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Sequence and expression analysis of histone deacetylases in rice

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Abstract

Histone acetylation levels are determined by the action of histone acetyltransferases and histone deacetylases (HDACs). Sequence similarity and profile searching tools were used to analyze the genome sequence of rice (*Oryzae sativa*) for genes encoding HDAC proteins. The rice RPD3/HDA1-family HDAC proteins can be divided into four classes based on sequence similarity and phylogenetic analysis of sequences obtained from the rice genome. The spatial expression pattern of rice *HDACs* genes indicated that some *HDAC* genes have different expression profiles. Furthermore, our analysis indicated that expression of *HDA705*, *HDT701,* and *HDT702* could be affected by salicylic acid, jasmonic acid or abscisic acid. Expression of *HDA714, SRT702*, and *SRT701* could be modulated by abiotic stresses, such as cold, mannitol and salt. These results indicate that different *HDAC* genes have distinct expression patterns and members of rice HDAC families may be involved in plant response to environmental stresses.

Keywords: Histone deacetylase; RPD3/HDA1 family; SIR2 family; HD2 family; Expression; Rice

Acetylation and deacetylation are catalyzed by histone acetyltransferases (HATs) and histone deacetylases (HDACs), respectively. Both enzymes are members of distinct gene families and exist as multiprotein complexes. Many of the recently identified HATs and HDACs turned out to be transcriptional co-activators and co-repressors, thus establishing a direct link between histone acetylation and regulation of gene transcription mechanisms. Acetylation of the histones is often associated with increased gene activity; whereas deacetylation of histones is correlated with transcriptional repression.

Eukaryotic HDACs can be grouped into three major families, namely RPD3/HDA1 superfamily, SIR2 family, and HD2 family, based on their primary homology to the yeast HDACs, RPD3/HDA1, SIR2, and the plant-specific HDAC, HD2 [1]. In *Arabidopsis*, mutations in a *RPD3*/*HDA1*-type *HDAC*, *HDA6*, affected transgene expression, DNA methylation, and regulation of rRNA genes [2–4]. Another *Arabidopsis RPD3*/*HDA1*-type *HDAC, HDA19*, is involved in a range of plant development processes and plant response to environmental stresses [5–9]. A recent study indicates that another *RPD3*/*HDA1*-type *HDAC*, *HDA18*, was required for the cellular patterning in the root epidermis in *Arabidopsis* [10]. These studies demonstrate that members of RPD3/HDA1 HDAC family play essential roles in plant development and plant response to environment.

Previously, Pandey [1] reported sequence analyses of HDAC families from *Arabidopsis*. In this paper, we analyzed genes encoding RPD3/HDA1, SIR2, and HD2 families of HDACs in rice, a model monocot species. We also investigated the expression profiles of the rice *HDAC* genes. Our analysis indicates differential expression patterns among members of the *HDAC* gene families in rice. In addition, some *HDAC* genes also respond differently to plant hormones and environmental stresses.

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Materials and methods

Domain predictions. The protein sequences of all HDAC proteins were analyzed for recognizable domains using BLAST-based NCBI conserved domain searches (http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi) [11]. The low-complexity filter was turned off and the expect value was set at one in order to detect short domains or regions of less conservation in this analysis. The *E* value determined by these searches that indicates the strength of the alignment to the Pfam version 11.0 (pfam01429) or CDD version 2.02 (cdd1396). Domains were also verified using the HMMER-based SMART Web site (http://smart.embl-heidelberg.de) to search both SMART and PFAM domains [12].

Phylogenetic analysis. The complete group of nonreduntant *Arabidopsis* and rice HDAC proteins was aligned using Clustal X [13]. For all proteins analyzed, the regions of the HDACs used for the alignment began at the conserved HDAC domain. Neighbor joining was then performed with a bootstrap analysis of 1000 replicates using MEGA 2.0 [14].

Plant materials. seven-day-old seedlings of Pi-1 rice were sprayed with 100 μM salicylic acid (SA), jasmonic acid (JA) or abscisic acid (ABA) in the closed pots at a growth chamber. Water-spray was used as mock controls. Leaves were collected at 24 h after treatments. For treatments with abiotic stresses, seven-day-old seedlings of Pi-1 were treated with 0.5 M mannitol, 0.3 M NaCl or cold (4 °C) for 24 h.

