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Expression analysis of *OsbZIP* transcription factors in resistance response by the rice blast resistance gene *Pi36*-mediated

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Plant basic leucine zipper (bZIP) proteins play an essential role in the genes expression and regulation in higher plants. They have been shown to regulate diverse plant specific phenomena, including germination, floral induction and development, seed maturation, photomorphogenesis, biotic and abiotic stresses. Resistance response mediated by the rice blast resistance gene *Pi36* is a typical signal transduction, in which 12 *OsbZIP* genes were differentially expressed by microarray analyses. To understand the potential function of *OsbZIP* genes during the defense responses against rice blast, the expression analysis of these *OsbZIP* genes, in response to the blast fungus inoculation and the related defense signal molecules induction, were further conducted using real-time fluorescent quantitative polymerase chain reaction (PCR) technique. Our data indicates that among the 12 *OsbZIP* genes, the expression level eight tested genes were differentially regulated and maintained to 96 h points post inoculation in rice resistant and susceptible cultivars during *Magnaporthe oryzae* infection, and all of them were also significantly up-regulated by one or several kinds of exogenous plant hormones stresses. Although, these genes were induced only at early time points (1 to 24 h); it is evident that the *OsbZIP* genes may be involved in different signaling pathway, and play potential important functions in the defense response to rice blast.

Key words: OsbZIP transcription factors, rice blast, resistance response, plant hormones stresses.

INTRODUCTION

The plant defense responses is regulated via a network of signaling pathway involving salicylic acid (SA), abscisic acid (ABA), jasmonate (JA) and ethylene (ET). When the plants are suffering drought, high salt, external hormones, diseases, transcription factors were stimulated to combine with the cis-acting elements of downstream gene promoter through a series of signal transmission (Bari and Jones, 2009; Pieterse et al., 2009), and the target gene was directly regulated to express, or form homologous, heterologous dimers, or interact with other

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Abbreviations: SA, Salicylic acid; **ABA,** abscisic acid; **JA,** jasmonate; **ET,** ethylene; **CC,** coiled-coil domain; **NBS,** nucleotide binding site; **LRR,** leucine-rich repeat; **LTH,** Lijiangxintuanheigu; **MeJA,** methyl jasmonate; **BTH,** benzothiadiazole **qRT-PCR,** quantitative reverse transcriptions polymerase chain reaction.

# These authors contributed equally to this work

protein becomes a activated form and involved in JA, SA, ABA and other signal transduction pathways, forming a regulation of gene expression networks. More and more evidences show that, in the microbial pathogenic fungus, bacteria and insect resistance, different defense signaling pathways have complicated interactions with each other (Seabolt et al., 2011).

The plant basic leucine-zipper (bZIP) proteins compose a large family of transcriptional regulators exclusively in eukaryotes, which shared two common structures: a DNA-bonding basic region and the Leu zipper dimerization (Nijhawan et al., 2007). bZIP proteins play an essential role in the genes expression and regulation in higher plants, which have been shown to regulate diverse plant-specific phenomena, including photomorphogenesis and light signaling (Jakoby et al., 2002), defense response against pathogens (Zhang et al., 2003; Kesarwani et al., 2007; Thurow et al., 2005) as well as ABA and/or stress signaling (Lu et al., 2009; Xiang et al., 2008). So far, over 120 bZIP transcription factors have been identified in different plants. As a model species of monocotyledonous plants, about 100 bZIP sequences were predicted in rice database, and 89 of them take different roles in rice stress response and plant hormone signal transduction, 16 of those function have been identified (Nijhawan et al., 2007; Lu et al., 2009; Zou et al., 2008).

Plant defense responses are regulated through a network of signaling pathways. To defeat pathogens, the plant has to regulate transcription factors in a timely manner after recognizing the pathogen in order to activate a flood of defense-related genes (Liu et al., 2010). It has been reported that Xa21, an R-protein against *Xanthomonas oryzae pv. oryzae* (*Xoo*) of receptor kinase structure, also interact with a WRKY TF (OsWRKY62) in yeast two hybrid assay (Peng et al., 2008). Barley CC-NBS-LRR protein MLA10 interacts by CC domain with HvWRKY1/2 transcription factor (Shen et al., 2007). Rice blast, caused by the filamentous ascomycete *Magnaporthe oryzae*, remains the most serious pathogen in most rice producing (*Oryza sativa L.*) regions. Genetic resistance has been and undoubtedly will continue to be the major means of disease control for blast. To date, more than 80 major blast resistance genes have been identified (Zhai et al., 2011). Among them, 17 blast *R* genes have been characterized. With the exceptions of *pi21* and *Pid-2*, all of them are predicted to encode intracellular proteins with a coiled-coil (CC) domain at the N terminus and a nucleotide binding site (NBS) and leucine-rich repeat (LRR) domains at the C terminus. CC-NBS-LRR genes might be the most important genes to respond to the rice blast pathogens. Although so many resistance genes have been cloned, the mechanism of resistance remains unknown.

