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Isolation, characterization and chromosomal location of a novel zinc-finger protein gene that is down-regulated by salt stress

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Abstract mRNA transcripts from salt-stressed and unstressed rice seedlings were detected by differential display to show alterations in abundance. One transcript, designated *OsZFP1*, was found to be significantly down-regulated by salt stress. *OsZFP1* encodes a protein of 145 amino acids with three putative Cys_2/Cys_2-type zinc-finger domains. A homology search of GenBank databases showed that OsZFP1 is homologous to the rat and human ZIS (zinc-finger, splicing) proteins and the human nucleopore complex protein Nup358 in the zinc-finger domains. Genomic Southern analysis indicated that the *OsZFP1* gene was present as a single-copy sequence in the rice genome. Restriction fragment length polymorphism mapping assigned the *OsZFP1* gene to the distal position of chromosome 6. A RT-PCR assay showed that the *OsZFP1* transcripts were more abundant in rice shoots than in the roots. Decreases in the level of *OsZFP1* transcripts were detected in the shoots after 6 h of salt stress and in the roots after 3 h of salt stress. In addition, the expression of *OsZFP1* in rice shoots was significantly repressed by exogenous application of abscisic acid. The results suggest that *OsZFP1* represents a novel type of zinc-finger protein gene in plants and that it is implicated in the responses of rice plants to salt stress.

Keywords Differential display · Down-regulation · Rice (*Oryza sativa* L.) · Salt stress · Zinc-finger protein

Introduction

Plant responses to environmental factors are often accompanied by changes in gene expression (Shinozaki and Yamaguchi-Shinozaki 1997). During the past decade, a number of genes that are induced by salt and drought stresses have been isolated and characterized from different plant species (Claes et al. 1990; Chen et al. 1994; Lippuner et al. 1996; Urao et al. 1999; Zhang et al. 1999; Li and Chen 1999, 2000). In addition, several types of upstream regulatory elements responding to the stress signals have been identified (Shinozaki and Yamaguchi-Shinozaki 1997). However, reports on the isolation of genes that are down-regulated by osmotic stress are rather scarce, except for the case of a novel tomato gene being negatively regulated by water stress (Yu et al. 1996).

Many types of the zinc-finger transcription factor genes have been characterized in plants (Reviewed by Takatsuji 1998). The term "zinc finger" represents the sequence motif in which the cysteine residues and/or the histidine residues coordinate a zinc atom to form local peptide structures that are implicated either in DNA binding for example, zinc-finger of the TFIIIA- and GATA-types – or in protein-protein interactions – for example, zinc-finger of the LIM- and RING-finger types. (Takatsuji 1998). Differential expression of a plant zinc-finger protein gene in response to salt stress has been observed. For example, the *Arabidopsis* zinc-finger protein gene *STZ* was salt-inducible and able to complement the yeast calcineurin mutants (Lippuner et al. 1996).

We are interested in the regulation of rice gene expression by salt stress. Using a differential display (DD) technique (Liang and Pardee 1992) Li and Chen (1999, 2000) isolated and characterized two salt-inducible genes from rice. One gene is a new member of the rice translation elongation factor 1A gene family and is significantly up-regulated by salt and drought stress (Li and Chen 1999). The second gene encodes *S*-adenosylmethionine decarboxylase (SAMDC), which is a rate-limiting enzyme in the polyamine biosynthesis pathways. We have demonstrated that the differential expression of SAMDC gene in rice seedlings is positively correlated with the salt tolerance of rice varieties (Li and Chen 2000).

In this article we report the identification and characterization of a novel rice gene, designated *OsZFP1*,

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which encodes a protein with three putative Cys_2/Cys_2-type zinc-finger domains. We investigated the expression of *OsZFP1* in rice seedlings in response to salt stress and determined its chromosomal location.

Materials and methods

Plant materials, growth conditions and stress treatments

Seeds of rice (*Oryza sativa* L. cv. ZYQ8) were germinated at 37°C for 3 days and grown hydroponically at 26°C under a photoperiod of 12 h (light):12 h (dark). At the three-leaf stage, rice seedlings were grown for 3 days either in solutions containing 1% (about 171 m*M*) NaCl or in water. Total RNA was extracted from the shoots and used for differential display analysis.

Rice seedlings at the three-leaf stage were transferred into solutions containing 171 m*M* NaCl or 10 µ*M* abscisic acid (ABA) for salinity and ABA treatments, respectively. The shoots and roots were harvested after being subjected to varying durations of stress treatments, quickly frozen in liquid nitrogen and stored at –70°C for RNA extraction.

