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Research article

Overexpression of *VvLRK10L* affected the development of *Arabidopsis thaliana* ☆

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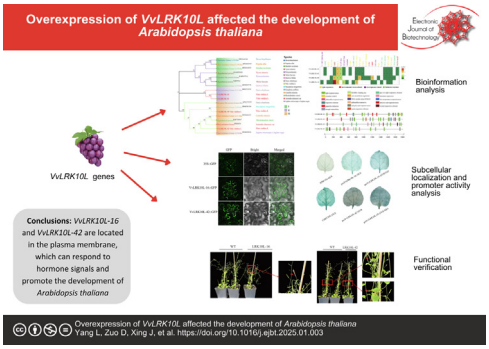
GRAPHICAL ABSTRACT

Overexpression of *VvLRK10L* affected the development of *Arabidopsis thaliana*.



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ABSTRACT

Background: Receptor-like kinase (RLK), as a phosphotransferase, is widely involved in plant growth and development and stress response. RLK in plants could be divided into different types according to the sequence characteristics. LRK10 kinase is a subfamily of RLKs and has been considered to be associated with plant disease resistance. LRK10 is differentially expressed during ABA-mediated grape berry ripening, showing its possibility with plant development.
Results: To explore the relationship between *VvLRK10L* genes and plant development, 4 *VvLRK10L* genes were cloned, and their conserved domains, subcellular localization and promoter activity were analyzed. *VvLRK10L-16* and *VvLRK10L-42* were localized to the plasma membrane. GA3 and ABA treatments enhanced their promoter activity, respectively, and the overexpression of these two genes promoted plant growth.
Conclusions: *VvLRK10L-16* and *VvLRK10L-42* are located in the plasma membrane, which can respond to hormone signals and promote the development of *Arabidopsis thaliana*.
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1. Introduction

Receptor-like kinase is a membrane protein located on the plasma membrane [1]. Its extracellular ligand binding domain can specifically sense and bind to various extracellular signals such as pathogens, peptides or hormones, and transmit extracellular signals to cells, thereby regulating the development process of plants [2,3]. For example, *MdHXK1* and *MdSnRK1* regulate anthocyanin biosynthesis in different tissues by sensing exogenous glucose and sucrose signals in apple, respectively [2,3]. According to the sequence characteristics, RLKs can be divided into different types [4] and are widely involved in plant growth process, including development, stress response and intracellular signal transduction [5].

Recently, RLKs, as one of the largest gene families in plants, are also considered to be involved in the regulation of plant fruit ripening [5,6]. FERONIA-like Receptor Protein Kinase (FERLs) belongs to the CrRLK1-L receptor-like protein kinase subfamily, the overexpression and silencing of *FaMRLK47* can inhibit and promote the ripening process of strawberry fruit, respectively [7]. Apart from FERLs, *FaRIPK1*, as a leucine-rich repeat receptor-like protein kinase (LRR-RLKs) isolated from strawberry, can interact with ABA receptor *FaABAR* to regulate strawberry fruit ripening [8].

Table 1
Physical and chemical specifications of *VvLRK10L*.

Protein Name	Gene ID	CDS length (bp)	Amino acid length (aa)	molecular weight (Da)	PI	Protein instability	Lipid-binding protein index	Average hydrophobicity index	Transmembrane structure
VvLRK10L-16	VIT_16S0098g00160	1782	593	67389.15	8.98	34.83 (stabilization)	91.73	−0.157	1
VvLRK10L-40	VIT_16S0098g00400	1647	548	62239.44	6.00	48.34 (destabilization)	92.70	−0.152	1
VvLRK10L-41	VIT_16S0098g00410	1707	568	65002.87	6.66	37.57 (stabilization)	85.76	−0.218	0
VvLRK10L-42	VIT_16S0098g00420	1200	399	45554.87	8.73	45.09 (destabilization)	90.12	−0.162	1