RNA isolation and semi-quantitative RT-PCR analysis. Total RNA was prepared using Trizol reagent (Invitrogen, http://www.invitrogen.com). RNA was treated with the DNase and then used for the synthesis of first strand cDNA with an oligo-dT primer. Gene-specific primers used for PCR were listed in Table 1. Conditions of the PCR were as follows: 94 °C for 2 min, 30 cycles of 94 °C for 30 s, 56 °C for 30 s, 72 °C for 2 min, followed by 72 °C for 10 min for most *HDAC* genes. For *HDA714* and *HDT701,* annealing temperature of 53 °C was used. For RT-PCR analysis, at least three experiments with similar results were performed for each gene. RT-Q-PCR analysis was amended by McGrath et al. [15] and was performed by the Quantity One software.

Results and discussion

Identification of HDACs encoded by rice genome

We obtained the sequences of HDACs from the plant chromatin databases (http://www.chromdb.org). According to the ChromDB nomenclature, *Arabidopsis* genes are numbered between 1 and 99, and rice genes are numbered 701–799.

The similarity of the HDACs to current domain models was evaluated by National Center for Biotechnology Information (NCBI) conserved domain searches [16] and HMMER-bases searches using SMART [12]. A total of 14 representatives possessing the complete HDAC domain (Pfam designation PF00850) that defines the RPD3/HDA1 superfamily were identified in rice (Table 2). Iterative TBLASTN searches were performed between these species using all HDAC proteins to find the complete complement of HDAC proteins in the rice genomes. The *E* value for presence of an HDAC is indicated in Table 2 using two different alignment methods (BLAST and HMMER) to either the PFAM HDAC or the CDD HDAC.

Phylogenetic analysis and identification of putative HDAC motifs of RPD3/HDA1 superfamily HDACs

The HDACs from the *Arabidopsis* and rice sequences were aligned using Clustal X [13]. Fig. 1 shows an unrooted phylogenetic tree illustrating the relationships among the *Arabidopsis* and rice RPD3/HDA1 superfamily proteins, produced by aligning their HDAC domains. The plant proteins were classified into four different classes according to the phylogenetic analysis and consideration of the protein structure and sequence similarity outside of the HDAC (Table 2). Eight Class I proteins of rice can be group into four distinct branches (Fig. 1). Among them, *HDA701*, *HDA707*, and *HDA709* are grouped into one branch.

Class I motif

Most mammalian HDACs contain nine conserved domains [17] and a histidine residue (e.g., His^{141} in

Table 1
Primers used for RT-PCR

Gene name	Forward primer sequence	Reverse primer sequence
HDA701	ACTCCATAGACGGCATCAGG	AAGTAGAGCTTCCGGTGCAG
HDA702	GTTGGGTTGCTTCAACCTGT	GAGCTCATGACCAAGTGCAA
HDA703	ATTACTGCCTGAATGTCCCG	GCAGCGTGCAACATTTCTTA
HDA704	GAGCTGGTGCCAAGAAAGTC	AACTCCCACCTCATTTGCTG
HDA705	ATGCTTTAAATGTGCCCCTG	GCAGTCTGCATGACCTTTCA
HDA706	ATGCAAGTTCCTCACCAAGG	AGGAATGAATGCCACAGGAG
HDA707	CCGGAGTACGTCAACCTCAT	ATTGTCGTCGCCGAGTAAAC
HDA709	CAGAACGCCTTCTTGGACTC	CACGTTCACGCTGTAGTGCT
HDA710	ATTACTGCCTGAATGTCCCG	GCAGCGTGCAACATTTCTTA
HDA711	CTATTTCTCGACGCGACTCC	TGCGAGCTCTGTTGGATATG
HDA712	GTGCCAAGAAGCTGTGTGAA	AGTAACCATCAGCACGGTCC
HDA713	TGCTGTACGACGAGAGGATG	CTGAGGAGCCCTTGTTGAAG
HDA714	CTATCCTGGCACCGGTAAGA	GGCTGAAACGAGGATGATGT
HDA716	GTAGACGCACGACGGAAAAT	AGCTTACCCGCCCACTTATT
HDT701	CCCACCTCCCTTTTCTTTTC	AGCCTGAGAAAGGTGCAAAA
HDT702	CTGGGCAATCCTGTGTAGGT	AATGAAACGTGCAACATCCA
SRT701	TGGCTATGCCGAGAAGCTAT	GATGCACCAGGAACACCTTT
SRT702	CTGGGCTAGGAGCTATGCTG	TCCTGGAATGATTCTCGGTC
PR10a	ACCATCTACACCATGAAGCTTAAC	GTATTCCTCTTCATCTTAGGCGTA
Actin	CGTGACCTTACCGACAACCT	GCACCTGAACCTTTCTGCTC

