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# Characterization of a S-locus-related Receptor-like Kinase Cluster in Rice Chromosome 4

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**Abstract:** We have identified 14 *S*-locus glycoprotein (SLG)-related protein kinase genes in a 323 kb contig of rice (*Oryza sativa* L.) chromosome 4 and we detected the transcription pattern of this gene cluster by reverse transcription-polymerase reaction (RT-PCR). RT-PCR results revealed that nine putative genes were transcribed in rice and these genes had the different expression patterns: two genes are expressed predominantly in reproductive tissues while the other seven genes are expressed in both reproductive and vegetative tissues. Analysis of the predicted amino acid sequences demonstrated that the extracellular receptor domains are highly homologous to SLG of *Brassica*, whereas the cytoplasmic kinase domains contain conserved amino acids present in serine/threonine kinases.

**Key words:** *Oryza sativa* receptor-like protein kinase; *S*-locus receptor kinase; *S*-locus glycoprotein; rice (*Oryza sativa*)

Receptor-like protein kinases (RLKs) are a diverse group of proteins that span the plasma membrane and allow cells to recognize and respond to their extracellular environment. A number of similar genes predicting to encode RLKs have been identified in plants. Five different classes of plant RLKs have been identified, as defined by the predicted amino acid sequences of their extracellular domains (Walker, 1994; Becraft, 1998). One of the largest and well-studied classes of RLKs is characterized by the leucine-rich repeat (LRR) motif, which is implicated in protein-protein interactions. Another class contains the family of *S*-locus receptor kinases (SRKs) in *Brassica*. They have an extracellular *S*-domain with high similarity to *S*-locus glycoproteins (SLG) and play a role in the self-incompatibility response (Nasrallah, 1997). Other classes are represented by the maize CR4, which has a tumor necrosis factor (TNFR)-like motif (Becraft *et al*, 1996), the *Arabidopsis* WAK with an epidermal growth factor (EGF)-like motif (He *et al*, 1998), or the *Arabidopsis* lecRK with a motif similar to legume lectin (Herve *et al*, 1996).

Plant *S*-locus-related receptor-like kinase genes have been isolated from a wide range of both dicotyledonous and monocotyledonous plant species. This class includes the *SRK* of *Brassica* (Stein *et al*, 1991), *SFR2* of *Brassica* (Pastuglia *et al*, 1997), *ZmPK1* of maize (for *Zea mays* protein kinase 1) (Walker and Zhang, 1990), *ARK1*, *ARK2* and *ARK3* of *Arabidopsis* (for *Arabidopsis* receptor kinases;) (Tobias *et al*, 1992; Dwyer *et al*, 1994) and *OsPK10* of rice (for *Oryza sativa* protein kinase 10) (Zhao *et al*, 1994). These receptor-like kinases of the *S* gene family have diverse roles in plants. In *Brassica*, *SRK* is thought to be involved in the pollen-pistil recognition step of the self-incompatibility response and expressed exclusively in the papilla cells (McCubbin and Kao, 1996). In *Arabidopsis*, *ARK2* and *ARK3* that were expressed in vegetative tissues are likely involved in cell-cell communication systems (Dwyer *et al*, 1994). Pastuglia *et al* (1997) have shown that *SFR2*, a novel member of the *S* gene family encoding a receptor-like kinase, is induced by a range of stimuli inducing plant defense genes.

In this study, a 323 kb contig of rice chromosome 4 was completely sequenced and analyzed. A large gene cluster consisting of 14 predicted SLG-related protein kinase genes in a tandem array was found to be located in a 108 kb region of the contig. Expressions of nine putative genes were confirmed by RT-PCR and revealed that they had different expression patterns: two genes are expressed predominantly in reproductive tissues while the other seven genes are expressed in both reproductive and vegetative tissues. This is the first large *S*-locus-related *RLK* gene cluster found in plant. Studies are in progress to analyze whether the *Oryza sativa RLK* (*OsRLK*) gene cluster involve in the plant defense response.

## 1 Materials and Methods

### 1.1 Plant materials and growth conditions

Seeds of rice (*Oryza sativa* ssp. *indica* Guangluai 4) were germinated at 37 °C and the seedlings were grown in the light at 30 °C for 3 d for RNA extraction from root and bud. Leaves were collected after 10 d of germination.

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Flowers and young panicles were prepared from 3-month-old plants.