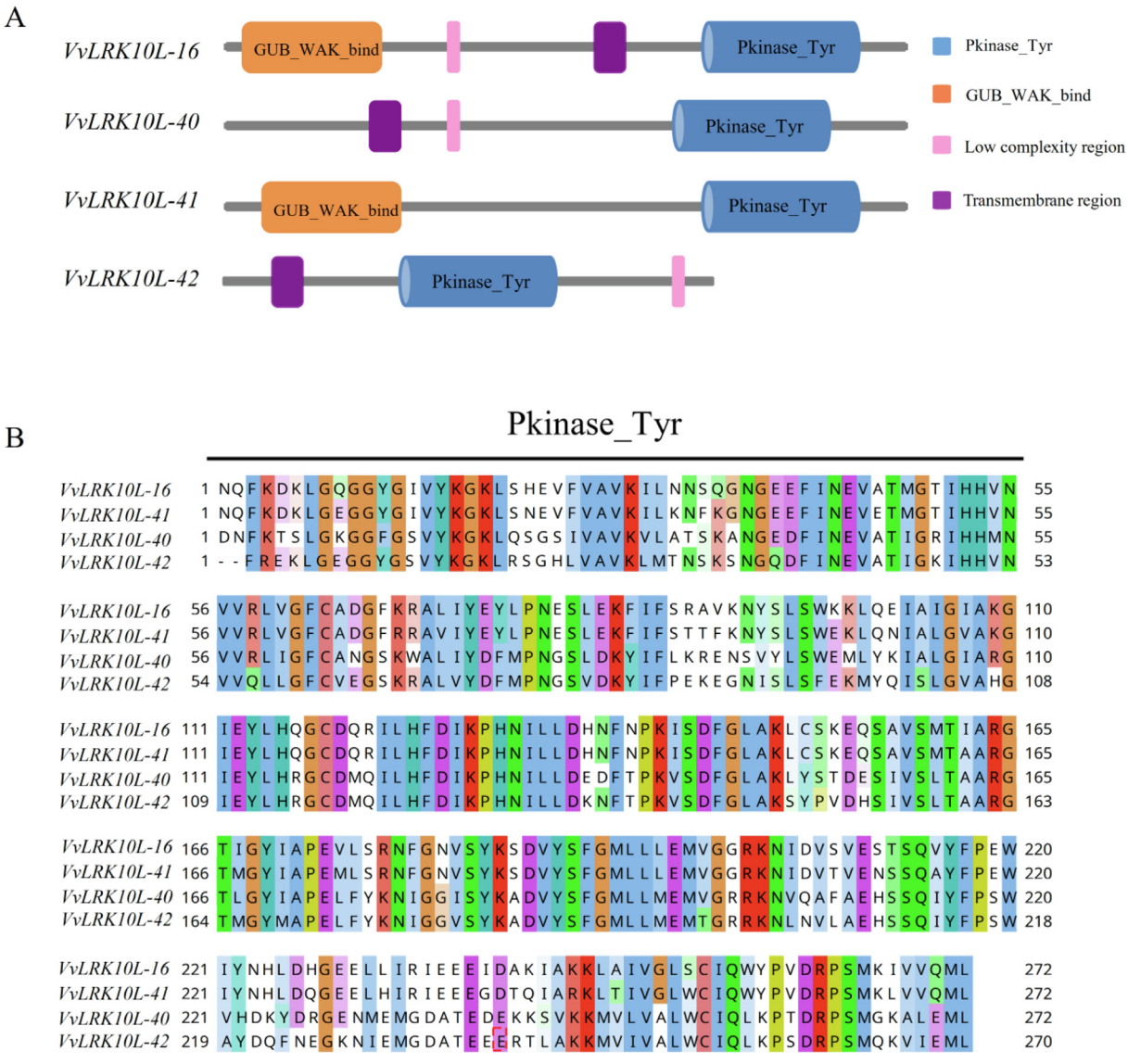

Fig. 1. Conserved domain analysis of *LRK10L* in grape. (A) Conserved domain diagrams of *VvLRK10L-16*, *VvLRK10L-40*, *VvLRK10L-41* and *VvLRK10L-42*. (B) Comparison of Pkinase_Tyr domain motifs in *VvLRK10L-16*, *VvLRK10L-40*, *VvLRK10L-41* and *VvLRK10L-42*.

LRR and FERL-type receptor-like protein kinases are also key factors in regulating apple ripening [7,9]. Thus, other types of RLKs may also have certain potential in fruit ripening regulation.

In wheat, the first identified RLK gene was located at the Lr10 resistance locus of wheat and co-segregated with the resistance locus of leaf rust pathogen, resulting in the naming of leaf rust-associated receptor-like protein kinase gene LRK10 [10]. The existing research on LRK10 is mainly related to stress response. *TtdLRK10L-1* contributes to resistance to powdery mildew and is described as an important regulator of wheat development [11]. In *Arabidopsis*, *AtLR10L1.2* may affect the tolerance to drought stress through the ABA signaling pathway and regulate stomatal pore size [12]. ABA is not only involved in the response of grapes to stress [13] but also a major regulator of fruit ripening [14,15]. The expression of LRK10 was significantly up-regulated during ABA-mediated grape fruit ripening, indicating that LRK10 played a role in this process [14]. Based on previous studies, the genome-wide identification of LRK10 in grapes was completed and named as *VvLRK10L* [4,16].

Grape is widely cultivated in the world and has high economic and nutritional value [17]. Among them, 'Kyoho' is one of the main varieties in production, with large fruit grains and delicious taste [18]. As the early bud mutation of 'Kyoho', the maturity period of 'Fengzao' is 20 d earlier than that of 'Kyoho', which also provides an ideal material for the study of developmental regulation genes [18]. We have identified the expression pattern of 109 *VvLRK10L* genes identified from *Vitis vinifera* in 'Kyoho' and 'Fengzao' [16]. Among them, four genes were up-regulated during fruit development, and the expression in 'Fengzao' was significantly higher than that in 'Kyoho' [16], which was considered to be the candidate gene for regulating fruit ripening.

In this study, to explore the function of *VvLRK10L* genes previously identified from 'Kyoho' and 'Fengzao', we overexpressed these genes in *Arabidopsis thaliana* and analyzed their subcellular localization and promoter activity. In fact, the overexpression of *VvLRK10L-16* and *VvLRK10L-42* significantly promoted the development of *Arabidopsis* and showed potential in promoting grape ripening.

2. Materials and methods

2.1. Plant material

The 'Kyoho' grapefruits were collected from the experimental field under natural cultivation conditions of Henan University of Science and Technology (Luoyang, China) in 2020. After the sampling, the fruits were wrapped in tin foil and stored in liquid nitrogen immediately, and then stored at −80°C.

The seeds of tobacco (*Nicotiana tabacum*) and *Arabidopsis* (Colombian) were from the samples preserved in our laboratory. Subcellular transient localization and promoter activity analysis were performed on 6-week-old tobacco. *Arabidopsis* and tobacco plants were cultured in soil pots at 25°C, 16:8 h light–dark photoperiod conditions. The transgenic plants were obtained by transforming the inflorescence of *A. thaliana*.

2.2. Analysis of promoter cis-acting elements and gene sequence

TBtools was used to extract the 2000 bp sequence upstream of the initiation codon of *VvLRK10L-16*, *VvLRK10L-40*, *VvLRK10L-41* and *VvLRK10L-42* genes as promoters [19]. The analysis of cis-acting elements was established with Plant Care (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/) and visualized them with TBtools and R packages [19]. The conserved domain of the cloned target gene sequence was analyzed in SMART website, and the conserved domain sequence of the target gene was further compared and visualized with MEGA7.0.