Table 2
Rice HDAC proteins

Family	Gene	Length (amino acid)	BAC Accession No.	cDNA Accession No.	Chromosome	Class	HMMER (PFAM)	BLAST (CDD)
RPD3	*HDA701*	483	P0700A11	NM_192536	1	I	2.20e-126	2e-84
/HDA1	*HDA702*	518	P0498C03	AF513382	6	I	1.10e-185	6e-123
	HDA703	510	OJ1006_D05	AF513384	2	I	4.80e-176	4e-118
	HDA704	623	P0428D12	XM_476712	7	II	1.20e-114	5e-69
	HDA705	452	OJ1119_B10	XM_481792	8	I	2.10e-166	6e-113
	HDA706	352	P0610D01	NM_188519	6	III	1.10e-24	2e-37
	HDA707	300	P0443E05	NM_188519	1	I	6.10e-04	1e-15
	HDA709	456	OSJNBb0058H17	NM_192536	12	I	4.80e-125	6e-89
	HDA710	509	B1307A11	AF513383	2	I	3.00e-179	1e-119
	HDA711	430	OSJINBa0042I15	XM_479060	4	I	4.90e-168	1e-112
	HDA712	392	B1110B01	AF25571	5	IV	8.60e-74	2e-53
	HDA713	665	OSJNBb0018H10	AK060337	7	II	4.30e-112	1e-82
	HDA714	443	OSJNBb0089D09	AK067069	12	II	7.40e-88	1e-62
	HDA716	395	B1110B01		5	IV	2.80e-57	4e-50
HD2	*HDT701*	297	OSJNBa0035I01		5		1.10e-03	—
	HDT702	273	P0456E05		1		—	—
SIR2	*SRT701*	483	OSJNBboo67G11		4		9.20e-24	2e-93
	SRT702	393	OSJNBb0028H07		12		2.80e-47	3e-88

HDAC1), which are essential for catalytic activity [18]. In rice, HDA702, HDA710, and HDA703 (OsHDAC1-3) contains these nine conserved domains and the histidine residue [17,19]. In addition to the nine conserved domains and the histidine residue, a conserved cysteine residue was also found in HDA701 (Cys^{177}), HDA705 (Cys^{164}), HDA709 (Cys^{169}), HDA711 (Cys^{147}), except for HDA707 of rice (Fig. 2A). These observations suggest that most Class I RPD3/HDA1 HDAC proteins are functional enzymes in rice and the plant RPD3/HDA1-type Class I domains are actually deacetylase domains.

Several potential post-transcriptional modification sites including a potential *N*-glycosylation site (NWS) at Asn have been identified in the mammalian [17]. This site is also found in HDA701, HDA703, HDA709, and HDA710 of rice. This site is changed into NWA in HDA702, HDA705, and HDA711, but cannot be found in HDA707.

Class II motif

The Class II HDACs have been well conserved in higher eukaryotes [20]. There are five clearly conserved sequence motifs, i.e., RPPGHHA, GFCXXN, DøDøHHGXGTQ, VX(Y/F)SXH, øEGGY in the yeast or mammalians, which are limited to the catalytic regions and does not extend to the N-terminal domains (X represents any amino acid while ø indicates a hydrophobic residue) [20]. The five conserved domains, the histidine residue and the cysteine residue were also found in HDA704 (His^{331}, Cys^{341}), HDA713 (His^{144}, Cys^{154}), and HDA714 (His^{222}, Cys^{232}) (Fig. 2B), suggesting that Class II HDAC proteins are also functional enzymes in rice. This evolutionary conservation suggests that these enzymes may perform critical functions [20].

