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The phenome analysis of mutant alleles in *Leucine-Rich Repeat Receptor-Like Kinase* genes in rice reveals new potential targets for stress tolerant cereals

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ABSTRACT

Plants are constantly exposed to a variety of biotic and abiotic stresses that reduce their fitness and performance. At the molecular level, the perception of extracellular stimuli and the subsequent activation of defense responses require a complex interplay of signaling cascades, in which protein phosphorylation plays a central role. Several studies have shown that some members of the Leucine-Rich Repeat Receptor-Like Kinase (LRR-RLK) family are involved in stress and developmental pathways. We report here a systematic analysis of the role of the members of this gene family by mutant phenotyping in the monocotyledon model plant rice, *Oryza sativa*. We have then targeted 176 of the ~320 *LRR-RLK* genes (55.7%) and genotyped 288 mutant lines. Position of the insertion was confirmed in 128 lines corresponding to 100 *LRR-RLK* genes (31.6% of the entire family). All mutant lines harboring homozygous insertions have been screened for phenotypes under normal conditions and under various abiotic stresses. Mutant plants have been observed at several stages of growth, from seedlings in Petri dishes to flowering and grain filling under greenhouse conditions. Our results show that 37 of the *LRR-RLK* rice genes are potential targets for improvement especially in the generation of abiotic stress tolerant cereals.

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1. Introduction

Nowadays, rice of Asian origin (*Oryza sativa* L.) is the staple food for more than half of the human population. In less than 40 years, the world's population is predicted to reach 9 billion, raising the so-called "9-billion-people" issue [1]. For sustainable rice production in the years to come, a number of challenges need to be addressed by the entire rice community with the common goal of creating new elite rice varieties [2,3]. Large efforts have focused in the last years to complete sequencing of several *Oryza* genomes [4–10]. In functional genomics, the challenge is now to system-

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atically assign a biological function to all genes in the genomes. To help in this task, the rice community worldwide has started to share efforts in the late 90's to produce insertion mutant collections required for gene functional analyses [11,12]. These mutant collections are available in several laboratories around the world: CSIRO in Australia [13], NIAS in Japan [14], OSTID in Europe [15], OTL in France [16], POSTECH [17] and PMBBRC [18] in Korea, RMD in China [19], TRIM in Taiwan [20], and UCD in USA [21]. These mutant collections contain insertion lines created with T-DNA, Tos17, Ds, and dSpm inserts mutagens and the engineered mutagens may additionally carry gene traps, enhancer traps and/or activation tags. They have been generated in different cultivars: Nipponbare (NB), DongJin (DJ), HwaYoung (HW), Zhonghua 11 (Z11), Zhonghua 15, Tainung 67 (TNG) and Kitaake. All these lines are listed based on their flanking sequence tags (FSTs) in two databases: RiceGE (http://signal.salk.edu/cgi-bin/RiceGE) and Ory-GenesDB (http://orygenesdb.cirad.fr). In total, ~225,000 FSTs are precisely positioned on the ssp. japonica cv. Nipponbare sequence

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Abbreviations: LRR-RLK, leucine-rich repeat receptor-like kinase; MS, Murashige and Skoog medium; DJ, DongJin; HW, HwaYoung; Z11, Zhonghua 11; TNG, Tainung 67; FST, flanking sequence tag.

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Table 1 List of LRR-RLK genes with known functions in rice.

