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ORIGINAL ARTICLE

The AP2/ERF transcription factor SlERF.J2 functions in hypocotyl elongation and plant height in tomato

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Abstract

Key message **Our findings indicated that the SlERF.J2-IAA23 module integrates hormonal signals to regulate hypocotyl elongation and plant height in tomato.**

Abstract Light and phytohormones can synergistically regulate photomorphogenesis-related hypocotyl elongation and plant height in tomato. AP2/ERF family genes have been extensively demonstrated to play a role in light signaling and various hormones. In this study, we identified a novel AP2/ERF family gene in tomato, *SlERF.J2*. Overexpression of *SlERF.J2* inhibits its hypocotyl elongation and plant height. However, the plant height in the *slerf.j2*^{ko} knockout mutant was not significantly changed compared with the WT. we found that hypocotyl cell elongation and plant height were regulated by a network involving light, auxin and gibberellin signaling, which is mediated by regulatory relationship between SlERF.J2 and IAA23. SlERF.J2 protein could bind to *IAA23* promoter and inhibit its expression. In addition, light–dark alternation can activate the transcription of *SlERF.J2* and promote the function of *SlERF.J2* in photomorphogenesis. Our findings indicated that the SlERF.J2-IAA23 module integrates hormonal signals to regulate hypocotyl elongation and plant height in tomato.

Keywords Hypocotyl · Dwarfism · SlERF.J2 · INDOLE-3-ACETIC ACID (IAA23) · Gibberellin · Tomato

Introduction

Light and darkness have different effects on seedlings after germination. Photomorphogenesis is characterized by suppressed hypocotyl elongation, cotyledons open and green, without apical hooks; skotomorphogenesis is characterized by hypocotyl elongation, cotyledons closed and yellowish, apical hooks (Von Arnim and Deng 1996). Cells in the apical meristem divide and elongate resulting in the growth of the hypocotyl (de Wit et al. 2016). Light is the most important energy and signal source for plant development (Li and He 2016). Light signals can be perceived by families of photoreceptors, including phytochromes, cryptochromes, phototropins, and UV resistance locus 8 (UVR8) (Casal 2013). Downstream of these photoreceptors are several transcription factors, including the bHLH

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protein phytochrome-interacting factor (PIFs) (Leivar and Quail 2011) and the bZIP protein elongating hypocotyl 5 (HY5) (Osterlund et al. 2000). PIFs (phytochrome-interacting factors) are a family of basic helix–loop–helix (bHLH) transcription factors that promote hypocotyl elongation in the dark, and phytochromes regulate light responses by promoting the degradation of PIFs (Lorrain et al. 2008). The basic leucine zipper (bZIP) transcription factor (*HY5*) is required to inhibit hypocotyl growth under light conditions (Shi et al. 2011). Many targets of *HY5* are modulators of hormone signaling, including modulators of auxin, gibberellin (GA), abscisic acid (ABA), ethylene, brassinolide (BR), and jasmonic acid (Wang et al. 2012; Lau and Deng 2010).

Plant hormones are the main regulators of plant growth and development. The signaling pathway of the plant hormone auxin and gibberellin (GA) has been studied extensively (Sun 2010; Weijers and Wagner 2016). Auxin has long been regarded as a major regulator of plant growth and development. AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) and auxin response factors (ARF) were two transcriptional regulators of auxin signaling (Liu et al. 2018). The Aux/IAA protein plays a pivotal role in the perception and signaling of the plant hormone auxin (Audran-Delalande et al. 2012), and Aux/IAA gain-of-function mutants display multiple auxin-related phenotypes such as apical dominance, root formation, and hypocotyl elongation (Chaabouni et al. 2009; Bassa et al. 2012; Deng et al. 2012; Su et al. 2014). Silencing of *Sl-IAA27* resulted in impaired auxin sensitivity and reduced leaf chlorophyll content in tomato (Bassa et al. 2012). Silencing of *Sl-IAA3* exhibits altered apical dominance, decreased auxin sensitivity, and exaggerated curvature of the apical hook in the dark (Chaabouni et al. 2009). ARFs bind to auxin response elements to activate or repress transcription of target genes (Zouine et al. 2014). The double mutant *arf6 arf8* displayed a short hypocotyl phenotype in the dark (Nagpal et al. 2005).

