

Expression analysis of cold-induced transcription factor genes in rice (*Oryza sativa* L.)

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ABSTRACT

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Rice plants are injured at the seedling stage in early spring in northern Iran. In order to study rice response to cold stress, the expression of *OsDREB1A*, *OsAP37*, *OsMYB3R-2*, and *OsNAC6* genes encoding transcription factors was observed in 14-day-old seedlings of cold-tolerant genotype PR and cold-sensitive cv. Hashemi during cold stress (5°C for 24 h) using the differential display method and three replications for each genotype. PCR products were quantified using Total Lab (ver. 1.10) software and significant differences in gene expression were found using Wilcoxon Test of SPSS (ver. 18) software. Transcription factors play an important regulatory role in the response to abiotic stress and interact with *cis*-elements in the promoter regions of several stress related genes. Different genes displayed different expression patterns in tolerant and susceptible plants during cold stress. While the expression level of *OsNAC6* gene increased in both genotypes after cold stress, the expression level of *OsDREB1A*, *OsAP37*, and *OsMYB3R-2* genes upregulated significantly in PR and decreased in the Hashemi genotype. Results suggest that the expression of genes encoding transcription factors changes in response to cold stress and so could be an informative resource in breeding and biotechnology projects aimed at developing cold tolerance in rice.

Keywords: cold stress, differential display, gene expression, *Oryza sativa*, transcription factor

INTRODUCTION

Rice seedlings are particularly sensitive to chilling in early spring, which causes slow development, yellowing, withering, reduced tillering, and stunted growth (Andaya and Mackill, 2003). Plant response to cold stress is accompanied by morphological, biochemical, and molecular changes (Wang *et al.*, 2003). Abiotic stress-related genes can be classified into three groups: genes encoding for signal transduction components; functional proteins; and transcription factors (Gao *et al.*, 2008).

The expression of stress-related genes is largely regulated by specific transcription factors (Oh *et al.*, 2009). The promoters of stress responsive genes typically have *cis*-regulatory elements such as DRE/CRT, ABRE, and MYCRS/MYBRS and are regulated by various upstream transcriptional factors (Dai *et al.*, 2007). Transcription factors such as *OsDREB1A*, *OsAP37*, *OsMYB3R-2*, and *OsNAC6* are proteins that act together with other transcriptional regulators, including chromatin remodeling/modifying proteins, to employ or obstruct RNA polymerases to the DNA template (Udvardi *et al.*, 2007). Transcription factors thus

upregulate the expression of many downstream genes resulting in abiotic stress tolerance (Agarwal and Jha, 2010).

The dehydration responsive element binding proteins (DREBs) are important AP2/ERF plant transcription factors that induce a set of abiotic stress-related genes through ABA-independent pathways, thus imparting stress tolerance to plants. DREB1 and DREB2 are two main subgroups of the DREB subfamily, that are involved in two different signal transduction pathways under cold and dehydration, respectively (Yamaguchi-Shinozaki and Shinozaki, 1994). Aspartic Protease (AP2) factors appear to be widespread in the genomes of plants such as rice and Arabidopsis (Nakano *et al.*, 2006). Members of the AP2 family have been implicated in diverse functions in cellular processes such as flower development, spikelet meristem determinacy, plant growth, and stress tolerance (Gutterson and Reuber, 2004).

Another transcription factor family, NAC, is reported to participate in abiotic and biotic responses. The NAC family of plant-specific transcription factors is one of the largest in the plant genome, with 106 and 149 members in Arabidopsis

and rice, respectively (Xiong *et al.*, 2005). The MYB family of proteins is universally found in both plants and animals; these transcription factors play important roles in many physiological processes under normal or unfavorable growth conditions. The R1R2R3-type MYB protein is induced by cold, drought, and salt stress in rice (Yanhui *et al.*, 2006).

Identification of novel genes and screening for differentially expressed genes in response to stress is a straight forward approach for studying the molecular basis of a biological system (Lievens *et al.*, 2001). Subtractive hybridization, microarray, and differential display are different methods for detecting, isolating, and studying gene expression in response to abiotic stresses (Kim *et al.*, 2007). A method used to isolate genes induced by special stresses is a PCR-based differential display method that is based on the detection of differentially expressed cDNA from two or more samples that are separated in adjacent lanes of sequencing gels (Liang and Pardee, 1992).

