

Review

Receptor-like Kinases (LRR-RLKs) in Response of Plants to Biotic and Abiotic Stresses

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Abstract: Plants live under different biotic and abiotic stress conditions, and, to cope with the adversity and severity, plants have well-developed resistance mechanisms. The mechanism starts with perception of the stimuli followed by molecular, biochemical, and physiological adaptive measures. The family of LRR-RLKs (leucine-rich repeat receptor-like kinases) is one such group that perceives biotic and abiotic stimuli and also plays important roles in different biological processes of development. This has been mostly studied in the model plant, *Arabidopsis thaliana*, and to some extent in other plants, such as *Solanum lycopersicum*, *Nicotiana benthamiana*, *Brassica napus*, *Oryza sativa*, *Triticum aestivum*, *Hordeum vulgare*, *Brachypodium distachyon*, *Medicago truncatula*, *Gossypium barbadense*, *Phaseolus vulgaris*, *Solanum tuberosum*, and *Malus robusta*. Most LRR-RLKs tend to form different combinations of LRR-RLKs-complexes (dimer, trimer, and tetramers), and some of them were observed as important receptors in immune responses, cell death, and plant development processes. However, less is known about the function(s) of LRR-RLKs in response to abiotic and biotic stresses. Here, we give recent updates about LRR-RLK receptors, specifically focusing on their involvement in biotic and abiotic stresses in the model plant, *A. thaliana*. Furthermore, the recent studies on LRR-RLKs that are homologous in other plants is also reviewed in relation to their role in triggering stress response processes against biotic and abiotic stimuli and/or in exploring their additional function(s). Furthermore, we present the interactions and combinations among LRR-RLK receptors that have been confirmed through experiments. Moreover, based on GENEINVESTIGATOR microarray database analysis, we predict some potential LRR-RLK genes involved in certain biotic and abiotic stresses whose function and mechanism may be explored.

Keywords: abiotic stress; biotic stress; stress tolerance; LRR-RLK receptors; *Arabidopsis*



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1. Introduction

Biotic and abiotic stresses have detrimental effects on growth and development in plants that are at risk of biotic and abiotic stresses. To counteract these adversities, plants have developed diverse stimuli and activation strategies. The receptors in plants are one of the primary components of plant–environment interaction that transduces the information and makes the plant aware of its surroundings. In plants, a large number of different types of receptor-like kinases (RLKs) have evolved, and they are classified based on their kinase domain and extracellular domain sequences [1–3]. Among the RLKs, the biggest group are the Leucine-rich-repeats–RLKs (LRR-RLKs), which have an extracellular domain LRR motif that facilitates the binding of ligands (proteins, signaling peptides, hormones, etc.). In addition to their regulatory role in plant development, shoot and root apical meristem, xylem differentiation, and BL (Brassinolide) pathways, they also play a role in the immune system and activation of cell death [4–9]. A small number of LRR-RLKs have been shown

to be involved in the abiotic stress response of plants [2,10–12]. It is mainly achieved through the investigation of *LRR-RLK* mutant lines by inserting tDNA fragments into their exon [8,13,14], intron, UTR (untranslated region), or into the promoter region [8,15,16] and then testing them under different stresses (Tables S1 and S2). There are plenty of genetic tools that are used for the investigation of *LRR-RLK* gene function, but these studies were mostly conducted in model plant *Arabidopsis thaliana*, and thereafter in tomato (*Solanum lycopersicum*) and tobacco (*Nicotiana benthamiana*). The ubiquitous presence of *LRR-RLK* with varying sequences across the plant genera underscores the need for its investigation in other plants in order to expand the knowledge and thereby to understand their role more specifically. *RLKs* were classified into different groups based on their functions, such as growth and development processes and biotic and abiotic stress responses (reviewed Yuriko Osakabe, and Beg Hab Kim review articles [2,17]). Some of the well-studied *LRR-RLKs*, such as *BRASSINOSTEROID INSENSITIVE 1 (BRI1)* or *SOMATIC EMBRYOGENESIS RECEPTOR KINASE 3 (SERK3)*; *SOMATIC EMBRYOGENESIS RECEPTOR KINASE 1, 2, and 4 (SERK1/2/4)*; *BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1)*; *BAK1-INTERACTING RECEPTOR-LIKE KINASE1 (BIR1)*; and *SUPPRESSOR OF BIR1-1 (SOBIR1)*, *ELONGATION FACTOR-Tu (EF-Tu) RECEPTOR (EFR)* were discussed as being essential for immune responses [2,17,18]. Credible evidence has been provided to demonstrate that some of the *RLKs*, such as *RECEPTOR-LIKE PROTEIN KINASE1 (RPK1)* and *RECEPTOR-LIKE KINASE 7 (RLK7 or other name LRR XI-23)*, are involved in water stress [2,16], and *PHLOEM INTERCALATED WITH XYLEM-LIKE 1 (PXL1)* in cold stress [19]. Notably, some of the above-mentioned *LRR-RLKs*, such as *BAK1/SERK3*; *SERK1,-2, and -4*; and *BRI1*, share the same signaling pathways in Mitogen-Activated Protein Kinase (MAPK) activation, Ca^{2+} influx, and the production of reactive oxygen species (ROS) in order to initiate plant responses to biotic or abiotic stresses and/or developmental cues (see review [20]). Among the *SERK*-mediated signaling pathways, crosstalk occurs at multiple levels, and it is possible to have crosstalk with other *LRR-RLKs*. Recent *LRR-RLK* studies showed additional crosstalk of *LRR-RLKs*, and also new achievements for additional functions of known *LRR-RLKs*. Despite the exploration of so many *LRR-RLKs* from *A. thaliana* over a period of time, the functional role of several of these has not yet been explored.

The *in silico* studies have shown that *LRR-RLK* harbors a transmembrane domain (TM), intracellular kinase domain (KD), and *LRR*-containing extracellular domain (ECD) [21]. This extracellular domain of *LRR-RLKs* was classified according the structure of *LRR*, where the *LRR* II, III, VI, IX, X, XI, XII, and XIII sub-families contained the cysteine residues in the amino-terminal of the *LRR* motifs [21]. This extracellular domain could have an impact on oligomerization [21]. Moreover, it was shown that *LRR-RLKs* with short extracellular domains are mainly co-receptors [22], which help to hold the ligand and stabilize and enhance transduction of the intracellular signal together with the ligand-binding receptor [23–25]. Some of the *LRR-RLKs* interact with each other, which allows for the formation of different heterodimers or trimers, thereby allowing them to become multi-functional [26,27]. *In vitro* and *in vivo* studies confirmed the heterodimer complexes of *LRR-RLK* and few trimeric complexes [15,16,28–32]. These formations are important for triggering immune responses, metabolic pathways, stem development, etc. Therefore, the use of double, triple, or quadruple mutants proved to be a useful tool for achieving their function and/or interactions [16,29–33]. The interaction of *LRR-RLKs* and its mechanism was mainly studied in *A. thaliana*.