It has been well studied that the synergistic regulation of GA, auxin, and light signaling of cell elongation during seedling morphogenesis (Bai et al. 2012; de Lucas et al. 2008; Chaiwanon et al. 2016). GA and auxin are inextricably regulated in plant growth and development, and auxin appears to alter GA responses by interacting with DELLA proteins that act as repressors of GA signaling (Fleet and Sun 2005). DELLA interacts with PIF and inhibits its DNA-binding activity (Feng et al. 2008). GA is sensed by GA-INSENSITIVE DWARF1 (*GID1*) (Shimada et al. 2008). Upregulation of *AtGA20ox1*, *AtGA20ox2* and *AtGA20ox3* increased hypocotyl length by increasing GA production in *Arabidopsis* (Huang et al. 1998). Overexpression of *GA2oxs* results in a dwarf phenotype in *Arabidopsis* (Schomburg et al. 2003). *GID2* is a positive regulator of gibberellin signaling, and inhibition of this gene can lead to a dwarf phenotype in tomato (Liu et al. 2016).

The AP2/ERF TFs (APETALA2/ETHYLENE RESPONSIVE FACTOR) family plays an important role in plant development processes and stress response (Licausi et al. 2013; Muller and Munne-Bosch 2015). There have been many studies on the AP2/ERF family of genes involved in the regulation of light and hormone signals. For example, it has been reported that *Sl-ERF.B3* integrates ethylene and auxin signaling by regulating the expression of the auxin signaling component *Sl-IAA27*, and overexpression of *Sl-ERF.B3* inhibits the expression of *Sl-IAA27* to suppress hypocotyl length and plant height (Liu et al. 2018). ERF109 binds directly to the GCC-box in the promoters of *ASA1* and *YUC2*, two key enzymes in auxin biosynthesis. Overexpression of *ERF109* resulted in a root phenotype similar to auxin overproduction mutants (Cai et al. 2014). *SlERF.F12* negatively regulates fruit ripening by regulating the transcription of ripening-related genes 1-aminocyclopropane-1-carboxylic acid synthase 2 (*ACS2*), *ACS4*, *POLYGALACTURONASE 2a* and *PECTATE LYASE* (Deng et al. 2022). *SlERF.D6* regulates the expression of multiple genes in the SGA synthesis pathway, affects the SGA (Steroidal glycoalkaloids) content of the fruit, and promotes fruit ripening (Guo et al. 2022). *SlERF.E4* can transcriptionally regulate tomato fruit ripening specific expression of the β-D-N-acetylhexosaminidase (*β-Hex*) gene (Irfan et al. 2022). The genes of the AP2/ERF family play an important role in plant growth and development. Recently, more and more gene functions of this family have been revealed, and it has become increasingly important to study the function of this family of genes.

In this study, we found that transgenic tomato seedlings overexpressing of *SlERF.J2* (Solyc02g090790) exhibited the constitutive photomorphogenesis phenotype of a short hypocotyl, and open cotyledons in darkness compared with wild type (WT). In addition, our data revealed that *SlERF.J2* is involved in the regulation of auxin and GA homeostasis, and plays a role in the dwarf phenotype affecting plant growth and development. We further demonstrated that SlERF.J2 could repress the transcription of *IAA23*. Our results suggested that the SlERF.J2-IAA23 module is involved in integrating hormone signaling pathways to control hypocotyl cell elongation and plant height in tomato.

