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RESEARCH ARTICLE

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Cloning and expression analysis of a ribosomal protein S7 in wheat under the stress of *Puccinia triticina*

Abstract A gene was isolated from the suppression subtractive hybridization (SSH) cDNA library of wheat by reverse northern blotting. Full length cDNA was obtained by RACE technique, and the result showed that all sequences consisted of 471 bp and encoded 157 amino acid. Subsequently, the gene expression was enhanced according to quantity real-time PCR (qRT-PCR) in response to leaf rust stress as the time over. All the results above suggested that the gene might play important role in wheat hypersensitive response (HR) to leaf rust.

Keywords wheat, ribosomal protein, cloning, expression

1 Introduction

There are extensive ribosomes in cytoplasm, chloroplasts, and mitochondrium, and the analysis of the synthesis of ribosomal proteins (RPs) in isolated chloroplasts has shown that a chloroplast genome encodes about one-third of the ribosomal proteins in higher plant species (Eneas-Filho et al., 1981). Although they possess various conformations and molecular weights, their functions were considered as simple as a worker of protein synthesis years ago (Cashmore, 1976). Since the identification and sequencing of more ribosomal protein genes were completed, the functions of ribosomal proteins have become obscure, and much more studies are focusing on uncovering the complex functions of different ribosomal proteins. Many results showed that ribosomal proteins were involved in several additional life processes such as duplication, transcription, translation, DNA repair, and PCD regulation (Chiaruttini et al., 1989; Wool, 1996; Clemens, 2004). Knogsuwna et al. established a series of *PR* gene mutations using fruit fly successfully; they reported that it did affect the cell physiologic function when *PR* genes were mutated and deleted without the normal translation hurt (1985). The changed expressions on transcription level in abnormal cells were reported recently. For example, 18 of the ribosome-related genes increased, and 6 genes decreased in the expression profile of liver cancer cells (Xu et al., 2008). According to Robert, the somatic abnormality of fruit fly would be induced by knocking down of *RPL14* gene (Espen et al., 2003).

Most researches about RPs were concerned on studies of bacteria, fungi, cancers, and pests. However, new discoveries in plant were reported in recent years. Transcripts for several ribosomal proteins such as S4, S15, and L25, combined with transcripts for histones and chaperones, were expressed to be up-regulated by UV-B in maize (Paula and Virginia, 2003). The other PRs, S7 and S9, were expressed to be up-regulated in rice under salt stress (Kawasaki et al., 2001). All results above suggested that PRs may take part in plant responses to external environment, but few reports on PRs involving in plant resistance response to biostress were reported yet. The colon 4h35 in our experiment related with PRs was isolated from the wheat SSH cDNA library induced by leaf rust, and then, its full sequence and expression profiling were detected, approaching the key function preliminary. This is the first time to explore the function of the PRs under biostress.

2 Materials and methods

2.1 Materials and treatment

Wheat (*Triticum aestivum* L.) NIL TcLr19 and leaf rust race 366 constituted the incompatible combination, and the Thatcher-366 was considered as the compatible combination, which was obtained according to Qi et al. (2008). Wheat seeds were planted in organic soil in pots with

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diameter of 10 cm and grown under greenhouse conditions at 24°C with a 16-hour-day and 8-hour-night photoperiodic regime. Seven-day-old seedlings were used for infection with leaf rust fungus. Then, fresh rust urediospores suspension was brushed onto the surface of the first leaves of seedlings. Control plants were brushed with water only, referred to as placebo inoculation. Finally, inoculated seedlings were kept in a humid chamber for 16 h in the dark at 25°C to allow infection to occur. After 16 h of infection, the seedlings were returned to greenhouse with the conditions as described above. The mock and treated plant leaves were sampled at 2, 4, 8, 16, and 24 hours post-inoculation (hpi), quickly frozen in liquid nitrogen, and then stored at −80°C.

2.2 RNA extraction

Total RNAs were extracted from the samples harvested above, and the extraction method using TIANGEN RNAplant and the isolation of poly (A) RNA using oilgotex were operated according to the manufacturer's protocol (Qiagen, Germany). The quality and quantity of RNA and mRNA were measured by nucleonic acid and protein detection instruments. As the initial material, mRNA was cadenced to 0.5 $\mu g \cdot \mu L^{-1}$.

