



Pepper G-type Lectin Receptor-like Kinase, CaRLK1, Modulates ABA-Mediated Stomatal Closure and Drought Tolerance

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Lectin receptor-like kinases (LecRLKs) are plant-specific kinases that play critical roles in stress signaling. G-type LecRLKs, which possess an α -mannose-binding bulb lectin domain, are implicated in diverse stress responses; however, their roles in drought responses in pepper plants remain poorly understood. Therefore, this study aims to identify and functionally characterize a pepper G-type LecRLK, CaRLK1. *CaRLK1* expression was significantly induced by multiple abiotic stresses, particularly dehydration. Additionally, functional analysis using virus-induced gene silencing revealed that *CaRLK1*-silenced pepper plants showed reduced drought tolerance and increased leaf water loss, associated with impaired stomatal closure and attenuated leaf temperature increases following abscisic acid (ABA) treatment. Moreover, *CaRLK1* silencing reduced the expression of several drought-responsive genes, including

CaOSR1, *CaDREBLP1*, and *CaLOX1*, under dehydration conditions. Collectively, these findings suggest that CaRLK1 functions as a positive regulator of drought stress responses in pepper plants by modulating ABA-dependent stomatal aperture dynamics and drought-responsive gene expression.

Keywords : abscisic acid, drought, lectin receptor-like kinase

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Receptors play a crucial role in plant stress responses by perceiving and transmitting external signals that activate physiological pathways enabling environmental adaptation (Soltabayeva et al., 2022). Receptor-like kinases (RLKs) constitute a large protein family that mediates plant stress responses and hormone signaling (Zhu et al., 2023). RLKs are classified based on their extracellular domains (Shiu and Blecker, 2001). Lectin receptor-like kinases (LecRLKs) are plant-specific proteins that contain an extracellular lectin domain capable of binding carbohydrates (Liu et al., 2023; Navarro-Gochicoa et al., 2003; Sun et al., 2020; Vaid et al., 2013). LecRLKs consist of an extracellular lectin domain, a transmembrane region, and kinase domains (Navarro-Gochicoa et al., 2003). Based on their lectin domains, LecRLKs are classified into three groups: L-type, G-type, and C-type (Vaid et al., 2012). L-type LecRLKs contain a legume-like lectin domain; G-type LecRLKs possess an α -mannose-binding bulb lectin domain; and C-type LecRLKs have a calcium-dependent lectin domain (Sun et al., 2020). Previous studies show that several G-type LecRLKs are involved in abiotic stress responses. For example, the G-type LecRLK GsSRK enhances salt tolerance in *Glycine soja* (Sun et al., 2013), while PWL1, a G-type LecRLK in *Oryza sativa*, positively regulates heat

stress (Xu et al., 2023). However, the role of G-type LecRLKs in drought stress remains poorly understood.

Abscisic acid (ABA) is a plant hormone that regulates drought responses primarily by inducing stomatal closure to reduce transpirational water loss (Abhilasha and Roy Choudhury, 2021; Hussain et al., 2018). ABA signaling comprises three main components: pyrabactin resistance 1 (PYR1)/PYR1-like (PYL)/regulatory components of ABA receptors (RCAR), sucrose non-fermenting 1-related protein kinase 2 (SnRK2s), and clade A type 2C protein phosphatases (PP2Cs) (Ma et al., 2009; Umezawa et al., 2010). PYR/PYL/RCAR receptors perceive ABA and form complexes with PP2Cs, leading to SnRK2 activation and subsequent phosphorylation of downstream drought-responsive targets, including transcription factors and ion channels (Fujii et al., 2007; Nakashima et al., 2009).

Therefore, this study aimed to identify and functionally characterize the pepper G-type LecRLK, *CaRLK1*, and to investigate its role in drought tolerance, with particular emphasis on ABA-dependent stomatal regulation and drought-responsive gene expression.

Results and Discussion

Isolation and molecular characterization of *CaRLK1*.

Previous studies show that G-type LecRLKs play important roles in water-deficit stress (Karlik, 2023; Sun et al., 2020; Wang et al., 2024). However, the identification and functional characterization of pepper G-type LecRLKs have not been reported. Thus, this study aims to identify pepper G-type LecRLKs involved in water-deficit stress responses. We identified a pepper G-type LecRLK, designated *CaRLK1* (*Capsicum annuum* G-type lectin receptor-like protein kinase 1), and first characterized its expression before functional analysis.