| Accession numbers | Names | Orthologous relationships described | Functions/comments | References |
|---|--|--|---|-----------------|
| Os11g36180 | Xa21 | | Resistance to Xanthomonas oryzae pv. | [61] |
| Os02g34790 | Xoo-INDUCED KINASE 1 (XIK1) | | oryzae Positively regulates XA21-mediated immunity | [62] |
| Os11g47000 | Xa3/Xa26 | | Immune receptor playing the same | [63,64] |
| Os04g52780 | Os FLAGELLIN SENSING 2 (OsFLS2) | AtFLS2 | As in Arabidopsis mediates flagellin | [65] |
| Os01g52050 | Os BRASSINOSTEROID INSENSITIVE 1 | AtBRI1 | Cell elongation and cell division in | [66] |
| Os09g12240 | Os BRI1-LIKE 1 (OsBRL1) | AtBRL1 | Cell elongation and cell division in shoot and root in conjunction with OsBR11 | [67] |
| Os08g25380 | Os BRI1-LIKE 3 (OsBRL3) | AtBRL3 | Cell elongation and cell division in shoot and root in conjunction with OsBRI1 | [67] |
| Os06g50340 Os01g68870 | FLORAL ORGAN NUMBER 1 (FON1) MULTIPLE SPOROCYTE 1 (MSP1) | AtCLAVATA1 (AtCLV1) At EXTRA SPOROGENOUS CELLS / EXCESS MICROSPOROCYTES1 (EXS/EMS1) | Regulates floral meristem size Necessary to restrict the number of cells entering into male and female sporogenesis and to initiate anther wall formation | [68] [55] |
| Os02g10100 | MSP-LIKE 1 (MSL1) | At EXTRA SPOROGENOUS CELLS / EXCESS MICROSPOROCYTES1 (EXS/EMS1) | Necessary to restrict the number of cells entering into male and female sporogenesis and to initiate anther wall formation in conjunction with MCD1 | [69] |
| Os03g12730 | BLAST RESISTANCE-RELATED (BRR1) | At BARELY ANY MERISTEM (BAM1 and BAM2) | Involved in blast resistance | [70] |
| Os03g50810 | Os TRANSMEMBRANE KINASE (OsTMK) | four members of the TRANSMEMBRANE KINASE (TMK) | Role in plant growth | [71] |
| Os04g38480 | Os SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE 2 (OsSERK2) | AtSERKs | Required for both Xa21, Xa3/Xa26 and FLS2 signaling and | [72] |
| Os08g07760 | Os SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE 1 (OsSERK1) also named Os BRI1-ASSOCIATED KINASE 1 (OsBAK1) | AtSERKs | Functions in rice development, affecting growth and angle of lamina joint; brassinosteroid signaling? | [73–75] |
| high degree of similarity but not identical to Os08g07760 | BENZOTHIADIAZOLE-INDUCED SOMATIC EMBRYOGENESIS RECEPTOR KINASE 1 (BISERK1) | AtSERKs | Up-regulated upon <i>Magnaporthe</i> inoculation | [76] |
| Os08g34380 | COMMISSURAL VEIN EXCESSIVE 1 (COE1) | AtSERKs | Responsible for commissural vein pattern formation in rice | [77] |
| Os02g14120 | DEFECTIVE IN OUTER CELL LAYER SPECIFICATION 1 (DOCS1) also named OsSERK-like 4 (OsSERL4) | | Involved in the proper development of root outer cell layers | [75,78,79] |
| Os02g40240 Os02g12440 | LEAF PANICLE 2 (LP2) GAMMA-RAY INDUCED LRR-RLK 1 (GIRL1) | | Negative regulator in drought response Highly induced by gamma irradiation, by several abiotic stresses (salt, osmotic, and heat), by hormonal treatment with salicylic acid or abscisic acid, but downregulated in response to iasmonic acid treatment | [80,81] [82] |
| Os05g40770 | OsRPK1 | | A salt-responding protein, whose expression is also induced by cold, drought, and abscisic acid; affects root architecture by negatively regulating polar transport and accumulation of auxin in roots | [83,84] |
| Os07g41140 | RECEPTOR-LIKE PROTEIN KINASE 1 (RPK1) | AtRPK1 | Overexpression of both Arabidopsis and rice RPK1 receptors induces a reduction in salt tolerence in Arabidopsis transgonic plants | [85,86] |
| Os06g03970 | STRESS-INDUCED PROTEIN KINASE GENE 1 (OSSIK1) | | Affects stomatal density in leaf epidermis and plays important roles in salt and drought stresses | [87] |
| Os04g48760 | XIAO ("small" in Chinese) | | Regulates brassinosteroid signaling | [88] |
| Os11g07225-like1 and Os11g07225-like2 | 25L1 and 25L2 | | Specific to wild <i>Oryza rufipogon</i> rice; responsible for the high temperature-dependent expression of | [89] |
| Os02g05980 | LEUCINE-RICH REPEAT RECEPTOR-LIKE KINASE 1 (LRK1) | | hybrid weakness Cluster of 8 genes; LRK1 present in Dongxiang wild rice, but absent in Guichao2; Overexpression of LRK1 improved quantitative yield components | [90] |

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