2.3. Analysis of phylogenetic and protein physicochemical properties

The protein sequence of the cloned gene was predicted with NCBI (https://www.ncbi.nlm.nih.gov/), and the protein sequence was further subjected to Blast. 3–4 protein sequences from each group were selected with the closest homology for phylogenetic

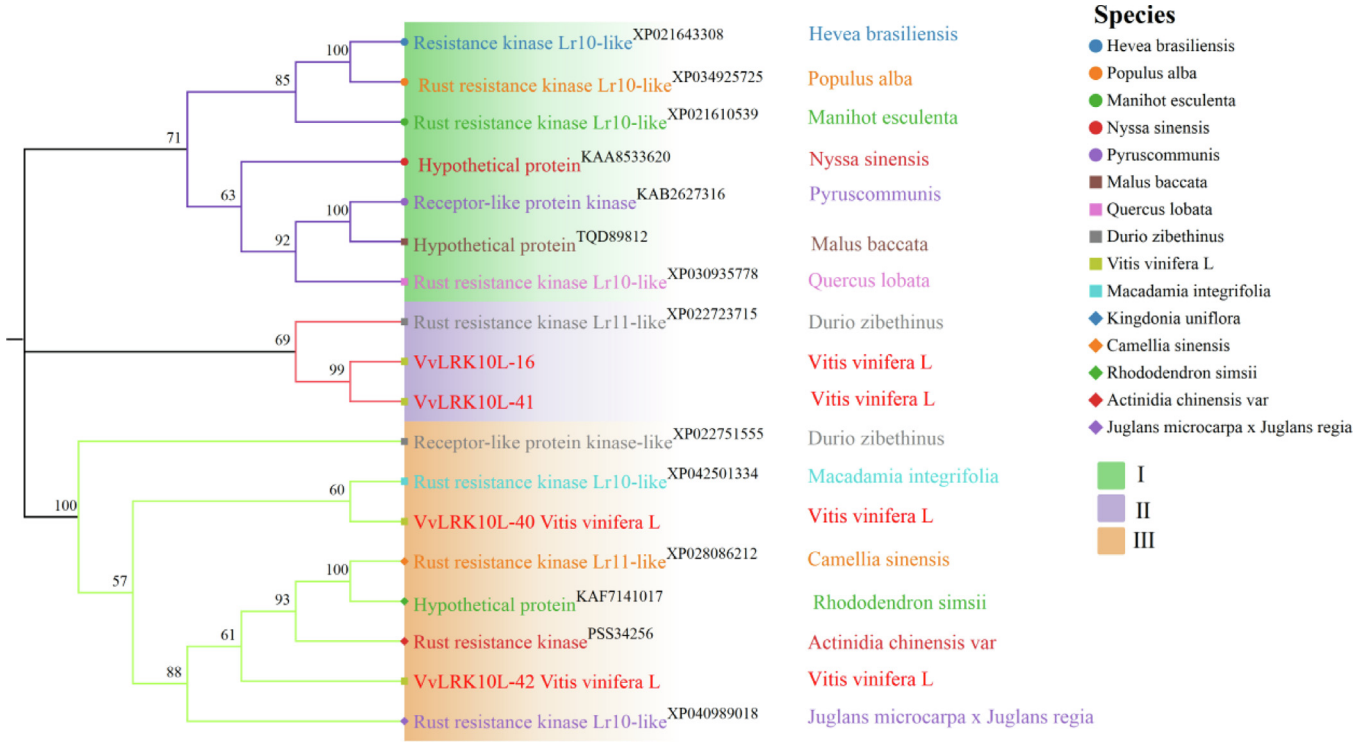

Fig. 2. Phylogenetic tree of *VvLRK10L* and other known proteins in different species. Different species are represented in different color shapes. The upper right corner of the gene represents its ID in the NCBI database, and the species name is behind the gene.

analysis. The alignment of *VvLRK10L* with known functional proteins in different species was performed in MEGA7.0 and visualized in Chiplot (https://www.chiplot.online). The amino acid sequence encoded by the cloned gene was further analyzed in ExPASy (https://web.expasy.org/protparam/).

2.4. Subcellular localization analysis

The RNA of 'Kyoho' berries was extracted with Spectrum™ Plant Total RNA Kit (SIGMA, Beijing, China) and reverse transcribed with rime Script™ RT Reagent Kit (Takara, Dalian, China). Primers designed with Premier 5.0 software were synthesized by sangon biotech (Shanghai, China). *VvLRK10L-42* and *VvLRK10L-16* were inserted into p1300-35S-GFP vector under the control of 35S promoter, respectively. Primer information is shown in Table S1. The recombinant plasmid was introduced into *Agrobacterium tumefaciens* (GV3101) and transiently transformed into tobacco leaves. After co-cultured for 24 h under dark conditions, tobacco was transferred to 16:8 h light–dark photoperiod conditions for 1–2 d. The green fluorescence signal of leaves was observed with a laser confocal scanning microscope (FV3000).

2.5. Promoter activity analysis

An improved CTAB method contributed to the extraction of DNA from 'Kyoho'berries [20]. Similarly, the promoter sequences of *VvLRK10L-42* and *VvLRK10L-16* were inserted into the 0390-35S-GUS vector. Primer information is shown in Table S1. The 6-week-old detached tobacco leaves were used for *A. tumefaciens*-mediated transient genetic transformation. The recombinant plasmid was introduced into tobacco leaves by injection and co-cultured for 2–3 d in 16:8 h light–dark photoperiod conditions. Half of the leaves containing *VvLRK10L-16* and *VvLRK10L-42* transgenic tobacco were treated with GA3 and ABA solutions, respectively. According to the instructions, GUS Blue KIT (Huayueyang, Beijing) was used to treat tobacco leaves and observe the leaves after decolorization with 70% absolute ethanol.