2.3 Reverse northern high-density blots and screening

The synthesis of dscDNA was performed by the TaKaRa's manufacturer. The PCR products of actin and 4h35 were denatured in boiling water for 10 min after being detected by agars gel electrophoresis; subsequently, 1 μL was loaded onto nylon membrane, which was baked for 30 min at 120°C to fix DNA. The filters were hybridized under stringent conditions with equivalent amount probes made by DIG-labeled double-stranded cDNA that is "approximately equal to," which is derived from driver and tester mRNA, respectively. Next, all hybridization steps all followed the introduction of DIG-High Prime DNA Labeling and Detection Starter Kit I (ROCHE).

2.4 Quantitative real-time PCR analysis

qRT-PCR was carried out with Sybgreen I as staining (TaKaRa). The expected sizes of resulting PCR products were 103 and 101 bp for 4H35 and actin, respectively. Transcript abundance was assessed with three independent biological replicates. Each real-time PCR mixture (10 μL) contained 5 μL premix (Premix Ex TaqTM, TaKaRa), 3.6 μL distilled H_2O, 0.2 μL 10 $\mu mol \cdot L^{-1}$ forward primer, 0.2 μL 10 $\mu mol \cdot L^{-1}$ reverse primer, and 1 μL cDNA as a template. The Chromo4 System (biorad, USA) was used for PCR reactions under the condition of consisting 1 cycle at 95°C for 10 s and 45 cycles at 95°C for 30 s, 58°C for 30 s, and 72°C 30 s. The primer sequences were as followed: 4h35 (F: GATTCTTTACTGCGACAGC; R: GAACCTCTTTCACGCTCAT) and actin (F: AGGAGAAGCTCGCTTACGTG; R: ACCTGACCATCAGGCATCTC). The transcript level of selected ESTs was calculated by the $2^{-\Delta\Delta Ct}$ method with the wheat actin gene endogenous reference for normalization. Relative quantification of these ESTs was computed with their transcript levels at different stages in comparison to that in wheat.

2.5 Full length sequence

The full sequence of 4h35 followed the protocol of RACE kit (Clonetech). UPM: the primer was 5′-CTAATACGACTCACTATAGGGCAAGCAGTGGTATCAACGCAGAGT-3', the short sequence primer was 5′-TAATACGACTCACTATAGGGC-3′, and the special primer was 5'-GAGGTTATTCGTACCTGCCCGGGC-3′. PCR reactions were under the conditions of consisting 1 cycle at 95°C for 1 min and 30 cycles at 95°C for 30 s, 65°C for 90 s, and 72°C for 3 min. The product sequence was blasted in NCBI.

2.6 Construction of prokaryotic expression vector

Primers were designed according to the full length sequence (5'-CGGGATCCATGTCACGTCGAGGTACTGC-3' and 5'-CCCAAGCTTCACGAAAATGTGCAAGAGCTC-3'), the sequence underline was enzyme sites (*Bam*HI and *Hin*dIII, respectively). PCR mixture (25 μL) contained 12.5 μL, 7.5 μL distilled H_2O, 1 μL 10 $\mu mol \cdot L^{-1}$ forward primer, 1 μL 10 $\mu mol \cdot L^{-1}$ reverse primer, 1 μL 10 $\mu mol \cdot L^{-1}$ dNTPs, and 2 μL the cDNA template. PCR reaction was consisted of 5 min at 95°C (1 cycle) and 40 cycles of 95°C for 30 s, 68°C for 45 s and 72°C 30 s, and 72°C 10 min finally. The purified product was cut by *Bam*HI and *Hin*dIII, cloned into pET28a$^+$ vector cut with the same enzymes, and the construct was transformed into the cells of *E. coli* strain Roseeta. The transformed cells were selected and verified by PCR as described by Joseph and David (2001) and further confirmed by sequence analysis.