Materials and methods

Plant materials and growth conditions

The WT tomato (*Solanum lycopersicum* Mill. cv. Ailsa Craig) and transgenic seedlings (*SlERF.J2*-OE, *slerf.j2*^{ko} mutant) were grown in a greenhouse under standard conditions (16-h day (28 °C)/8-h night (18 °C) cycle, 80% relative humidity). All seeds were surface sterilized and sown on 1/2

MS medium after incubation and germination. and incubated for 7 days under white light (60 µmol m^{-2} s^{-1}, 16-h day (28 °C)/8-h night (18 °C) cycle, 80% relative humidity), red light (60 µmol m^{-2} s^{-1}, 16-h day (28 °C)/8-h night (18 °C) cycle, 80% relative humidity) and dark (24-h night, 16-h day (28 °C)/8-h night (18 °C) cycle, 80% relative humidity) conditions. For the light-to-dark transition experiments, seedlings were grown under continuous light or dark conditions for 6 days and then transferred to the opposite condition. Hypocotyl length was measured using the ImageJ software. All these samples were collected and immediately frozen in liquid nitrogen and then stored at − 80 °C freezer.

Construction of overexpression and CRISPR/Cas9 knockout vectors and plant transformation

For construction of the *SlERF.J2* overexpression vector, the ORF sequence of the *SlERF.J2* gene was amplified using SlERF.J2-all-F/R primers. Then, the open reading frame (ORF) sequence was cloned into the plant binary vector pBI121 with CaMV 35S as its promoter. The knockout target of SlERF.J2 was designed on the first exon sequence using targetdesign (http://skl.scau.edu.cn/targetdesign). Then the CRISPR/Cas9-SlERF.J2 vector was constructed. The constructed vector was transformed into *Agrobacterium tumefaciens strain LBA4404*. Finally, the constructed vector was transformed into WT tomato cotyledons using the method previously described (Chen et al. 2004). Plants with transgenes were selected using kanamycin and positive transgenic plants were identified by PCR using NPTII-F/R primers. All primers used in this study are listed in Table S1.

Total RNA extraction and qRT-PCR analysis

Trizol reagent (Invitrogen, Shanghai, China) was used to extract total RNA. The RNA extraction method was based on previous research (Xie et al. 2014). RNA was reverse transcribed into cDNA using a kit (Promega, Beijing, China).

Quantitative reverse-transcription PCR (qRT-PCR) was performed by using a CFX96™ RealTime System (Bio-Rad, USA) (Zhang et al. 2020). Relative gene expression levels were analyzed using the $2^{-\Delta\Delta CT}$ method (Nicot et al. 2005) and normalized with the *SlCAC* (Solyc08g006960) gene (Exposito-Rodriguez et al. 2008). Three independent biological replicates were performed for each sample. All primer sequences used in this experiment are listed in Table S1.

Determination of chlorophyll content

Chlorophyll was extracted from frozen tissue in 80% acetone. The extraction method was determined according to previous studies (Arnon 1949). The content of chlorophyll was extracted from cotyledons and hypocotyls (0.1 g) of WT and *SlERF.J2*-OE lines. For the determination of chlorophyll content, total Chl (mg mL^{-1}) = 20.29 × A646 + 8.02 × A663.

Gibberellic acid and paclobutrazol treatment

To test the response of *SlERF.J2* to gibberellins (GA3), 4-week-old WT and *SlERF.J2*-overexpressing tomato seedlings were sprayed with GA3 (50 µM) every 2 days for 8 days. These GA3-sprayed leaves were collected for RNA extraction. The plant height was measured. All samples were subjected to three biological replicates.

Transient expression assay in tobacco leaves

The ORF sequence of *SlERF.J2* gene was amplified and cloned into the pGreen II 62-SK vector and used as an effector. The promoter fragment of *IAA23* and *IAA27* were amplified and cloned into the pGreen II 0800-LUC vector and used as a reporter (Hellens et al. 2005; Xu et al. 2018). The effector and reporter were co-transformed into *N. benthamiana* leaves. Firefly luciferase and Renilla luciferase were measured using a dual-luciferase reporter assay (Promega) according to the manufacturer's instructions. The binding activity was calculated by detecting the LUC–REN ratio. All primer sequences used in this experiment are listed in Table S1.

