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Review Article

How *Arabidopsis* Receptor-Like Kinase 7 (RLK7) Manifests: Delineating Its Structure and Function

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Like animals, plants customarily utilize cell surface-localized receptors to keep track of environmental stimuli, specifically by plasma membrane-associated receptor-like kinases (RLKs). In comparison to other organisms, plants own a variety of RLKs, which insinuates that ligand-receptor-facilitated molecular mechanisms regulate an array of processes during plant development. Here, we take up *Arabidopsis* receptor-like kinase 7 (RLK7), which shares the archetypal structure of transmembrane receptor kinases accompanied by a receptor-like ectodomain comprising of leucine-rich repeats (LRRs) along with a functional intracellular kinase domain. Interestingly, this distinctive receptor-like kinase not only orchestrates crucial steps during plant development, including the regulation of seed longevity, dormancy, and seed germination speed, but also plays a role in oxidative stress tolerance, salt stress tolerance, and pattern-triggered immunity. This review deciphers the sequence and structure and evaluates existing knowledge of the function and expression pattern of RLK7.

1. Introduction

Receptor-like kinases (RLKs) are an indispensable part of communication between cells [1–4] and intercellular signal transduction [5, 6]. They can operate as hetero or homodimers [7], adding to their regulatory potential, sensing, and signaling, suggesting that plants can distinguish a vast range of signals [8]. The maiden RLK in plants was spotted in *Zea mays* [9]. Subsequently, RLKs and their functions have been discerned and characterized in *Arabidopsis thaliana* and other plant species [10]. The development of the *Arabidopsis* genome sequence unveiled an exceptionally vast disposition of RLK genes [11]. The RLKs form one of the most abundant protein families [5] and account for roughly 60% of the complete kinase superfamily in *Arabidopsis* [10]. One of the probable reasons for plants to own such an enormous number of RLKs is that plants confront a raft of environmental stresses [12], fluctuating atmospheric changes, and different pathogens in soil [13]. Plants must cope incessantly with their living conditions to survive. Because of their vast numbers and their varied functions, including the roles in the development [14], pathogen resistance [15], stress [16], and hormone perception [12, 17], RLKs have turned out to be a fundamental interest among researchers.

RLKs structure can be defined by the presence of a signal peptide, one extracellular domain, a single-pass transmembrane domain, and one kinase domain accompanied by the serine/threonine consensus sequence [18, 19]. They contrast considerably in their sequence identity and domain organization among the extracellular domains. In RLK, a broad range of extracellular domains exist, and they have been categorized into 15 groups [20]. Among all RLKs, LRR-RLKs (leucine-rich repeat receptor-like kinase) are the most meticulously analyzed subfamilies [21, 22]. It was corroborated that LRR-RLKs have a paramount role to play in diverse plant signal transduction pathways throughout growth and development [23].

In *A. thaliana*, LRR-RLKs symbolize the colossal class of RLK with more than 218 LRR-RLKs members, and they have been divided into 13 subfamilies (LRR I–XIII) and grouped

as per domain organization [24]. Additionally, RLK can also be categorized based on conserved residues in the kinase domain [25]. The *Arabidopsis thaliana* genome possesses 28 types of XI LRR-RLKs genes [26], among which six are triggered off by pathogen invasion: PEPR1, PEPR2, At5g25930, SOBIR1, RLK5 (HAESA), and RLK7 [27, 28]. The RLK7 recognizes that PIPs, peptides secreted by *Arabidopsis*, can mediate innate immunity in plants against both bacteria and fungi [29]. RLK7 is also associated with the control of germination speed, salt stress tolerance, and stomatal closure [30, 31]. Other similar well-characterized LRR-RLKs are FLS2, BRI1, and Xa21, which recognize flg22, brassinolide, and RaxX21-sY, respectively [32–36]. Though RLK7 shows various functionalities from development to immunity, very little research has been conducted on this receptor protein.

This review provides an updated and comprehensive analysis of the structure and function of RLK7. Here, we elucidate the recent advancements that correspond to RLK7 in *Arabidopsis* and discuss future research directions in this field.