2.7 Optimization of the expression condition

Overnight culture of Roseeta cells with pET28 (a + 4h35) was inoculated to LB media in the ratio of 1∶50 (v/v) and incubated in a shaker (150 $r \cdot min^{-1}$) for 2 h at 37°C until the OD value reached 0.5–0.8. IPTG was added into the culture media to make the final concentration at 0.8 $mmol \cdot L^{-1}$, and the culture was incubated for additional 2, 5, and 8 h, respectively. The cells were harvested by centrifuging 1.5 mL of culture for 5 min at 2000 $r \cdot min^{-1}$ and resuspended in 100 μL Tris-HCl. The latter was ultrasonicated in ice bath, and both the supernatant and pellet were collected after centrifugation for 10 min at 12000 $r \cdot min^{-1}$.

2.8 SDS-PAGE electrophoresis

15% separation gel was prepared according to the published protocol (Sambrook and Russell, 2002). The supernatant and pellet samples were mixed or dissolved with 4×SDS-PAGE loading buffer, and the gel was stained by Coomassie brilliant blue R250 as described in the protocol.

3 Results

3.1 Reverse northern blotting

The products of colony PCR of 4h35 and actin were loaded on two nylon membranes, respectively, to test the positive points. cDNA of both TcLr19 and TcLr19 inoculated with 366 were used as a probe to hybrid. As showed in Fig. 1, the color of hybridization with TcLr19 inoculated with 366 as probe (B1) is significantly darker than that with TcLr19 (A1), and otherwise, the hybridization result of actin did not appear different in color (A2, B2), indicating the expression of the 4h35 is significantly different in two treatments at 4 hpi.

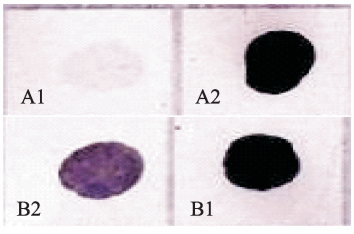

Fig. 1 The result of hybridization of wLR4h35
Note: A represents responses to the cDNA probes of TcLr19; B represents responses to TcLr19 inoculated with 366; 1 represents responses to PCR products of 4h35; and 2 represents responses to PCR products of actin.

3.2 Quantitative real-time PCR analysis (qRT-PCR)

3.2.1 PCR products of actin and 4h35

To conform to the expression changes at different time points, the quantitative real-time PCR was performed by using actin gene as endogenous reference. The PCR products of special fragments of actin and 4h35 detected in qRT-PCR gel electrophoresis, as shown in Fig. 2, and the results showed that both of them were about 100 bp.

3.2.2 Expression profiling of 4h35

According to the result of qRT-PCR (Fig. 3), compared with the treatment of Tc inoculated with 366, the expression profile of 4h35 at different hpi in TcLr19 changed significantly, the relative expression increased at 2 hpi until 4 hpi, and decreased gradually until the coincidence with Tc at 24 hpi.

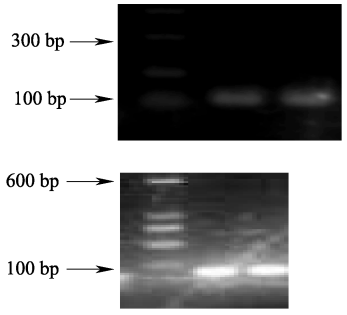

Fig. 2 PCR result of actin gene of wheat
Note: Upper and lower represent actin and 4h35, respectively.

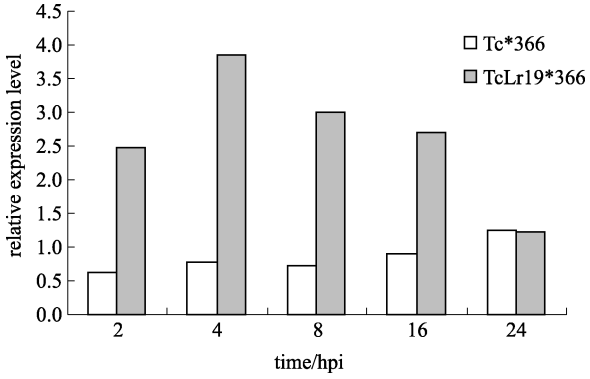

Fig. 3 Global expression of wLR4h35 in early stage of HR

3.3 Full length sequence of 4h35

3.3.1 RACE result of 4h35

The full length sequence of 4h35 was obtained by RACE, and the products were subjected to electrophoresis on agro gel (Fig. 4). The total length consisted of 486 bp according to the sequencing result.