Differential display

Total RNA was extracted using the acid guanidinium thiocyanate-phenol-chloroform method (Chomczynski and Sacchi 1987). First-strand cDNAs were synthesized from 0.4µg total RNA (pre-treated with DNase I) with M-MLV reverse transcriptase (Promega). Differential display was performed according to procedures described previously (Li and Chen 2000). The differential cDNA fragments were recovered from the sequencing gel and eluted. The elusions were used as templates for reamplification using the same sets of primer pairs. The reamplified fragments were purified from the agarose gel and cloned into pGEM-T easy vector (Promega) according to the manufacturer's instructions.

Rapid amplification of cDNA end (RACE)

5′-RACE was performed with the 5′/3′ RACE kit (Boehringer Mannheim) according to the manufacturer's instructions. The amplified cDNA fragment was purified from the agarose gel and cloned into pGEM-T easy vector for sequencing.

Reverse transcription-PCR (RT-PCR)

Oligonucleotide primers were designed to amplify both a part of the cDNA sequence of *OsZFP1* to give a 700-bp PCR product and a part of the constitutively expressed actin gene *RAc1* (McElroy et al. 1990) to generate a 800-bp PCR fragment. First-strand cDNAs were synthesized from 4 µg total RNA (pre-treated with DNase I) with M-MLV reverse transcriptase (Promega). The PCR conditions were a pre-denaturation of 3 min at 94°C; 28 cycles of 1 min at 94°C, 1.5 min at 55°C, 1 min at 72°C; an extension for 10 min at 72°C. The PCR products were separated on a 1% agarose gel containing ethidium bromide and visualized under UV light. The sequences of the primers are as follows:

OsZFP1: sense: 5′-CCTAGTACTAAGAACAGC-3′
anti-sense: 5′-TACAACGATCTTGGAAGC-3′
RAc1: sense: 5′-GGAACTGGTATGGTCAAGGC-3′
anti-sense: 5′-AGTCTCATGGATAACCGCAG-3′

Genomic Southern analysis

DNA extraction and Southern blot hybridization followed the methods of McCouch et al. (1988). Three micrograms of genomic DNA was completely digested, fractionated on a 0.8% agarose gel and blotted onto Hybond N^+ nylon membranes (Amersham). Southern hybridization was carried out overnight at 65°C using an α-[^{32}P]-dCTP-labeled *OsZFP1* cDNA as a probe. The filters were washed at 65°C with 2× SSC, 0.1% SDS; 1× SSC, 0.1% SDS and 0.5× SSC, 0.1% SDS each for 15 min.

Restriction fragment length polymorphism (RFLP) mapping

The chromosomal position of *OsZFP1* was determined with an *indica*/*japonica* rice (ZYQ8/JX17) doubled haploid (DH) population and its molecular linkage maps (He et al. 1999). The *Sca*I-digested genomic DNA of the 127 DH lines was separated on a 0.8% agarose gel and transferred onto nylon membranes for Southern hybridization using *OsZFP1* cDNA as a probe. Linkage analysis was conducted using the MAPMAKER/EXP. 3.0 software (Lander et al. 1987).

DNA sequencing and data analysis

Double-strand cDNA sequences were determined using the Taq Dye Primer Cycle Sequencing Kit (Amersham) and the ABI 373 A automatic sequencer. The nucleotide and deduced amino acid sequences of *OsZFP1* were compared with those released in GenBank databases using the Gapped BLAST analysis program. Alignment of the amino acid sequences was generated by the BLAST program.

Results

Differential display

Differential display was performed to detect changes in the transcripts in rice seedlings under salt stress conditions. We used five 3′ anchor primers ($dT_{12}GG$, $dT_{12}CG$, $dT_{12}AG$, $dT_{12}GC$ and $dT_{12}CC$) and ten arbitrary oligonucleotide primers (10 mer) to carry out DD-PCR amplification. Of the 31 differential bands displayed on the sequencing gel, 26 were up-regulated and 5 were down-regulated by salt stress. One down-regulated fragment (shown in Fig. 1) was further characterized. Sequence analysis revealed that this fragment was 245 bp in length and had no significant homology to the sequences released in GenBank databases.