2. Structural Elucidation of RLK7

RLK7 (UniProt entry: F4I2N7) [37] contains one signal peptide, 20 leucine-rich repeats (LRR) domains, a single transmembrane domain, a potential juxtamembrane domain, and one cytoplasmic kinase domain in its structure (Figures 1 and 2) [38].

The extracellular LRR domain of RLK7 is distinguished by the consensus sequence LxxLxLxxNxLxx (Figure 2), which matches well with other RLK-LRR consensus sequences found in *Arabidopsis* [20]. With our previously developed multiple-template modeling approach, namely, HHpred [39, 40], the top five templates (4Z5W_A, 5IXO_A, 4MNA_A, 4LXR_A, and 5JFK_A) were selected and then used to predict the 3D structure of RLK7 ectodomain (Figure 3).

Our predicted structure showed that the LRR domains form an extremely ordered solenoid "horseshoe-like" arrangement, along with a structural backbone comprised of an α-helix and connecting residues on the outer convex part of the horseshoe structure and a β-strand/β-turn (Figure 3) with the LxxLxLxxN sequence on the internal concave portion. However, the solvent-exposed residues, x, are assumed to be associated with ligand binding. The predicted 3D structure of RLK7 is similar to other similar RLKs available [40–45].

Moreover, in RLK7, the extracellular domains of LRR receptors hold cysteine residues that are salient to the protein structure [46], since these can develop disulfide bridges, which are imperative for the stability and folding, resistance to proteolytic degradation, and tertiary structure of fully fledged proteins. Cysteines can often pair up, and two such pairs generally flank the LRRs [26, 43].

Characteristically, in RLK, the amino (N-) terminal paired cysteines emerge immediately before the first LRR, and the carboxy (C-) terminal pair appears precisely after the last LRR [26, 47, 48]. Surprisingly, a conserved motif (CxWxGVt/sC), which is exclusive to plants, appears in the N-terminal pair of cysteines of most of the LRR subfamilies (II, III, VI, IX–XIII) as well as in some unclassified LRR-RLKs, where the C-terminal cysteine pair is much less conserved [7, 26]. The first and second pairs of cysteines of RLK7 are ^{61}CSFIGVTC^{68} (N-terminal) and ^{587}CSTTIKSFNRC^{597} (C-terminal), respectively (Figures 1 and 2).

Though not confirmed, a juxtamembrane domain may reside between the transmembrane and kinase domains (Figure 2) and may play a significant role in RLK7 kinase regulation. This juxtamembrane is also present in other RLKs [40, 49]. There is a lack of research discussing the structure of the transmembrane domain and the signal peptide of RLKs. Both are presumed to be essential for the proper localization of the plasma membrane. The transmembrane domain's presence has been suggested to be crucial for the structural stability of the ectodomain, thus facilitating interaction with the ligand [50]. The 3D structure of juxtamembrane, transmembrane, and kinase domains of RLK7 was not modeled in this study due to its complexity of modeling.

3. Functional Characterization of RLK7

3.1. Controlling Seed Development and Maturation. In wild-type seeds, RLK7 takes part in promoting germination as well as decreasing dormancy. The question remains about which phase of development is controlled by RLK7. A slowdown or setback in the germination rate may be the phenotypic effect of the control defect of several factors in seed maturation. In *Arabidopsis thaliana*, it has been observed that initially, during seed development, dormancy is initiated and that it is achieved via two consecutive processes. First, embryo growth ceases, which is constrained by the transcription factors FUS3 and LEC1, and second, embryo dormancy under the control of ABA (abscisic acid) and ABI3 [51]. Another ABA-dependent growth arrest is executed at germination by ABI5 (abscisic acid-insensitive 5) [52]. RLK7 might be involved in these two crucial stages of seed growth and maturity.

