

Published with Open Access at **Journal BiNET**

Vol. 09, Issue 02: 827-836

**Journal of Bioscience and Agriculture Research**Home page: [www.journalbinet.com/jbar-journal.html](http://www.journalbinet.com/jbar-journal.html)

## Functional analysis of plants *srg-genes*/transmembrane protein (RLKs) under stress condition

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### ABSTRACT

Stress perception and plant response occurs via signal transduction pathways, regulates expression of several classes of stress responsive genes (*srg-genes*). The products of *srg-gene* include chaperones, osmotins, anti-freeze proteins, mRNA binding proteins, enzymes involved in osmolyte biosynthesis, water channel proteins, sugar and proline transport proteins, detoxification enzymes, a variety of proteases, proteins and protein kinases/ or receptor-like kinases (RLKs). Out of these *srg-gene* products, protein kinases (RLKs) are transmembrane proteins and they play an important role in optimizing plant responses under different types of stress. Protein kinases (RLKs) make up a large super-family of homologous proteins, which are subdivided within the two super-family (i) Protein-serine/ threonine kinases and (ii) Protein-tyrosine kinases. Plant RLKs are further classified into the six different classes (*S-domain*, *LRR*, *TNFR*, *WAKs*, *PR*, *LecRLK*), which performed different functions in plants. This review explored how stress-specific 'ligands' of different types of RLKs coordinately control various molecular events under stress conditions.

**Key Words:** Abiotic and biotic stress, Signaling, Receptor-like kinases and Stress responsive genes

**Cite article:** Garg, G. & Kumari, R. (2016). Functional analysis of plants *srg-genes*/ transmembrane protein (RLKs) under stress condition. *Journal of Bioscience and Agriculture Research*, 09(02), 827-836.



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### I. Introduction

Natural environment is composed of a complex set of abiotic stresses and biotic stresses and plants are exposed to a wide range of these environmental stresses. Such stresses give rise to imbalances in the ability of a plant to perform normal metabolic processes (Marshall *et al.*, 2012). Stress perception and plant response occurs *via* signal transduction pathways, regulates expression of several classes of stress responsive genes (*srg-genes*). The products of *srg-gene* include chaperones, osmotins, anti-freeze proteins, mRNA binding proteins, enzymes involved in osmolyte biosynthesis, water channel proteins, sugar and proline transport proteins, detoxification enzymes, a variety of proteases, proteins and protein kinases or receptor-like kinases (RLKs). Out of these *srg-gene* products, protein kinases (RLKs) are transmembrane proteins and play an important role in optimizing plant responses under different types of stress. They are considered as key regulators of plant architecture and growth behavior in stress conditions (such as regulation of many physiological changes in plants such as self-

incompatibility, endosperm and pollen development, brassinosteroid sensing, anthoptosis, disease resistance etc.)

In the eukaryotes, protein kinases (RLKs) make up a large super-family of homologous proteins, which are subdivided within the two super-family (i) Protein-serine/threonine kinases and (ii) Protein-tyrosine kinases. Serine/threonine protein kinase phosphorylate the OH groups of serine or threonine and been classified as Cyclin-dependent kinases (CDKs), Ca<sup>2+</sup> calmodulin-dependent protein kinase-II (CaM kinase II or CaMKII), Mitogen activated kinases (MAPK), receptor like kinase (RLKS). The network of protein-serine/threonine kinases act as a “central processor unit” (CPU), accepting input information from receptors that sense environmental conditions, phytohormones, and other external factors, and converting it into appropriate outputs such as changes in metabolism, gene expression, and cell growth and division (Hanks and Hunter, 1995; Hardie, 1999).

Protein-tyrosine kinases, catalyze the phosphorylation of tyrosine residues in proteins and classified into two groups: (i) receptor tyrosine kinase (transmembrane proteins, which are involved in the control of animal cell growth and differentiation) and (ii) non receptor tyrosine kinase (lack transmembrane domains). Tyrosine- kinases function in many signal transduction cascades. In the cytosol, the nucleus, and the inner surface of the plasma membrane it act as critical component in the regulation of the immune system. Inside the nucleus tyrosine kinase is involved in cell cycle control. Elucidation of the functions of these kinases in different types of stress condition will provide a better understanding of stress-sensing mechanisms in plants and help to identify potential candidate genes for genetic engineering of improved stress-tolerant crops. In this review, we summarized very briefly the structure, classification, types and functions of different families of RLKs under different types of stress conditions.

## II. Methodology

This review paper is prepared based on primary and secondary published materials of various sources.