The blast resistance gene *Pi36* encodes a CC-NBS-LRR disease resistance protein which confers a stable and high level of resistance against isolates of the rice blast pathogen *M. oryzae* in Northern China (Liu et al., 2010; Liu et al., 2007). In this study, the expression profiles of 12 *OsbZIP* genes were reported, which were differentially expressed by microarray analyses, in various stages before and after rice blast pathogen *M. oryzae* inoculated in resistance cultivar (cv.) Kasalath with *Pi36* and susceptible cv. Lijiangxintuanheigu (LTH), which carries no known major resistance genes, as the susceptible one. The cv. Kasalath was also detected the treatments with three exogenous plant hormones ABA, methyl jasmonate (MeJA) and benzothiadiazole (BTH) which is fuctional analogues of SA, by real-time PCR analysis using gene-specific primers. A better understanding of the gene network associated with *Pi36* may help in the elaboration of strategies to promote durable resistance against rice blast, and the *OsbZIP* genes at transcriptional level are important for resistance to the rice blast.

MATERIALS AND METHODS

Plant materials, growth condition and stress treatments

The rice *indica* cv. Kasalath was used for this study because this culture was the donor of resistance gene *Pi36* (Liu et al., 2010; Liu et al., 2007), and the cv. Lijiangxintuanheigu (LTH), which carries no known major resistance genes, as the susceptible one. Seeds were sterilized in 1.5% NaClO and germinated at 28°C for three days and then transferred to plant growth chamber to grow for 14 days before treatments. For the hormone treatments, seedlings were fully sprayed with 0.05 mM ABA, 0.1 mM MeJA, 0.05 mM BTH, respectively, and covered with a plastic film over 48 h to keep a humidity environment more than 95%. And leaves were harvested at 0, 1, 3, 6, 12, 24, 48 and 72 h after treatment. For *M. oryzae* isolate treatment, three week-old seedlings were infected with a suspension of (1 to 2) × 10^5 spores per mL in 0.02% (v/v) Tween 20. Negative control leaves were sprayed with 0.02% (v/v) Tween 20. After inoculation, the seedlings were maintained at 24°C in darkness for 24 h, and then under a 14/10 h (light/dark) regime at 95% humidity. Leaf samples were taken at 0, 1, 2, 3, 6, 12, 24, 48, 72 and 96 hpi.

RNA extration and reverse transcription

Total RNA was extracted from a sample of leaf tissue at each time point using the TRIzol reagent (Invitrogen). The RNA was reverse transcribed using an avian myeloblastosis virus (AMV) reverse transcriptase kit (Promega Inc., Madison, WI, USA), following the manufacturer's instructions. For each sample, two independent reverse transcription (RT) reactions were pooled. All quantitative reverse transcriptions polymerase chain reaction (qRT-PCR) were based on the same pooled cDNA, and three technical replicates were run for each cultivar/time point combination. Three biological replicates (independent experiments) were included in the analysis.

Quantitative reverse transcriptions polymerase chain reaction (qRT-PCR)

Gene-specific primer sets were designed from nucleotide sequences available in the public domain (Table 1). All the primers were also designed to span intron-splicing sites in order to reduce

Table 1. The primer sets sequences used in this study.