To determine whether water-deficit stress regulates *CaRLK1* expression, reverse transcription-quantitative polymerase chain reaction (RT-qPCR) was performed on six-leaf-stage pepper plants subjected to NaCl (200 mM), mannitol (600 mM), dehydration, or ABA (100 μ M; Fig. 1A). Pepper plants were carefully uprooted and treated with NaCl or mannitol, exposed to dehydration, or sprayed with ABA for the indicated time points. First leaf of pepper was sampled for RNA extraction and total RNA was isolated from the first leaf using TRIzol Reagent. For cDNA synthesis, 1 μ g of RNA was used with the iScriptTM cDNA Synthesis Kit (Bio-Rad, Hercules, CA, USA). Quantitative RT-PCR was conducted using gene-specific primers (Supplementary Table 1) and iQ SYBR Green Super mix on a CFX96 Touch Real-Time PCR Detection System (Bio-

Rad). RT-qPCR analysis revealed that, as shown in Figure 1A, *CaRLK1* expression was strongly induced in all treatments, with dehydration causing the most rapid and sustained increase that remained high over time. Upon ABA exposure, *CaRLK1* expression peaked at 6 h and remained approximately tenfold higher than baseline after 24 h. Under NaCl treatment, *CaRLK1* transcript levels rapidly increased at 2 h, decreased, and then showed a second strong induction at 24 h. Mannitol treatment gradually increased *CaRLK1* expression until 24 h, followed by a decline.

Next, we examined *CaRLK1* expression in different pepper organs. Leaves, stems, and roots were collected from plants at the five-leaf stage, whereas flowers were harvested at the ten-leaf stage. As shown in Fig. 1B, *CaRLK1* expression was highest in flowers—sixfold higher than in leaves—while stems had relatively low expression and roots displayed expression levels similar to those in leaves. In a previous study, *Arabidopsis thaliana* G-type LecRLKs were classified into eight clades, and *Solanum lycopersicum* G-type LecRLKs into 13 clades (Teixeira et al., 2018). Based on this classification, a phylogenetic tree was constructed using G-type LecRLKs from *Arabidopsis*, tomato, and pepper to determine the phylogenetic positions of pepper G-type LecRLKs (Supplementary Fig. 1). Additionally, we identified nine pepper G-type LecRLK genes sharing over 70% similarity to *Arabidopsis* G-type LecRLKs and included them in the phylogenetic analysis. G-type LecRLKs from *Arabidopsis*, tomato, and pepper were clustered into 13 clades. In particular, pepper G-type LecRLKs were distributed among clades 2, 3, 5, 7, 10, and 13, with *CaRLK1* placed in clade 2. The closest *Arabidopsis* clade member identified in our phylogenetic analysis was AT5G60900; however, no functional studies have reported its involvement in drought stress or ABA signaling.

Decreased tolerance of *CaRLK1*-silenced pepper plants to drought stress.

CaRLK1 expression was highly induced after dehydration treatment (Fig. 1A); therefore, a functional analysis was performed to determine whether this upregulation resulted in phenotypic differences under drought stress. Pepper plants were grown under controlled greenhouse conditions (24°C, 16 h light/8 h dark photoperiod, 60% relative humidity) until reaching the five-leaf stage. Because pepper is technically challenging to transform genetically, a virus-induced gene silencing (VIGS) system was employed to evaluate the phenotype under drought stress conditions. The Tobacco rattle virus (TRV) vector was used, into which a 300-bp *CaRLK1*-specific fragment was inserted, as previously described (Bae et al., 2023; Lim et al., 2026; Senthil-Kumar and Mysore,