Here, we update the functioning of *LRR-RLKs* in response to biotic and abiotic stresses in *A. thaliana*, and in other plants as well, such as *N. benthamiana*, *S. lycopersicum*, *Oryza sativa*, *Triticum aestivum*, *Hordeum vulgare*, *Brachypodium distachyon*, *Brassica napus*, *Medicago truncatula*, *Gossypium barbadense*, *Phaseolus vulgaris*, *Solanum tuberosum*, and *Malus robusta*. Additionally, we compiled the information on genetic tools used in the investigation of *LRR-RLK*'s role in biotic and abiotic stress response. The Microarray data analysis (GENEINVESTIGATOR, <https://geneinvestigator.com/>, accessed on 3 August 2022) of the *LRR-RLK* genes, which responded to biotic and abiotic stimuli, suggested

the possibility of additional functions and their cross-link in triggering different signaling processes. Furthermore, we have presented the information on stress-related LRR-RLKs as dimer, trimer, and tetramer complexes, which were experimentally achieved in *A. thaliana*. Furthermore, an ATTED databases (<https://atted.jp/hclust/>, accessed on 2 February 2022) analysis for protein interactions pointed towards additional possible interactions among the LRR-RLKs, however, these need to be validated experimentally [33].

2. Abundance of LRR-RLKs Genes in the Plant Genome

The abundant availability of genome and RNA sequences allowed us to identify the potential LRR-RLK in different plants, such as annual and perennial plants, crops, trees, herbs, etc. (Table 1). In primitive plants such as *Sedum alfredii*, *Selaginella moellendorffii*, *Amborella trichopoda*, and *Physcomitrella patens*, there are about 60–134 genes. In higher plants, the identified LRR-RLK gene numbers vary from 200 to 600 (LRR-RLK genes) (See Table 1). It was shown that algae do not contain any LRR-RLK genes similar to plants and it was suggested that the structural combination of LRRs and kinase domains (KD) to form new genes may have occurred after the divergence of land plants from green algae [34]. An in silico analysis revealed that the expansion in LRR-RLKs is a result of tandem and segmental duplication events (Table 1). Additionally, the exon/intron compositions and motif arrangements were considerably conserved among members in the same groups or subgroups in plants (Table 1).

Table 1. Number of LRR-RLKs present in different plants. Whole genome sequence data of the enlisted plant species was analyzed for the identification of LRR-RLKs. The identified LRR-RLK genes (numbers) with their expansion characteristic (presence of tandem duplication, motif conservation, and duplication) were based on different studies. Genome size for each species was given. Mb indicates mega base pairs. “-” indicates no data available.

Numbers of LRR-RLK	Plant Species	Genome Size	Presence of Tandem Duplication	LRR-RLK Organizations	References
0	<i>Chlamydomonas reinhardtii</i>	120 Mb	-	-	[34]
60	<i>Sedum alfredii</i>	39.1 Mb	-	motif conservation	[35]
67–81	<i>Selaginella moellendorffii</i>	100 Mb	present	motif conservation	[34]
94	<i>Amborella trichopoda</i>	870 Mb	present	motif conservation	[36]
134	<i>Physcomitrella patens</i>	500 Mb	-	-	[34,37]
176	<i>Phoenix dactylifera</i>	658 Mb	present	-	[37,38]
180	<i>Cucumis sativus</i>	367 Mb	present	segmental duplication	[37,39]
201	<i>Fragaria vesca</i>	240 Mb	present	-	[40]
211	<i>Medicago truncatula</i>	465 Mb	present	exon/intron organization, motif conservation	[37,41]
215	<i>Vitis vinifera</i>	500 Mb	present	segmental duplication	[37,42]
226	<i>Arabidopsis thaliana</i>	133 Mb	present	-	[37,43]
227	<i>Jatropha curcas</i>	320 Mb	present	-	[37,44]
230–236	<i>Vernicia fordii</i> <i>Vernicia montana</i>	1310 Mb	Present (<i>V. fordii</i>)	motif conservation (both), segmental duplications (<i>V. fordii</i>)	[45,46]
239	<i>Solanum lycopersicum</i>	900 Mb	present	-	[37,47]
247	<i>Theobroma cacao</i>	430 Mb	present	motif conservation	[37,48]
250	<i>Zea mays</i>	2400 Mb	present	random chromosomal distribution	[37,49]
267	<i>Prunus mume</i>	280 Mb	present	-	[40]
268	<i>Solanum tuberosum</i>	840 Mb	present	lineage-specific expansion	[37,50]
268	<i>Prunus persica</i>	265 Mb	present	-	[37,40]
292	<i>Raphanus sativus</i>	574 Mb	present	motif conservation	[51]
298	<i>Gossypium arboreum</i>	1750 Mb	present	conserved exon/intron organization	[52]

Table 1. Cont.