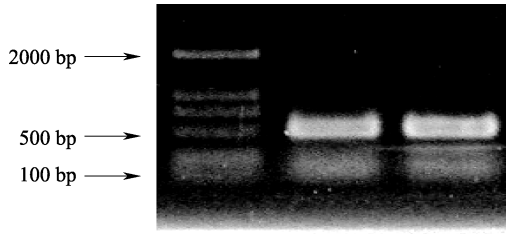

Fig. 4 Full length sequence PCR result of 4h35

3.3.2 sequence result of 4h35

The nucleotide sequence including 1277 bp was obtained according to the sequencing result of 4h35, and all the nucleotides were shown as below:

GTAATACGACTCACTATAGGGCACGCGTGGTC-
GACGGCCCGGGCTTGTATCGTCCGATTCTCCTTC-
TATTGATTCTTTTCCGATCGAGATGTACGGATC-
CATGTGTCTACATACATAGATTCTGTTCATGGAT-
TAACGAAAATGTGCAAGAGCTCTATTTGCCTCT-
GCCATTCTATGAGTCGCTTCCTTTTTGCGTATGG-
CACCCCCACTCCCTTTGGCAGCATCTACTAATTC-
GGAACTTAATTTGAAAGCCATATTTCGACCCG-
GACGCTTTTGGGATGCTTCTAATAACCAAC-
GAATGGCAAGTGCTCTTCCTTGTTTAGATCC-
TATTTCAATCGGAACTTTCCGCGTCGATCCTTTTT-
TATTACGTCTTGTTTTTACTCCTATATTGGGAGT-
TACTCTACGTATTGCTTGACGTAAAACCAA-
TAGTGGATTTGTTTCTGTCTTTTGTTGAATCTTTTT-
CACGGCCCGATAGAGAATTTGATAAGCCAAT-
GATTTTTTTCCGTCTTTCATAATACGGTTAACCAC-
CATGTTAACTAATCGATTACGAAAAATTGGATCG-
GATTTTGCAGTTCTTTTTTCTGCAGTACCTC-
GACGTGACATGAGCGTGAAAGAGGTTCAA-
GAATCCGTTTTCTTTTTATAAGGGCTAAAATCACT-
TATTTTTTTTGGCTTTTTGACCCCATATTG-
TAGGGTGGATCTCGAAAGATAGGAAAGATC-
TCCCTCCAAGCCGTACATACGACTTTCATCGAA-
TACGGCTTTCCACAGAATTCTATAGGGATCTATGA-
GATCGAGTATGGAATTCTGTTTACTCACTT-
TAAATTGAGTATCCGTTTCCCTCCTTTTCCCGC-
TAGGATCGGAAATCCTGTATTTTCCATATCCATAC-
GATCGAGTCCTTAGGTTTCCGAAATAGTGTAATG-
GAAAAAGAAGTGCTTCGAATCATTGCTATTT-
GACTCGGACCTGTTCTGAAAAAGTCGAGGTAT-
TTCGAATTGTTTGTTGACACGGACAAAGTAAGG-
GAAAACCTCTGAAAGAATTTCCATATTGACCTTG-
GACATATAAGAGTTCCGAATCGAATCTCTTTA-
GAAAGAGGATCTTTTGTCTCATGGTAGCCTGCTC-
CAGTCCCCTTACGAAACTTTCGTTATTGGGTTA-
GCCATACACTTCACATGTTTCTAGCGATTCA-
CATGGCATCATCAAATGATACAAGTCTTGGATAA-
GAATCTACAACGCACTAGAACGCCCTTGTTGAC-
GATTCTTTACTGCGACAGCATCTAGGGTTCCTCG

3.3.3 Translated amino acid sequence of S7

According to the analysis of open reading frame (ORF), the cDNA sequence ranging from 133 bp to 603 bp was translated into the 157 amino acid with initial code of ATG and end code of TAA. The translated amino acid sequence is shown in Fig. 5.

