LecRKIII.1 and LecRKIII.2 formed homodimers to play physiological functions in Arabidopsis thaliana

Meiling Li[1],†, Xiaoxia Lin[1],†, Xiutao Lu[1],†, Shucan Liu[1], Huili Li[1], Cheng Zhang[1], Yan Lu[1], Xinhong Guo[1]*, Jiazhuo Ye[1]*

[1] College of Life Sciences, Hunan University, Changsha 410082, P.R. China

[2] College of Electrical and Information Engineering, Hunan University, Changsha 410082, P.R. China

†These authors contributed equally to this work

CORRESPONDENCE AUTHOR
Xinhong Guo, Email: gxh@hnu.edu.cn
Jiazhuo Ye, Email: yjz@hnu.edu.cn

CONFLICTS OF INTEREST
There are no conflicts of interest for any of the authors.

ABSTRACT

Receptor-like kinases (RLKs), an important family that plant cell sense and transmit extracellular signals, are fundamental to plant cell life and play critical roles in various biological processes, such as response to abiotic stress, development and hormonal response. Among RLKs, the lectin receptor-like kinases (LecRLKs) possess a characteristic extracellular carbohydrate-binding lectin domain and play important roles in plant immune, stress and hormone responses. However, little is known about the genes *LecRKIII.1* and *LecRKIII.2* of LecRLK family up to now. Here, we founded that *LecRKIII.1* and *LecRKIII.2* were localized in plasma membrane and played the physiological roles by forming a homodimer. Real-time fluorescence quantitative PCR analysis of the expression level of *LecRKIII.1* and *LecRKIII.2* in response to exogenous ABA, MeJA, SA, NaCl, mannitol and dehydration suggested that *LecRKIII.1* and *LecRKIII.2* may play important roles in response to various stresses. It will lay a good foundation for further studies on physiological functions of *LecRKIII.1* and *LecRKIII.2*.

Key words： LecRLK, Yeast two hybrid, BiFC, cDNA library, qRT-PCR

INTRODUCTION

Compared with mobile animals, sessile plants evolved developmental plasticity as an important strategy to adapt to different environmental conditions [1]. In other words, plants must depend on a complicated signaling system in response to external stimuli. *Arabidopsis thaliana* receptor-like kinases (RLKs) are widespread proteins family in all kingdoms of plant life and are represented by 610 genes in *Arabidopsis* genome [2]. RLKs contain an extracellular receptor domain, a single transmembrane domain and an intracellular kinase domain in plant [3]. The extracellular receptor domain specifically recognizes and binds extracellular signal molecules to alter the conformation

of the intracellular kinase domain by homologous or heterodimerization, and then activate intracellular serine /threonine kinase domain and phosphorylate downstream proteins, which will recongnize and transfer the extracellular signal into the cell [3]. Generally, in plants, RLKs are the ideal candidates to percept extracellular stimuli and further initiate signaling pathways [4,5,6]. RLKs are generally divided into 6 categories: S RLKs, Ieucine-rich repeats RLK(LRRs), Chitinase-related RLKs (CR4), WAK-1ikeRLKs, TNFR.1ike RLKs, PR5-RLKs, LecRLKs, based on the difference of the RLKs extracellular receptor domain.

LecRLKs, which are characterized by an N-terminal lectin domain and are represented by 75 members in *Arabidopsis* [7,8,9]. On the basis of the extracellular lectin domains'difference, the LecRLKs family could be further subdivided into three categories: L-type, G-type and C-type LecRLKs [10]. Here, *LecRKlll.1* and *LecRKlll.2* belong to L-type LecRKs, which are ubiquitous in plants and have been identified in avarieties of plant species, such as cotton and rice [11,12]. Thus far, with the continuous study of LecRLKs family, they are thought to be play important roles in microbial identification and response [13]. For example, plants could respond to pathogens by activation of plasma membrane-localized receptor-like kinases (RLKs) that function as pattern recognition receptors (PRRs) to initiate defense [14,15,16]. Recently, it has been demonstrated that *LecRK-VI.2* (At5g01540) recognized the pathogen-related molecular component β-aminobutyric acid induce stomatal closure to enhance the resistance of plants to pathogens such as pseudomonas syringae [17,18]. *A. thaliana LecRK-I.8* played a great role in defense triggered by eggderived elicitors of the cabbage butterfly Pieris brassicae [19]. In addition, few L-type LecRKs are involved in plant other biotic and abiotic stress. The LecRLKs responding to wounding were reported for *Arabidopsis LecRK-V.5* and Populus nigra *PnLPK* genes [20,21,22]. *Arabidopsis* LecRLKs family A4 subfamily member gene *LecRK-b2* participated in plant hormone abscisic acid signal transduction pathway [23].