Numbers of LRR-RLK	Plant Species	Genome Size	Presence of Tandem Duplication	LRR-RLK Organizations	References
297–300	<i>Citrus clementina</i> <i>Citrus sinensis</i>	370 Mb 380 Mb	present	-	[53]
300	<i>Brassica rapa</i>	455 Mb	present	intron/exon pattern organization, motif conservation	[37,54]
310	<i>Setaria italica</i>	515 Mb	present	motif conservation, segmental duplication	[37,55]
312	<i>Brassica nigra</i>	522 Mb	present	intra-chromosomal duplication, conserved loci duplication	[56]
332	<i>Oryza sativa</i>	430 Mb	present	exon duplication, mutation, and exon shuffling	[37,57]
367	<i>Glycine latifolia</i>	939 Mb	present	-	[58]
384	<i>Gossypium raimondii</i>	761 Mb	present	motif conservation	[37,59]
427	<i>Pyrus bretschneideri</i>	512 Mb	present	exon/intron organization, motif conservation	[60]
441	<i>Populus trichocarpa</i>	500 Mb	present	segmental duplication, exon/intron organization and motif conservation	[37,61]
484	<i>Brassica juncea</i>	920 Mb	present	segmental duplications, intra-/inter-genomic duplications	[62]
485	<i>Malus domestica</i>	750 Mb	present	-	[37,40]
494	<i>Glycine max</i>	1100–1150 Mb	present	exon/intron organizations, motif arrangements	[37,63]
531	<i>Triticum aestivum</i>	17,000 Mb	present	segmental duplications, intra-genomic duplications	[64]
548	<i>Arachis hypogaea</i>	2700 Mb	present	segmental duplication, exon/intron organization and motif conservation	[65]
589	<i>Thinopyrum elongatum</i>	4780 Mb	present	segmental duplications	[66]

The research on LRR-RLKs were mainly conducted in *A. thaliana* due to the availability of a large dataset. The increase in DNA and RNA sequencing in different crops and *A. thaliana* allowed for the identification of the numbers of stress-related LRR-RLKs (Table S1) and their sequence in other plants such as *O. sativa*, *G. max*, *M. truncatula*, *Populus*, *V. vinifera*, *S. lycopersicum*, *B. napus*, and *Z. mays* (Table S2). Note that some of the stress-related LRR-RLKs in *A. thaliana* have bigger numbers of orthologs in some plants, such as *G. max*, *M. truncatula*, *O. sativa*, and *Z. mays*, as compared to *A. thaliana* (Table S2). Only a few orthologs of stress-related LRR-RLK genes were investigated under biotic and abiotic stresses and their functions were elucidated in different plants by using different mutants of LRR-RLKs (Table S3).

3. Stress-Related LRR-RLKs in Plants

From a pool of 223 LRR-RLKs identified in *A. thaliana* (Table 1), some were clustered as regulators of various growth and development processes (stem cell maintenance, anther development, determination of the fate of a cell and organ development, cell expansion, stem stomata development) [67–71], while others were shown or suggested to be important in biotic and abiotic stress responses (Figure 1). One of the extensively studied genes among LRR-RLKs is *BAK1/SERK3*, which regulates multiple processes such as Brassinosteroid (BR) signaling, growth and development, and stomatal patterning, and also activates the expression of antimicrobial proteins [20,72]. Recently, the role of BAK1 in guard cell ABA signaling was demonstrated and *bak1* mutants showed more loss of water as compared to wild-type. The ABA increased the formation of a complex between BAK1 and OPEN STOMATA1 (OST1) near the plasma membrane [73]. In addition, *bak1-5* mutants revealed

that the post-invasive resistance of *A. thaliana* to *Alternaria brassicicola* is independent of pathogen-triggered indole-3-carboxylic acid and its derivatives (ICAs) and camalexin biosynthesis [74]. Notably, the function of BAK1/SERK3 in the immune response was shown in tobacco and tomato plants against the late blight pathogen (*Phytophthora infestans*) and bacterial and nematode infection [75,76]. Other SERKs, such as SERK1 and SERK2, were also important genes for conferring resistance against bacterial leaf blight and fungal infection, respectively [20,77,78]. In rice, *OsSERK2* was shown as a positive regulator of immunity, interacting with the rice immune receptor kinases (XA21 and XA3) [78]. It was suggested that SERK2 could be a target for sRNAs of *Sclerotinia sclerotiorum* and the resulting action may contribute to the silencing of immune components in plants [79]. Recently, using the *serk2* mutant lines, it was observed that SERK2 is a component of BR signaling and it regulates BR signaling and salt resistance in rice [80]. Previously, SERK4 together with SERK3 were shown to trigger a series of defense responses [20], but in recent studies using knock-out and overexpressing lines of SERK4, it was observed that SERK4 negatively regulates the leaves senescence process [81].

Another well-studied LRR-RLK gene is *BRI1*, which interacts with SERK3 by mediating BR signaling through the BRI1/BAK1 complex [72], and it regulates stem elongation, vascular differentiation, seed size, fertility, flowering time, and senescence [8,17,82]. Moreover, the mutant of *BRI1* shows pleiotropic effects on disease resistance along with plant development regulation [83], and it displays ABA-hypersensitive primary root growth [84,85]. In *B. napus*, *S. lycopersicum*, and *B. distachyon*, the role of *BRI1* in BR signaling was confirmed [86–88]. Furthermore, *BRI1* was involved in BR signaling through MAPK and Ca²⁺-dependent protein kinases in rice [89]. Additionally, it was suggested that *SIBRI1* is related with systemin-mediated systemic defense response [90], however it was not established conclusively [87]. In tobacco, *NbBRI1* was involved in BR-mediated systemic defense signaling by regulating H₂O₂ and NO production [91]. Recently, *BRI1* manipulation in different cereals resulted in drought tolerance [86], and disease resistance [83]. Additionally, the overexpression of wheat *TaBRI1* in *A. thaliana* revealed early flowering and enhancement of seed production [92], while overexpression of *SIBRI1* promoted fruit ripening and ethylene production, and increased the levels of carotenoids, ascorbic acid, soluble solids, and soluble sugars during fruit ripening [93]. In potato (*S. tuberosum*), *BRI1* was involved in the regulation of tuberization, thus suggesting other possible roles of *BRI1* [94]. *BIR1* is another LRR-RLK that forms a complex with SERK3/BAK1 or with other SERKs, and these complexes were shown to repress the effector-triggered immunity (ETI) in the absence of pathogen effectors [72]. The LRR-RLK *SOBIR1* also interacts with SERKs, serving as a stabilizer of the protein complex and aids receptor complexes in triggering defense responses [18]. Notably, the homolog of *SOBIR1* activated the immune response in tomato against fungal infection [18], but not in antiviral infection [95]. In tobacco plants, *NbSOBIR1* was involved in the immunity of *N. benthamiana* through monitoring the production of ROS [96]. Furthermore, the manipulation of *GbSOBIR1* in cotton (*G. barbadense*) plants resulted in resistance to *Verticillium* [97]. While *EFR* regulated the immune response of plants after perceiving bacterial flagellin and EF-Tu by forming complexes with SERKs [72], it was observed that *A. thaliana efr* mutants lacking EF-Tu perception are more susceptible to transformation by *Agrobacterium tumefaciens* [98]. This revealed the importance of the EF-Tu perception system for plant defense. The homologs of *EFR* in tobacco and in tomato were also involved in pathogen-associated molecular patterns (PAMP)-triggered immunity, and suggesting transgenic expression of *EFR* could be used as an engineering tool against broad-spectrum bacterial infections [99]. In rice, it was shown that receptors *EFR* and XA21 recruit similar immune signaling [100]. The overexpression of *AtEFR* in different crops shows resistance to bacterial infection and/or symptoms. In wheat and apple, the overexpression of *AtEFR* enhanced resistance against bacterial disease, fire, and blight [101], respectively. Similarly, in *M. truncatula*, it reduced the bacterium infection [102] and in potato it enhanced bacterial wilt resistance [103].