## III. Discussion

### RLKs and its classification

Plant receptor-like kinases (RLKs) represents one of the largest gene families in the *Arabidopsis* genome, comprising at least 610 members (Shiu and Bleecker, 2001), with approximately 1,131 members in rice (Shiu *et al.*, 2004). Size variations of the RLK families have been affected by many factors such as natural and artificial selection, living environments, genome size variation, polyploidization (Zhang, 2010). RLKs having amino-terminal extracellular domains and carboxyl-terminal intracellular kinase domains, with striking resemblance in domain organization to the animal receptor tyrosine kinases such as epidermal growth factor receptor. These ecto and endo domain parts are involved in downstream signal transduction. The ectodomain part is thought to act as a ligand-binding site. Their N-terminal signal sequence varies in structure, a single membrane-spanning region, and a cytoplasmic protein kinase catalytic domain. On the bases of variations in N-terminal sequences, plant RLKs are classified into the following six different classes, which performed different functions in plants:

- (i) S-domain class, possess an extracellular S-domain homologous to the self-incompatibility-locus glycoproteins (SLG) of *Brassica oleracea*. It consists of 12 conserved cysteine residues, out of which ten are absolutely conserved. SLG protein of this class plays an important role in self-incompatibility recognition process between pollen and stigma, act as a receptor for the pollen-derived ligand<sup>9</sup> and in plant defense response (Nasrallah, 2000; Pastuglia *et al.*, 1997).
- (ii) LRR (leucine-rich repeats) class: the largest class of plant RLKs, having tandem repeats of approximately 24 amino acids with conserved leucines. This class of RLKs plays an important role in plant development. For e. g. ERECTA regulates organ shape, CLAVATA1, HAESA and BRI1 regulates shoot meristem cell differentiation, floral abscission process and brassinosteroid perception respectively (Torii, 2000; Clark *et al.*, 1997; Li and Chory, 1997; Jinn *et al.*, 2000). LRR-RLKs also play a role in disease resistance e. g. rice gene *Xa21* confers race-specific resistance to

*Xanthomonas oryzae* cv. *oryzae* (Song *et al.*, 1995), tomato  $C_f$  disease resistance gene products confer a race-specific resistance to *Cladosporium fulvum* (Jones and Jones, 1996)

- (iii) Tumor-necrosis factor receptor (TNFR) class having a conserved arrangement of six cyteines, and seven repeats of ~39 amino acids that display a weak similarity to the RCC GTPase. The maize *CRINKLY4* (*CR4*) gene product possess TNFR like repeats. *CR4* is required for a normal cell differentiation of the epidermis. The *Aragbidopsis* genome contains several genes related to *CR4* (Becraft *et al.*, 1996; McCarthy and Chory, 2000)
- (iv) The cell wall associated receptor kinases (WAKs) represent the EGF (epidermal growth factor) class. Motif of EGF is characterized by a conserved arrangement of six cysteine, play a role in protein-protein interactions, pathogenic responses (He *et al.*, 1996; He *et al.*, 1998).
- (v) PR class, *Arabidopsis* PR5K (PR5-like receptor kinase) is the known example of this class. The extracellular domain of PR5K exhibits sequence similarity to PR5 (pathogenesis related protein 5), whose expression is induced upon pathogen attack (Wang *et al.*, 1996). The structural similarity between the PR5K receptor domain and PR5 suggests a role for PR5K in pathogenesis response.
- (vi) The Lectin RLK (LecRLK) class, is believed to play crucial roles in saccharide signaling as well as stress perception (defense against various plant pathogens and pests). LecRLKs possess three domains: an N-terminal lectin domain, an intermediate trans-membrane domain, and a C-terminal kinase domain. On the basis of lectin domain variability, LecRLKs again sub grouped into three subclasses: L, G, and C type. Phylogenetic analysis has been shown that plant receptor-like kinases (RLKs) share an evolutionary origin with the animal interleukin-1 receptor-associated kinase (Klaus-Heisen *et al.*, 2011). RLKS are again sorted in four main types, which are further divide in subfamilies (Table 01).

#### Types and subfamilies of RLKs

- (a) LRR (leucine-rich repeat RLKs)
- (b) PERK (proline-rich-extensin-like-RLKs)
- (c) CRK/DUF26 (cysteine-rich RLK/ Domain of Unknown Function 26)
- (d) RLCK (Calcium/calmodulin-regulated RLKs).