2.6. Plant expression vector construction and Arabidopsis transformation

Under the control of the CaMV35S promoter, the full-length of *VvLRK10L-42* and *VvLRK10L-42* were inserted into the pSAK277

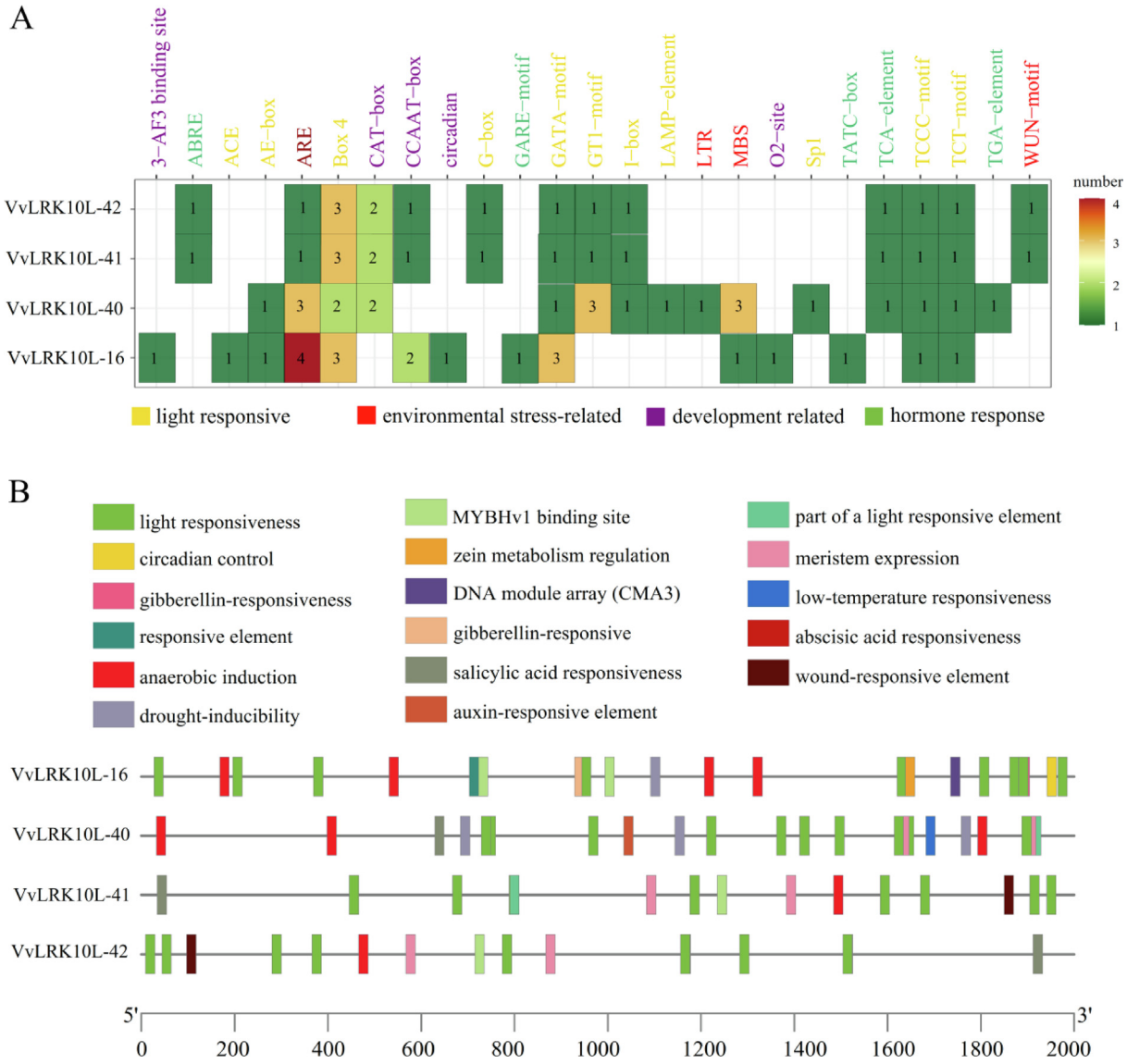

Fig. 3. Cis-acting elements of *VvLRK10L-16*, *VvLRK10L-40*, *VvLRK10L-41* and *VvLRK10L-42*. (A) Analysis of the number and type of cis-acting elements contained in four genes promoter; (B) Location distribution of different types of cis-acting elements on four genes promoters.

vector with homologous recombination method. Primer information is shown in Tab S1. Through the *Agrobacterium*-mediated method, transgenic *Arabidopsis* lines were obtained by the floral dip method. The *Agrobacterium* used for transformation was GV3101. *Arabidopsis* plants were cultured at 25°C in a greenhouse (16:8 h light–dark cycle). The obtained transgenic seeds were sown on MS medium; the control plants were cultured under the same conditions Table S1.

3. Results

3.1. Cloning and sequence analysis of VvLRK10L

The CDS sequences of *VvLRK10L-16*, *VvLRK10L-40*, *VvLRK10L-41* and *VvLRK10L-42* were obtained from 'Kyoho' and analyzed by SMART and EXPASY (Table 1). All genes contained a highly conserved Pkinase_Tyr domain. *VvLRK10L-16* and *VvLRK10L-40* are structurally similar and contain a GUB_WAK_bind domain. In addition, *VvLRK10L-16* and *VvLRK10L-41* are stable proteins, while *VvLRK10L-40* and *VvLRK10L-42* are the opposite. Except for *VvLRK10L-41*, the other three genes have transmembrane structures (Fig. 1).