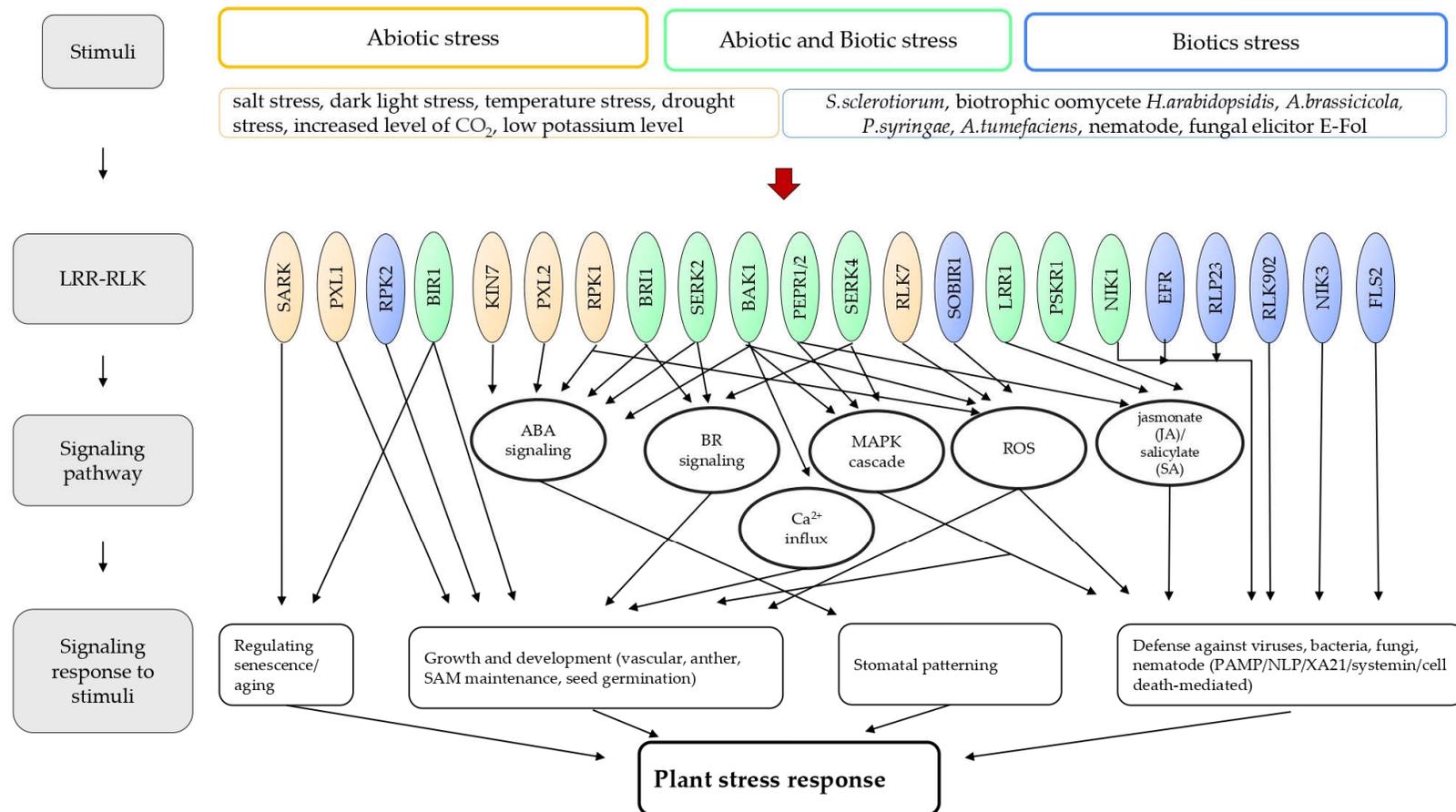


Figure 1. Scheme of signaling pathways triggered by biotic- and abiotic-stimulated LRR-RLKs and crosstalk among them. The LRR-RLKs regulate various plant processes, including growth, development, and responses to biotic and abiotic stresses. After perceiving abiotic and/or biotic stimuli by the LRR-RLKs, activation of diverse signaling, such as MAPK activation (BAK1, PEPR1/2, SERK4), Ca²⁺ influx (BAK1), reactive oxygen species (ROS) production (RPK1, BAK1, RLK7, SOBIR1), BR signaling (BRI1, SERK2, SERK4), ABA signaling (KIN7, PXL2, RPK1, BRI1, SERK2, BAK1), jasmonate (JA), and salicylate (SA) (PEPR1/2, LRR1, PSKR1) occurs. Some LRR-RLKs may activate several signaling pathways depending on the type of stimuli: RPK1-ABA and ROS pathways; BRI and SERK2—ABA and BR pathway; PEPR1/2—MAPK and JA/SA pathway, SERK4—BR and MAPK pathway, BAK1-BR signaling, Ca²⁺ and MAPK pathways. Senescence may be associated with SARK and BIR1. Defense mechanisms against biotic stress stimuli are mediated by JA, SA, ROS, and MAPK pathways, and also additionally followed by LRR-RLKs: NIK1, EFR, RLP23, RLK902, NIK3, and FLS2. Yellow color indicates tested abiotic stimuli, blue color is for tested biotic stimuli, and green for both stimuli.