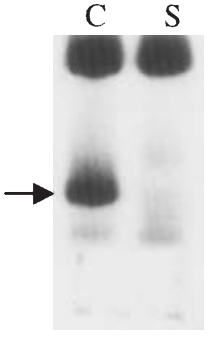

Fig. 1 Differential display of the transcripts from normally grown (*C*) and salt-stressed (*S*) rice seedlings. The anchor primer $dT_{12}GC$ and the arbitrary primer OPA20 were used for DD-PCR. The *arrow* indicates the differentially expressed partial cDNA fragment of *OsZFP1*

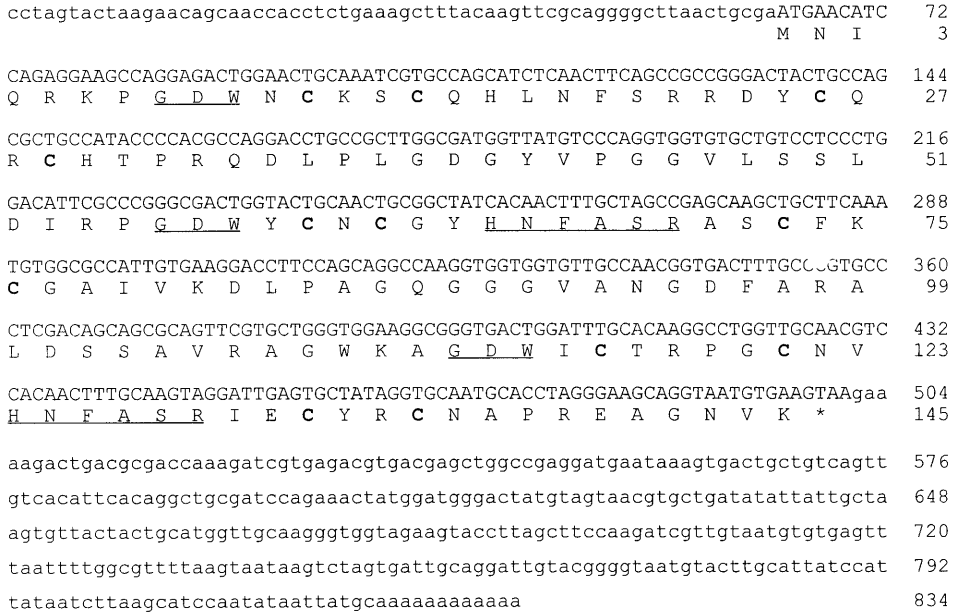

Fig. 2 The cDNA sequence and predicted amino acid sequence of the *OsZFP1* gene. *Bold C* residues in the amino acid sequence are the six cysteines of the three Cys_2/Cys_2-type zinc-finger domains. The internal amino acid sequence repeats are *underlined*. The nucleotide sequence of *OsZFP1* has been deposited in GenBank databases under the accession number AF171223

Isolation and characterization of the full-length cDNA sequence of *OsZFP1*

To obtain the full-length cDNA sequence of this fragment, we employed the 5′-RACE technique. Sequencing of the positive PCR fragment indicated that it contained a complete open reading frame (ORF). The reconstituted full-length cDNA was 834 bp in length, consisting of a 63-bp 5′-untranslated region (UTR), a complete ORF of 435 bp encoding a polypeptide of 145 amino acids, followed by a 3′-UTR of 336 bp (Fig. 2). A stop codon (TAA) at position 55, 9 bp upstream of the first ATG codon and in frame with the entire ORF, suggests that the ATG codon at position 64 is the start codon. Analysis of the deduced amino acid sequences revealed that this protein contained three putative Cys_2/Cys_2-type zinc-finger domains, which were arranged as $CX_{1-4}CX_{10}CX_2C$ (Fig. 3A). Therefore, we named this gene *OsZFP1* (*Oryza sativa* Zinc Finger Protein No. 1).

A homology search of GenBank databases showed that OsZFP1 is homologous to the rat and human ZIS (zinc-finger, splicing) proteins (Karginova et al. 1997; Nakano et al. 1998) in the zinc-finger domains (Fig. 3B). In addition, the zinc-finger domains of OsZFP1 also show a similarity to that of a human giant nucleopore complex protein (nucleoporin) Nup358 (Wu et al. 1995) (Fig. 3C). The rat and human ZIS proteins contain two zinc-finger domains and a splicing-factor domain. The Nup358 protein contains eight zinc-finger domains, three Ran-GTP binding sites, a cyclophilin A homologous domain and a leucine-rich region. However, the fact that OsZFP1 contains only the zinc-finger domains suggests that the function of OsZFP1 is different from that of the ZIS proteins and the Nup358 protein.