In conclusion, The *Arabidopsis* L-type LecRLKs family genes have important research sig-

nificance. However, the function of genes *LecRL-KIII.1* and *LecRLKIII.2* and function mechanism of the LecRLKs family have not been studied. In this study, we employed Yeast two-hybrid and BiFC experiments for confirming that *LecRKIII.1* can interact with itself to form homodimers and *LecRKIII.2* also have similar function. In addition, our datas suggested that the genes *LecRKIII.1* and *LecRKIII.2* may play important roles in response to multiple stresses.

Materials and Methods

Plant materials and growth conditions

Arabidopsis ecotype Columbia-0 (Col-0) was used as the materials. Seeds of the wild type Col-0 were surface-sterilized in 75% alcohol solution and 20% sodium hypochlorite for 8 min and then washed four times in sterile distilled water. They were plated on 0.8 % (w/v) solid agar MS medium at 4 °C for 3 d synchronization to promote their germination rate. After7 d, the green seedlings were transferred to soil and continually grown at 22 °C under long-day conditions (16 h light and 8 h dark) until the last siliques were dry, and seeds were harvested and stored as described [24].

For treatment analyses, seven-day-old wild-type seedlings were selected as the materials. Firstly, the seedlings were gently pulled out from the MS plate. After soaking, the seedlings were treated with 100 mM ABA, 100 mM MeJA, 100 mM SA, 100 mM mannitol and 100 mM NaCl in the MS liquid medium, respectively. Materials were collected at several time points. All samples were frozen shortly in liquid nitrogen to keep them fresh for the next experiments.

RNA isolation and qRT-PCR Analysis

Total RNA was extracted from the frozen samples of *Arabidopsis* by using a total RNA Purifcation System kit (Invitrogen) and cDNA was synthesized using a PrimeScriptTM RT reagent kit (Takara). For quantitative real-time PCR analysis, we carried out three biological replicates to guarantee precise statistical results. RNA accumulation of genes in each sample was normalized to that of Actin2 gene. The following amplifcation procedure was used: 94 °C for 10min, followed by 40 amplifcation cycles of 94 °C for 30 s, 55

°C for 30 s, and 72 °C for 30 s. Finally, we analyzed the qPCR results using software MXPro. The primers used in the qRT-PCR reactions are presented in Table1.

Table 1. Primer sequences were used in quantitative RT-PCR.

Gene	Primer Name	Sequence 5'-3'
LecRKIII.1	At2g29220QF	GACCGACCAGTTCTCACC
	At2g29220QR	GTGTTACCTTTCCCGTGT
LecRKIII.2	At2g29250QF	ACGACCTACCAGTTCTCA
	At2g29250QG	GTGTCCCGTAGTGCTGTG

Yeast two hybrid and BiFC

The pGBKT7 and pGADT7 vectors and the yeast strain AH109 were used for Yeast two hybrid assays. The C-terminal sequences and N-terminal sequences of *LecRKIII.1* and *LecRKIII.2* were both cloned into pGBKT7 and pGADT7. The recombinant constructs and empty vectors were transformed into yeast strain AH109 in pairs. Transformants spotted on plates of selective medium without Leu and Trp (SD-Leu-Trp) indicating that two vectors pGADT7 and PGBKT7 that expressed *LecRKIII.1* and *LecRKIII.2* of the N-terminal and C-terminal fusion proteins were successfully transferred, respectively. Next, the cells were plated on SD medium lacking leucine, tryptophan and histidine, (SD-Leu-Trp-His) supplemented with 3-amino-1,2,4-triazole for screening. All vectors and primers used in Yeast two hybrid and BiFC assays are presented in Table 2 and Table 3.

Subcellular Localization

To determine the subcellular localization of *LecRKIII.1* and *LecRKIII.2* in A*rabidopsis thaliana* cells, the coding sequence of *LecRKIII.1* and *LecRKIII.2* were amplified by PCR using the primer pair *LecRKIII.1*/*LecRKIII.2* (F/R) (Table 4) and then cloned into the vector pEZS-NL to generate pEZS-NL-*LecRKIII.1*/*LecRKIII.2*. Then, recombinant 35Spro-GFP-*LecRKIII.1* and 35Spro-GFP-*LecRKIII.2* were introduced into *Arabidopsis* protoplasts, respectively.