3.2. Phylogenetic analysis of VvLRK10L genes

The amino acid sequences of four *VvLRK10L* genes were BLAST in NCBI, and the sequences of other species with high homology were compared with MEGA7.0 software and the phylogenetic tree was constructed (Fig. 2). *VvLRK10L-16* and *VvLRK10L-41* are more closely related to rust resistance kinase Lr10-like of *Durio zibethinus*, while *VvLRK10L-40* is clustered with *Macadamia integrifolia*. The genes in the same cluster may contain similar functions.

3.3. Promoter sequence cloning and cis-acting element analysis

A total of 25 cis-acting elements were identified from four genes with PlantCare. As shown in Fig. 3, the number and types of light response-related cis-acting elements are the most abundant. In addition, each gene contained cis-acting elements related to hormone response, stress response and growth. Among them, the hormone-responsive cis-acting elements in *VvLRK10L-41* and *VvLRK10L-42* are related to ABA (ABRE and TCA-element), while *VvLRK10L-16* and *VvLRK10L-40* are related to GA3, SA and auxin (GARE-motif, TATC-box, TCA-element and TGA-element), respectively. The different cis-acting elements in the genes indicate that they may be involved in fruit development through different regulatory pathways.

3.4. VvLRK10L genes were localized in plasma membrane

The subcellular localization of *VvLRK10L-16* and *VvLRK10L-42* was detected with Plant-PLoc analysis. The recombinant plasmid was introduced into tobacco by *Agrobacterium*-mediated method and analyzed by Confocal Laser Scanning Microscopy (FV3000). *VvLRK10L-16* and *VvLRK10L-42* only had green fluorescence on the plasma membrane, indicating that they were localized on the plasma membrane, which was consistent with the predicted results (Fig. 4).

3.5. Promoter activity analysis

To explore the relationship between *VvLRK10L* genes and plant development, the promoter sequences of *VvLRK10L-16* and *VvLRK10L-42* genes containing hormone-related elements were cloned from 'Kyoho' grapes. The *Agrobacterium*-mediated method was used for the transformation of tobacco leaves, and then, the promoter activity was analyzed by GUS staining assay. The GUS reporter protein without any gene was used as a negative control, and the GUS reporter protein containing CaMV35S promoter was used as positive control. *VvLRK10L-16* and *VvLRK10L-42* could initiate GUS protein expression (Fig. 5). In addition, GA3 and ABA treatment enhanced the promoter activity of *VvLRK10L-16* and

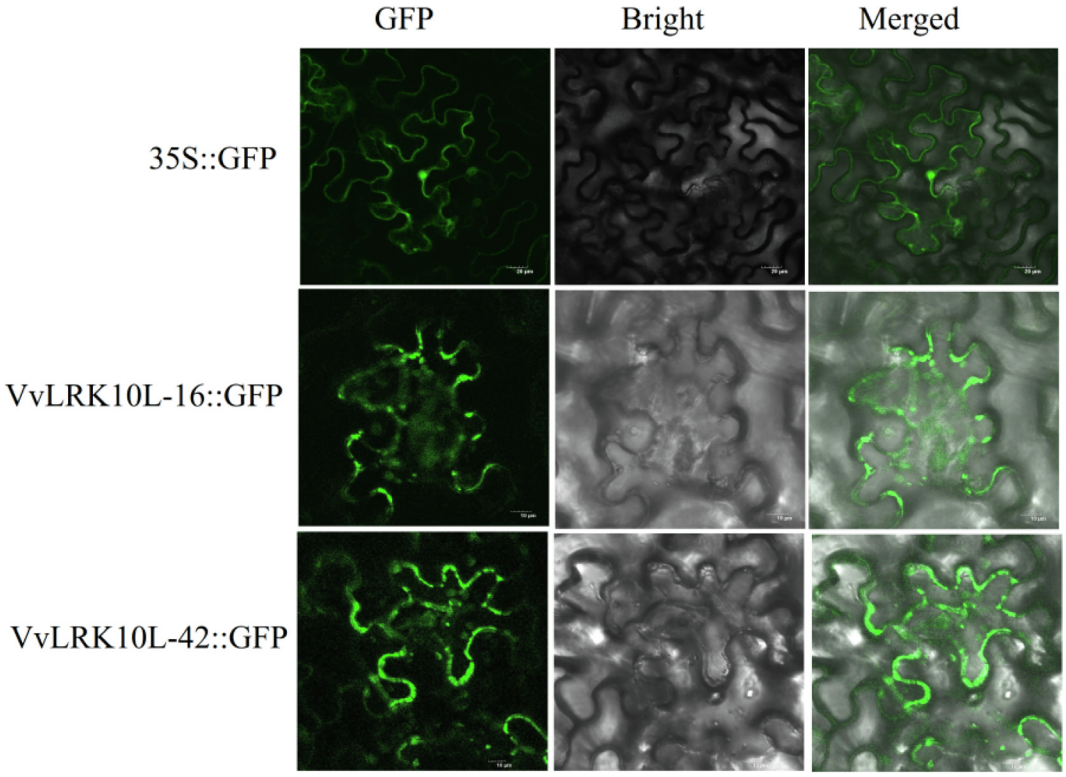

Fig. 4. The subcellular localization of *VvLRK10L-16* and *VvLRK10L-42*. The p1300-35S-GFP vector activated by 35S promoter was used as a control.