SERKs also form complexes with PHYTOSULFOKINE (PSK) RECEPTOR 1 (PSKR1), which is known to regulate root growth and hypocotyl elongation [20]. Moreover, *PSKR1* was also identified as an important component of plant defense [104]. *PSKR1* suppresses salicylate-dependent defense responses, where the *pskr1* mutants exhibit early senescence, a salicylate (SA)-associated response, and are impaired in wound healing, a jasmonate (JA)-associated response [104]. Moreover, *OsPSKR1* was involved in the immune response against bacterial leaf streak in rice through salicylic acid (SA) pathway signaling [105]. *PEP1 RECEPTOR 1 (PEPR1)* and *PEPR2* were involved in immune responses through interaction with *SERK3* through *AtPep1*-triggered ROS production and ethylene signaling [20]. Furthermore, *PEPR1* recognizes *AtPep3* and increases tolerance to salt stress as well as immune response [106]. Furthermore, it was suggested that *AtPeps-PEPR* signaling pathway is involved in stomatal closure through an *OST1*-independent mechanism under biotic stress [107]. *PEPR1/2 ORTHOLOG RECEPTOR-LIKE KINASE1* from *S. lycopersicum* was shown to regulate responses to systemin, necrotrophic fungi, and insect herbivory [108]. Previously, *RECEPTOR-LIKE PROTEIN KINASE1 (RPK1)* was linked to the water stress response [2], wherein it regulates ABA/stress signaling by controlling ROS homeostasis. Additionally, *RPK1* and *BAK1* form complexes with *OST1* to regulate ABA-induced stomatal closure [73,109].

The LEUCINE-RICH REPEAT PROTEIN 1 (*LRR1*) forms a complex with pathogenesis-related protein10 (*PR10*), and it leads to cell-death-mediated defense signaling [110]. Additionally, it was shown in vivo and in vitro that during plant responses to drought stress, *LRR1* and *KINASE 7 (KIN7)* are degraded by *PLANT U-BOX PROTEIN 11 (PUB11)*, an E3 ubiquitin ligase [111]. This *KIN7* phosphorylates and activates tonoplast-located channels during ABA- and CO_2 -mediated stomatal closure [112]. Recently, Leucine-rich receptor-like kinase homologs in cereals such as barley and wheat showed important components of defense responses against *Fusarium* by disbalancing salicylic acid signaling [113]. The silencing of *LRR1* in rice in the *XA21* genetic background (*XA21-LRR1Ri*, *XA21* is 21 amino acid tyrosine-sulfated epitope derived from the bacterial protein) compromises resistance to bacterial leaf blight, indicating involvement in *XA21*-mediated immune response [114]. Other *LRR-RLK*, *RECEPTOR-LIKE KINASE 902 (RLK902)* previously showed importance in resistance to *Hyaloperonospora arabidopsidis* (downy mildew) in *A. thaliana* [115]. *RLK902* associates with *ENHANCED DISEASE RESISTANCE 4 (EDR4)* and with *BRASSINOSTEROID-SIGNALING KINASE1 (BSK1)*, a key component of plant immunity [116]. Not much is known about *LRR-RLK*-like NSP-interacting kinases (*NIKs*), such *NIK1*, *NIK2*, and *NIK3*, and their interaction with geminivirus nuclear shuttle protein (*NSP*). The binding of *NSP* to *NIK* inhibits its kinase activity in vitro, and a phenotypic analysis of *NIKs* mutant lines suggests that *NIKs* are involved in the antiviral defense response [117]. It was shown that *At-FEI2* (cell wall receptor-like kinase) plays a positive role in *Arabidopsis* and in tomato defense against *Botrytis cinerea* based on the study using knockout mutants of the *Bc-siR37* [118].

The *LRR-RLK* genes have been shown to play important roles in response to abiotic stresses. In previous studies, *ERECTA-LIKE1 (ERL1)*, a member of the gene family closely related to *LRR-RLKs*, was shown to synergistically regulate plant development and morphogenesis and functions in response to abiotic stresses, especially for heat response and drought [2,119]. Recently, it was observed that the *ERECTA* family was involved in sensing salt and osmotic stresses [120]. Furthermore, other *LRR-RLK* genes like *PXY-Like 2 (PXL2)* have been proven to be essential in vascular development through recognizing small signaling peptides, and they play a role in ABA signaling [121]. While the *PHLOEM INTERCALATED WITH XYLEM-LIKE 1 (PXL1)* is essential in cold and heat stress (through the ROS), the *PXL1* regulates *HISTIDINE-RICH DEHYDRIN1 (AtHIRD1)* and *LIGHT-HARVESTING PROTEIN COMPLEX I (AtLHCA1)* by phosphorylation [122]. Another *LRR-RLK* gene, such as *SCHENGEN 3 (SGN3)*, is related with developmental processes, particularly with microdomain organization and enhanced suberization in the endodermis. Additionally, it was shown that the *sgn3* mutant was extremely sensitive to environmental

conditions, such as different temperatures and nutrient deficiency [123]. Moreover, the role of BRL1-LIKE3 (BRL3) was reported in sensing glucose and flg22, where BRL3 together with REGULATOR OF G-PROTEIN SIGNALING 1 (AtRGS1) prevents excess ROS burst and control growth inhibition [124]. Additionally, the overexpression of *BRL3* resulted in drought stress tolerance in *A. thaliana* through the accumulation of osmoprotectant metabolites, such as proline and sugars [125]. In rice, the *OsBRL1* and *OsBRL3* were shown to be partly involved in BR perception in the roots [126]. Another LRR-RLK, *RLK7/LRR XI-23*, was involved in the regulation of seed germination and oxidative stress [127]. Furthermore, the LRR-RLKs, RECEPTOR-LIKE PROTEIN KINASE 2 (RPK2) also known as TOAD2) together with CLAVATA3 (CLV3), regulate the development of anthers, embryo, and stem cell homeostasis in the shoot apical meristem [2]. Single mutants of *RPK2* and *CLAVATA1 (CLV1)* and *CLAVATA2 (CLV2)* showed importance in nematode parasitism [128]. Furthermore, RPK2 interacts with other LRR-RLK, such as SENESCENCE-ASSOCIATED RECEPTOR-LIKE KINASE (SARK)—also known as CLAVATA3 INSENSITIVE RECEPTOR KINASE 3 (CIK3)—to maintain stem cell homeostasis [129] and anther development [33]. SARK was shown to be a positive regulator of senescence through hormone imbalances [130]. Interestingly, *PpSARK* in moss was shown as a positive regulator of senescence in salt stress responses and was also suggested to be a negative regulator of senescence [131]. In common bean's SARK, it did not coordinate senescence in nodules [132].