Drought stress responsive genes (Tyagi and Chavdra, 2006) and cold related genes (Kim *et al.*, 2007) in rice have been identified using the RT-PCR method. Here, we studied the response at the molecular level of 14-day-old seedlings of two rice genotypes, PR (cold tolerant) and Hashemi (cold sensitive) to 24 h of 5°C cold stress and compared the expression changes of four genes encoding transcription factors (*OsDREB1A*, *OsAP37*, *OsMYB3R-2*, and *OsNAC6*) using the differential display method.

MATERIALS AND METHODS

Plant materials

This study was performed at the University of Guilan's biotechnology laboratory. Two rice genotypes were obtained from the Rice Research Institute (<http://berenj.areo.ir>) in Rasht, Iran. Cultivar Hashemi (HA) and genotype PR27137-CR153 (PR) are cold-sensitive and cold-tolerant, respectively (Alah gholipour *et al.*, 2010). Seeds were surface sterilized with ethanol (75% v/v) for 5 min and with diluted commercial bleach (1:3 v/v) NaOCl for 10 min, and then rinsed three times with sterile distilled water. Fourteen-day-old seedlings were exposed to 5°C cold for 24 h (Liu *et al.*, 2007). Seedlings were harvested, frozen in liquid nitrogen, and stored at -70 for further analysis.

RNA extraction

Total RNA was isolated from the cold-treated and control plants using RNX-Plus (CinnaGen Co., Iran) according to the manufacturer's instructions. The quality of RNA was analyzed on 1% agarose gel (Fig. 1).

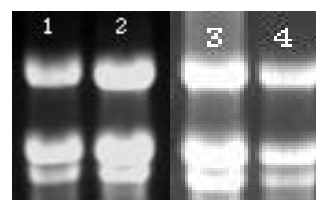


Fig. 1. Total RNA extracted from PR and Hashemi genotypes in 1) PR in 25°C, 2) HA in 25°C, 3) PR in 5°C, and 4) HA in 5°C.

RT-PCR

First-strand cDNA was synthesized using 50 ng RNA, Oligo-dt primer, and M-MLV reverse transcriptase (Fermentase). PCR reaction was set up in a 20- μ l volume of 2- μ l cDNA, 0.2 μ M of gene-specific primers, 10 mM of dNTP and one unit of Taq DNA polymerase. The reaction included an initial 5-min denaturation at 94°C, followed by 40 cycles of (94°C, 40 s; T_m of each primer, 40 s; 72°C, 2 min), and a final 5-min extension at 72°C. PCR products were then separated on a 1/5% agarose gel. The *OsGAPDH* (*Oryza sativa* glyceraldehyde-3-phosphate dehydrogenase) gene was used as the positive control (Jain *et al.*, 2006) to quantify the initial amount of RNA (Fig. 2). Four pairs of gene-specific primers were used in this study (Table 1). PCR bands were quantified using Total Lab software ver. 1.10 (Chivers *et al.*, 2006). Significant differences in gene expression were determined using Wilcoxon test of SPSS (ver. 18) software.



Fig. 2. The expression of *OsGAPDH* gene as a positive control: 1) PR in 25°C, 2) HA in 25°C, 3) PR in 5°C, and 4) HA in 5°C.

RESULTS AND DISCUSSION

The expression of four cold-induced genes encoding transcription factors, namely, *OsDREB1A*, *OsNAC6*, *OsAP37*, and *OsMYB3R-2* were screened in this study using the RT-PCR method; results displayed different expression patterns in PR and HA rice genotypes under cold stress.

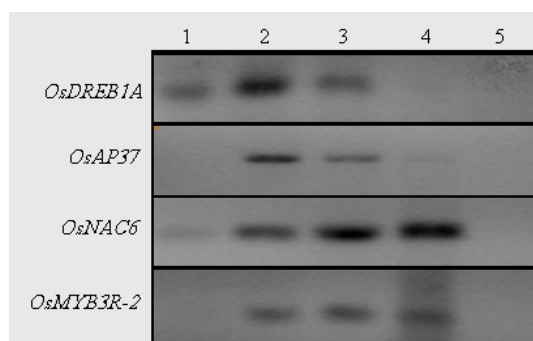
DREB: Dehydration responsive element binding; *AP*: Aspartic proteases; *MYB3R-2*: R1R2R3 MYB gene; *NAC* gene: NAM, ATAF1, -2, and CUC2 gene.

OsDREB1A gene

OsDREB1A expression was induced by cold treatment in the PR genotype but suppressed significantly in the HA cultivar (Fig. 3, Table 2). These expression patterns in two genotypes indicates that timing is an important factor in stress-related gene response in cold-tolerant genotypes

Table 1. Name and accession number of genes, specific primer sequences and T_m (melting temperature), and references for each primer used in this study.