Class III motif

Only rice HDA706 belongs to Class III HDAC members. The nine conserved domains, the histidine (His^{164}) and the cysteine (Cys^{174}) residues were also found in HDA706 (Fig. 2C).

Class IV motifs

Rice HDA712 and HDA716 belong to the Class IV HDAC members. Only seven conserved domains, the histidine residue and the cysteine residue were also found in HDA712 (His^{161}, Cys^{171}) and HDA716 (His^{164}, Cys^{174}) (Fig. 2D).

Domain architecture of RPD3/HDA1 superfamily HDACs from rice

Class I HDACs

The HDAC domains are located within 300 amino acids of the N-terminus in all class I HDAC domain proteins (Fig. 3). The C-terminal regions of the Class I proteins, HDA701, HDA702, HDA705, HDA707, HDA709, and HDA710, contain a low complexity. In addition, the N-terminal regions of HDA702, HDA703, and HDA709 also have a low complexity domain. HDA701 and HDA707

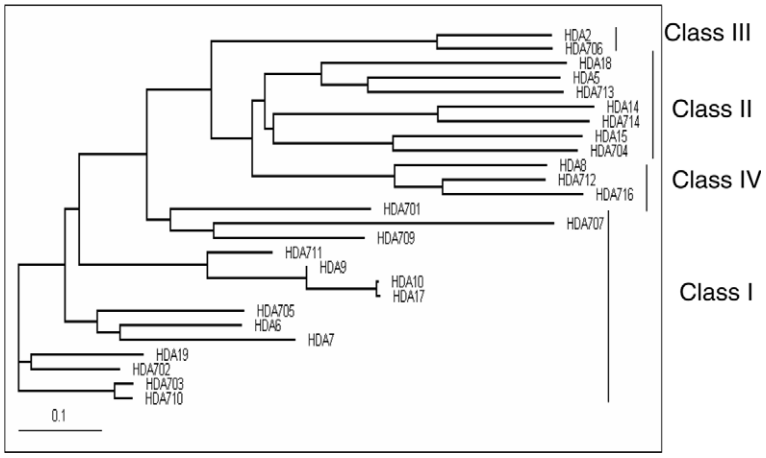

Fig. 1. Phylogenetic analysis of the members of RPD3/HDA1-type HDACs in *Arabidopsis* and rice. *Arabidopsis* proteins are numbered between 1 and 19, and rice proteins are numbered 701–716.

occur immediately adjacent to each other on chromosome I, suggesting a gene duplication event. Similarly, HDA703 and HDA710 also occur immediately adjacent to each other on chromosome II, suggesting another gene duplication event.

Class II HDACs

The rice genome possesses three Class II proteins, which are designated to HDA704, HDA713, and HDA714. All of them have a complete HDAC domain. HDA704 contains a RanBP zinc-finger domain that has been implicated in nucleocytoplasmic transport and nuclear envelope localization [1,21]. HDA704 also contains two low complexity regions—a Glu/Asp-rich region that forms a predicted amphpathic α-helical structure, and an Ala/Leu-rich region of hydrophobic α-helices in its N-terminal region. The C-terminal and N-terminal regions of Class II protein HDA713 both contain low complexity regions—an Ala-rich region that is essential for repression and also interacts with TBP (TATA-box binding protein), and a Ser-rich region that plays a crucial role in splicing and is implicated in splice site selection in metazoa [22].

Class III HDACs

A new class of HDAC proteins, designated Class III, is represented in rice by HDA706. HDA706 has a complete HDAC domain and a low complexity region—an Ala/Ser/Pro-rich region. The Pro-rich region is deeply involved in transcriptional regulation [23].