Yeast one-hybrid assay

Yeast one-hybrid (Y1H) assay was performed according to the instructions for the Matchmaker Gold Yeast One Hybrid System (TaKaRa). The ORF sequence of *SlERF.J2* gene was amplified and transferred into the pGADT7 vector as a prey vector. The IAA23 promoter sequence was amplified and transferred into pAbAi as a bait vector. According to the TaKaRa's instructions, the pAbAi-proIAA23 plasmid was linearized and transformed into the Y1H Gold yeast cells. Aureobasidin A (AbA) screened the minimum concentration that inhibits the bait strain. The prey vector was transformed into the bait yeast strain and screened on SD/-Leu (with or without AbA) medium. The pAbAi-p53 (+) and pGADT7-p53 (+) plasmids were used as positive controls. Incubate in the dark (30 °C) for 2–3 days. All primer sequences used in this experiment are listed in Table S1.

Statistical analysis

Data were subjected to analysis of variance with SPSS 26.0. Student's *t* test (*$P < 0.05$, **$P < 0.01$) was performed to analyze the significant difference. ANOVA statistical analyses were performed using SPSS 26.0. Significant differences ($P < 0.05$) between treatments, as determined by Tukey's tests, are indicated with different letters. All data are taken from the average of at least three independent biological replicates.

Results

Light/dark regulates transcription of *SlERF.J2*

Light and darkness are the primary regulators of photomorphogenesis and skotomorphogenesis in plant. To explore the effects of specific light and darkness on tomato seedling growth, we evaluated seedling growth of WT under continuous white light (WL), red light (RL) and dark conditions. Under WL and RL conditions, WT seedlings exhibited short hypocotyls, open cotyledons, and no apical hooks. Under dark conditions, WT seedlings exhibited long hypocotyls, yellowed cotyledons, and apical hooks (Fig. 1A–C). Under light conditions, the seedlings maintained photomorphogenesis and their hypocotyl length was shorter than that of seedlings under dark conditions (Fig. 1D). To obtain some clues of whether *SlERF.J2* was involved in the morphogenesis of seedlings under different light conditions, we investigated the expression patterns of *SlERF.J2* under different light treatments by quantitative RT-PCR technique (qRT-PCR). The results showed that the expression level of *SlERF.J2* in hypocotyls under WL and RL treatments was higher than that of under dark treatments (Fig. 1E).

To further investigate the expression of *SlERF.J2* under different light conditions, we transferred light-grown seedlings to the dark and dark-grown seedlings to light (Fig. 1F, G), and qRT-PCR was performed to detect the expression of *SlERF.J2*. As shown in Fig. 1H, the expression level of *SlERF.J2* in light-grown seedlings was lower than that in dark-grown seedlings. After the seedlings were transferred to dark conditions, *SlERF.J2* expression increased for 24 h and then decreased up to 48 h. In contrast, after seedlings were transferred from dark to light conditions, *SlERF.J2* expression decreased within 12 h and a low level was maintained up to 48 h. These results suggested that the increased expression level of *SlERF.J2* was mainly caused by the light-to-dark transition. To verify whether *SlERF.J2* has functional redundancy with other tomato ERFs genes, a phylogenetic tree of tomato ERF family proteins was constructed (Fig. S1). The results showed that SlERF.J2 did not have high homology to other ERF family proteins. We speculate that the function of the *SlERF.J2* gene may not be affected by other homologous genes in tomatoes.

