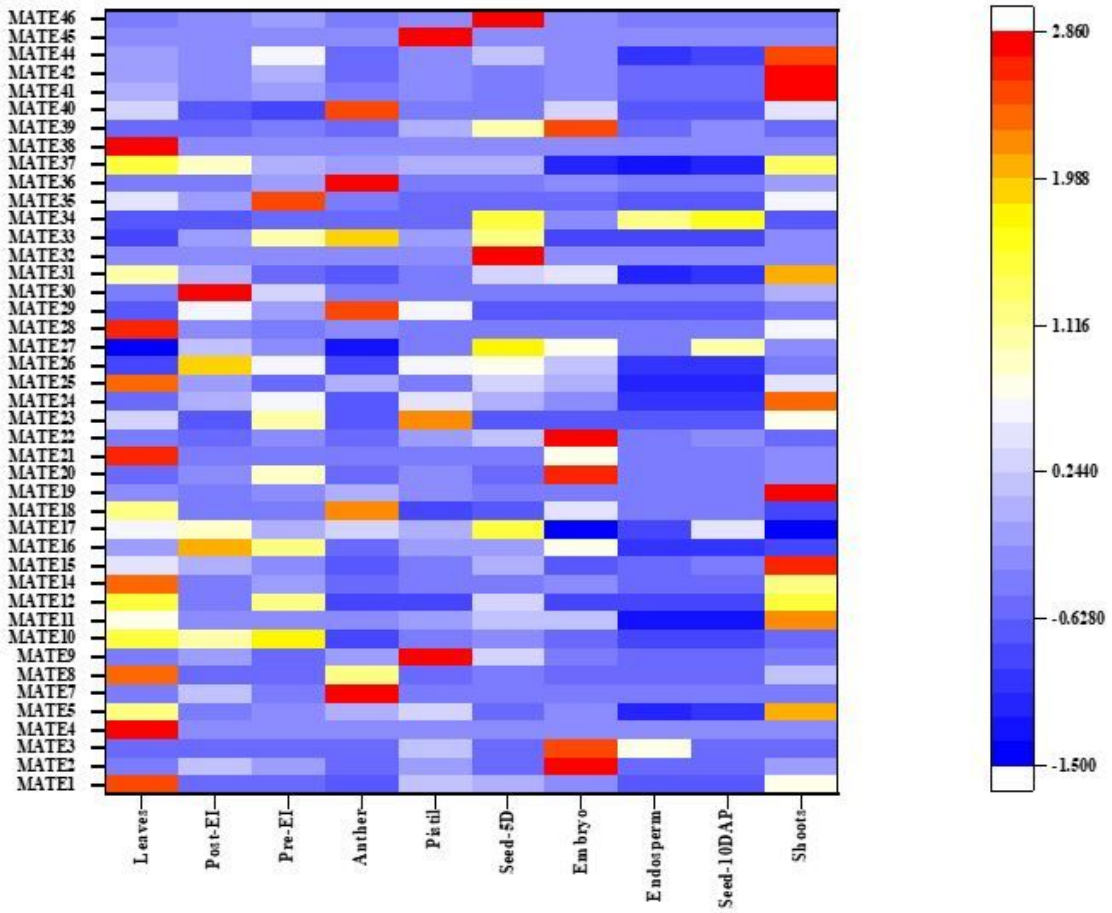

Figure 5

Expression pattern of rice MATE genes. Expression level is expressed by color and intensity: dark red indicates highest expression level, dark blue indicates lowest expression level. Other colors represent intermediate levels of expression..

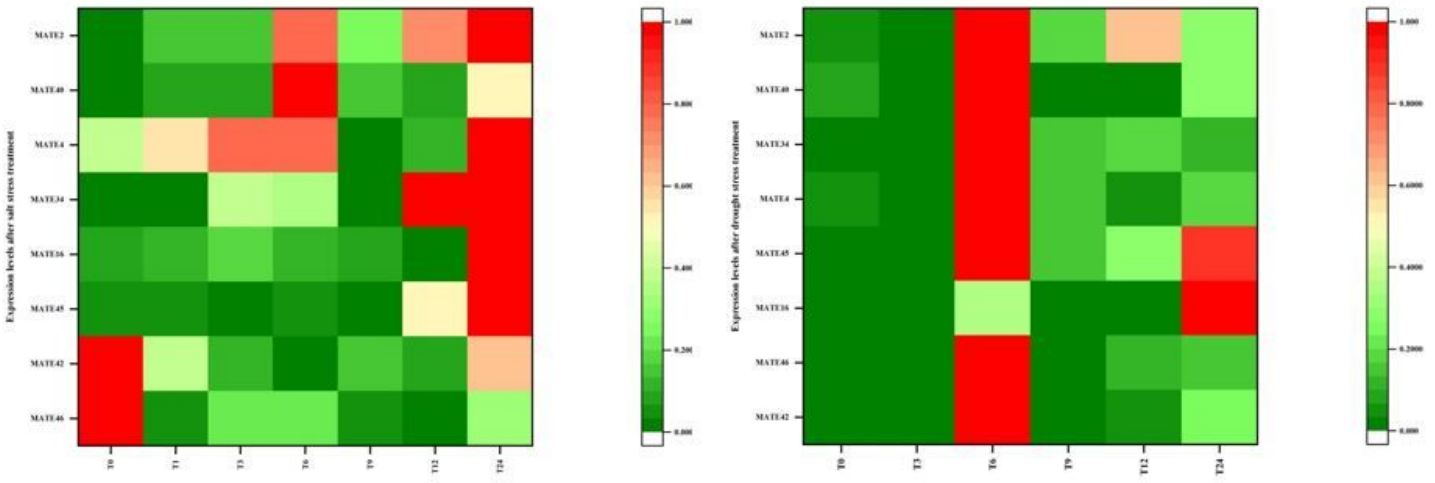

Figure 6

Expression pattern of genes after salt stress and drought stress. Eight OsMATE genes representing four subfamilies were randomly selected and their relative expression in different periods was verified by qRT-PCR. The gene before treatment was used as an internal control, and its relative expression was one. All data were normalized.