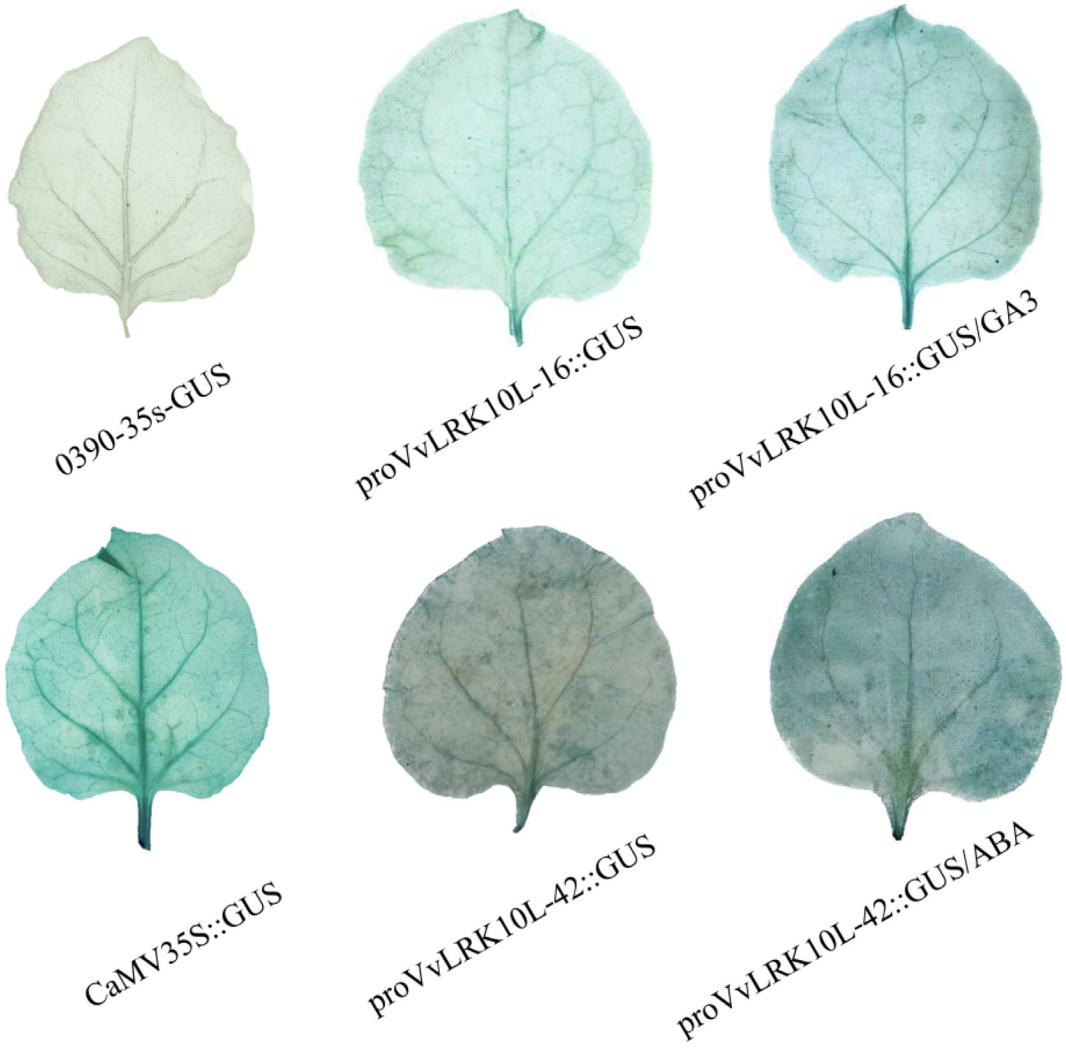

Fig. 5. Analysis of promoter activity of *VvLRK10L-16* and *VvLRK10L-42* in grape. 0390-35S-GUS was negative control and CaMV35S::GUS was positive control.

VvLRK10L-42, respectively. These results indicated that the functions of *VvLRK10L-16* and *VvLRK10L-42* in plant development are mediated by GA3 and ABA.

3.6. Overexpression of VvLRK10L-16 and VvLRK10L-42 promoted Arabidopsis growth

To identify the function of *VvLRK10L-16* and *VvLRK10L-42*, they were overexpressed in *A. thaliana* (Fig. S1). Compared with WT, the overexpression of *VvLRK10L-16* and *VvLRK10L-42* significantly increased the number of roots at the seedling stage (Fig. 6A,B,C, D). In addition, the overexpression of *VvLRK10L-42* also increased the number of rosette leaves (Fig. 6F,H). The above results indicated that *VvLRK10L-16* and *VvLRK10L-42* have the effect of promoting growth.

3.7. Transgenic plants showed early maturity

The phenotype of mature stage of *A. thaliana* was observed. It was found that the pods of *VvLRK10L-16* transgenic lines were fully mature at 70 d, while WT *A. thaliana* was not yet mature (Fig. 7A). At 73 d, the pods of *VvLRK10L-42* transgenic lines had matured and cracked, and WT *Arabidopsis* pods began to turn yellow, and the *VvLRK10L-42* transgenic lines were longer than the control (Fig. 7B). The transgenic lines matured 2–3 d earlier than WT *Arabidopsis*, indicating that *VvLRK10L* genes can promote maturation in plants.

4. Discussion

The LRK10 has been identified in many plants and is considered to be involved in a series of analytical mechanisms regulating plant development [4,6]. However, most of the studies on LRK10 have focused on the regulation mechanism of stress response, such as *PR5K* (LRK10) is similar to PR5 protein structure and participates in the immune regulation of plants against diseases in *A. thaliana* [21]. As one of the largest gene families in plants, RLK is involved in the regulation of most development processes in plants [5,6], and many of its subfamilies are the main factors regulating fruit development [6,7]. Furthermore, Lec-RLK and LRR-RLK also contribute to plant development [22,23]. In previous studies, a total of 109 *VvLRK10L* genes were identified from the grape genome. The expression of some of these genes gradually increased during the development of grape, especially in the early bud mutation, indicating that they have the potential to regulate plant development.