**Leucine-rich repeat RLKs (LRR-family):** LRR-RLKs involved mainly in water stress responses. Expression of LRR-RLK [a receptor-like protein kinase1 (RPK1)] is induced by ABA, dehydration, high salt, and low temperature. Loss of function of *RPK1* resulted in ABA insensitivity and reduced expression levels of various water stress-responsive genes, indicating that RPK1 positively regulates ABA/stress signalling. In an independent study Lee *et al.* (2011) reported that RPK1 functions in ABA dependent leaf senescence as well. RPK2 controls cell fate in anthers (Mizuno *et al.*, 2007), embryo development (Nodine *et al.*, 2007), and stem cell homeostasis in the shoot apical meristem through the mediation of CLV3 (Kinoshita *et al.*, 2010; Betsuyaku *et al.*, 2011). These studies indicate that RPK2 is another important RLKs governing plant development in various species. RLK7, an LRR-RLK member of the LRR XI sub-family, was identified as an important regulator in oxidative stress responses and shown to be involved in maintaining seed longevity (Pitorre *et al.*, 2010).

Recently, an LRR-RLK that controls ABA and H<sub>2</sub>O<sub>2</sub> regulated activation of S-type anion channels in guard cells has been identified (Hua *et al.*, 2012). This RLK, named GUARD CELL HYDROGEN PEROXIDE-RESISTANT1 (GHR1), physically interacted with and activated the S-type anion channel SLOW ANION CHANNEL-ASSOCIATED1 (SLAC1) by phosphorylation, resulting in stomatal closing in response to drought stress.

**Proline-rich-extensin-like-RLKs (PERK family):** A member of the proline-rich extensin-like receptor kinase family, PERK4, was identified as a positive regulator in ABA responses (Bai *et al.*, 2009). Decreased sensitivity to ABA with respect to seed germination, seedling growth, and root tip growth was observed in *perk4* mutant plants. ABA-induced elevation of the concentration of cytosolic free calcium and Ca<sup>2+</sup> channel activity were impaired in *perk4* root cells. PERK4 was shown to be an ABA and Ca<sup>2+</sup> activated protein kinase that functions at an early stage of ABA signaling, and this is involved in the inhibition of root cell elongation (Bai *et al.*, 2009). All detail suggesting that PERK4 may

perceive changes in the levels of ABA.

**Table 01. List of RLKs-families and subfamilies and their functions in plant system under stress condition**

Type of RLK	Sub family name	Gene Name	Full name	Organisms	Homologue expression	Functions	Reference
LRR	LRRIII	GHR1	Guard cell	Arabidopsis	Guard cell	Functions in ABA and H <sub>2</sub> O <sub>2</sub> regulated activation of S-type anion channels in guard cells	Hua et. al. (2012)
	LRRIX	SRLK	Salt induced	<i>Medicago truncatula</i>	Abiotic stress inducible	The RNAi prevents inhibition of root growth in Medicago under salt stress	De-Lorenzo et. al (2009)
	LRRXI	RLK7	Receptor like kinase 7	Arabidopsis	Abiotic stress inducible	Involved in the control of germination speed and the tolerance to oxidant	Pitorre et. al (2010)
	LRRXIII	OsSIK1	Oryza sativa stress induced protein kinase gene 1	<i>Oryza sativa</i>	Abiotic stress inducible	Rice OXa plants exhibited	Ouyang et. al. (2010)
	LRRXIII	OsSIK1	Stress induced protein kinase gene 1	<i>Oryza sativa</i>	Abiotic stress inducible	Rice OXa plants exhibited tolerance to salt and drought increased the level of superoxide dismutase and decreased ROS accumulation	Ouyang et. al. (2010)
	LRRXV	RPK1	Receptor like protein kinases 1	Arabidopsis	Abiotic stress inducible	Arabidopsis OXs showed enhanced ABA sensitivity and drought tolerance with increased SOD level and decreased ROS accumulation	Osakabe et. al. 2010
PERK	-----	PERK4	Proline rich extensin like receptor kinase 4	Arabidopsis	Abiotic stress inducible	Functions at early stage of ABA signaling to inhibit primary root cell elongation by perturbing Ca <sup>++</sup> homeostasis	Bai et. al. (2009)
CRK/DUF26	-----	CRK36	Cysteine rich receptor like kinase 36	Arabidopsis	Abiotic stress inducible	Forms a complex with ARCK1 and negatively controls ABA and osmotic stress signal transduction	Tanaka et. al (2012)
RLCK	-	ARCK1	ABA and osmotic stress inducible	Arabidopsis	Abiotic stress inducible	Forms a complex with CRK 36 and control negatively ABA and osmotic stress	Tanaka et. al (2012)