3.1.1. Promoting Germination. During embryogenesis, the *GUS* (β-glucuronidase) expression is driven by the *RLK7* promoter in the micropylar zone of ovules and developing seeds till the late heart phase [38]. A previous study showed that at germination, the micropyle is the location of radicle emergence, and the micropylar endosperm is a germination constraint [53]. In *A. thaliana*, it has been found that the endosperm regulates seed germination and *ABI5* expression, which is an indisputable agent of this control and acts as a micropylar endosperm marker [52, 54]. Furthermore, radicle protrusion is also constrained by the seed coat, and almost all seed coat mutants of *Arabidopsis* have shown decreased seed dormancy [55]. Thus, in the surrounding tissues of the embryo, the RLK7 receptor may be responsible for the initial forming of radicle protrusion, and therefore, its unavailability could inhibit germination [38].

3.1.2. Decreasing Dormancy. The precocity phenotype of the overexpressors of RLK7 (RLK7 Δ kin and RLK7Δ LRR lines)

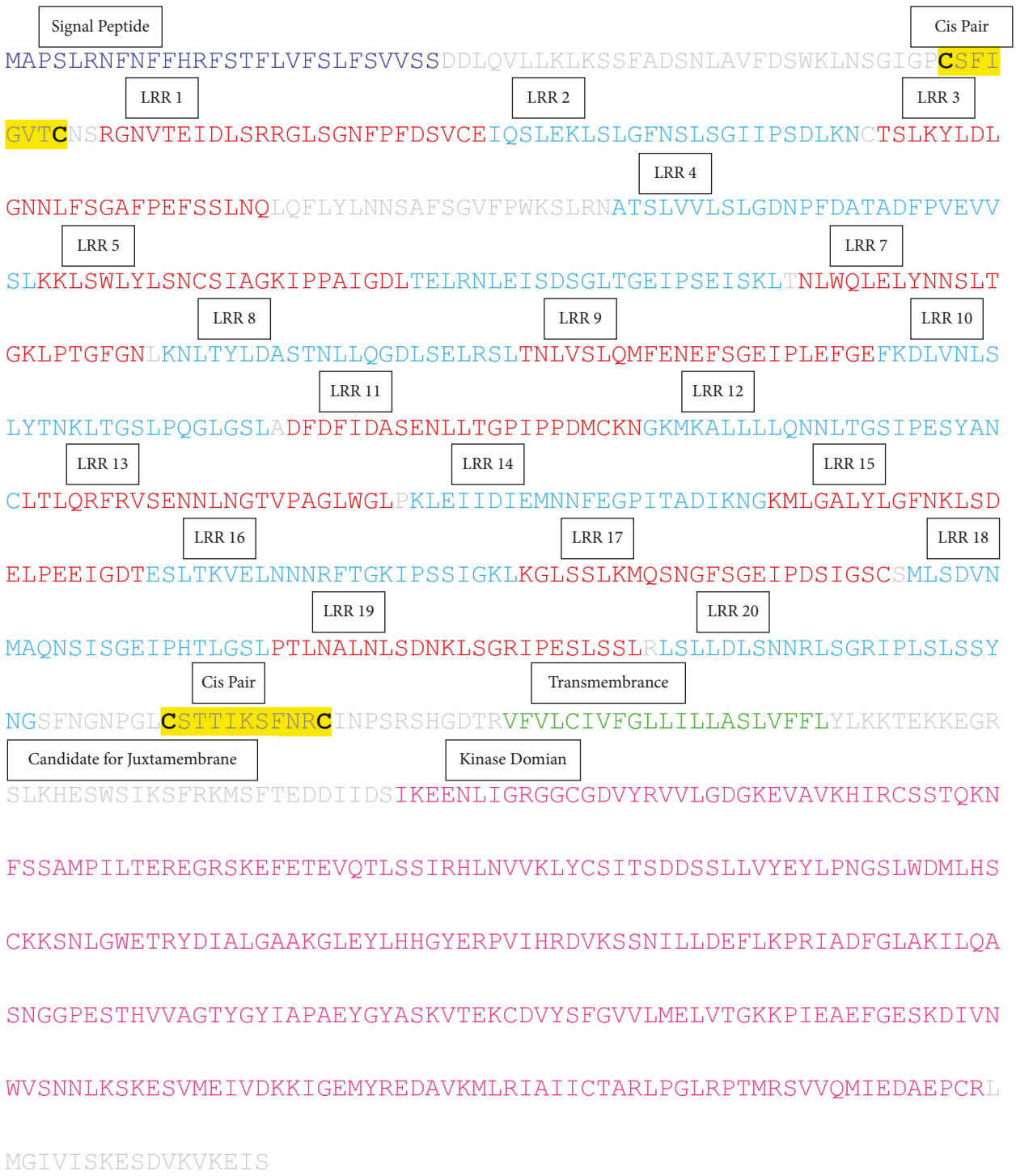

Figure 1: The amino acid sequence of RLK7. RLK7 carries a signal peptide, followed by an ectodomain composed of twenty LRRs, a transmembrane domain, a candidate for a juxtamembrane domain, and a kinase domain. The signal peptide is colored in blue, and the other twenty LRRs are colored in red and cyan alternatively. The transmembrane and kinase domains are colored in green and pink, respectively. The cysteine pairs that flanked the LRR domain are highlighted in yellow.

and the germination delay phenotype of the *rlk7* mutants were observed in the previous study [38]. In that study, for the expression pattern of *RLK7*, the transcript accumulation tends to increase at the desiccation phase to reach a peak in desiccated seeds, declining quickly at the time of imbibition [38], and thus leads to a conclusion that RLK7 may be involved in the dormancy-to-germination transition. The *RLK7* promoter is functional all over the embryo in dry and mature seeds [38]. It is assumed that in the initial phases of germination, proteins and mRNAs deposited in the desiccated seed can offer essential RNA species for the protein synthesis [56, 57]. Previous studies showed the resemblance