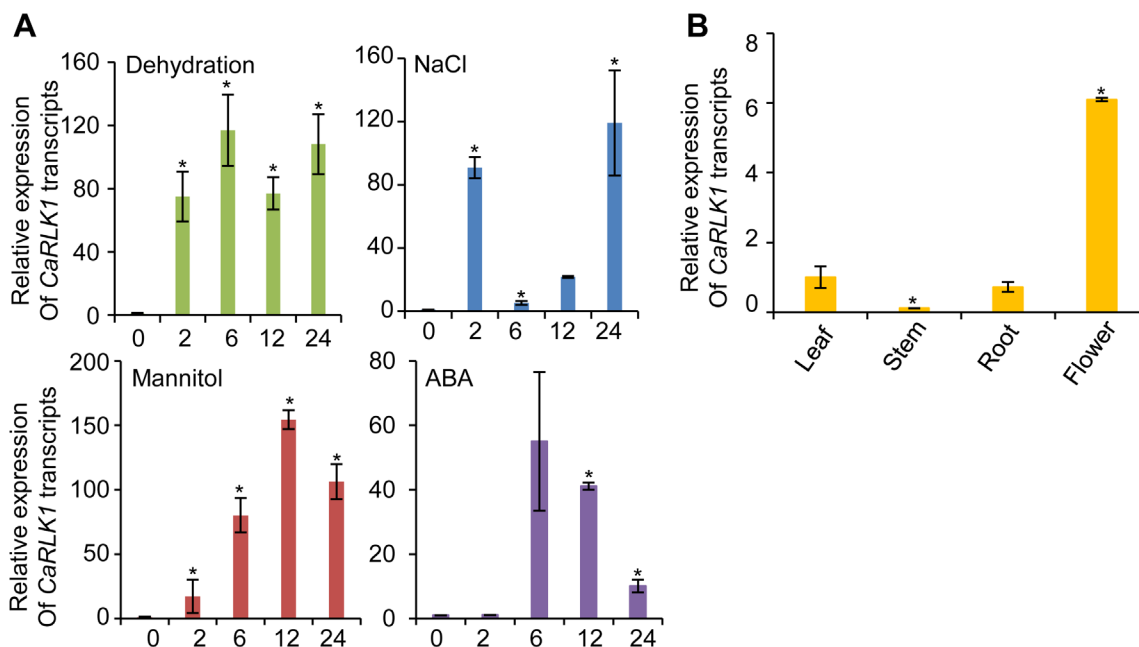


Fig. 1. Expression analysis of the *CaRLK1* gene in pepper. (A) Relative transcript levels of *CaRLK1* in pepper plants subjected to dehydration, ABA (100 μ M), NaCl (200 mM), or mannitol (600 mM). Expression levels were quantified by qRT-PCR using cDNA derived from the first and second leaves. The pepper *ACT1* (*CaACT1*) gene was employed as an internal control. (B) Organ-specific expression of *CaRLK1* in pepper. The relative expression of *CaRLK1* was normalized to that of *CaACT1*. Data are presented as means $\pm$ standard error from three independent experiments (Student's t-test; * $p < 0.05$).

2014). *Agrobacterium tumefaciens* carrying pTRV1 and pTRV2:CaRLK1 or pTRV2:00 as negative control was co-infiltrated into pepper plants using a needleless syringe ($OD_{600}=0.2$). Prior to phenotypic evaluation, VIGS efficiency was verified using a semiquantitative RT-PCR assay (Fig. 2A). The first leaf of five-leaf stage of *CaRLK1*-silenced and control pepper plants was used for RT-PCR. *CaRLK1*-silenced pepper plants showed lower expression of *CaRLK1* than control plants. Drought tolerance was then evaluated *CaRLK1*-silenced pepper (TRV2:CaRLK1) and control pepper (TRV2:00) plants at 2 weeks after agroinfiltration. Both plant lines were subjected to dehydration by withholding water for 12 days. After 2 days of re-watering, survival rates were determined based on the number of rehydrated leaves. Under normal growth conditions, no significant differences were observed between TRV2:CaRLK1 and TRV2:00 pepper plants (Fig. 2B, upper panel). In contrast, after 12 days of dehydration, the leaves of TRV2:CaRLK1 exhibited more severe wilting than those of TRV2:00 (Fig. 2B, middle panel). Furthermore, after re-watering, the survival rate of TRV2:CaRLK1 was nearly twofold lower than that of TRV2:00 (Fig. 2B, lower panel). Plants reduce transpiration water loss through their leaves to enhance drought resistance (Harb et al., 2010; Yamaguchi-Shinozaki and Shinozaki, 2006). Ac-

cordingly, the effect of *CaRLK1* silencing on leaf water-loss rates was evaluated (Fig. 2C). Furthermore, 2 weeks after infiltration, the first and second leaves were detached, and their fresh weights were recorded at regular intervals at room temperature over an 8-h period. The results showed that TRV2:CaRLK1 pepper plants exhibited a significantly higher rate of leaf water loss. Water loss from leaves occurs primarily through stomata, and ABA regulates stomatal opening and closure (Bharath et al., 2021). Accordingly, stomatal apertures were examined following exogenous ABA treatment. following exogenous ABA treatment (Fig. 2D and 2E). For stomatal aperture measurements, leaf peels obtained from these leaves were floated on a stomatal opening buffer containing 50 mM KCl, 10 mM $CaCl_2$, and 10 mM MES-KOH for 3 h. After confirming that stomata were open, the leaf peels were incubated with 20 μ M ABA for an additional 3 h. Stomata were observed under a microscope, and 70 stomata were randomly selected for measurement of stomatal width and length using ImageJ software. In the absence of ABA, no significant differences in stomatal aperture size were observed between TRV2:CaRLK1 and TRV2:00 pepper plants. However, after treatment with 20 μ M ABA, TRV2:CaRLK1 exhibited significantly larger stomatal apertures than TRV2:00 (Fig. 2D). Stomatal closure reduces transpiration water loss