3.4 Homology analysis

The result of Blastx showed that 4h35 was high homology with ribosomal protein S7 (prS7) of maize, rice, etc. The identity value was so high that 4h35 was proved as prS7.

3.5 Construction of expression vector

The amplified fragments were digested with *Bam*HI and *Hin*dIII and then inserted into pET28a$^+$ to construct the pET28a + 4h35. This expression vector was confirmed by digestion with *Bam*HI and *Hin*dIII to produce the 486 bp target DNA fragment (Fig. 6) and, subsequently, by sequence analysis of the inserts, which showed 96% identity to the published sequence (AB042240) after alignment (data not shown). This indicated that the cloned fragment was *rpS7*.

3.6 Prokaryotic expression

The time duration for the IPTG induction was quite important for yield. As shown in Fig. 7, the maximum yield was achieved 8 h after induction by IPTG, and this observation repeated in another two independent experiments (data not shown).

4 Discussion

Interests on discovering new functions about ribosome and ribosomal proteins are rising now; many subjects suggest that the ribosomal proteins play important roles in responses to various stresses. From small beans induced by low temperature, three 60S ribosomal protein genes of *GmRPS13*, *GmRPS6*, and *GmRPL37* were cloned. Our experiments showed that the ribosomal proteins encoded by these three genes could enhance the tolerance to low temperature via affecting the transcription or the process of ribosome assembling (Kim et al., 2004). Li et al. (2002) found that in the mutant of RPL24, an *E. coli* ribosome protein and the activities of β-galactosidase and glutathione-S-transferase were reduced, supposing that it might have an effect on the initial and ending process of translation to promote plant resistance to virus.

It was confirmed that the RPS7 protein could regulate the initial translation process in plant chloroplast, either at general or specific levels, but rarely referred to wheat. This regulation role could even be significant at the early stage of stress. Kawasaki et al. (2001) reported that a remarkable increase of the expression of *rpS4* and *rpS7* gene under salt stress in one hour was detected in rice. It was the first time to report *rpS7* gene in view of plant resistance to biostress. Our result suggested that the wheat *rpS7* gene might participate at the early stage HR, but the tendencies might be changed with different plant species. Thomas et al. (2000) discovered that the expression of rye *ScRPS7* gene decreased sharply, and then, it ascended gradually until 30 d after low temperature treatment; from then on, the expression of *ScRPS7* gene achieved the prior level. However, the expression of *OsRPL14* gene kept rising