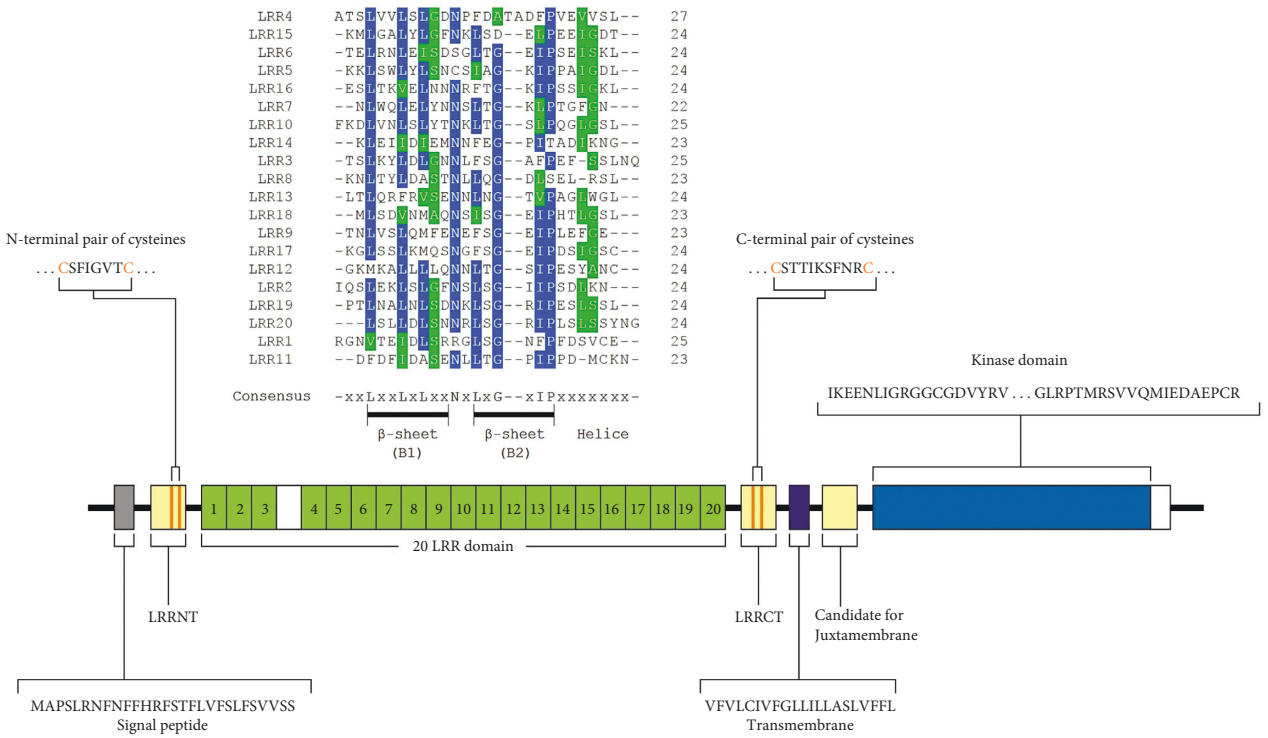

Figure 2: RLK7 functional domain. RLK7 carries a signal peptide, an ectodomain composed of twenty LRRs flanked by an amino (N) terminal cysteine pair and a carboxy (C) terminal cysteine pair, a single transmembrane domain followed by a potential juxtamembrane domain candidate, and a kinase domain. The cysteine pairs are colored in orange. LRRNT and LRRCT are the LRR N-terminal domain and LRR C-terminal domain, respectively. The alignment of the twenty LRR domains is shown above. The gaps represent the spaces introduced for better alignment. The identical and similar amino acids are boxed in blue and green, respectively.

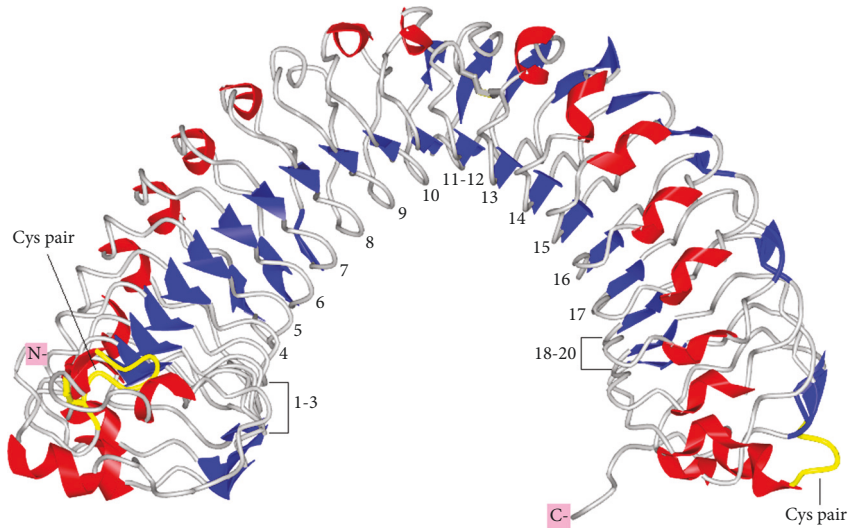

Figure 3: The 3D structure of RLK7 extracellular domain. The model was generated using a multiple-template modeling approach (HHpred) [39]. The β-sheets are shown in blue, α-helices in red, and cysteine pairs in yellow. The LRRs are numbered/marked with the numbers from 1 to 20. "N" and "C" denote the amino and carboxy terminus, respectively.

in the expression kinetics of *RLK7* and *ABI5* in imbibed and developing seeds [38]. It has been observed that during the initial phases of germination, to track the water condition of the environment, the ABI5 protein exerts its activity by arbitrating a growth inhibition [52]. RLK7 may correspondingly take part in the regulation of the initial germination events. Alternately, RLK7 may be active in the desiccated seed embryo field during the after-ripening process [38].

3.2. Tolerating Oxidative Stress and Maintaining Seed Longevity. In *Arabidopsis* biology, another feature of the

role of RLK7 is its association with tolerance to oxidative stress. Hydrogen peroxide (H_2O_2) is known to induce oxidative stress. The *rlk7* mutants displayed improved sensitivity to H_2O_2 treatment. The *rlk7* mutants tend to accumulate a smaller quantity of some enzymes (vacuolar $H+$-ATPase (subunit-E), ribulose-bisphosphate carboxylase, glutathione S-transferase F6, glutathione S-transferase F8, manganese superoxide dismutase, and chlorophyll a/b-binding), which are indirectly or directly associated with reactive oxygen species detoxification, in comparison to the wild-type control [38, 58].