The transient GFP fluorescence in *A. thaliana* leaf cells was observed under a Leica SPE confocal microscope as described previously [25,26].

Table 2. C/N-terminal primers of *LecRKIII.1* and *LecRKlII.2* were used in Yeast two hybrids.

Primer Name	Sequence 5'-3'	RestrictionEnzymeCutting Site g Site Cutting Site
220C-pGBKT7 F	CGGAATTCTGGTTCTTAC-GTAGAGACAAAATATTC	*EcoR I* EcoR I
220C-pGBKT7R	CGGGATCCTTAGACTCCA-TAGAAGAGGTAGTCATC	*BamH I*
250C-pGBKT7 F	CGGAATTCTGCTTTTTTCG TAGAACGGAAAACTTC	*EcoR I* EcoR I
250C-pGBKT7 R	CGGGATCCTTAGACGAC-GTAGTCATCATGAGGGAG	*BamH I*
220C-pGADT7 F	CGGAATTCTGGTTCTAC-GTAGAGACAAAATATTC	*EcoR I* EcoR I
220C-pGADT7 R	CGGGATCCTTAGACTCCA-TAGAAGAGGTAGTCATC	*BamH I*
250C-pGADT7 F	CGGAATTCTGCTTTTTTCG TAGAACGGAAAACTTC	*EcoR I*
250C-pGADT7 R	CGGGATCCTTAGACGAC-GTAGTCATCATGAGGGAG	*BamH I*
250N-pGBKT7 F	GGAATTCCATATGCAACA ACAAACCAAATTTCTTAC C	*Nde I*
250N-pGBKT7 R	CGCG-GATCCCATCGTGTTACTC GAATTTTTCAT	*BamH I*
220N-pGBKT7 F	GGAATTCCATATGCAAC-GACAGACCAAGTTTCTTA ACC	*Nde I*
220N-pGBKT7 R	CGCGGATCCCATCGTGTT-GTTCGACTTCTTCTC	*BamH I*
250N-pGADT7 F	GGAATTCCATATGCAACA ACAAACCAAATTTCTTAA CC	*Nde I* □
250N-pGADT7R RR	CGCG-GATCCATCGTGTTACTCG AATTTTTCAT	*BamH I*
220N-pGADT7 F	GGAATTCCATATGCAAC-GAGAGACCAAGTTTCTTA ACC	*Nde I*
220N-pGADT7R RRR	CGCGGATCCCATCGTGTT-GTTCGACTTCTTCTC	*BamH I*

Table 3. All primers were used in BiFC assays.

Primer Name	Sequence 5'-3'	Restriction Enzyme Cutting Site
250-3308-F	GGGGTACCTCATGGCTAATACCTATAAATCGA-TAGCTG	*Kpn I*
250-3308-R	TCCCCCGGGGACGACGTAGTCATCATGAGGGAG	*Sma I*
250-3349-F	GGGGTACCTCATGGCTAATACCTATAAATCGA-TAGCTG	*Kpn I*
250-3349-R	TCCCCCGGGGACGACGTAGTCATCATGAGGGAG	*Sma I*
220-3308-F	GGGGTACCTCATGATTAC-CTTCAAATCTATAGCTCTAAC	*Kpn I*
220-3308-R	TCCCCCGGGGACTCCATAGAAGAGGTAG-TCATCAT	*Sma I*
220-3349-F	GGGGTACCTCATGATTAC-CTTCAAATCTATAGCTCTAAC	*Kpn I*
220-3349-R	TCCCCCGGGGACTCCATAGAAGAGGTAG-TCATCAT	*Sma I*

Table 4. Primer sequences used in the coding sequence were amplification of *LecRKIII.1* and *LecRKlII.2* in subcellular localization.