### 1.2 Cloning and sequencing of BAC clones

A bacterial artificial chromosome (BAC) contig, which was anchored on the region from 110.0 centimorgan (cM) to 111.5 cM of chromosome 4, was constructed by using colony hybridization and chromosome walking. The contig consisted of 20 BAC clones which came from two BAC libraries of *O. sativa* Guangluai 4, and the genetic markers used as probes were provided by rice genome program (RGP) in Japan (Tao *et al*, 1994; Hong *et al*, 1997; Sasaki, 1998). Six tiled BAC clones (BAC H0410G08, H0315F07, H0613A10, B0808H03, H0105C05, H0323C08) with minimum overlaps were sequenced and analyzed. The BAC DNA was purified by Cesium Chloride gradient centrifugation, and subcloned into pBluescript II plasmid vector (Stratagene) after sonication. Subclones were sequenced at both ends using the DYEnamic™ ET dye terminator kit (Amersham pharmacia) and analyzed on Megabase100 (Amersham pharmacia). The sequence data were assembled using PHRED/PHRAP software. Homology searches were performed using the BLAST program (Altschul *et al*, 1997). GENSCAN program was used to predict possible genes in this contig (Burge and Kalin, 1997).

### 1.3 Oligonucleotides

All oligonucleotides used in this study were synthesized by Sangon company, China, except for Oligo dT-Adaptor primer which was provided by RNA RCR Kit. The sequences of all oligunucleotides are shown in Table 1.

### 1.4 RT-PCR

Total RNA of roots, buds, leaves, flowers, and young panicles of rice were extracted following the manufacture's instruction (Qiagen RNeasy Plant mini kit). For RT-PCR, 1 μg of DNase-treated total RNA was reverse-transcribed with gene-specific antisense primers and AMV reverse transcriptase using an RNA PCR Kit (Takara, Japan), and the entire reaction mixture was used as a template in the subsequent PCR. Each PCR cycle consisted of 94 ℃ denaturation for 30 s, 60 ℃ annealing for 30 s, 72 ℃ extension for 2 min, for 30 cycles.

## 2 Results and Discussion

### 2.1 Identification of a OsRLK gene cluster in the 108 kb fragment

Six overlapping BACs representing a 323 kb region of rice chromosome 4 were sequenced and analyzed by using the gene identification software GENSCAN to predict the location of the genes. The prediction results showed that 14 receptor like kinase genes were clustered in a 108 kb fragment. This gene cluster was designated as *OsRLK* (*O. sativa* receptor-like kinase), and each gene of this cluster was named according to their order in the 108 kb fragment. Sequence analysis of the deduced protein revealed that the structures of *OsRLK2-14* were similar and their extracellular domains all had high similarities with *S*-domain of *SRK* in *Brassica*. *OsRLK1* encoded a serine/threonine receptor kinase but it lacked a SLG-like extracellular domain. Table 2 shows the sequence comparisons of *OsRLK2-14* and the relevant protein features of *OsRLK1-14* are shown in Table 3. Thirteen *OsRLK* genes had the same direction of transcription except *OsRLK6*. Two retrotransposons were found in the *OsRLK* cluster. The length of the two retrotransposons is 13 kb and 14.22 kb respectively. Retrotransposon-1 was located between *OsRLK2* and *OsRLK3*; Retrotransposon-2 was found to be located in the first intron of *OsRLK8* and this gene was disrupted by the 14.22 kb retrotransposon.

To date, only *OsPK10* from rice (Zhao *et al*, 1994) and *ZmPK1* from maize (Walker and Zhang, 1990) were reported as *S*-locus-related receptor-like kinase genes in monocotyledonous plant species. The