To evaluate the physiological effect of the deficiency in proteins in *rlk7* mutants, in the presence of H_2O_2, seedlings were grown in vitro, and findings revealed that all were less resistant towards this treatment, certainly indicating noticeable phenotypes varying from chlorosis of the cotyledons to delayed growth [38]. Such results suggest that, for typical tolerance to oxidative stress, RLK7 is mandatory. Moreover, *rlk7* mutants demonstrated a decreased germination potential compared to their corresponding wild types, with some severities, which affirm that the unavailability of RLK7 affects the seed longevity [38].

3.3. Role in PTI (Pattern-Triggered Immunity) Amplification. Three PAMP-induced secreted peptides, PIP1, PIP2, and PIP3, derived from the processing of the representative prePIP (precursors of PAMP-induced peptides) family members prePIP1, prePIP2, and prePIP3 can enable immunologic responses in *A. thaliana* as well as promote resistance toward *Fusarium oxysporum* and *Pseudomonas syringae* [29, 30, 59]. The biochemical and genetic analyses demonstrated that RLK7 operates as a receptor of PIP1. A reverse genetics screen detected RLK7 accountable for PIP1 and PIP2-induced responses [29]. The prePIP1 expression pattern clarifies that the RLK7-PIP1 mediated resistance is more distinctive to pathogens proliferating in the vascular tissue or infecting via the hydathodes. RLK7 is necessary for PIP1 and PIP2-driven immune activation, and PIP1-RLK7 has a significant role in PTI (pattern-triggered immunity) amplification [29, 60].

In PTI immune activation, the receptor kinase BAK1 (brassinosteroid-associated kinase 1) contributes to forming heteromeric complexes with many LRR-RLK receptors [27, 61, 62]. Previous research revealed that both the PIP1-induced root growth inhibition and ROS (reactive oxygen species) production were limited in *bak1* mutant plants (T-DNA insertion mutants) compared to wild-type plants, which denote PIP1-RLK7 signaling is reliant on BAK1 to some extent. The PIP1 initiates overlapping and distinctive immune signaling responses when perceived by RLK7 [29]. Furthermore, a recent study showed that BAK1 might act as a critical player in the PIP1-RLK7 signaling [31].

An LRR-RLK from subfamily XII, FLS2 (flagellin-sensitive 2), attaches to flg22, the functional epitope of Gram-negative bacterial flagellin [44]. Previously, an additive impact in the buildup of host resistance toward *Pseudomonas syringae* DC3000 was noticed in plants pretreated concomitantly with PIP1 and flg22, in contrast to every individual peptide elicitor. Moreover, activation of two genes *PR1* and *WRKY33*, consecutively representing late and early response immune reporters, by flg22 was decreased in *rlk7* mutant plants in comparison to wild-type plants, as well as the degree of flg22-triggered host resistance toward *P. syringae* DC3118 (a coronatine deficient *P. syringae* DC3000 mutant) was much less pronounced in the mutant *rlk7* [29]. These indicate that PIP1 signals via RLK7 play a vital role in increasing FLS2-initiated immunity.

PIP1 (often collectively with PEP1) enhances the immunological response induced by flg22. Both peptides, PIP1 and PIP2, trigger identical immunological responses like flg22 (and also like PEP1), which include ROS production, expression of marker genes, MAPK (mitogen-activated protein kinases) activation, and callose deposition. Not to mention, flg22-triggered immunity seems to have been impaired in the *rlk7* mutants [29]. All these lead to the conclusion that PIP1-RLK7 may increase PAMP signaling.

Besides exchanging gas and water, the plant stomata play a crucial role in different abiotic and biotic stress fields [63]. RLK7 in complex with the PIP1 interacts with salicylic acid to control the stomatal immunity to protect itself from bacteria [29, 60]. An S-type anion channel SLAC1 is activated during this process, and BAK1 may play a vital role in this process [31]. During this process, RLK7 may share OST1, a downstream component to increase ROS production, activate Ca^{2+}, and activate the SLAC1 channel to close stomata.The mitogen-activated protein kinase MPK3/MPK6 is actively involved [31] (Figure 4). In a recent study, a close phylogeny of RLK7, AT5G25930, which is a cognate receptor "kinase plant screw unresponsive receptor" (nut), was found to be induced after pathogen exposure and dehydration, and it interacts with the secreted peptides "small phytocytokines regulating defense and water loss"(-SCREWs) to control the stomata opening in *Arabidopsis* [64]. On the other hand, RLK7, in the presence of *Fusarium graminearum*, upon chitin perception, interacts with APEX and promotes the immune signaling [59].