Class IV HDACs

The rice genome encodes two additional HDAC proteins in the RPD3/HDA1 superfamily, respectively, namely HDA712 and HDA716. Both of them contain a complete HDAC domain. HDA712 has a low complexity—Ser/Ala-rich region in its N-terminal region (Fig. 3). HDA712 and HDA716 in rice occur immediately adjacent to each other on chromosome V, suggesting a gene duplication event.

Analysis of the rice HDAC expression

To investigate the expression of rice *HDAC* genes, the mRNA accumulation patterns were examined for all of the rice *HDAC* genes by RT-PCR. As shown in Fig. 4A, *HDA702, HDA704, HDA712, HDT701*, and *SRT701* mRNAs were detected in leaves, stems, and roots; however, the levels of accumulation differed among different organs. *HDA706* and *SRT702* mRNAs were detected in leaves and stems but not in roots. In comparison, *HDA705* and *HDT702* mRNAs were only detected in roots. The transcripts of *HDA701*, *HDA703, HDA707, HDA709, HDA711, HDA713,* and *HDA716* were not detected (data not shown). The differences in expression patterns may reflect specific functions of different HDACs.

Response of HDAC genes to SA, JA, and ABA

SA and JA mediate plant defense response, whereas ABA is the major plant hormone in water stress signaling and regulates plant water balance and osmotic stress tolerance [24]. In *Arabidopsis*, it has been demonstrated that the expression of *HDA6* and *HDA19* can be induced by JA [8], whereas the expression of *AtHD2C* (*HDT3*) was repressed by ABA [25]. RT-PCR was conducted using total RNAs isolated from leaves of seven-day-old rice seedling subjected to SA, JA, and ABA treatment. *PR10a* gene was selected as a control since previous study has shown that it can be induced by JA and SA [26]. As shown in Fig. 4B, *PR10a* gene can be induced by JA, SA, and ABA. In the *RPD3/HDA1* family, the expression of *HDA705*, which has a high sequence homology with *Arabidopsis HDA6* (67%) and *HDA19* (58%), was induced by JA. In addition, the expression of *HDA702* and *HDA704* was induced by SA, JA, and ABA. In HD2 family members, the expression of *HDT701*, which has a high sequence