Primer Name	Sequence 5'-3'	Restriction Enzyme Cutting Site
PEZS-250F	GGGGTACCTATGGCTAATACCTATAAATCGA-TAGCTG	*Kpn I* *Kpn I*
PEZS-250R	CGGGATCCGGGACGACGTAG-TCATCATGAGGGAG	*Bam HI*
PEZS-220F	GGGGTACCTATGATTAC-CTTCAAATCTATAGCTCTAAC	*Kpn I*
PEZS-220R	CGGGATCCGGGACTCCATAGAAGAGGTAG-TCATCAT	*Bam HI*

RESULTS

LecRKIII.1 and *LecRKIII.2* were localized on plasma membrane

We predicted that 97.5% of *LecRKIII.1* and 97.1% of *LecRKIII.2* are located on the plasma membrane, respectively by softberry website (http://linux1.softberry.com/) . To further verify the authenticity of the prediction, subcellular localizations of LecRKIII.1 and LecRKIII.2 have been completed. We expressed GFP-*LecRKIII.1* and GFP-*LecRKIII.2* fusion protein under the control of the 35S promoter in wild-type plants, respectively. Transient expression of GFP-*LecRKIII.1* or GFP-*LecRKIII.2* in *Arabidopsis* leaf protoplasts showed that both *LecRKIII.1* and *LecRKIII.2* were localized in the plasma membrane (Fig. 1), this is consistent with the previous bioinformatics analysis results.

LecRKIII.1 and *LecRKIII.2* can interact with themselves in the form of homodimer

Here, we have already proved that *LecRKIII.1* and *LecRKIII.2* were localized on plasma membrane, and *LecRKIII.1* and *LecRKIII.2* were predicted to contain a N-terminal extracellular domain (amino acids residues

24 to 303) with glycosylation site and ATP Binding site, a C-terminal cytoplasmic domain(residues 324 to the final amino acid) and single transmembrane proteins through the UniProt Web site (http://www.uniprot.org/). These are common with the existing receptor kinases, its extracellular glycosylation site and ATP Binding site can combine with extracellular signal molecules and have kinase domain, separately. Moreover, receptor kinases usually conduct biological functions in the form of dimers. To clarify whether *LecRKIII.1* and *LecRKIII.2* play a role through forming dimers, we conducted yeast two hybrid. As shown in Fig. 2A, only the yeast cell that contained C-terminal domain of *LecRKIII.1*/2 and C-terminal domain of *LecRKIII.1*/2 could grow appropriately on SD/-Trp−Leu−His screening medium, suggesting that the C-terminal domain of *LecRKIII.1*/2 can able to interact with themselves to form homodimers. To further explore this result, we conducted biomolecular fluorescence complementation (BiFC), no green fluorescence was found in the negative control, whereas when the vectors that expressed fusion protein *LecRKIII.1* or *LecRKIII.2* were transferred into *Arabidopsis* protoplasts, green fluorescence was observed (Fig. 2C) . The results are consistent with those obtained above in yeast two hybrid experiments. These findings demonstrated that proteins *LecRKIII.1* and *LecRKIII.2* were able to interact with themselves to form homodimers.

*LecRKIII.1*and *LecRKIII.2* are predicted to have 85% gene sequence and 82% protein sequence similarity, suggesting these two genes have high homology (https://www.arabidopsis.org/Blast/). We have proved that *LecRKIII.1* can interact with itself to form homodimers and *LecRKIII.2* also has similar function. To further ask whether *LecRKIII.1* and *LecRKIII.2* can also interact with each other, we performed yeast two-hybrid assays again. The results showed that both N-terminal and C-terminal of *LecRKIII.1* were not able to interact with N-terminal and C-terminal of *LecRKIII.2* (Fig. 2B), demonstrating that *LecRKIII.1* and *LecRKIII.2* didn`t form a heterodimer.
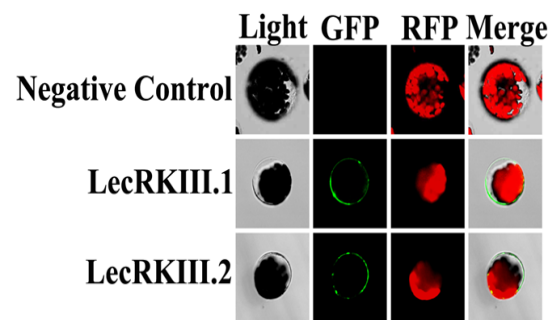