RLK7 also regulates lateral root initiation by interacting with PIP2 in *Arabidopsis*. TOLS2, another peptide, can interact with RLK7 in the same manner to mediate the same signaling. After interacting with RLK7, these peptides trigger MPK3/MPK6 phosphorylation [65].

A recent study showed that RLK7 interacts with PIP3 to module salt tolerance in *Arabidopsis*. RLK7 physically interacts with PIP3 and makes a complex with PIP3 in the presence of salt and activates MPK3/MPK6 for signal amplification, thus mediating the salt tolerance [30]. The presence of salt significantly enhanced RLK7-PIP3 interaction, induced RLK7 phosphorylation, and enhanced salt tolerance in *Arabidopsis* (Figure 4) [30].

3.4. Negatively Regulating the Formation of Lateral Root Founder Cells. Lateral organs in plants, including lateral roots (LRs), flowers, and leaves, emerge from founder cells, a group of plant cells that contributes to the development of organs [66, 67]. The founder cells' location in the shoot and root apices influences the structure of the lateral organs.

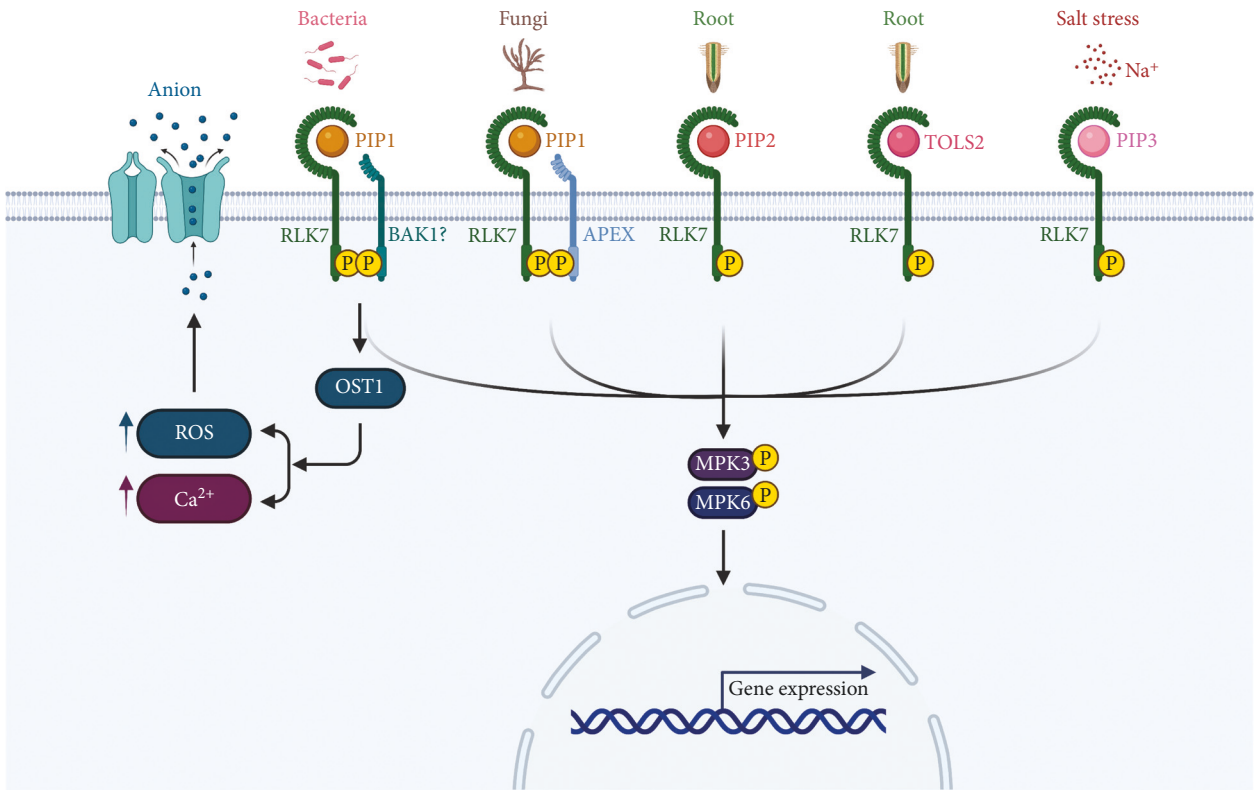

Figure 4: Interaction of RLK7 with peptides. Upon sensing bacteria, RLK7 interacts with PIP1 and triggers a downstream signal. While BAK1 may interact with the PIP1-RLK7 complex, both are phosphorylated, OSTI increases ROS production, and Ca^{2+} ion carriers activate the SLAC1 channel and close the stomata. RLK7-PIP1 may also interact with APEX upon detection of fungal chitin. Moreover, RLK7 can also interact with either PIP2 or TOLS2 to control lateral root initiation. Furthermore, RLK7 interacts with PIP3 and induces salt tolerance in the presence of salt. MPK3/MPK6 is phosphorylated to initiate the respective gene expressions in all cases.

Auxin, an indole acetic acid (IAA) responsible for plant growth, promotes the founder cells [68–70]. While RLK7 is expressed in the LR initiation zone, it is restrained transcriptionally and posttranscriptionally when auxins specify LR founder cells. The RLK7 mutation appears to increase the concentration of LR founder cells [71], indicating that RLK7 negatively controls the number of LR founder cells.

RLK7 is also associated with LR spacing. In the xylem precursor cells of the oscillation zone, DR5, a synthetic auxin-responsive promoter, is temporarily activated and reactivated in the xylem pole pericycle cells, which eventually become LR [72, 73]. To secure the desired spacing of LR, RLK7 contributes by inhibiting the congestion of DR5 sites [71].