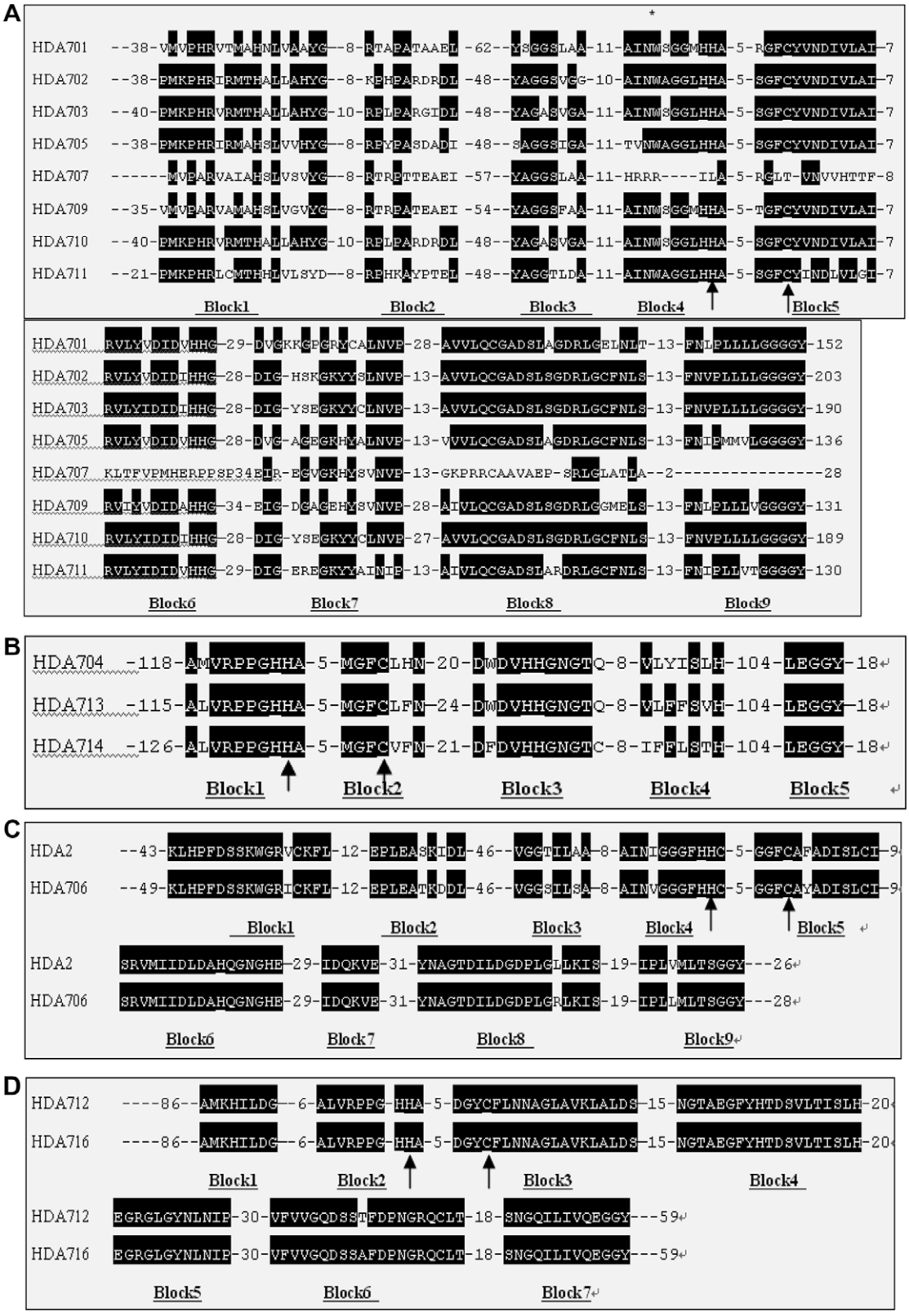

Fig. 2. Alignment of the blocks of RPD3/HDA1-type HDACs from rice or *Arabidopsis*. Amino acid sequences for Class I HDACs from rice were aligned using the DNAMAN program. Identical amino acids are boxed in white letters on a black background. Arrows indicate amino acids identified by mutagenesis to play an important catalytic and/or structural role in human HDAC1 [18]. (A) Alignment of the blocks of Class I HDAC from rice. A potential *N*-glycosylation site (NWS) at Asn in the mammalian HDACs [17] was also found in rice HDACs and was indicated by an asterisk. (B) Alignment of the blocks of Class II HDAC from rice. (C) Alignment of the blocks of Class III HDAC from rice and *Arabidopsis*. (D) Alignment of the blocks of Class IV HDAC from rice.