Thus, the mentioned *LRR-RLK* gene(s), which were tested in different biotic or abiotic stress/senescence processes, shared similar signaling pathways, such as reactive oxygen species (ROS) production, Ca^{2+} influx, activation of MAPK, regulation of defense genes, regulation of stomatal patterning, hormonal regulation, and regulation of senescence-related gene(s), to trigger the response of plants (See the scheme in Figure 1). Remarkably, some *LRR-RLK* genes show crosstalk in triggering different programs (Figure 1) and their numbers increased compared to the most recent review articles, which mentioned *LRR-RLK* genes in biotic and abiotic stresses [17,20]. Therefore, we have additionally collected all of the known single mutants of *LRR-RLK* genes and enlisted their phenotypic changes under experimentally tested biotic and/or abiotic stresses in Table S1, where their crosstalk can be easily observed. The information was gathered from the available microarray and RNA sequencing data (online available GENEINVESTIGATOR), which is also useful in predicting the potential role of genes for a particular stress stimulus [133]. Several *LRR-RLK* genes were identified in biotic or abiotic stresses (Table S1). The microarray data analysis of these *LRR-RLK* genes showed the alterations in expression under both types of stress stimuli i.e., biotic and abiotic (Figure S1). For example, *FEI2*, *NIK3*, *RLK902*, *RPK2*, *EFR*, *SOBIR1*, and *NIK1*, which were tested only in biotic stresses, showed a change in the expression under abiotic stress as well (Figure S2). Similarly, the reverse was observed for genes involved in abiotic stresses, such as *RPK1*, *BRL3*, *ERL1*, *PXL1*, *PXL2*, *SARK*, *RLK7/LRR XI-23*, *SGN3*, *KIN7*, and *PEPR1*, as it showed a change in expression for biotic stress too (Figure S3). The detailed characterization of these *LRR-RLK* genes under both stresses is likely to provide additional information on their mechanistic role and may give insight into the crosstalk among the LRR-RLKs.

4. Interactions among the Stress-Related LRR-RLKs

Several mutant lines, such as single, double, triple, and/or quadruple mutants, were generated (Table S1) to investigate the function of these genes [8,15,33,134,135]. In these studies, it was shown that the formation of complexes (dimer, trimer, or tetramer) is important in relaying the signals to the downstream components [13,14,28–31]. The genetic evidence for interactions was confirmed by pull-down, gel filtration, bimolecular fluorescence complementation (BiFC), co-immunoprecipitation (CoIP), and protein kinase assay, as presented in Table 2, Figures S4–S7. Most of the known functional interactions among the LRR-RLK were shown as heterodimers and, in a few cases, as homodimers, e.g., SERK 1 and SERK2 (Table 2). The trimers were also shown and they perform different functions, e.g., SOBIR-BAK1-RLP23, BON1-BAK1-BIR1, ER-BAK1-TMM, BIK1-BAK1-ERL1/2, FLS2-

BAK-BIK1, and FLS2-BIK1-RBOHD play a role in the immune system [14,28,29,31,136,137]; and CLV1-CLV2-CRN in stem cell regulation [32,138]. The formation of some of the LRR-RLK complexes were dependent on ligand stimulation, for example, ligands such as flg22 [fragment of bacterial flagellin that binds the FLAGELLIN SENSITIVE 2 (FLS2) receptor] and elf18 (the N-terminal of EF-Tu) stimulate the formation of BAK-FLS2 or BAK-EFR dimers, respectively [16]. Similarly, SCFE1 (SCLEROTINIA CULTURE FILTRATE ELICITOR1) or nlp20 (peptide motif) ligands stimulate the formation of the BAK1-SOBIR1-RLP23 complex [14], while the binding of AtPep1 (endogenous peptide elicitor) induces PEPR1-BAK1 heterodimerization [139]. The INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) stimulate the formation of heterodimers of SERK1 and SERK2 with HAESA (HAE) and HAESA-LIKE2 (HSL2), and Cf-4 of the SERK1-SOBIR1 complex [14,30] (see Figures S4–S7). Steroids may induce the generation of a LRR-RLKs complex, such as SERKs and TETRATRIPEPTIDE-REPEAT THIOREDOXIN-LIKE 3 (TTL3), which activate the BR signaling pathway [16,140,141], and an application of brassinolide (BL) stimulates the formation of BAK1-BRI1 [16]. However, it was shown that the formation of heterotrimers, BAK1-ER-TMM, BAK1-ERL1-TMM, and BAK1-ERL2-TMM, are not dependent on stimulation ligands (EPF1 and EPF2) [29].

The formation of heterodimers with other LRR-RLKs, so-called co-receptors that usually have short extracellular domains, is important for holding the ligand and stabilizing it for the enhancement of the transduction of the intracellular signal [22]. The role of heterodimers was mainly as a defense response, development process, BR signaling, or cell death (Figures S4–S7). For example, BRI1 generated complexes with SERKs (BAK1/SERK3, SERK1, and SERK4) and TTL3—only for BR pathway activation [16,140,141], BIR1 can interact with BAK1, SERK1, SERK2, and SERK4 to inhibit plant cell death [14,30], and EFR with SERK1, BAK1, and SERK4/BKK1 can activate the immune response [16,98] and EFR with GLYCINE-RICH PROTEIN7 (GRP7) activates the PAMP-triggered immune (PTI) response against *Pseudomonas syringae* [142]. SOBIR1 forms a complex with BAK1 for immune responses against *P. infestans* and *S. sclerotiorum* [14,30], and the heterotrimer with AtRLP23 is formed in the absence of BIR1 to activate cell death [14]. Additionally, PSKR1 may interact with SERK1/2 and BAK1 [143]. Furthermore, CLV1 forms heterodimers with BAM1 (BARELY ANY MERISTEM1), SARK, and CRN (CORYNE), RPK2 [32,138,144,145], which are important for apical and young floral meristem development. Conversely, other LRR-RLKs that form variant complexes were shown to perform different roles. For example, BAK1 interacts with FLS2, SOBIR1, NIK1, BKK1, BIR2, PEPR1, PSKR1, EFR, BIK1, RLP23, ERL2, ERL1, ER, and TMM to activate immune responses [14,16,28–31]; with BIR1 to inhibit plant cell death; with RPK1, BIR1, BON1 (BONZAI1), SOBIR1, and HSL2 to activate cell death [30,109,146]; with BRI1 to activate BR pathway [8,16]; and with ER or ERL1 to regulate stomatal patterning [147] (Figure S4). Other multifunctional LRR-RLK genes are SERK1 and SERK2, which interact with EXCESS MICROSPOROCYTES 1 (EMS1) for anther development [135]; with PXY to regulate procambial cell proliferation [23,148]; with ER or ERL1 to regulate stomatal patterning; and with FLS2 and EFR, BRI1 and BAK1 for other functions (Figure S5).