4. Expression Pattern of RLK7

At the differentiation region, the expression of RLK7 usually initiates and then consistently spreads to the shoot in the pericycle, endodermis, and cortex. It is less expressed in the lateral root primordia than in the flanking pericycle cells but not in the root meristem and oscillation region [71, 74].

RLK7 expression is observed at the micropylar zone of ovules and developing seeds until the late heart phase and in the embryo from the heart phase to desiccated seeds. Nevertheless, the expression is not seed-specific. The histochemical analysis of in situ hybridization and GUS (β-glucuronidase) activity displayed the face of RLK7 at every transition or junction between the organs: the insertion regions of sepals, petals, and stamens, along with the floral pedicel/stem, silique/pedicel, and cauline leaves/flowery stem transitions [38, 74].

5. Conclusion

In plants, because of the functional redundancy between the receptors, deciphering the function of the receptor-like kinase is sophisticated. Although *A. thaliana* alone has more than 218 LRR-RLKs, just a handful have been involved in plant functions, and RLK7 is one of them. Evaluating the phenotypic characteristics triggered by the mutation of a specific gene with inserted elements, such as T-DNA insertion, often clarifies the exact role the RLK7 plays.

The main objective of this study was to gain insight into the structure of RLK7 and the mechanisms associated with its response to different environmental stimuli. In this study, we reviewed the recent research on the role of RLK7 in regulating seed development and maturation, maintaining seed longevity, and its response to oxidative stress. It is also somewhat responsible for PIP-induced immune activation and the arrangement and density of lateral root founder cells.

Despite considerable progress in our understanding of the structure and function of RLK7, much remains to be

investigated regarding how the RLK7 extracellular domain interacts with its ligand and how RLK7 forms a heteromeric complex with the coreceptor. With structure-guided functional analysis, structures of the extracellular domain and kinase domains in bound and free forms will provide more crucial insights into how RLK7 dictates its subcellular localization, activation process, and signal translation.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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