Gene	Forward (5'-3')	Reverse (5'-3')	Product size/bp	Tm/℃
OsNIF1	CCTGAGTTCTCTCTGGCTTGC	ACTGAGCCACCAATCTTCTGC	141	62
OsNIF2	GTGGTCCGTCAGGGAGATT	TGCTCTCTCCTTTCTGCCA	131	62
OsNIF3	CAATGACGGAGTTCTTACACCC	CTGTCCTAGGGCTCATATCTGC	139	61
OsNIF4	TCAGTAGTTGACCCTCAGACAC	TCCTTGGACTTGTATCAGCC	121	56
OsbZIP5	CATCCAGCCCTTAGTCCATACC	CAAGATCCCTGGGCCGTAAT	65/160*	62
OsbZIP10	CGGTGGTAGCCTGGAATTCTT	ACGCAACTTTGGTTCCATGAA	76	63
OsbZIP36	GCTGCAGATGCACTAAATGAC	GCATTAACCTGACCTGTTGCAA	73	60
OsbZIP45	GGAACCAGCCAAGTCTGCCAA	CAGCCCCATCAACTTCCTTAAG	70	61
OsbZIP47	CAGGGAATCTTCATTGCAACTG	GCGCGTACTCAAGGTCGAA	90/187*	64
OsbZIP58	TGCTTGGCATGAGCATCTG	AAGTCCTGGCCCAAATGGA	65	60
OsbZIP62	AACAAGATCTCGCGGTTGGA	TCAGGAAATCGACGCAGCTA	97/743*	63
OsbZIP76	CTCGTGTTGAGTGATCCGAAGA	TTGGACCTCGCAGCAGATCT	67/403*	61
Actin1	TGCTATGTACGTCGCCATCCAG	AATGAGTAACCACGCTCCGTCA	209/458*	60

*The intron size if genomic DNA is used as the template.

the effect of potential genomic DNA contamination. Each PCR reaction was prepared as follows: 1 µL cDNA as template, 0.4 µL primer pair, 5 µL SYBR® Green Real-time PCR Master Mix (TOYOBO, Japan) and 3.6 µL ddH$_2$O. The reaction was initiated by pre-denaturation 5 min at 94°C, then followed by 40 cycles of 30 s at 94°C, 30 s at 55°C, and 30 s at 72°C. At the end of each extension step, the fluorescence signal was detected, and used to generate an amplification profile.

The rice *Actin1* gene, a constitutively expressed housekeeping gene, was used to normalize samples. The comparative C_t method, as described by Reyna and Yang (2006), was used to describe all genes within a sample relative to the time 0 sample. Briefly, the relative C_t method consists of the following formula

$$2^{-(\Delta Ct\ \text{treatment} - \Delta Ct\ \text{control})}$$

Where, (C_t $^{\text{target gene}}$ to C_t $^{\text{normalizer}}$) and (C_t $^{\text{time zero}}$ to C_t $^{\text{normalizer}}$) represent ΔC_t $^{\text{treatment}}$ and $\Delta C_t^{\text{control}}$, respectively.

Real-time PCR analysis was based on at least three technical replicates and a repetitive average C_t value was taken no more than 0.5. In this study, only genes that showed five-fold increase compared with the 0 h control were considered to have been induced.

RESULTS

Expression profiles of OsbZIPs challenged with *M. oryzae*

The expression profiles of 12 OsbZIP genes in cv. Kasalath and LTH challenged with blast isolate RB11, which is avirulent on Kasalath and virulent on LTH, were examined by qRT-PCR at a series of time points postinoculation (p.i.). The TGA transcription factors were documented to involve in basal resistance and PR gene expression (Zhang et al., 2003; Kesarwani et al., 2007). Of the four TGA type OsbZIP genes (*OsNIF1*, *OsNIF2*, *OsNIF3* and *OsNIF4*) assayed, *OsNIF1* was rapidly induced in cv. Kasalath, and reached a peak of expression at 2 hpi. Thereafter, its expression was temporarily reduced, before increasing again to a second maximum between 24 and 48 hpi. In cv. LTH, this same gene was down-regulated throughout the measurement period. *OsNIF2* was strongly up-regulated in cv. Kasalath by 1 hpi, and reached a peak of expression at 12 hpi, followed by a gentle decline, but maintaining a level above background throughout. In cv. LTH, this same gene was down-regulated throughout; while *OsNIF3* was rapidly up-regulated (peaking at 1 hpi) in cv. Kasalath, its expression level fell rapidly thereafter; in cv. LTH, the same gene was induced gradually, reaching 500-fold of the background level by 12 hpi. *OsNIF4* was down-regulated in both cv. Kasalath and cv. LTH at most of the measurement times, with the exception of 1, 3 and 12 hpi. in cv. LTH, when its expression level was somewhat raised (Figure 1). Therefore, our results reveal that OsNIF1 and OsNIF2 may be involved in the rice blast resistance response.