**Table 1** The sequences of primers designed for RT-PCR

| Name | Sequence | Name | Sequence |
|---|---|---|---|
| *OsRLK1* 5′ | 5′- cta tcc aaa ctg caa cac cg-3′ | *OsRLK1* 3′ | 5′- cgt aag agc ata tgg tgc cc-3′ |
| *OsRLK2* 5′ | 5′- ggg tga agc tgc cag aca c-3′ | *OsRLK2* 3′ | 5′- gcc act tct ctg gcg aaa tc-3′ |
| *OsRLK3* 5′ | 5′- tca cgg tgg agg agt gca g-3′ | *OsRLK3* 3′ | 5′- tgg tgt agc cgt ttt aca ge-3′ |
| *OsRLK4* 5′ | 5′- gca taa cgc gac ggt gga c-3′ | *OsRLK4* 3′ | 5′- cga cat cat ctc cac ctc tc-3′ |
| *OsRLK5* 5′ | 5′- caa act tga cca tag ccg gc-3′ | *OsRLK5* 3′ | 5′- aca agt cct cta gct act cc-3′ |
| *OsRLK6* 5′ | 5′- ttg ggg ttc atc tct cca tc-3′ | *OsRLK6* 3′ | 5′- cct aca cct act tga ccg c-3′ |
| *OsRLK7* 5′ | 5′- gtg ctt gct ttg ggt tgg tg-3′ | *OsRLK7* 3′ | 5′- ttc cgc caa aga ttc ttg cc-3′ |
| *OsRLK8* 5′ | 5′- gac gtt cgg tat gtc gac aaa g-3′ | *OsRLK8* 3′ | 5′- cag cag caa tgt ctc caa aac-3′ |
| *OsRLK9* 5′ | 5′- gct ctt ctg cag ctg cat g-3′ | *OsRLK9* 3′ | 5′- gtg gca gca gca att tct cc-3′ |
| *OsRLK10* 5′ | 5′- gca act tga cca aag ccg ac-3′ | *OsRLK10* 3′ | 5′- gtt gcc gcg aca acg tat tc-3′ |
| *OsRLK11* 5′ | 5′- cag caa ctg ctc ttg caa gg-3′ | *OsRLK11* 3′ | 5′- cgt gcc tcc ctc caa tat tc-3′ |
| *OsRLK12* 5′ | 5′- cag gaa cag aac ctt tga gg-3′ | *OsRLK12* 3′ | 5′- ccc ctt gct cag aat cct tg-3′ |
| *OsRLK13* 5′ | 5′- cct acg ctt acg cca act tg-3′ | *OsRLK13* 3′ | 5′- ccc aag cat gtt gtg atc ag-3′ |
| *OsRLK14* 5′ | 5′- gca caa ctg ctc ttg cac ag-3′ | *OsRLK14* 3′ | 5′- tcc ttg ccc aga acc ctt ac-3′ |
| *Actin* p1 | 5′- cat gct atc cct cgt ctc g-3′ | *Actin* p2 | 5′- cgc act tca tga tgg agt tg-3′ |
| *Oligo dT primer* | 5′- $(dT)_n$ gttttcccagtcacga c-3′ | | |

**Table 2** Comparison of putative amino acid sequences of the OsRLK protein excluding OsRLK1

| | OsRLK3 | OsRLK4 | OsRLK5 | OsRLK6 | OsRLK7 | OsRLK8 | OsRLK9 | OsRLK10 | OsRLK11 | OsRLK12 | OsRLK13 | OsRLK14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *OsRLK2* | 66.93 | 63.65 | 45.52 | 40.48 | 45.31 | 54.65 | 63.65 | 42.39 | 40.48 | 46.99 | 49.39 | 48.80 |
| | 62.11 | 58.27 | 38.03 | 32.89 | 38.02 | 48.11 | 58.27 | 35.63 | 32.89 | 38.82 | 41.99 | 41.04 |
| *OsRLK3* | | 65.74 | 43.90 | 39.95 | 47.23 | 55.79 | 58.23 | 41.98 | 46.66 | 46.33 | 48.44 | 47.48 |
| | | 60.69 | 37.06 | 34.28 | 40.60 | 49.64 | 52.61 | 35.42 | 39.54 | 38.53 | 40.97 | 38.85 |
| *OsRLK4* | | | 45.59 | 40.05 | 46.28 | 56.72 | 57.58 | 43.21 | 46.38 | 45.47 | 46.31 | 44.80 |
| | | | 38.82 | 32.63 | 39.23 | 50.88 | 51.06 | 35.32 | 37.87 | 37.57 | 39.07 | 37.22 |
| *OsRLK5* | | | | 67.61 | 76.20 | 50.78 | 52.95 | 79.03 | 76.20 | 64.81 | 75.00 | 65.21 |
| | | | | 62.68 | 72.39 | 45.19 | 46.90 | 76.46 | 72.39 | 59.08 | 69.88 | 59.16 |
| *OsRLK6* | | | | | 65.81 | 45.39 | 47.46 | 65.23 | 57.33 | 56.38 | 57.33 | 58.93 |
| | | | | | 59.61 | 38.80 | 40.78 | 59.84 | 49.67 | 50.36 | 49.67 | 50.67 |
| *OsRLK7* | | | | | | 57.02 | 58.13 | 74.62 | 69.44 | 67.17 | 74.05 | 69.09 |
| | | | | | | 51.40 | 51.60 | 71.21 | 63.36 | 60.71 | 69.47 | 61.96 |
| *OsRLK8* | | | | | | | 81.27 | 50.67 | 52.37 | 49.92 | 51.18 | 53.84 |
| | | | | | | | 78.73 | 44.72 | 44.81 | 41.89 | 44.82 | 46.32 |
| *OsRLK9* | | | | | | | | 53.93 | 56.28 | 56.51 | 57.12 | 55.17 |
| | | | | | | | | 47.64 | 49.93 | 48.48 | 50.45 | 48.55 |
| *OsRLK10* | | | | | | | | | 64.24 | 62.67 | 70.30 | 63.02 |
| | | | | | | | | | 56.67 | 55.30 | 65.20 | 55.68 |
| *OsRLK11* | | | | | | | | | | 61.24 | 69.85 | 68.86 |
| | | | | | | | | | | 53.93 | 62.62 | 62.28 |
| *OsRLK12* | | | | | | | | | | | 67.31 | 61.98 |
| | | | | | | | | | | | 61.38 | 55.85 |
| *OsRLK13* | | | | | | | | | | | | 72.88 |
| | | | | | | | | | | | | 66.99 |