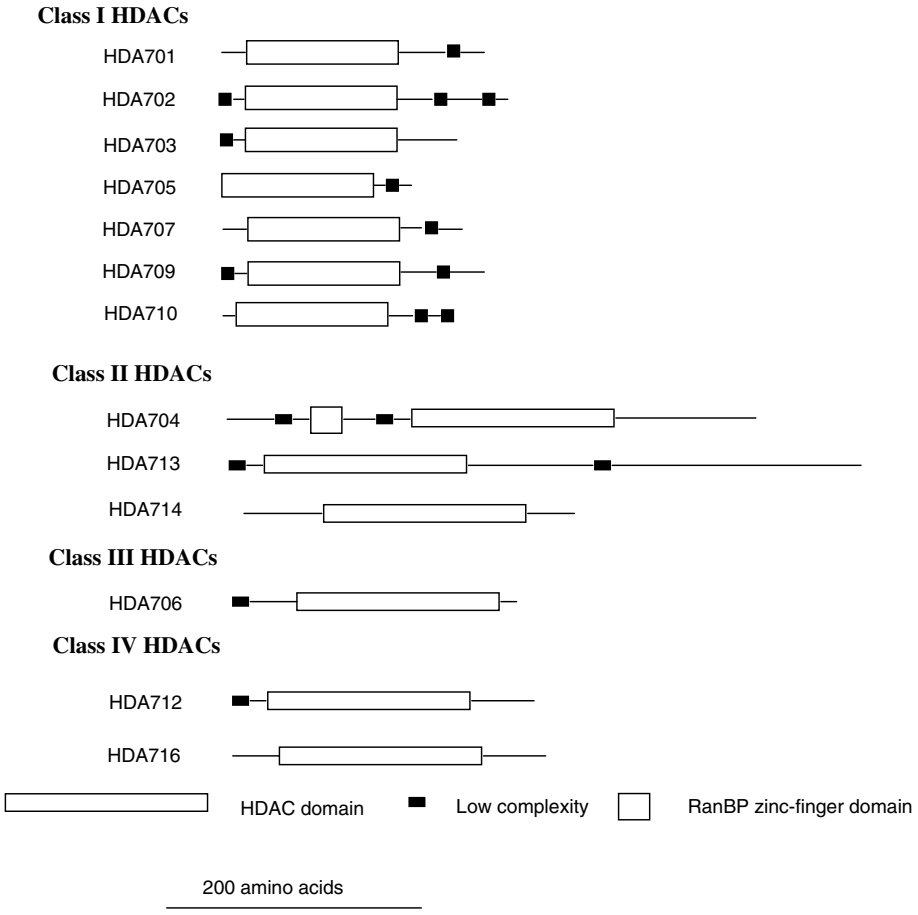

Fig. 3. Domain organization of the RPD3/HDA1-type HDACs proteins in rice. The locations and size of domains are shown by the use of different shape as indicated. The proteins belonging to each class are grouped together.

homology with *Arabidopsis HDT1* (43%) and *HDT3* (41%), was also induced by JA. In addition, the mRNA accumulation of *HDT702*, another HD2 family member, was induced by both SA and JA. In SIR2 family members, the expression of *SRT701* was induced by JA but decreased by SA and ABA, whereas the expression of *SRT702* was decreased by SA, JA, and ABA.

Response of HDAC genes to abiotic stress treatments

To investigate the expression pattern of *HDAC* genes in response to environmental stress conditions, RT-PCR was conducted using total RNA isolated from leaves of seven-day-old rice seedlings that were subjected to cold (4 °C), mannitol and salt (NaCl) treatment. After cold treatment, the expression of *HDA704, HDA712, SRT701, SRT702*, and *PR10a* was decreased, while the expression of *HDA702*, *HDA706*, *HDA714*, and *HDT701* was increased (Fig. 4C). After mannitol treatment, the expression of *HDA704, HDA706, HDA712, HDT701, SRT701, SRT702*, and *PR10a* was decreased, while the expression of *HDA702* was increased. After NaCl treatment, the expression of *HDA702* was increased, whereas the expression of *HDA704, HDA706, HDA712, HDA714, HDT701, SRT701, SRT702,* and *PR10a* was decreased. These results suggest that the expression of members of *HDAC* gene families can be modulated by abiotic stresses and some of them may be involved in the plant response to abiotic stresses.

Comparison of transcript profiles in various rice tissues by RT-PCR analysis indicates that members of the *HDAC* genes are expressed at different levels. Previously, it was found that the rice RPD3/HDA1-type *HDAC*, *HDA702,* the maize *ZmRPD3/HD1B-I*, the *Arabidopsis HDA19*, and the *Arabidopsis* HD2-type *HDACs*, *AtHD2A*, *AtHD2B*, and *AtHD2C* were all constitutively expressed [19,27–30]. Similarly, we found that rice *HDA702, HDA704, HDA712, HDT701*, and *SRT701* were expressed in all the tissues tested, suggesting that these genes may be necessary for the plant growth and development. In comparison, *HDA705*, *HDA706*, *HDA714, HDT702*, and *SRT702* were expressed in specific tissues only, suggesting that some rice *HDAC* genes may have adopted different functions.