Some multifunctional LRR-RLKs, such as BAK1, SERK 1, SERK2, SERK4, SARK, NIK1, and NIK3, were classified as co-receptors based on the length of the extracellular domain (ECD) [22], which are able to interact with other LRR-RLKs, and they are grouped as the LRR (II) family. Some of the examples of members belonging to a particular family are as follows: LRR (II)—SERK 4, NIK1, NIK3, SARK, and SERK5; LRR(III)—RPK1, RLK902, PRK1, PRK2A, PRK4, PRK5, PRK6, MRLK; LRR(VII)—HYDROGEN PEROXIDASE-RESISTANT 1 (GHR1); LRR(IX)—BIR1; and LRR(V)—SRF1, SRF2, SRF3, SRF5, SRF6, SRF7, and SRF8 (STRUBBELIG-RECEPTOR FAMILY 1–3, 5–8). Other LRR-RLKs such as SOBIR1, FEI1, EFR, FLS2, BRI1, CLV1, ERL1, ERL2, ER, HSL2, PXY, BAM1, BAM2, PEPR1, GSO1 (GASSHO1), PSKR1, EMS1, RPK2, BRL1, BRL2, BRL3, PSY1R (PHYTOSULFOKINE RECEPTOR), and IOS1 (IMPAIRED OOMYCETE SUSCEPTIBILITY1) (Table 2 and Table S4), which are classified as ligand-perceiving receptors with long ECD and are grouped as LRR (I), LRR

(X), LRR (XI), and (LRR XII) [22]. Mainly, these co-receptors potentially bind with ligand-perceiving receptor groups for the activation and stabilization of complexes that sense signals [8,13,16,22,28]. They also enhance signaling through sequential reciprocal receptor transphosphorylation [149]. Different combinations of interactions among co-receptors with different ligand-binding LRR-RLKs allows for the substitution of each other. This creates difficulties in using a single mutant line for LRR-RLK gene studies. For example, SERK1, SERK2, and BAK1 share the same players, like EFR and FLS2, although BAK1 is preferred by FLS2 among other SERKs, whereas EFR does not show preference to BAK1 [16]. Yet, SERK1 and SERK2 could easily substitute each other for activation of a similar plant response [16]. This regulation of stability of complexes is less studied, with only a few reported cases. For example, BAK1 interacts with BIR1 or BIR2 to prevent heterodimerization of the BAK1-FLS2 complex, and thereby inhibits an immune system response [14,30]. Furthermore, BRI1 and SERK3 do not ubiquitously interact, they only show interaction in the endosomes and in restricted areas on the plasma membrane. In these sites, BAK1 is shown as a redistributor of BRI1 receptors [15]. Thus, most LRR-RLKs form complexes, and some of the LRR-RLK in the complexes play key roles in the complex, such as BAK1 [16,28], and some components in the complexes are able to substitute for each other.

Additionally, the ATTED database showed different interactions among the proteins based on various experiments and data (Table 2). The analysis of these interactions confirmed the known interactions of BAK1, SERK 1, SERK 2, SERK 4, NIK1, NIK3, and SARK (Figures S4–S7), but also the additional potential heterodimerizations for these co-receptors (Table 2). The less investigated co-receptors, like NIK1 and SARK, according to this database, have a potential for binding with BAK1. Importantly, the CIKs, such as NIK1, NIK3, and SARK, were shown in the stress response and in natural senescence [4,22], but their co-receptors' (heterodimers or homodimer) involvement in senescence or the stress response was not shown (Table 2). It will be exciting in the future to reveal the additional functions of these CIKs and to show the new interactions of the collected LRR-RLKs mentioned in Table S4. The interactions among the LRR-RLKs in other plants are less studied, and only a few were confirmed in tomato and tobacco [75,150], rice [77], *M. truncatula* [151], and wheat [92] (Table S4), and that was mainly done by using the yeast two-hybrid assays, co-immunoprecipitation, and BiFC methods. Altogether, the study of new interactions of LRR-RLKs in *A. thaliana* and other plants and the generation of new double or triple mutants could help in functional and interactional analyses of LRR-RLKs.

Table 2. Experimentally proven and potential interactions of stress-related LRR-RLKs with LRR-RLK co-receptors from LRR II. Data taken from different well-studied research manuscripts and from ATTED database. The formation of heterodimers between the LRR-RLKs were labeled as “heterodimer” inside of box cross between two LRR-RLKs one from column and second from row. Below the heterodimer formation were shown the method/s of identifications heterodimer formation such as CoIP—coimmunoprecipitation; BiFC—bimolecular fluorescence complementation, gel filtration, pull-down, in vivo, genetically (by mutants analysis), kinase assay, co-sedimentation in solution, solid-phase assay. NA indicates not available data reported the formation of heterodimer/s. Grey colored box indicates that information taken from ATTED database about interaction was confirmed experimentally (published data), and white zone was not confirmed experimentally.