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603 atgtcacgtcgaggtactgcagaaaaaagaactgcaaaatccgat
    M  S  R  R  G  T  A  E  K  R  T  A  K  S  D
558 ccaatttttcgtaatcgattagttaacatggtggttaaccgtatt
    P  I  F  R  N  R  L  V  N  M  V  V  N  R  I
513 atgaaagacggaaaaaaatcattggcttatcaaattctctatcgg
    M  K  D  G  K  K  S  L  A  Y  Q  I  L  Y  R
468 gccgtgaaaaagattcaacaaaagacagaaacaaatccactattg
    A  V  K  K  I  Q  Q  K  T  E  T  N  P  L  L
423 gttttacgtcaagcaatacgtagagtaactcccaatataggagta
    V  L  R  Q  A  I  R  R  V  T  P  N  I  G  V
378 aaaacaagacgtaataaaaaaggatcgacgcggaaagttccgatt
    K  T  R  R  N  K  K  G  S  T  R  K  V  P  I
333 gaaataggatctaaacaaggaagagcacttgccattcgttggtta
    E  I  G  S  K  Q  G  R  A  L  A  I  R  W  L
288 ttagaagcatcccaaaagcgtccgggtcgaaatatggctttcaaa
    L  E  A  S  Q  K  R  P  G  R  N  M  A  F  K
243 ttaagttccgaattagtagatgctgccaaagggagtgggggtgcc
    L  S  S  E  L  V  D  A  A  K  G  S  G  G  A
198 atacgcaaaaaggaagcgactcatagaatggcagaggcaaataga
    I  R  K  K  E  A  T  H  R  M  A  E  A  N  R
153 gctcttgcacattttcgttaa 133
    A  L  A  H  F  R  *
```

Fig. 5 ORF cDNA sequence and amino acid of wLR4h35

Table 1 Blastx result of 4h35

accession	description	query coverage	E value
ref|NP_043077.1|	ribosomal protein S7 [*Zea mays*]	302	1e-80
ref|NP_039433.1|	ribosomal protein S7 [*Oryza sativa*]	300	4e-80
gb|ABR23110.1|	ribosomal protein S7 [*Danthonia californica*]	300	5e-80
dbj|BAD17338.1|	rice chloroplast ribosomal protein S7 [*Oryza sativa*]	298	1e-79
gb|ABR23128.1|	ribosomal protein S7 [*Streptochaeta angustifolia*]	297	4e-79
gb|ABJ52164.1|	ribosomal protein S7 [*Phyllostachys pubescens*]	293	8e-78
gb|ABR23125.1|	ribosomal protein S7 [*Anomochloa marantoidea*]	292	1e-77
gb|ABR23131.1|	ribosomal protein S7 [*Joinvillea plicata*]	282	1e-74
gb|AAS65712.1|	ribosomal protein S7 [*Ecdeiocolea monostachya*]	275	1e-72
gb|AAQ64532.1|	ribosomal protein S7 [*Mahonia aquifolium*]	258	2e-67
gb|AAS46086.1|	ribosomal protein S7 [*Oryza sativa*]	254	3e-66
gb|AAN31967.1|	ribosomal protein S7 [*Tofieldia glutinosa*]	254	3e-66
gb|AAS65704.1|	ribosomal protein S7 [*Petrosavia* sp. SWG-2004]	254	4e-66
sp|Q9GFM9.1|	RR7_CABCA RecName: Full = 30S ribosomal protein S7	253	5e-66

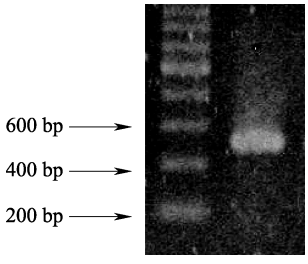

Fig. 6 Digestion of pET28a (+) with rpS7

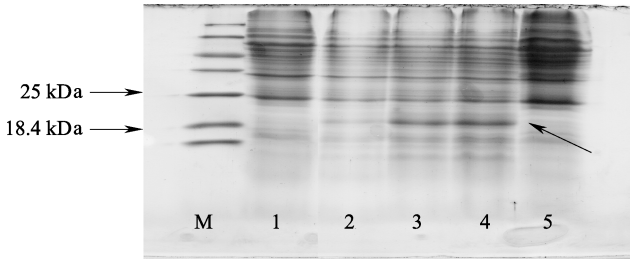

Fig. 7 SDS-PAGE analysis of expressed wLR4h35 product
Note: M represents protein MW marker (Low); 1 represents protein of the uninduced *E. coli* with 4h35; 2–4 represent proteins of the *E. coli* with wLR4h35 induced after 2 h, 5 h, and 8 h, respectively; 5 is inclusion body; and the arrow indicates the expressed proteins.

gradually in the root and stem of rice (Du et al., 2008). In our experiment, the result of qRT-PCR revealed that the expression of *rpS7* (4h35) was up-regulated notably 4 h after the TcLr19 was infected by leaf rust race 366, then

decreased at normal level at 24 hpi. It could be speculated that this gene may participate in the resistance to the fungi in the early infection stage. However, there remain many questions including which protein RPS7 combines with and whether or how RPs affect the physiological and biochemical reactions of infected plant. Besides, the reasons why the ribosomal proteins have exribosomal functions are still unrevealed. Considering the questions above, we expressed the *rpS7* gene in *E. coli* to step the primary research of the exact biological function of *rpS7*.

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