Of the eight other structural type *OsbZIPs* genes, which were reported to be involved in light regulation and abiotic stress signaling (Kesarwani et al., 2007; Lu et al., 2009), *OsbZIP62* displayed the similar expression profiles between cv. Kasalath and LTH. *OsbZIP45* was weakly up-regulated in cv. Kasalath at late period, whereas the gene was down-regulate throughout the measurement period. As for the other six genes, *OsbZIP5*, *OsbZIP10*, *OsbZIP36*, *OsbZIP47*, *OsbZIP58* and *OsbZIP76*, the expression of level strongly up-regulated in resistant cv. Kasalath, with a peaking of, respectively, 320-, 500-, 45-, 450-, 650- and 250-fold of the background level at 24 hpi, respectively. Notably, the expression level of these genes in cv. Kasalath was maintained to 96 hpi, but the six genes were down- regulated in cv. LTH throughout the measurement period (Figure 1).

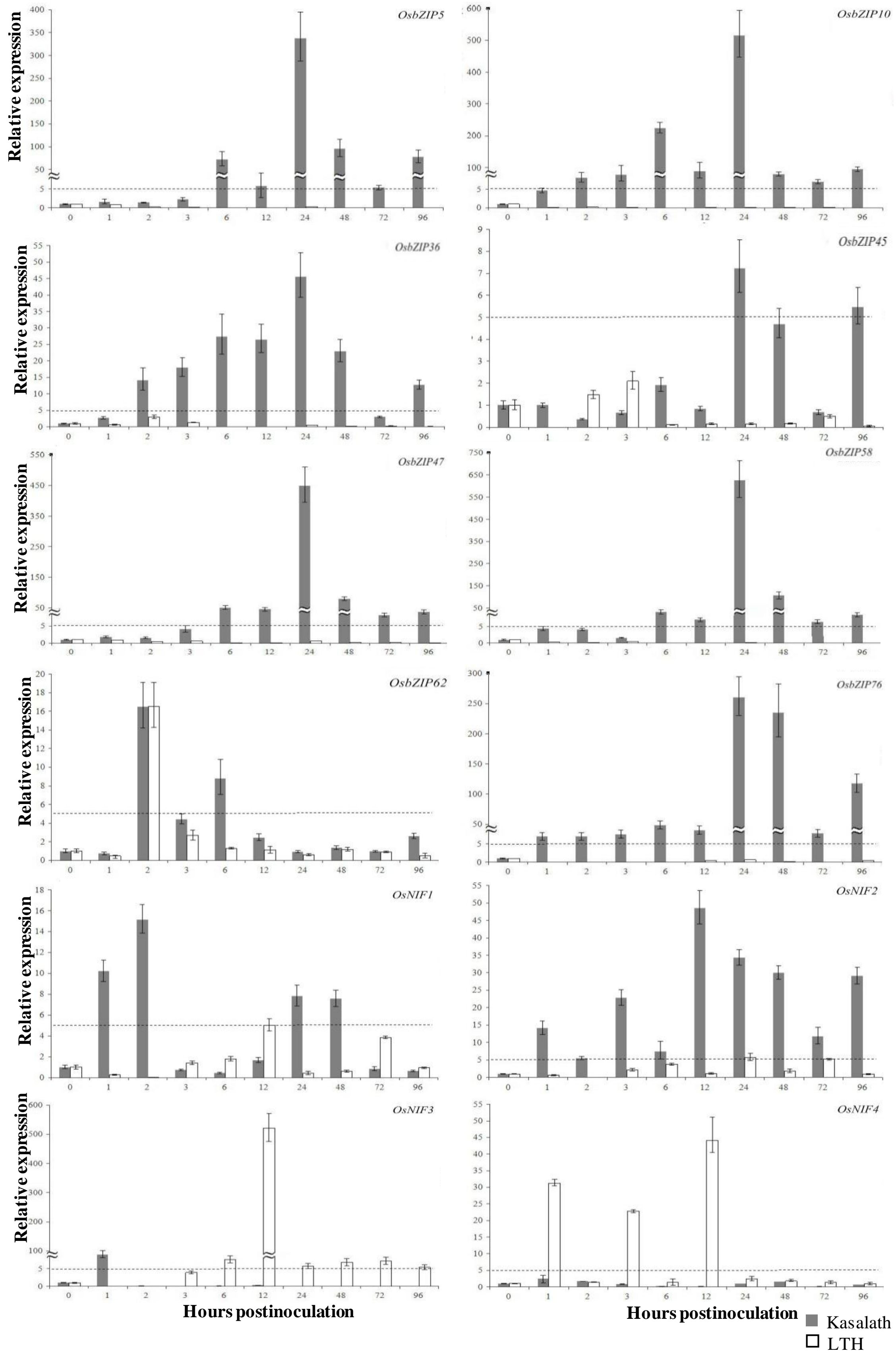

Figure 1. *OsbZIP* genes induced by rice blast infection

To our knowledge, this is the first report of the involvement of these bZIP transcriptional factors in the blast-induced defence response.