LRR-RLK	SERK2	SERK1	SERK4/BKK1	SERK3/BAK1	SARK/Cik3	NIK1	NIK3/Cik1	References
co-receptors (LRR-RLKs from LRR II family accordingly classification of [22])								
BIR1	heterodimer (BiFC)	heterodimer (BiFC)	heterodimer (BiFC)	heterodimer (genetically, in vivo, pull-down)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[14,152]
FLS2	NA	heterodimer (in vivo)	heterodimer (in vivo)	heterodimer (in vivo, CoIP, gel filtration)	NA	heterodimer (in vitro, pull down)	NA	[16,153,154]
ERL1	heterodimer (CoIP)	heterodimer (CoIP)	heterodimer (CoIP)	heterodimer (in vivo, CoIP)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[147,152,153]
BRI1	NA	heterodimer (genetically, in vivo)	heterodimer (in vivo)	heterodimer (genetically, in vivo, in vitro)	NA	NA	NA	[146,149,155]
EFR	NA	heterodimer (in vivo)	heterodimer	heterodimer (genetically, CoIP, in vivo)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[16,152,156]
ER	heterodimer (genetically, CoIP)	heterodimer (genetically, CoIP)	heterodimer (solid-phase assay)	heterodimer (genetically, pull-down, in vivo)	heterodimer (solid phase assay)	heterodimer (solid-phase assay)	NA	[29,147,152,153]
PXY	heterodimer (genetically, in vivo, in vitro)	heterodimer (genetically, in vivo, in vitro)	NA	heterodimer (genetically, in vivo, in vitro)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	[23,153]
co-receptors (LRR-RLKs from LRR II family accordingly classification of [22])								
HSL2	heterodimer (CoIP)	heterodimer (CoIP)	NA	heterodimer (CoIP)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[152,157]
BAK1	heterodimer (genetically, CoIP)	heterodimer (BiFC, CoIP)	heterodimer (genetically)	NA	heterodimer (solid-phase assay)	heterodimer (genetically, in vivo, in vitro)	heterodimer (solid-phase assay)	[127,130–132]
SERK1	heterodimer (genetically, in vivo)	homodimer (genetically, in vivo)	heterodimer (solid-phase assay)	heterodimer (BiFC, CoIP)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[152,153,155,158]
SERK2	homodimer (genetically, in vivo)	heterodimer (genetically, in vivo)	NA	NA	NA	NA	heterodimer (solid-phase assay)	[152,158]
EMS1	heterodimer (genetically, kinase assay, BiFC)	heterodimer (genetically, kinase assay, BiFC)	NA	NA	NA	NA	NA	[135]

Table 2. Cont.

LRR-RLK	SERK2	SERK1	SERK4/BKK1	SERK3/BAK1	SARK/Cik3	NIK1	NIK3/Cik1	References
SERK4	heterodimer (genetically, CoIP)	heterodimer (solid-phase assay)	NA	heterodimer (genetically)	Heterodimer (solid-phase assay)	Heterodimer (solid-phase assay)	NA	[16,152]
NIK1	NA	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	Heterodimer (genetically, in vivo, in vitro)	Heterodimer (solid-phase assay)	NA	NA	[152–154]
PSKR1	heterodimer (solid-phase assay, co-sedimentation in solution)	heterodimer(molecular sieving)	NA	heterodimer (genetically, CoIP, gel filtration)	heterodimer (solid-phase assay)	NA	NA	[143,153]
co-receptors (LRR-RLKs from LRR II family accordingly classification of [22])								
SOBIR1	heterodimer (solid-phase assay)	NA	NA	heterodimer (genetically, CoIP)	NA	NA	NA	[30,153]
RPK1	NA	NA	NA	heterodimer (genetically, pull-down, kinase assay)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[109,152]
PEPR 1	NA	NA	NA	heterodimer (pull-down, gel filtration)	NA	NA	heterodimer (solid-phase assay)	[153,159]
ERL2	NA	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	heterodimer (genetically)	heterodimer (solid-phase assay)	heterodimer (solid-phase assay)	NA	[29,152]
RPK2	NA	NA	NA	NA	heterodimer (in vivo, pull-down)	heterodimer (solid-phase assay)	heterodimer (genetically)	[129,153]
CLV1	NA	NA	NA	NA	heterodimer (in vivo, pull-down)	NA	heterodimer (genetically)	[129]
BAM1	heterodimer (solid-phase assay)	NA	NA	NA	heterodimer (pull-down)	heterodimer (solid-phase assay)	heterodimer (genetically, BiFC, CoIP)	[33,153]
BAM2	NA	NA	NA	NA	heterodimer (pull-down)	heterodimer (solid-phase assay)	heterodimer (genetically, BiFC, CoIP)	[33,153]

5. Conclusions

Plants must evolve to adapt and tolerate harsh environments. The perception of biotic and abiotic stimuli is crucial for the survival of plants. Among the large numbers of receptors, the LRR-RLK are not only involved in different development biological processes but also in stress response processes. The rapid development of genome and RNA sequence analyses have allowed for the identification of the many LRR-RLKs genes in different monocot and dicot plants. As compared to *A. thaliana*, not much is known about the functions of LRR-RLKs in other plants such as tomato, tobacco, wheat, rice, *H. vulgare*, *B. distachyon*, etc. Additionally, stress-related LRR-RLKs in *A. thaliana* are mainly shown to play a role in biotic stresses, and to some extent in abiotic stresses. For the functional study of LRR-RLKs, a single mutant is of little use to capture all their functions, and, as LRR-RLKs can be substituted by other members, they do not have non-specific ligand binding and they have the ability to make different protein complexes (di-, tri-, or tetramer). The double, triple, and quadruple mutant generation for LRR-RLKs in *A. thaliana* and/or crop plants is a powerful tool for identifying the function role of LRR-RLKs.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/plants11192660/s1>, Figure S1: Microarray analysis of the biotic and abiotic stress related LRR-RLK genes transcripts in response to biotic and abiotic stresses in WT (Col ecotype). Figure S2: Microarray analysis of the biotic stress related LRR-RLK genes transcripts in response to biotic and abiotic stresses in WT (Col ecotype). Figure S3: Microarray analysis of the abiotic stress related LRR-RLK genes transcripts in response to biotic and abiotic stresses in WT (Col ecotype). Figure S4: Protein interactions of BAK1/SERK3 with other LRR-RLK with experimental proved functional role. Figure S5: Protein interactions of SERK1 and SERK4 with other LRR-RLK with experimental proved functional role. Figure S6: Protein interactions of SERK2 with other LRR-RLK with experimental proved functional role. Figure S7: Protein interactions of CIK's (NIK1, NIK3 and SARK) with other LRR-RLK with experimental proved functional role. Table S1. Phenotypes of single mutants of LRR-RLK genes in *A. thaliana* tested under different biotic and abiotic stresses. Table S2. Orthologous of stress related LRR-RLKs genes in *A. thaliana*, *O. sativa*, *G. max*, *M. truncatula*, *Populus*, *V. vinifera*, *S. lycopersicum*, *B. napus*, *Z. mays*. Table S3. Genetic tools in different crop plants in investigation of stress-related LRR-RLKs. Table S4. Potential interactions of stress-related LRR-RLKs (from LRR II family) with other LRR-RLKs. References [160–181] are cited in the supplementary materials.

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