**Cysteine-rich rlk/domain of unknown function 26 (CRK family):** The DUF26 (Domain of Unknown Function 26; PFAM domain PF01657) RLKs, also known as Cysteine-rich RLKs (CRKs), form a large subgroup of the RLK family with more than 40 members (Shiu and Bleecker, 2003; Chen *et al.*, 2004). The extracellular region of the protein contains two copies of the DUF26 domain which has four conserved cysteines (three of them form the motif C-8X-C-2X-C) that may form disulphide bridges as potential targets for thiol redox regulation. The *CRKs* are transcriptionally induced by oxidative stress, pathogen attack and application of salicylic acid (SA) (Chen *et al.*, 2003; Chen *et al.*, 2004; Czernic *et al.*, 1999).

#### Calcium or calmodulin-regulated RLKs (RLCK family)

Calcium-mediated signaling plays a pivotal role in plant responses to abiotic stresses, including cold and drought stress. Calcium/calmodulin-regulated RLCKs have been shown to be involved in abiotic stress signaling. For instance, the cold-responsive *CRLK1*, which encodes an RLCK with two sites for calcium/calmodulin binding to stimulate kinase activity, was reported to regulate cold stress signaling

(Yang *et al.*, 2010b). The *crlk1* knock-out mutant plants exhibited an increased sensitivity to chilling and freezing stress, and cold-responsive genes were down-regulated in *crlk1* mutants<sup>40</sup>. Calcium-dependent calmo-dulin-binding RLCKs have also been isolated from *Glycine max* (GmCaMK1) (Defalco *et al.*, 2010) and *Glycine soja* (GsCBRLK) (Yang *et al.*, 2010a). GmCaMK1 and GsCBRLK activities are regulated by its calcium/calmodulin binding, and the overexpression of these genes in transgenic *Arabidopsis* enhanced plant tolerance to high salinity and ABA, as well as increasing the expression level of stress marker genes.

## Functions of RLKS

**RLKs and plant growth regulation:** Kinases transfer phosphoryl groups onto target proteins and altering their activity. Protein phosphorylation or dephosphorylation is the basic of many critical processes, including enzyme activation or inactivation, protein localization and protein degradation signal transduction, cell differentiation, cell proliferation and cell cycle progression. Kinases act as receptors on the cell membrane. Activation of a cell surface transmembrane receptor kinase by its ligand leads to changes in gene transcription and cell response. A fundamental aspect of plant growth regulation is cell cycle control and this involves the activity of several receptors like kinases protein. The receptor like kinases GS01 and GS02 together regulate root growth in *Arabidopsis* through control of cell division (Racolta *et al.*, 2013).

**RLKs and environmental stress:** RLKs have been known to have a major role in integrating environmental and plant hormone signalling (Dievart and Clark, 2004). Recent studies suggested that the rapid evolution and diversification of RLK-encoding genes in the plant genome might be enhanced by various environmental associations (Alcazar *et al.*, 2010; Smith *et al.*, 2011) (Table 02 & Table 03).

- RLKs convey signal to their target proteins in the cytoplasm by catalytic processes of protein kinase activity. RLKs like RPK1, CYSTEINE-RICH RLK, PROLINE-RICH-EXTENSIN-LIKE RLK4 (PERK4), and GHR1 (GUARD CELL HYDROGEN PEROXIDE-RESISTANT1) have been reported to control water stress signalling directly in *Arabidopsis* (Hua *et al.*, 2012; Bai *et al.*, 2009; Osakake *et al.*, 2010).
- LRR-RKs regulate a wide variety of developmental and defense-related processes (host-specific as well as non-host-specific defense response, wounding response, and symbiosis). PNAS, SR160, a tomato LRR-RLK, has been identified as the receptor, involved in systemic wounding signalling.
- RLK7 (the leucine-rich repeat class of receptor-like kinase [LRR-RLKs]) is involved in the control of germination speed and the tolerance to oxidant stress (Pitorre *et al.*, 2010).
- Lectin RLK (LecRLK) is believed to play crucial roles in saccharide signaling as well as stress perception. Over-expression of LecRLK has been demonstrated to improve germination rate, pigment content, and biochemical status of the salt-stress-affected plants (Deng *et al.*, 2009; Sun *et al.*, 2012). Stomatal closure is one of the most commonly employed defense mechanisms to limit the pathogen entry but this could result in a drop in CO<sub>2</sub> uptake, thus negatively affecting plant physiology. The *Arabidopsis* *LecRK-V.5* gene has been recently found to reverse the stomatal closure induced by bacterial infection and relieve the plant from CO<sub>2</sub> deficiency (Arnaud *et al.*, 2012). The potential role of LecRLK in symbiosis is evidenced in *Medicago* plants upon infection with *Sinorhizobium meliloti* (Navarro *et al.*, 2003).
- RLKs also participate in the recognition of pathogen a virulence factors (Avr genes) produced by specific strains of plant pathogens (Lee *et al.*, 2006). Recently a B-lectin RLK, termed Pi-d2, was identified as an R gene conferring resistance to the fungal pathogen *Magnaporthe grisea* (*M. grisea*) strain ZB15 (Chen *et al.*, 2006).
- Chen *et al.*, (2013) reported OsSIK2, an S-domain RLK from rice, play an important role in senescence process (in abiotic stress). Certain Cysteine- rich receptor kinases (CRK) proteins from *Arabidopsis thaliana* have been implicated in defense responses, for instance, over expression of *Arabidopsis* AtCRK5 was correlated with enhanced leaf growth and displayed enhanced resistance