Recent studies have shown that some subfamilies of RLK are involved in the regulation of plant development and ripening, such as Lec-RLK and LRR-RLK [22,23]. In apple, FERONIA-Like receptor kinases (FERLs) promote fruit ripening by modulating ethylene production [7,24]. Several researches proved that different kinds

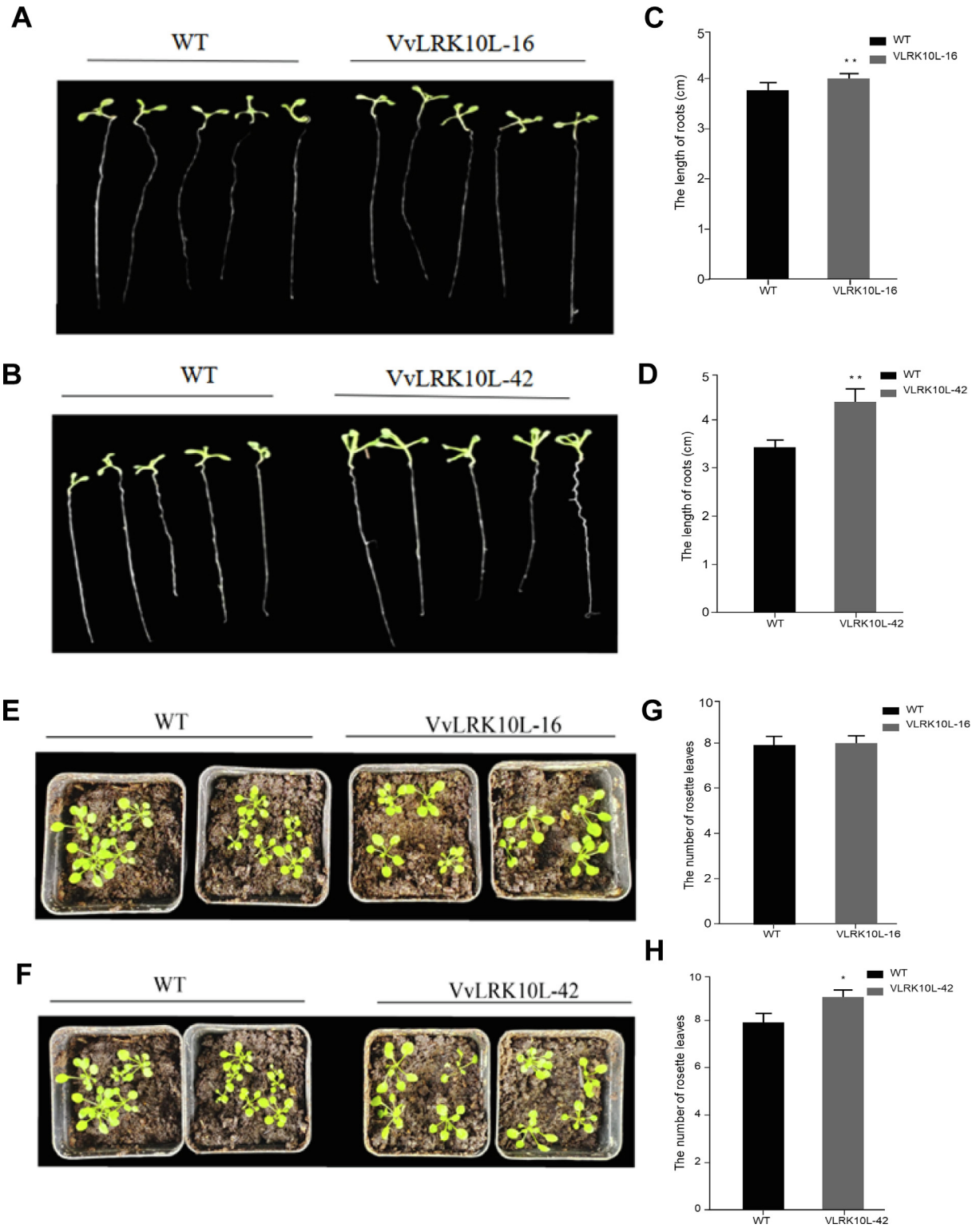

Fig. 6. Overexpression of *VvLRK10L-16* and *VvLRK10L-42* promoted *Arabidopsis* growth. (A), (C), (E) and (G) are the phenotypes of *VvLRK10L-16* transgenic *Arabidopsis*, while (B), (D), (F) and (H) are the phenotypes of *VvLRK10L-42* transgenic *Arabidopsis*.

of RLKs kinase may be involved in the fruit ripening [25,26]. Compared with other protein kinases, little is known about the function of LRK10 in fruit ripening. To explore the function of LRK10 kinases in grape, combined with LRK10 genes in other species, the phylogenetic tree analysis of these 4 genes was established. Among them, *VvLRK10L-16* and *VvLRK10L-41* are closer to the function of rust resistance kinase Lr10-like in *D. zibethinus* and the function of *VvLRK10L-42* may be more similar to that of Rust resistance kinase. However, at present, the known function of rust resistance kinase Lr10-like or Rust resistance kinase in different species is mostly related to plant disease resistance [27,28], and its direct effect on plant growth and development is poorly understood.