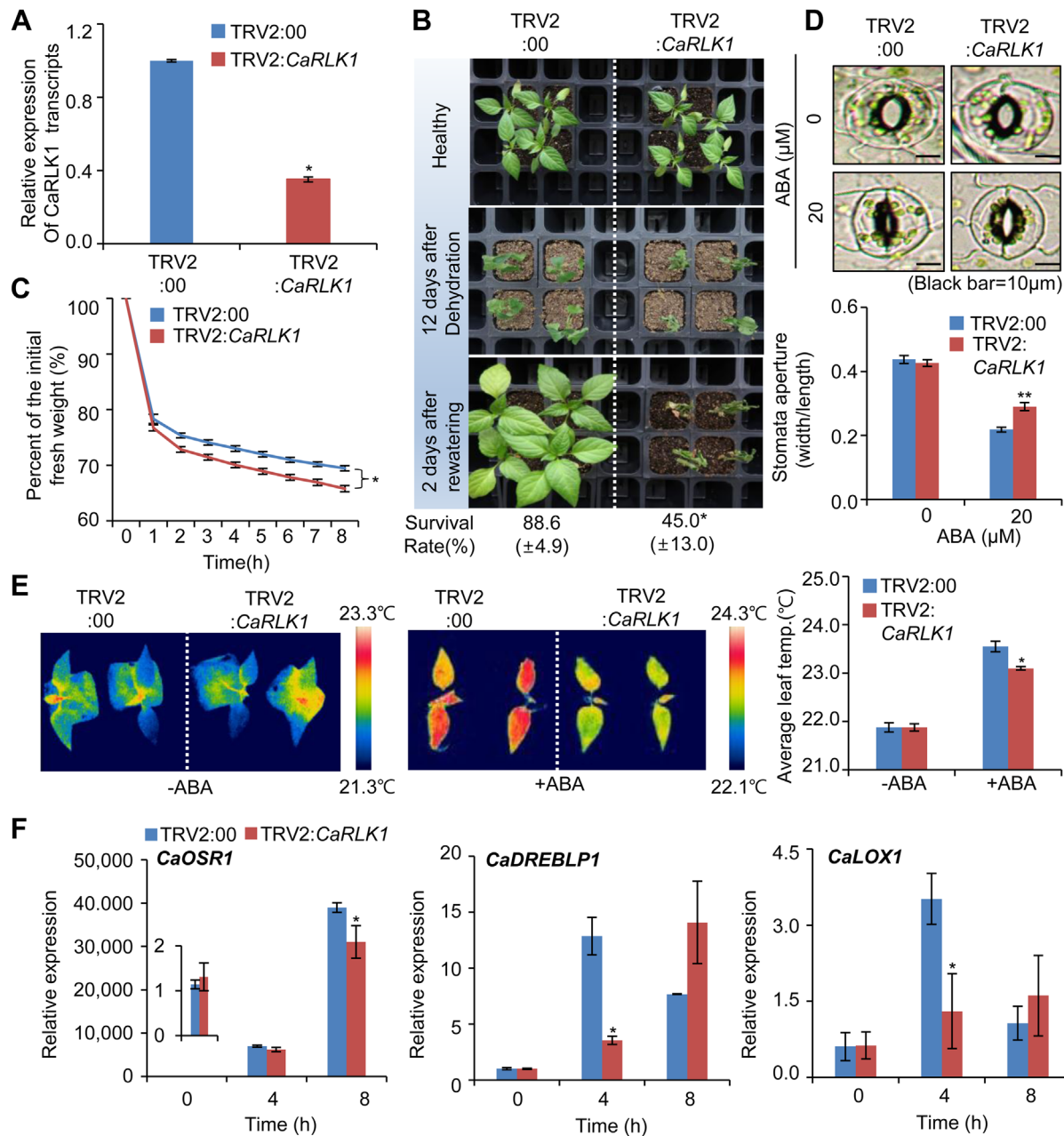


Fig. 2. Decreased tolerance of *CaRLK1*-silenced pepper plants to drought stress. (A) Semiquantitative RT-PCR analysis of *CaRLK1* expression in the leaves of control (TRV2:00) and *CaRLK1*-silenced (TRV2:*CaRLK1*) pepper plants. *CaACT1* was used as an internal control gene. (B) Drought sensitive phenotypes of TRV2:00 and TRV2:*CaRLK1* pepper plants. Three-week-old pepper plants were subjected to drought stress by withholding water for 12 days, followed by re-watering for 2 days. Representative images were captured before drought (upper), after drought (middle), and after re-watering (lower). Survival rates were calculated after re-watering. Data are presented as mean $\pm$ standard error from three independent experiments. (C) Time-course analysis of transpirational water loss in detached leaves of TRV2:*CaRLK1* and TRV2:00 plants. (D) ABA-induced stomatal closure in TRV2:*CaRLK1* and TRV2:00 plants. Leaf epidermal peels were incubated in SOS buffer containing 0 or 20 μ M ABA for 3 h. Representative images (upper) and quantitative measurements of stomatal apertures (lower) are shown. Stomatal apertures were measured from five independent plants, with at least 70 stomata analyzed per plant. (E) Leaf temperature responses to ABA treatment. Representative thermal images were captured 3 h after treatment with 100 μ M ABA, and leaf temperatures were quantified from the first and second leaves. (F) Relative expression levels of drought-responsive genes (*CaOSR1*, *CaLOX1*, and *CaDREBLP1*) in TRV2:*CaRLK1* and TRV2:00 plants following dehydration treatment. Transcript levels were normalized to *CaACT1*, and expression in control plants at 0 h was set to 1.0 (Student's t-test; * $p < 0.05$, ** $p < 0.01$).

from leaves, thereby decreasing evaporative cooling and increasing leaf temperature (Lim et al., 2017; Schroeder et al., 2001). Therefore, we measured leaf temperature using a T420 thermal imaging camera as a proxy of stomatal conductance (Fig. 2E). Prior to ABA treatment, no significant differences in leaf temperature were observed between TRV2:*CaRLK1* and TRV2:00 pepper plants, as determined using FLIR Tools+ ver. 5.2 software. Both plant lines were sprayed with 100 μ M ABA to examine the effects of exogenous ABA treatment. Conversely, after treatment with 100 μ M ABA for 3 h, TRV2:*CaRLK1* showed a smaller increase in leaf temperature than TRV2:00, consistent with a more open stomatal phenotype. These results suggest that TRV2:*CaRLK1* exhibit reduced stomatal closure, resulting