Gene name/ accession no.	Primer sequence	Temp.	Reference
<i>OsDREB1A</i> (Os09g35030)	5'-GCT CCG ATT ACG AGT CTT C-3' 5'-TTC TCC GAC GAA CTC CTC-3'	60°C	Dubouzet et al., 2003
<i>OsAP37</i> (AK061380)	5'-ATG GCG CCC AGA GCA GCT AC-3' 5'-CTA GTT CTC TAC CCG CGG CG-3'	66°C	Oh et al., 2009
<i>OsNAC6</i> (AV028185)	5'-CAT GGC CGG TGA ACT TTG AC-3' 5'-CTC GTC GTC GTT CAG TCC AG-3'	65°C	Liu et al., 2007
<i>OsMYB3R-2</i>	5'-CAT GGC CGG TGA ACT TTG AC-3' 5'-CTC GTC GTC GTT CAG TCC AG-3'	64°C	Dai et al., 2007
<i>OsGAPDH</i> (AK064960)	5'-AAG CCA GCA TCC TAT GAT CAG ATT-3' 5'-CGT AAC CCA GAA TAC CCT TGA GTT T-3'	63°C	Jain et al., 2006

**Fig. 3.** PCR product of *OsDREB1A*, *OsAP37*, *OsNAC6*, *OsMYB2-3R* genes: 1) PR in 25°C, 2) PR in 5°C cold stress, 3) Hashemi in 25°C, 4) Hashemi in 5°C, 5) negative control.**Table 2.** Quantification results of gene expression using Total Lab software.

Gene name	bp	PR in 25°C (ng)	PR in 5°C (ng)	HA in 25°C (ng)	HA in 5°C (ng)
<i>OsDREB1A</i>	198	35.295 ± 0.4	82.217 ± 1.5	38.948 ± 0.5	0.0
<i>OsAP37</i>	700	0	88.302 ± 5.4	69.966 ± 1.4	13.27 ± 0.6
<i>OsNAC6</i>	162	129.037 ± 0.5	239.964 ± 1.2	274.155 ± 0.9	285.067 ± 0.3
<i>OsMYB3R-2</i>	162	0	22.168 ± 0.7	30.878 ± 0.5	17.612 ± 0.4

Note: The average value of the gene expression measured in three replicates is given in the table. Expression levels of genes that are undetectable by the software are equal to zero.

(Kiedrowski et al., 1992) such as PR, compared with cold-sensitive ones. The *OsDREB1A* gene encoding one of the important transcription factors causes the expression of cold responsive genes by identifying C-repeat regions in the promoter of these genes. DRE contains the TACCGACAT core sequence shown to be linked to dehydration, low temperature, and high salt responses, as well as abscisic acid treatment (Yamaguchi-Shinozaki and Shinozaki, 1994). CBF/DREB1 transcription factors have also been identified in wheat, rye, tomato, and rice, and all of them showed a rapid response to cold stress (Dubouzet et al., 2003). The overexpression of *OsDREB1A* in rice induces the accumulation of soluble sugars, including raffinose, sucrose, glucose, and fructose, which may act as osmoprotectants (Ito and Kurata, 2006). *AtDREB1* in Arabidopsis was induced within 10 min at 4°C (Liu et al., 1998). *OsDREB1A* and *OsDREB1B* were induced early (within 40 min) after cold exposure, but not on ABA treatment (Dubouzet et al., 2003). Transgenic Arabidopsis and rice plants overexpressing

OsDREB1A also displayed tolerance to low temperatures, high salinity, and drought (Dubouzet et al., 2003; Ito et al., 2006).

OsAP37 gene

The expression of *OsAP37* gene was up-regulated in PR but significantly suppressed in HA after cold stress (Fig. 3, Table 2). AP2 factors are widespread in plants, with the genomes of rice and Arabidopsis predicted to contain 139 and 12 AP2 genes, respectively (Nakano et al., 2006). The AP2 family has been found to be involved in diverse functions such as plant growth and stress tolerance (Gutterson and Reuber, 2004). Based on these diverse functions, the involvement of the AP2 family in stress response has been relatively well characterized. Oh et al. (2009) showed that *AP37* gene encoding a transcription factor caused increased tolerance to low temperatures, drought, and salinity during the vegetative phase. The expression of *OsAP37* as a transcription factor may prevent cold injury indirectly through induction and expression of stress responsive genes, which often

encode osmoprotectants.