Expression analysis of OsbZIP gene after plant hormone treatments

To investigate expression profiles of the 12 *OsbZIP* genes in cv. Kasalath response to plant hormones treatments, we further treated the rice cv. Kasalath with ABA, MeJA and BTH (Figure 1). When the seedling were treated with ABA, most of the *OsbZIP* genes which displayed the similar expression pattern, *OsbZIP5*, *OsbZIP10*, *OsbZIP45*, *OsbZIP47*, *OsbZIP58* and *OsbZIP76* were up-regulated rapidly to reach the expression peaks at 6 or 24 h, but not so remarkable, only *OsbZIP58* and *OsbZIP76* got to 45- and 55-fold, respectively. *OsbZIP36* and *OsNIF2* were weakly induced at 6 and 24 h, respectively, but *OsbZIP62*, *OsNIF1*, *OsNIF3* and *OsNIF4* were not induced (Figure 2).

When the rice cv. Kasalath was treated by MeJA, the expression of *OsNIF3* and *OsNIF4* showed no significant changes, but *OsNIF1* and *OsNIF2* were up-regulated 5.5-fold at 3 and 6 h, respectively, while *OsbZIP76* was up-regulated 22-fold only at 6 h. The other OsbZIPs displayed different expression profiles. *OsbZIP5* and *OsbZIP45* were rapidly induced at 1 hpi and the expression level increased up to maximum by 6 and 12 hpi, respectively; whereas *OsbZIP10*, *OsbZIP36*, *OsbZIP47* and *OsbZIP62* were induced at 3 hpi and reached a peak of expression by 6 hpi and then followed by a gently decline by 24 hpi. *OsbZIP58* was strongly induced at 6 hpi reaching 175-fold of the background level and then slightly decreased by 24 hpi (Figure 3).

To investigate the expression pattern of OsbZIPs in cv. Kasalath under BTH stress, the results showed that the expression level of eight genes increased up to maximum by 12 hpi at different degree, and decreased slightly by 48 hpi. Among these genes, *OsbZIP62* and *OsbZIP76* were up-regulated only at 12 h and reached 6 and 7-fold, respectively. Whereas *OsbZIP5* and *OsbZIP45* were rapidly induced at 1 hpi and reached a peak by 12 hpi with 175 and 27-fold, decreased slight by 24 hpi. And, *OsbZIP10*, *OsbZIP36* and *OsbZIP47* were induced at 6 h and increased up to maximum by 12 hpi and declined slight by 24 hpi. As for *OsbZIP58*, the expression was induced at 3 hpi and reached a peak by 12 hpi, finally declined by 48 hpi. While the four genes *OsNIF1*, *OsNIF2*, *OsNIF3* and *OsNIF4* were not induced (Figure 4).

DISCUSSION

In many higher plants, bZIP proteins play crucial roles in the genes expression and regulation, which have been shown to regulate diverse plant-specific phenomena, as well as biotic and abiotic stresses (Nijhawan et al., 2007; Jakoby et al., 2002; Kesarwani et al., 2007). So far, most of the *OsbZIP* genes identified are related to drought, low temperature, high salt and other abiotic stress (Fujita et al., 2005; Achuo et al., 2006; Asselbergh et al., 2008). In the present study, 12 OsbZIP possible differentially expressed by microarray analyses involved in resistance response *Pi36*-mediated were analyzed by two induction patterns, such as *M. oryzae* infection and exogenous hormones induction. Our results reveal that, except *OsbZIP45*, *OsbZIP62*, *OsNIF3* and *OsNIF4* which were not induced among 12 *OsbZIP* tested genes, the other genes were up-regulated in the incompatible *Pi36/AvrPi36* interaction, indicating that these genes are active in the response of *Pi36* to the infection with an avirulent race of blast. To our knowledge, this is the first report of the involvement of bZIP transcriptional factors in the blast-induced defence response.

Plant defense responses are regulated through a network of signaling pathways that involve endogenous plant signaling molecules such as SA, JA, ET, and ABA (Mauch-Mani and Mauch , 2005; An and Mou, 2011). In this study, among 12 *OsbZIP* genes, they were up-regulated by blast fungus and could also be induced by one or more hormones resulting to expression. Interestingly, it was observed that the expression was induced by blast fungus in early time points (1 to 24 h) and lasted to late period (24 to 96 h) in resistance response, whereas all expression was up-regulated by the early time points. Apparently, our data is beneficial to dissect the roles of plant hormones in resistance response.