Fig. 1 *LecRKIII.1* and *LecRKIII.2* Localize to plasma membrane. From top to bottom, Negative control, fusion protein GFP- LecRKIII. 1+LecRKIII. 1, fusion protein GFP-LecRKIII. 1+LecRKIII. 2. From left to right, the light, fluorescence of GFP, fluorescence of RFP and merging of GFP and RFP.
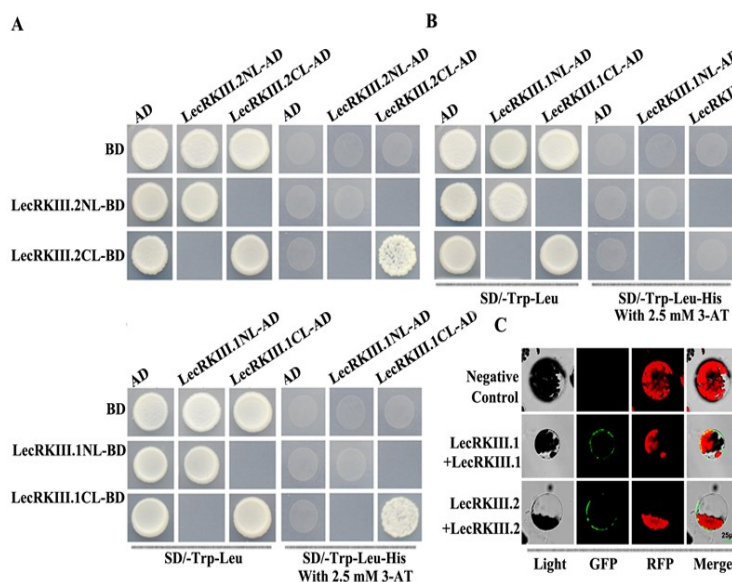

Fig. 2 Protein protein interact analysis of LecRKIII.1 and LecRKIII.2 by Y2H and BiFC.
(A) LecRKIII.1 and LecRKIII.2 play a role through forming dimers using yeast two-hybrid screening. AD, activationdomain; BD, DNAbindingdomain. Transformed yeasts were spotted on control medium(SD-Leu-Trp) or selective medium (SD-Leu-Trp-His) supplemented with 3-amino-1,2,4-triazole for screening. The empty vectors were used as controls.
(B) Testing of interactions between LecRKIII.1 and LecRKIII.2.
(C) BIFC assays proved that LecRKIII.1 and LecRKIII.2 were able to interact with themselves to form homodimers.
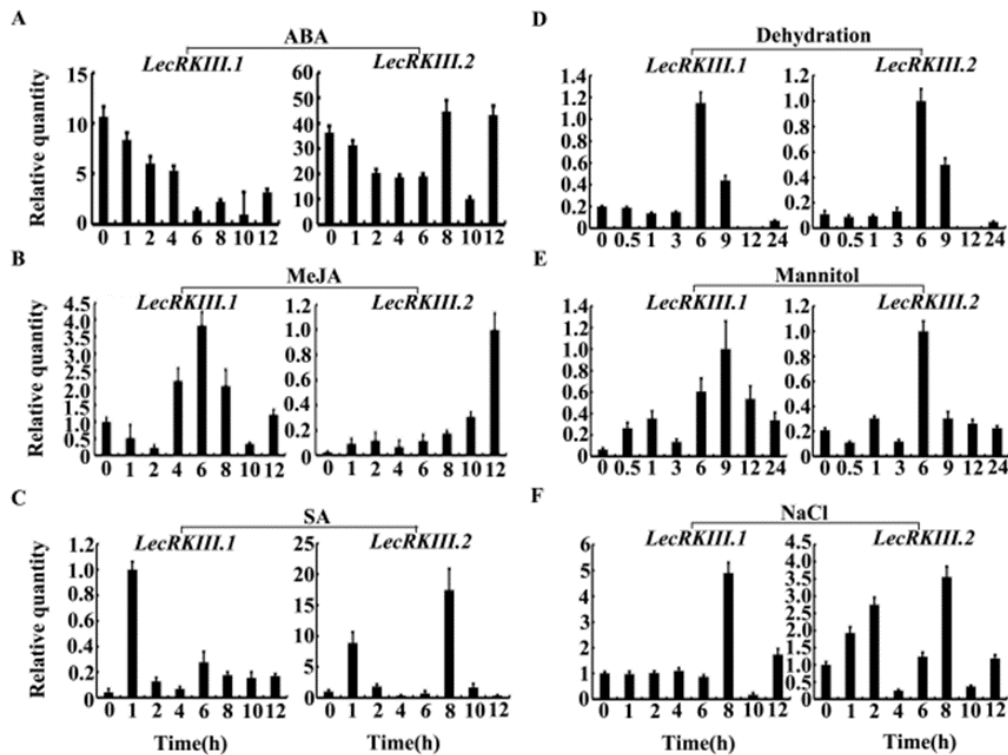
Fig. 3 Real-time fluorescence quantitative PCR analysis of the expression level of *LecRKIII.1* and *LecRKIII.2* in response to exogenous ABA (A), MeJA (B), SA (C), dehydration stress (D), mannitol (E) and NaCl (F) respectively. Actin-2 was used as control.