The plant hormones ABA, JA, SA and ethylene are involved in regulating defense gene expression during adaptive responses to abiotic and biotic stresses in plants [31–33]. Recent studies suggested that HDACs and histone acetylation may play a key role in the integration of ethyl-

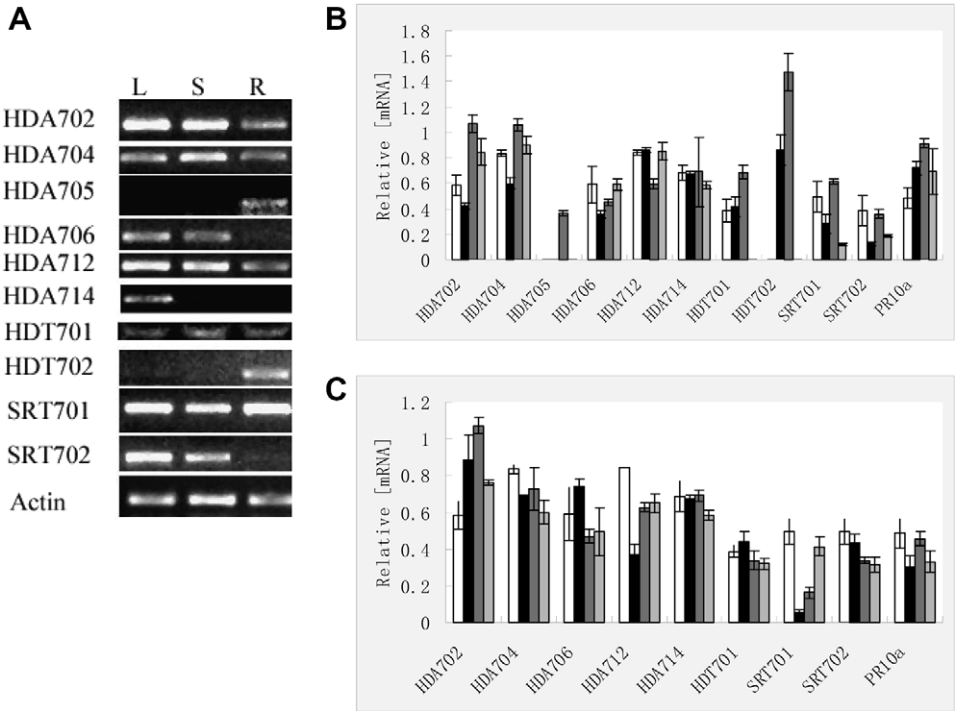

Fig. 4. RT-PCR analysis of *RPD3*/*HDA1*-type *HDAC* expression in tissue and treatment with plant hormone and abiotic stresses. (A) Total RNAs were isolated from the leaves (L), stems (S), and roots (R) of 7-day-old seedlings. The *actin* was used as a control. (B) Total RNAs were isolated from rice 7-day-old seedling leaves treated without hormone (CK, white bars), or with 100 μM SA (black bars), JA (dark gray bars) and ABA (gray bars) for 24 h. (C) Total RNAs were isolated from rice 7-day-old seedling leaves treated with no hormone (CK, white bars), cold (4 °C) (black bars), 0.5 M mannitol (dark gray bars), 0.3 M NaCl (gray bars) for 24 h. RT-PCR amplified as outlined in Materials and methods, using gene-specific primers. The *actin* and *PR10a* were used as controls. Average data with standard errors from three independent biological replicates are shown.

ene, JA and ABA signals for the regulation of stress response genes [25]. We found that different rice *HDAC* genes responded differently to environmental stresses and to hormones, SA, JA, and ABA. For examples, JA induced the accumulation of *HDA705* and *HDT701* as well as *PR10a* transcripts. SA and JA induced the expression of *HDT702*. On the other hand, ABA repressed the expression of *HDT701, HDT702, SRT701,* and *SRT702*. These observations suggested that some *HDAC* genes may play a role in the plant defense response.

More recent studies suggested that histone acetylation and deacetylation are involved in plant response to abiotic stresses [25,34–37]. Our results indicate that cold stress decreased the expression of *HDA712, SRT702*, and *SRT701*. Mannitol induced the expression of *HDT701*, but repressed the expression of *SRT701* and *SRT702*. High salt stress induced the expression of *HDT701* and *HDA714*, whereas decreased *SRT701* and *SRT702*. These observations suggested that members of *HDT* family and *SIR2* family may be involved in the abiotic stress signal pathways.

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