***OsNAC6* gene**

Upregulation of *OsNAC6* was a result of cold treatment in the PR genotype, but expression was not significantly enhanced in the HA cultivar under the same treatment (Fig. 3, Table 2). NAC family transcription factors are plant-specific and contain a highly conserved N-terminal DNA-binding domain and a diversified C-terminal domain (Hu *et al.*, 2008); they are reported to participate in plant response to abiotic and biotic stress. One hundred and forty NAC or NAC-like genes were identified in rice and divided into five subgroups based on phylogenetic analysis (Fang *et al.*, 2008). All of the known stress-related NAC genes were grouped into family III, including two well-characterized stress-responsive NAC genes, *SNAC1*, and *OsNAC6/SNAC2*. Unlike other transcription factors, NAC expression pathway is ABA-dependant (Zheng *et al.*, 2009). Some members of the NAC family have been shown to be involved in plant stress responses (Lu *et al.*, 2007). Using Northern blot analysis, Xiong *et al.* (2002) found that *OsNAC6* is strongly induced by cold. Ohnishi *et al.* (2005) showed that *OsNAC6* is induced by salt, cold, drought, and abscisic acid in rice. Hence NAC transcription factors play a crucial role in physiological adaptation that allows successful plant propagation under abiotic stress conditions.

***OsMYB3R-2* gene**

The expression of *OsMYB3R-2* was up-regulated in the PR genotype after cold treatment, but was not significantly enhanced in the HA cultivar. The suppression of *OsMYB3R-2* gene in the HA cultivar may be an indication of weak signal perception or a signal transduction pathway that may cause HA's sensitivity to cold-stress (Fig. 3, Table 2). The MYB transcription factors participate in the ABA-dependent pathway. A MYB domain is usually composed of one to three imperfect repeats, each with about 52 amino acid residues that adopt a helix-turn-helix conformation intercalating in the major groove of the DNA (Yanhui *et al.*, 2006). Plant MYB proteins are categorized into three major groups: (1) R2R3-MYB with two adjacent repeats; (2) R1R2R3-MYB with three adjacent repeats; and (3) MYB-related proteins, usually containing a single MYB repeat (Stracke *et al.*, 2001). The R1R2R3-type MYB protein is located in the nucleus in rice and is induced by cold, drought, and salt stress. The enhanced stress tolerance of *35s::OsMYB3R-2* Arabidopsis plants reveals that *OsMYB3R-2* could mediate signal transduction, regulating some stress-responsive genes involved in CBF-dependent or CBF-independent pathways (Dai

et al., 2007). *OsMYB3R-2* transgenic plants showed enhanced tolerance to freezing, drought, and salt stress and decreased sensitivity to ABA (Dai *et al.*, 2007). Ma *et al.* (2009) showed that *OsMYB3R-2* functions in both stress and developmental processes in rice. Transgenic plants overexpressing *OsMYB3R-2* exhibited enhanced cold tolerance. Cold treatment greatly induced the expression of *OsMYB3R-2*, which encodes an active transcription factor.

CONCLUSIONS

The differential expression of various stress-induced genes was studied in one cold-tolerant and one cold-sensitive genotype. This investigation showed that cold induced genes encoding transcription factors expressed in higher levels and that genes encoding transcription factors may confer stress tolerance in tolerant genotypes through the activation of genes whose products are involved either in the regulation of gene expression for cold adaptation or for protection of cells from chilling injury. Our observations suggest that the differences between the studied genotypes regarding cold tolerance may be due to the timing of expression. Kiedrowski (1992) suggested the hypothesis of quantitative differences in the resistant and susceptible responses of genes to abiotic stress. Thus quantitative differences in the expression of genes involved in tolerance induction during abiotic stress could also be the result of the timing and intensity of transcriptional activation of involved genes rather than their presence/absence or other mechanisms. Thus it is important to enhance the genetic control capability of one or several key regulatory factor(s) to make the plant achieve multiple stress resistance (Qiang *et al.*, 2000).

This investigation showed that cold induced genes encoding transcription factors, namely *OsDREB1A*, *OsAp37*, *OsNAC6*, and *OsMYB3R-2* that regulate various stress responsive gene expressions, showed higher levels of expression in tolerant genotype. Functional analysis of these transcription factors should thus provide more information on the intricate regulatory networks involved in abiotic stress responses, and the cross-talk between different signaling pathways during stress adaptation.

Furthermore, considering transcription factors as candidate genes in breeding and other crop improvement programs will give us a clear understanding of abiotic stress related signal transduction events and will eventually lead us to develop crop varieties with superior stress tolerance through genetic manipulation (Lata *et al.*, 2011). The results of this study suggest that the expression

of genes encoding transcription factors changes in response to cold stress and so could be an informative resource in breeding and biotechnology projects aimed at developing cold tolerance in rice.

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