It has become evident that SA and JA signaling pathways are mutually antagonistic in *Arabidopsis* (Kunke and Brooks, 2002). Recently, ABA has been reported to have an antagonistic interaction with SA signaling pathways in the rice-*M. oryzae* interaction (Achuo et al., 2006; Asselbergh et al., 2008; Fan et al., 2009; Jiang et al., 2010). In this study, our results show that in rice, some of the OsbZIP members were differentially regulated in rice plants in different hormones signaling pathway, implicating that OsbZIPs may be involved in SA, JA and ABA-dependent pathway, consistent with the suggestion that SA, JA and ABA-dependent defence signals interact with one another, either synergistically or antagonistically (Kunke and Brooks, 2002; Fujita et al., 2006).

The redundant function of *OsbZIP* genes may be beneficial in protecting the cell or organism under various stress conditions and in eliciting the multiple pathways that lead to the wide array of physiological responses that occur following infection with pathogens. Recently, we have produced transgenic rice plants with overexpression or RNAi construct for each differentially regulated OsbZIP. These lines provide the opportunity to study the contribution of each OsbZIP under normal or defined stress condition, and should eventually lead to the determination of the functions of *OsbZIP* genes.

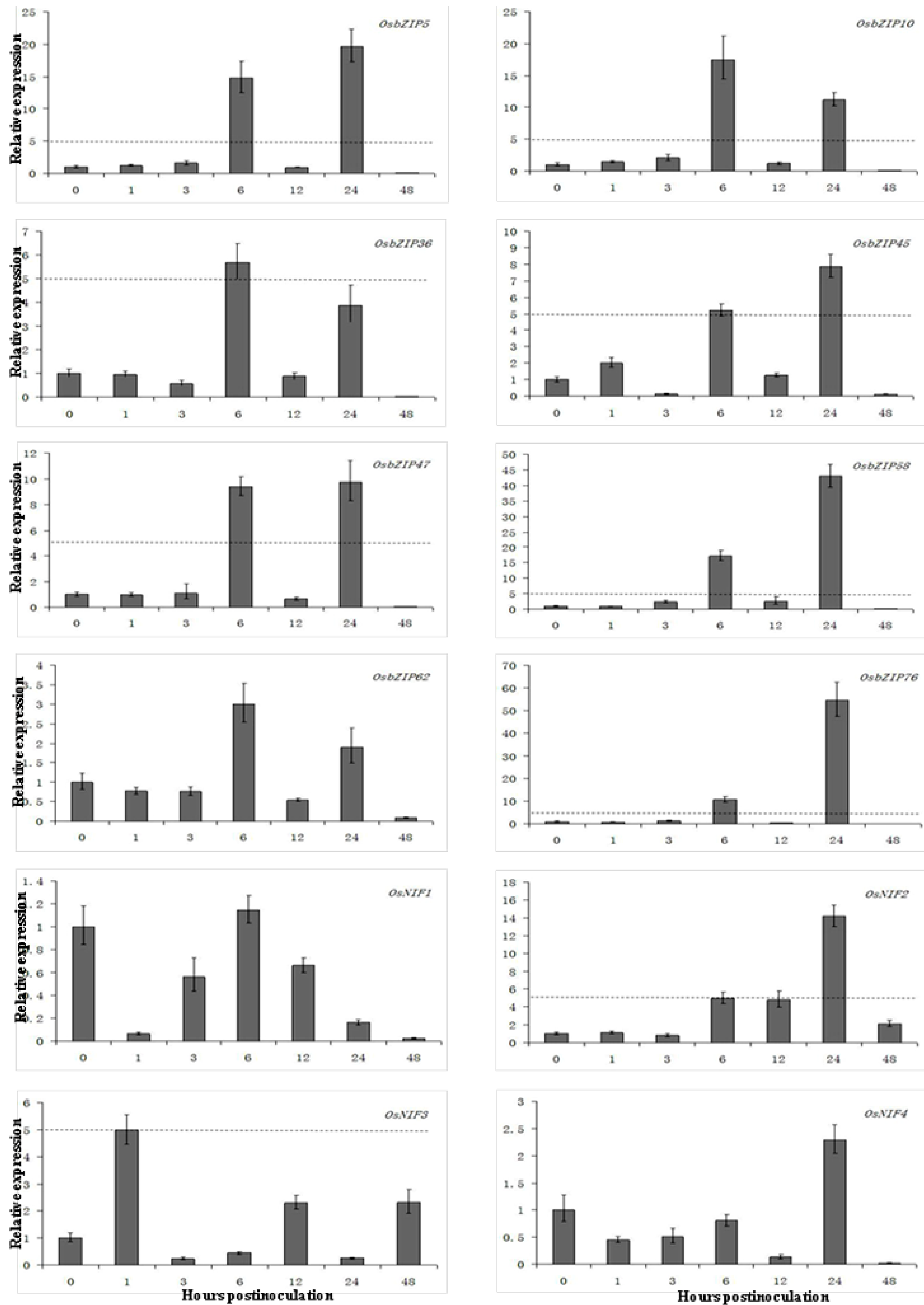

Figure 2. *OsbZIP* genes induced by abscisic acid (ABA) treatment.

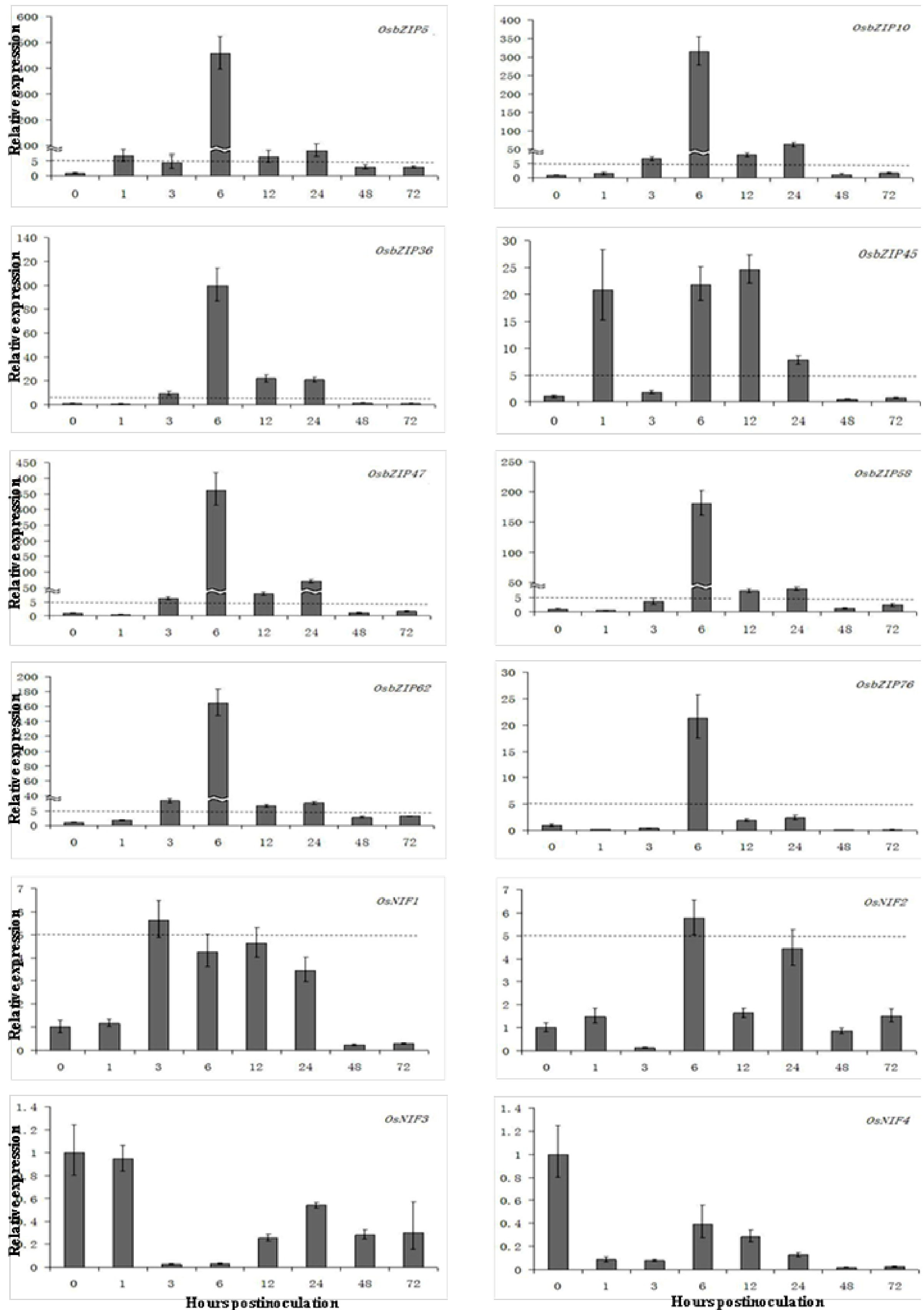

Figure 3. *OsbZIP* genes induced by methyl jasmonate (MeJA) treatment.