Recently, the entire nucleotide sequence of the rice P1-derived artificial chromosome (PAC) clone P0535G04, which contains a homologous sequence of the *OsZFP1* gene, was determined (Accession No. AP000399.1). We compared the nucleotide sequence of *OsZFP1* with the genomic sequence, and found two introns in the coding region and one intron in the 5′-UTR of the *OsZFP1* cDNA clone. The amino acid sequence of OsZFP1 was 99% identical to that deduced from the genomic sequence.

Genomic Southern analysis and RFLP mapping

Genomic DNA gel blot analysis was carried out to investigate the genomic organization of the *OsZFP1* gene. It was observed that only one band was detected under high-stringency conditions (Fig. 4), suggesting that the *OsZFP1* gene is present as a single-copy in the rice genome.

The chromosomal location of the *OsZFP1* gene was determined by an RFLP mapping approach using a rice DH population and its molecular linkage maps (He et al. 1999). Figure 5 shows the chromosomal position of the *OsZFP1* locus on chromosome 6. This map position is consistent with the report that the PAC clone P0535G04, which also carries the *OsZFP1* gene, is located on chromosome 6 (http://www.dna.affrc.go.jp).

Expression of *OsZFP1* was down-regulated by salt stress and exogenous ABA application

Because the level of the *OsZFP1* transcript is too low to be detected by Northern blot analysis, we performed RT-PCR to investigate its expression in rice seedlings stressed by salinity. PCR amplification generated a 700-bp fragment from cDNA and a 2.0-kb fragment from genomic DNA (data not shown). Using RT-PCR, we observed that *OsZFP1* transcripts were more abundant in rice shoots than in the roots, and were signifi-

Fig. 3A–C Deduced structural features of OsZFP1. **A** Alignment of the three putative zinc-finger domains in OsZFP1. *Numbers* at *left* and *right* refer to amino acid residue positions in the deduced OsZFP1 protein from **Fig. 2**. The cysteine residues are in *bold*. *Gaps* are introduced to maximize the similarity. **B, C** Alignment of the zinc-finger domains of OsZFP1 with that of the rat ZIS protein, human ZIS1, ZIS2 proteins and Nup358 protein. Identical residues are marked by *asterisks*, and the cysteine residues of the zinc-finger domains are in *bold*

(A)

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Zinc-finger 1    8 GDWNCKS--CQHLNFSRRDYCQRC  29
Zinc-finger 2   56 GDWYCN---CGYHNFASRASCFKC  76
Zinc-finger 3  112 GDWICTRPGCNVHNFASRIECYRC 135
Consensus          GDW.C X1-4C...NF..R..CX2C
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(B)

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OsZFP1  NIQRKPGDWNC--KSCQHLNFSRRDYCQRC---HTPRQDLPLGDGYVPGGVLSSLD---I 53
Zis     NFRVSDGDWICPDKKCGNVNFARRTSCNRCGREKTTEAKMMKAGGTEIGKTLAEKSRGLF 64
ZIS1    NFRVSDGDWICPDKKCGNVNFARRTSCNRCGREKTTEAKMMKAGGTEIGKTLAEKSRGLF 64
ZIS2    NFRVSDGDWICPDKKCGNVNFARRTSCNRCGREKTTEAKMMKAGGTEIGKTLAEKSRGLF 64
        *     *** *  * *   ** **  * **    *         *   *  *

OsZFP1  RPGDWYC-NCGYHNFASRASCFKCGA---IVKDLPAGQGGG  89
Zis     SANDWQCKTCSNVNWARRSECNMCNTPKYAKLEERTGYGGG 105
ZIS1    SANDWQCKTCSNVNWARRSECNMCNTPKYAKLEERTGYGGG 105
ZIS2    SANDWQCKTCSNVNWARRSECNMCNTPKYAKLEERTGYGGG 105
           ** *  *   * * *  *  *            * ***
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(C)

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OsZFP1  KPGDWNCKSCQHLNFSRRDYCQRCHTPR-QDLPLGDGYVP---------------GGVLS   49
Nup358  KEGQWDCSACLVQNEGSSTKCAACQNPRKQSLPATSIPTPASFKFGTSETSKTLKSGFED 1538
        * * * *  *   *      *  *  ** * **      *                 *

OsZFP1  SLDIRPGDWYC-NCGYHNFASRASCFKCGAIVKDLPAGQGGGVANGDFARALDSSAVRAG 108
Nup358  MFAKKEGQWDCSSCLVRNEANATRCVACQNPDKPSPSTSVPAPASFKFGTSETSKAPKSG 1598
              * * *  *   * *    *  *    *  *       *   *     * *  *