The similarity is shown in the upper row and the identity is in the lower row.

**Table 3** Relevant features of protein sequences deduced from the *OsRLK* gene cluster

| | OsRLK1 | OsRLK2 | OsRLK3 | OsRLK4 | OsRLK5 | OsRLK6 | OsRLK7 | OsRLK8 | OsRLK9 | OsRLK10 | OsRLK11 | OsRLK12 | OsRLK13 | OsRLK14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AA length | 699 | 817 | 782 | 803 | 713 | 791 | 816 | 714 | 1086 | 750 | 771 | 743 | 792 | 758 |
| Isoelectric point | 8.14 | 8.15 | 6.68 | 4.99 | 7.04 | 7.00 | 6.92 | 7.39 | 7.36 | 8.11 | 6.44 | 6.54 | 7.06 | 6.68 |
| Molecular weight (kD) | 75.2 | 88.4 | 84.2 | 87.1 | 79.6 | 88.7 | 90.9 | 77.1 | 119.2 | 84.3 | 85.6 | 83.1 | 88.4 | 83.9 |

extracellular domains of *OsPK10* from rice and *ZmPK1* from maize had about 20 % and 25 % similarity to SLG of *Brassica*, respectively. However, these 13 *OsRLK* genes (except *OsRLK1*) had higher similarities (45 %) to SLG than the similarities of *ZmPK1* and *OsPK10*. Therefore, the gene cluster could be classified as *S*-locus-related receptor like kinase cluster (*OsRLK*).

### 2.2 Structural features of the OsRLKs

Computer analysis of the 14 *OsRLK* amino acid sequence revealed that except *OsRLK1*, other 13 genes were all composed by three domains: the large extracelluar SLG like domain; the transmembrane domain; the cytoplasmic kinase domain. The putative extracellular domains of these 13 genes all contained 12 cysteine residues clustered near the membrane-spanning segment. These 12 cysteine residues are invariant in the *Brassica SLG* and *SRK* gene products and are probably involved in disulfide bond formations that would have an important role in determining the secondary and tertiary structure of the *SLG* extracellular domain. The putative cytoplasmic domain contained all 11 conserved subdomains and 15 invariant amino acids of eukaryotic protein kinases in the proper order (Hanks *et al*, 1988).

The predicted *OsRLK* proteins were all serine/threonine specific kinases. It is interesting to note that the enzymatic activities of most plant receptor-like protein kinases were serine/threonine specific. If not coincidental, this might be suggestive that protein-serine/threonine phosphorylation rather than protein-tyrosine phosphorylation was the main scheme of transmembrane signal in plants. This in turn indicated that a unique signal-transducing component interplay pattern might exist in plant cells.

### 2.3 Transcript levels of OsRLK gene cluster

The expression of the *OsRLK* gene cluster in different tissues of rice was examined by Northern hybridization. Total RNAs were extracted from roots, buds, leaves, flowers, and young panicles. However, no obvious signal was detected in the Northern hybrid experiment. Therefore, to raise the sensitivity of detection, amplification by RT-PCR was performed using total RNA extracted from the organs described above. These RNAs

were all treated with DNase to remove any contaminated genomic DNA. The gene-specific primers (*OsRLK*s 5′/ *OsRLK*s 3′, Table 1) corresponded to the first and the third or fourth putative exon of each gene, respectively. As a control, amplification by RT-PCR was performed using two primers (*Actin*p1/*Actin*p2) specifically for the rice actin 1 gene (*ACT1*). An *ACT1*-specific fragment (340 bp) was amplified from all organs examined, and the intensities of the bands corresponding to these fragments were almost the same, indicating that an equal amount of total RNA of each organ was used for RT-PCR amplification (Fig. 1).