The main structure of LRK10 protein includes the Pkinase_Tyr domain and is located on the plasma membrane [29]. After binding

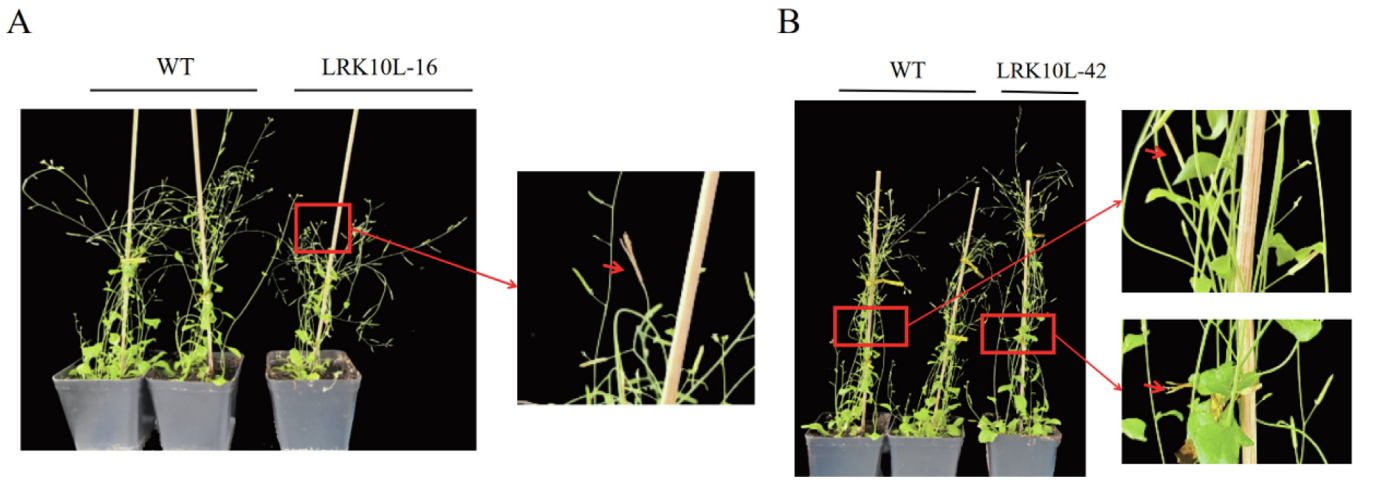

Fig. 7. Maturity analysis of transgenic *Arabidopsis* pods. (A) and (B) represent the transgenic plants of *VvLRK10L-16* and *VvLRK10L-42*, respectively. The long arrow shows an enlarged view in the red box, while the small red arrow points to the mature *Arabidopsis* seed pod. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to various extracellular signals, the phosphorylation activity of the intracellular kinase functional domain is activated to cause a phosphorylation cascade reaction, resulting in the regulation of plant development [12,29]. Consistent with previous studies on LRK10 [30], *VvLRK10L-16* and *VvLRK10L-42* identified from grapes were also localized in the plasma membrane, which is consistent with the predicted results. Through the analysis of cis-acting elements in the promoter region of four genes, it was found that there were multiple hormone-related cis-acting elements in the promoter region of each gene, including ABRE, TCA-element and TATC-box. Plant hormones are essential for plant development [31]. In many crops, the effects of FERONIA receptor kinases on plant growth and development depend on plant hormone signaling, including auxin, abscisic acid and ethylene [32]. There are hormone-related cis-acting elements in *VvLRK10L* genes, indicating that these genes may be involved in plant development by regulating various hormone-mediated signaling pathways. In grapes, ABA not only contributes to stress response but also participates in the regulation of fruit ripening [13,14], while some members of LRK10L are highly expressed after ABA treatment, indicating that they may be involved in this process [14]. In the analysis of promoter activity, GA3 and ABA can enhance *VvLRK10L-16* and *VvLRK10L-42*, respectively, which also indicated that plant hormones can mediate *VvLRK10L* to participate in the regulation of grape development.

In addition, the effects of *VvLRK10L-16* and *VvLRK10L-42* were verified by *Arabidopsis*-mediated stable genetic transformation experiments. As a result, the overexpression of *VvLRK10L-16* and led to 2 ~ 3 d early maturation of *A. thaliana*. Furthermore, the increase of transgenic plant roots indicated that RLK kinase plays an important role in promoting plant root elongation, which is consistent with previous research results [33,34]. *VvLRK10L-42* can also significantly promote the growth of *Arabidopsis* leaves at the seedling stage. These results demonstrated that *VvLRK10L* genes promoted fruit ripening. However, its molecular mechanism in promoting fruit ripening still needs further study.

In this study, we cloned the gene and promoter sequences of *VvLRK10L-16*, and *VvLRK10L-42*, analyzed the cis-acting elements of the promoter sequences, and performed promoter activity analysis and subcellular localization experiments on them. In addition, we also overexpressed *VvLRK10L-16* and *VvLRK10L-42* in *A. thaliana* and found that they can promote early ripening of pods. The results provide a theoretical basis for further research on the function of *VvLRK10L* genes in fruit development.

5. Conclusions

The subcellular localization and promoter activity of *VvLRK10L-16* and *VvLRK10L-42* were analyzed. The results of subcellular localization showed that they were located in the plasma membrane. They contained development-related cis-acting elements through promoter sequence analysis and their promoter sequences were active. Overexpression of *VvLRK10L-16* and *VvLRK10L-42* can promote the development of *Arabidopsis*, especially the maturation of pods.

CRediT authorship contribution statement

Lu Yang: Writing – review & editing, Visualization. **Ding-Ding Zuo:** Writing – original draft. **Jia-Ling Xing:** Writing – review & editing, Methodology. **Da-Long Guo:** Project administration, Methodology, Funding acquisition.

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Declaration of competing interests

No conflict of interest exists in the submission of this manuscript, and the manuscript is approved by all authors for publication.

Supplementary material

https://doi.org/10.1016/j.ejbt.2025.01.003.

Data availability

Data will be made available on request.

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