OsZFP1  W------KAGDWICTRPGCNVHNFASRIECYRCNAP  138
Nup358  FEGMFTKKEGQWDCS--VCLVRNEASATKCIACQNP 1632
              * * * *    * * * **   *  *  *
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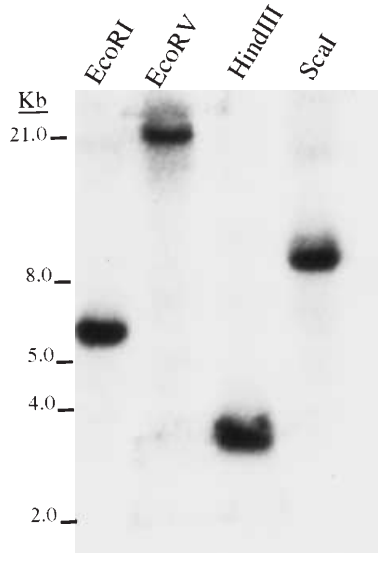
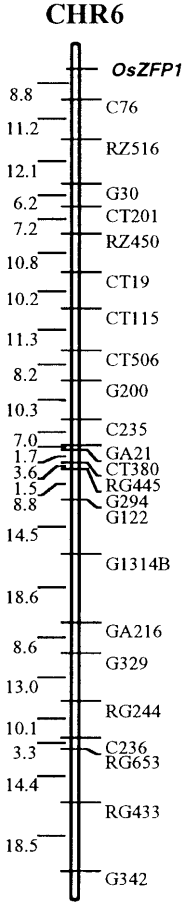


Fig. 4 Genomic DNA gel blot analysis of the *OsZFP1* gene. Rice genomic DNA was digested with *Eco*RI, *Eco*RV, *Hind*III or *Sca*I, and hybridized with the entire cDNA of *OsZFP1*

Fig. 5 Map position of the *OsZFP1* locus on chromosome 6. The RFLP map was based on an *indica*/*japonica* rice (ZYQ8/JX17) DH population consisting of 127 individuals. Map distances are presented in centiMorgans on the *left* of the chromosome and the RFLP markers on the *right*



cantly down-regulated by salt stress (Fig. 6). In the shoots, repression of *OsZFP1* gene expression was observed 6 h after salt stress, with the lowest level being reached at 24 h, after which there was a slight recovery (Fig. 6A). However, in the roots, the repression of its expression was detected 3 h after salt stress, and the

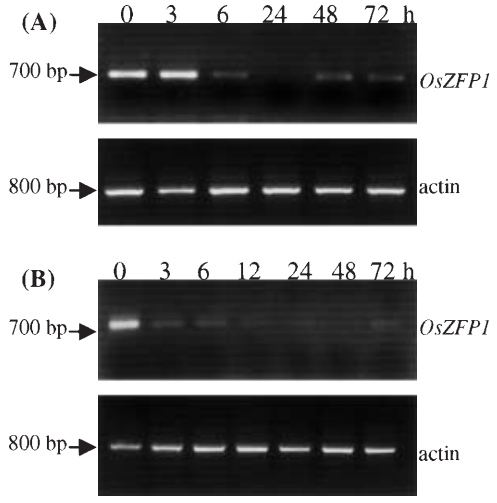


Fig. 6A, B Effect of salt stress on the expression of *OsZFP1* in rice shoots (**A**) and roots (**B**). RT-PCR products from the *OsZFP1* and actin (control) transcripts were separated on ethidium bromide-stained agarose gels and visualized under UV light

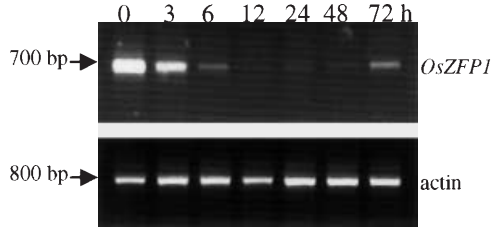


Fig. 7 Effect of exogenous ABA application on the expression of *OsZFP1* in rice shoots by RT-PCR assay

lowest level was observed between 12 h and 48 h of salt stress (Fig. 6B). It is obvious that the down-regulation of *OsZFP1* occurs earlier in roots than in shoots and that the recovery of *OsZFP1* expression is more difficult in roots than in shoots. These differences may be due to the fact that the roots are in direct contact with the stress and always remain in contact with it.