to bacterial pathogen *Pseudomonas syringae* through induction of expression of pathogenesis-related 1 (PR1) gene (Yang *et al.*, 2010a; Wang *et al.*, 1996).

**RLKs and BR signalling:** Beside the above functions, RLK also involve in brassinosteroid perception. Like animal steroids, BRs are plant hormones required for normal plant growth, reproduction and development, as well as responses to both abiotic and biotic stresses (Divi and Krishan, 2009; Wolters and Jurgens, 2009; Wang, 2012). Plants that are deficient either in the biosynthesis or perception of these hormones are typically dark green dwarfs with epinastic leaves, have reduced or no fertility, and exhibit delay development (Bishop and Koncz, 2002). BRs negatively regulate stomatal development, mediated by upstream signalling components including the BR receptor RLK BRI1, the protein phosphatase BRI1 SUPPRESSOR1 (BSU1), the BR SIGNALLING KINASE 1 (BSK1), and the GSK3-like kinase BRASSINOSTEROID-INSENSITIVE 2 (BIN2) (Tang *et al.*, 2008). BRs have also been shown to repress light-responsive gene expression and chloroplast development mainly through the BRASSINAZOLE RESISTANT 1 (BZR1)-mediated transcriptional network (Luo *et al.*, 2010; Sun *et al.*, 2010).

**Table 02. RLKs involved in the control of plant growth and development**

GENE	ORGANISM	RLK type	Function
BRI1	<i>Arabidopsis thaliana</i>	LRR	Brassinosteroid-mediated growth responses
CLAVATA1	<i>Arabidopsis thaliana</i>	LRR	Control of apical meristem proliferation
ERECTA	<i>Arabidopsis thaliana</i>	LLR	Organ initiation and elongation
HAESA	<i>Arabidopsis thaliana</i>	LLR	Delayed floral organ abscission
PRK1	<i>Petunia inflata</i>	LRR	Post meiotic development of microspores
CRINKLY4	<i>Zea mays</i>	CR4L	Epidermal cell development

**Table 03. RLKs involved in plant-microbe interactions and stress responses**

GENE	ORGANISM	RLK type	Function
FLS2	<i>Arabidopsis thaliana</i>	LRR	Flagellin insensitivity
PBS1	<i>Arabidopsis thaliana</i>	RLCK	Resistance to <i>Pseudomonas syringae</i> sp
WAKs	<i>Arabidopsis thaliana</i>	WAKL	Defense response and cell expansion
Pti	<i>Lycopersicon esculentum</i>	RLCK	Resistance to <i>P. syringae</i> pv. Tomato
Xa21	<i>Oryza sativa</i>	LRR	Resistance to <i>Xanthomonas oryzae</i>
LRK10	<i>Triticum aestivum</i>	LRK10L	Resistance to wheat rust fungi

#### IV. Conclusion

Environmental stress tolerance is an important agronomic trait and is essential for maintaining high yield under adverse conditions. It is important to understand how plants sense the environment and regulate signaling networks. Genetic engineering of plant membrane signaling factors, including RLKs can have a positive impact on stress tolerance by influencing many downstream signaling factors, multiple functions and signaling networking of RLKs in stress conditions. This review explored how stress-specific 'ligands' of different types of RLKs coordinately control various molecular events and down-stream cascades, such as phosphorylation cascades, activation of secondary messengers, gene expression, protein dynamics, and the other functions of different families of RLKs in stress conditions.

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