Expression of the *LecRKIII.1* and *LecRKIII.2* gene in response to various stresses

To understand and predict results of *LecRKIII.1* and *LecRKIII.2* in *Arabidopsis* in more detail, we performed RT-PCR analysis at several time points to explore their expression patterns under various abiotic stress treatments. Seven-day-old seedlings were treated with ABA, MeJA, SA, mannitol, NaCl and dehydration stress, respectively. The expressions of *LecRKIII.1* and *LecRKIII.2* in response to exogenous ABA, MeJA, SA, NaCl, mannitol and dehydration were shown in Fig. 3. The expression of *LecRKIII.1* and *LecRKIII.2* decreased when treated with ABA, whereas the expression of *LecRKIII.2* after 8h treatment fluctuated, which may be related with its negative feedback pathway (Fig. 3A). The expression of *LecRKIII.1* and *LecRKIII.2* were significantly induced by dehydration stress, peaking at 6 h (Fig. 3D), by NaCl at 8h (Fig. 3F), by MeJA at 6h and 12h (Fig. 3B) and by mannitol at 9 and 6h for *LecRKIII.1* and *LecRKIII.2*, respectively (Fig. 3E). Interestingly, there

are no regular changes when treated with SA, showing that *LecRKIII.1* and *LecRKIII.2* may don't participate in SA signal path (Fig. 3C). Collectively, the outcome strongly suggested that *LecRKIII.1* and *LecRKIII.2* might be involved in various stresses, but not in the SA stress response signaling pathways.

DISCUSSION

In this study, we identified that *LecRKIII.1* and *LecRKIII.2* have typical L-type LecRLK structure-an extracellular soybean lectin domain, a single transmembrane region and a cytoplasmic serine/threonine kinase domain by bioinformatics analysis. Sequence alligment demonstrated that *LecRKIII.1* and *LecRKIII.2* have a very high homology. Here, we proposed a function mechanism for *LecRKIII.1* and *LecRKIII.2* in which *LecRKIII.1*/2function as homogous dimers. However, the yeast two hybrid confirmed that *LecRKIII.1* and *LecRKIII.2* didn`t interact with each other to form a heterodimer.

Previous studies have shown that RLKs family function as homodimers, heterodimers or oligomers, but the function mechanisms of *LecRKIII.1* and *LecRKIII.2* were not investigated [27,28,29,30,31,32]. Our study demonstrated that *LecRKIII.1* and *LecRKIII.2* could interact with themselves to form homodimers. Although there were 85% gene sequence and 82% protein sequence similarity between *LecRKIII.1* and *LecRKIII.2*, they didn`t interact with each other to form a heterodimer, we speculated that *LecRKIII.1* may function in a redundant manner with *LecRKIII.2*, but they function independently.

Plants are often exposed to various adverse environment that greatly is harmful to growth. To adapt to all kinds of complex external conditions, they have formed a set of fine strategies for survival. One of the key measure is that RLKs transmit extracellular signals to intracellular. Therefore, RLKs are crucial in regulating plant reactions to biotic and abiotic stress [33,34], and previous studies have also proved this view [35,36]. However, no study showed that *LecRKIII.1* and *LecRKIII.2* are related to hormone and stress response in details. And largely, abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), MeJA, NaCl and mannitol are key regulations of plant growth and development. In our conclusion, we founded that there were certain regular expression level changes except SA under different treatment. We found that *LecRKIII.1* and *LecRKIII.2* have the same expression pattern under dehydration, NaCl and mannitol. The expression level of *LecRKIII.1* and *LecRKIII.2* peaking at 6, 8 or 9 h. However, they presented opposite expression mode when treated with MeJA. The expression level of *LecRKIII.1* reached maximum at 6 hours and then declined, but the expression of *LecRKIII.2* was activated and increased after the expression declining of *LecRK.III.1*. These results suggested that *LecRKIII.1* and *LecRKIII.2* may play important roles in response to multiple stresses.

In summary, the present research provides a significant work mechanism that *LecRKIII.1* and *LecRKIII.2* function as homogous dimmers. It is beneficial for deep research of LecRKs family. The expressions of *LecRKIII.1* and *LecRKIII.2* were induced with the above-mentioned different ways of treatment, suggesting that these two genes might modulate these various signalling pathways and ultimately enhance *Arabidopsis thaliana*'s tolerance in response to different intrinsic and environmental signals.

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