The plant hormone ABA plays an important role in the responses of plants to salt, drought and cold stress. It has been hypothesized that at least four independent signal pathways function in the activation of stress-responsive genes under dehydration conditions: two are ABA-dependent and two are ABA-independent (Shinozaki and Yamaguchi-Shinozaki 1997). We used a RT-PCR assay to investigate the effect of exogenous application of ABA on t he expression of *OsZFP1* in rice seedlings. As shown in Fig. 7, an initial steady decrease in the level of the *OsZFP1* transcript was observed between 3 h and 12 h after ABA treatment, and then a slight recovery of its expression was detected from 24 h to 72 h after ABA stress. This observation suggests that the regulation of *OsZFP1* by salt stress is through the ABA-dependent pathways.

Discussion

In this paper we report the isolation and characterization of a novel rice gene (*OsZFP1*) encoding a protein with three putative Cys_2/Cys_2-type zinc-finger domains. The *OsZFP1* gene reported here is 834 bp in length and contains a complete ORF encoding a small polypeptide of 145 amino acids (Fig. 2). A homology search of GenBank showed that the putative zinc-finger domains of OsZFP1 are similar to that of the rat and human zinc-finger, splicing proteins (Fig. 3B), the human nucleopore complex protein Nup358 (Fig. 3C) and many putative proteins from animals (data not shown). In addition, it also has homology to the zinc-finger domains of some plant hypothetical proteins such as a putative Ser/Thr protein kinase (Accession No. AC003105) and a putative nuclear protein (Accession No. AC003952) in *Arabidopsis* (data not shown). However, the functions of these plant sequences are not further characterized. On the other hand, although eight classes of the zinc-finger transcription factor genes have been isolated from plants (Takatsuji 1998), none of these genes has a similarity to the *OsZFP1* gene in the zinc-finger domains. We found that the differences among them occurred in the spacing and in the conserved amino acid sequences between the second and the third cysteine residues in the zinc-finger motifs. In the second and third zinc-finger domains of OsZFP1 HNF ASR sequence repeats were observed, which have not been found in other types of plant zinc-finger proteins. These observations suggest that *OsZFP1* represents a novel type of zinc-finger protein gene in plants.

The distinctive feature of the *OsZFP1* gene is the negative regulation of its expression by salt stress (Fig. 6), because most of the previously isolated stress-responsive genes are positively regulated (Shinozaki and Yamaguchi-Shinozaki 1997). This down-regulation of *OsZFP1* may be the consequence of transcriptional repression and/or the mRNA instability occurring at the post-transcriptional level. It has been reported that the negative regulation of the bean proline-rich protein gene *PvPRP1* by fungal elicitor occurs at the post-transcriptional level (Zhang et al. 1993) and that a U-rich sequence in the 3′-UTR is responsible for the down-regulation of *PvPRP1* expression (Zhang and Mehdy 1994). We found that the 3′-UTR of the OsZFP1 mRNA also contains a sequence similar to the U-rich sequence of the PvPRP1 mRNA (Fig. 8), suggesting that the regulation at a post-transcriptional level may be accountable for the repression of *OsZFP1* expression by salt stress.

The down-regulation of gene expression has also been observed in other plants. Yu et al. (1996) reported that a

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OsZFP1 mRNA  717 AGUUUAAU-UUUG-GCGUUUUAAGU 739
PvPRP1 mRNA  940 AUGUUAAUAUUUAUGUGUUUUCCGU 964
                 *  ***** ***  * *****  **
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Fig. 8 Comparison of the U-rich sequence in the 3′-UTR of OsZFP1 mRNA with that of the bean proline-rich protein PvPRP1 mRNA

tomato gene encoding a proline-, threonine-, and glycine-rich protein was negatively regulated by water stress. The bean proline-rich protein gene *PvPRP1* was found to be down-regulated by fungal elicitor (Sheng et al. 1991). However, what the physiological significance of the down-regulation of these genes is remains unclear. Chandler and Robertson (1994) suggested that positive and negative regulation of gene expression are equally important for plant growth under stress conditions and that certain genes are negatively regulated, probably owing to the fact that the gene products are inappropriate for the new physiological and biochemical changes caused by stress. We assume that the repression of *OsZFP1* expression may reflect the closure of some biochemical processes in rice cells so as to allow the rice seedlings to survive under saline conditions. Since OsZFP1 may function as a transcription factor, the determination of its target gene will be helpful to our understanding of the function of the *OsZFP1* gene in the stress tolerance of rice plants.

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