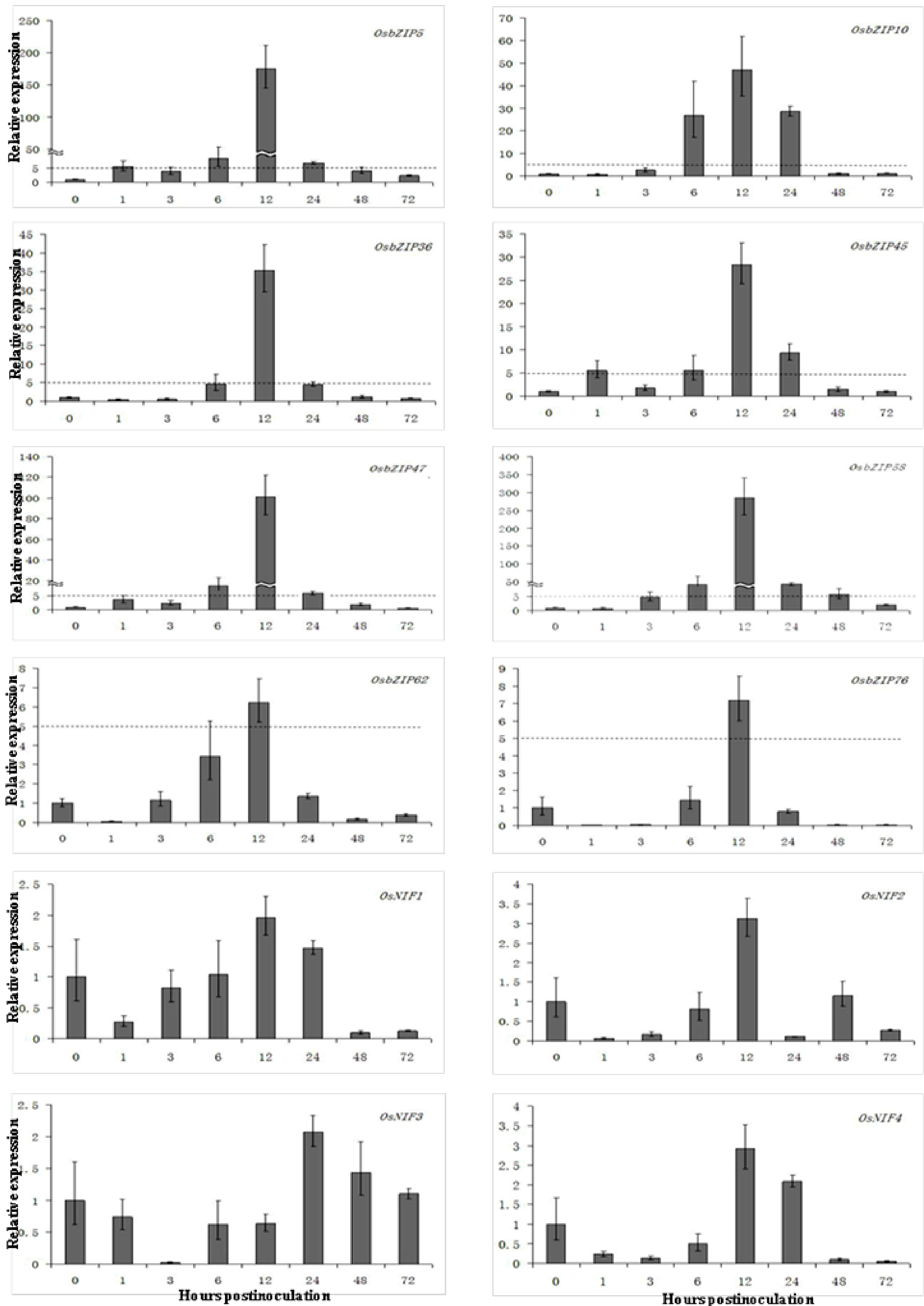

Figure 4. *OsbZIP* genes induced by benzothiadiazole (BTH) treatment.

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