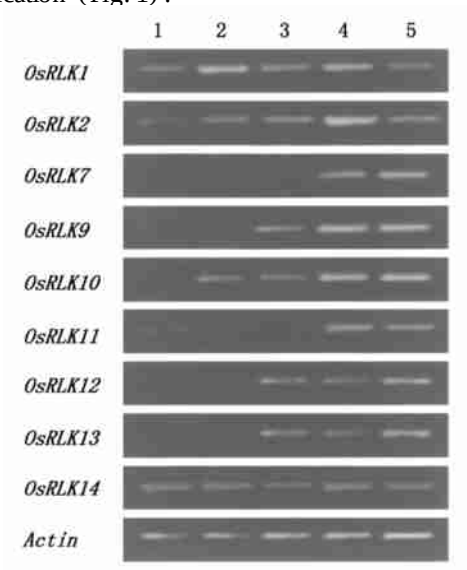


**Fig. 1.** Expression of the *OsRLK* cluster.
RT-PCR analysis was performed using primers designed for specific amplification of each gene. Tissues from which RNA being extracted are indicated atop the figure as follows: 1, root; 2, bud; 3, leave; 4, flower; 5, young panicle.

As shown in Fig. 1, PCR products corresponding to *OsRLK1*, *2*, *7*, *9*, *10*, *11*, *12*, *13*, *14* were detected in different tissues of rice. Comparison of the sequences of these amplified fragments with genomic DNA proved that the templates used for PCR amplification were not contaminated with genomic DNA. The transcripts of *OsRLK3*, *4*, *5*, *6*, *8* could not be detected in all tissues of rice. For *OsRLK8*, it is possible that the insertion of retrotransposon-2 led the inactivation of this gene. And for *OsRLK3*, *4*, *5*, *6*, this result indicated that these four genes might be pseudogenes or the transcription of these five genes could not be detected under normal conditions. It remains to be determined whether the expression of these five genes are enhanced by environmental changes. Transcripts of *OsRLK7*, *11* were detected in flowers and young panicles, but not in other tissues. Genes of *OsRLK1*, *2*, *9*, *10*, *12*, *13*, and *14* were detected to be transcribed in reproductive and vegetative organs.

In *O. sativa*, the *S*-locus-related RLK had quite distinct patterns of expression compared to the expression of the *Brassica SRK* genes. The differential expression of these RLK suggested that they had different physiological functions despite their related extracellular domains. In *Brassica*, *SRK* was thought to be involved in the pollen-pistil recognition step of the self-incompatible response and expressed exclusively in the papilla cell (McCubbin and Kao, 1996). In *Arabidopsis*, *ARK2* and *ARK3* were thought to function in specific aspects of plant growth or development but that their specific role in the plant was not known yet (Dwyer *et al*, 1994). Another possible function of *S* gene family members in vegetative tissues was suggested by the numerous similarities between self-incompatibility and the plant's response to pathogens attack (Hodgkin *et al*, 1988). Pastuglia *et al* (1997) had shown that *SFR2*, a novel member of the *S* gene family, is encoding a receptor-like kinase which is to be induced by a range of stimuli that induced plant defense genes. These stimuli included both wounding and bacterial attack. These results indicated that this gene might play a role in the response of the plant to mechanical and biological attack. Wound inducement, bacterial infection and SA treatment of rice are in detection to elucidate whether this gene cluster is involved in the plant defense.

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# 对水稻 4 号染色体一个编码 S 位点相关的受体样蛋白激酶基因簇的分析

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**摘要**: 通过对水稻(*Oryza sativa* L.) 4 号染色体一段 323 kb 的序列测定和分析,在其中 108 kb 的区域内发现了一个由 14 个编码 *S* 位点相关的受体样蛋白激酶(SRK)基因组成的基因簇。RT-PCR 实验证明了这 14 个基因中有 9 个基因表达,并且这 9 个基因有不同的表达模式:其中 2 个基因主要在生殖器官中表达,而另外 7 个基因在水稻的营养和生殖器官中均有表达。对这些基因的预测的氨基酸序列进行分析表明他们的细胞外受体部分均和甘蓝的 SLG 蛋白高度同源,而细胞内的激酶区都包含有丝氨酸/苏氨酸激酶中特异的氨基酸。

**关键词**: 水稻受体样激酶蛋白; *S* 位点受体激酶; *S* 位点糖蛋白; 水稻

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