in increased transpiration water loss and lower leaf temperature. Furthermore, the effect of *CaRLK1* silencing on the expression of drought-responsive genes was examined (Fig. 2F). Three drought-responsive marker genes—*CaOSR1*, *CaLOX1*, and *CaDREBLP1*—were selected because they are rapidly induced by drought stress and modulate drought response (Hong and Kim, 2005; Lim et al., 2015; Park et al., 2016). At the five-leaf stage, TRV2:*CaRLK1* and TRV2:00 pepper plants were uprooted and subjected to dehydration for 4 h and 8 h. In the absence of dehydration stress, the expression levels of these genes did not differ between them. However, after dehydration treatment, TRV2:*CaRLK1* pepper plants exhibited lower expression levels of these genes than TRV2:00 plants. Collectively, these results show that *CaRLK1* plays a positive role in the drought response by regulating ABA-mediated stomatal closure and downstream gene expression.

Consistent with previous reports in other plant species, *CaRLK1* expression is strongly induced by water-deficit stress, and its silencing produces pronounced drought-sensitive phenotypes (Sun et al., 2018, 2020; Vaid et al., 2013; Yang et al., 2016; Zhang et al., 2022). These findings support the emerging view that G-type LecRLKs function as key regulators of plant responses to dehydration stress. Notably, *CaRLK1* silencing reduces drought tolerance, which appears to result from impaired ABA-mediated stomatal closure and decreased expression of drought-responsive genes.

Given that LecRLKs are plasma membrane-localized proteins, *CaRLK1* likely functions as a sensor or signaling component that links extracellular drought-related cues to intracellular ABA signaling pathways. Similar regulatory roles are proposed for other G-type LecRLKs involved in abiotic stress responses (Sun et al., 2013; Xu et al., 2023). While the data clearly demonstrate a positive role for *CaRLK1* in drought tolerance, the molecular mechanisms

underlying *CaRLK1*-mediated signaling remain unresolved. Identification of *CaRLK1*-interacting proteins and downstream phosphorylation targets is essential for elucidating how G-type LecRLKs integrate drought signals with ABA signaling networks.

Conflict of Interest

The authors have no potential conflicts of interest to disclose.

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Electronic Supplementary Material

Supplementary materials are available at The Plant Pathology Journal website (<http://www.ppjonline.org/>).

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