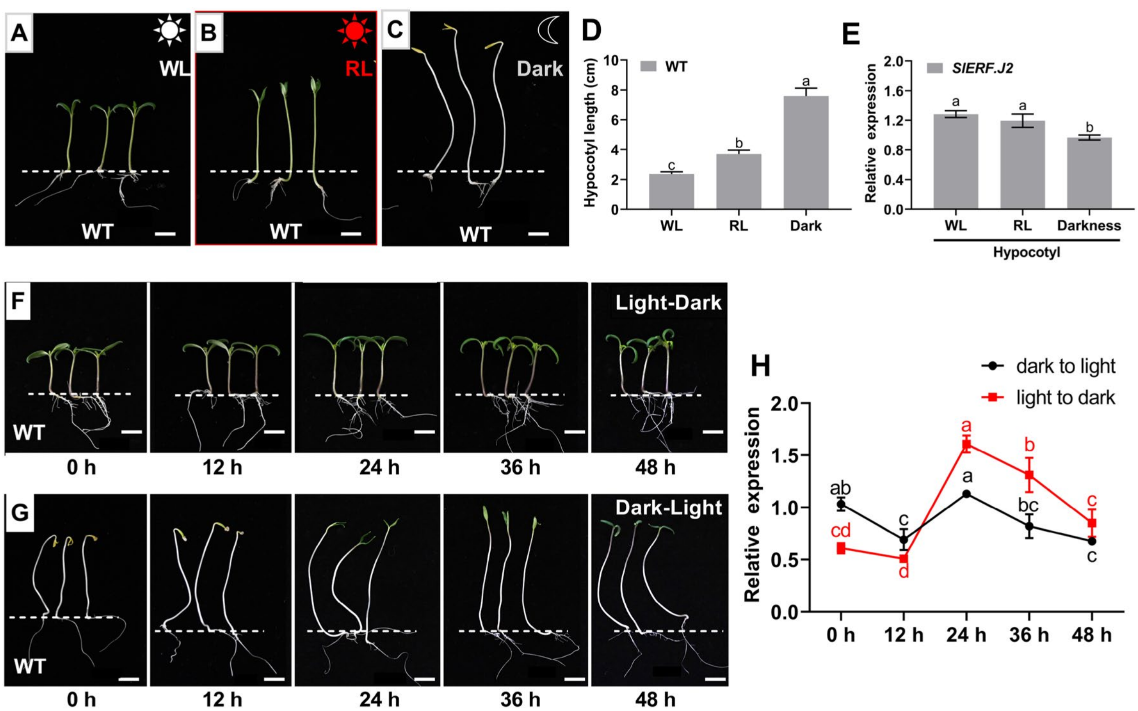

Fig. 1 Expression profile of *SlERF.J2* in WT. **A–C** Growth of WT seedlings for 6 days under continuous white light (WL), red light (RL) and dark. **D** Hypocotyl length of WT seedlings under the conditions of **(A–C)**. **E** Expression levels of *SlERF.J2* in the hypocotyls of WT seedlings under the conditions of **(A–C)**. **F, G** Seedlings were grown under continuous light or dark conditions for 6 d and then transferred to the opposite conditions for the indicated times. **H** The expression level of *SlERF.J2* was determined by qRT-PCR. Seedlings were grown under continuous light or dark conditions for 6 d and then transferred to the opposite conditions. Data are means (SD) of at least 20 seedlings. Scale bars are 1 µm. All data are means (± SE) of three independent biological replicates (**P* < 0.05, ***P* < 0.01)

Overexpression of *SlERF.J2* triggers a constitutive photomorphogenetic responses under dark and light conditions

To investigate the role of the *SlERF.J2* gene, we generated transgenic plants overexpressing of *SlERF.J2* (*SlERF.J2*-OE) (Fig. S2). Under light conditions, the hypocotyl length of *SlERF.J2*-OE plants was significantly shorter compared with WT (Fig. 2A). We further evaluated the growth of transgenic and WT seedlings under dark conditions. Consistent with the results under light conditions, the hypocotyl length of *SlERF.J2*-OE plants was significantly shortened and the apical hook were inconspicuous compared to WT (Fig. 2E). To further investigate the effect of light–dark alternation on the growth of *SlERF.J2*-OE and WT seedlings, we treated the seedlings with light–dark alternation. More interestingly, the hypocotyl length of *SlERF.J2*-OE seedlings did not change during transition from light to dark, while the hypocotyl length of WT seedlings became longer (Fig. 2B, I). During the transition from dark to light, the hypocotyl length of *SlERF.J2*-OE and WT seedlings did not change (Fig. 2F, I). In addition, during the transition from light to dark, the hypocotyls of WT seedlings were elongated and the chlorophyll content decreased compared with that of *SlERF.J2*-OE seedlings (Fig. 2C, D, J). During the transition from dark to light, the cotyledons of the *SlERF.J2*-OE seedlings opened and accumulated more chlorophyll than that of WT (Fig. 2G, H, J). These results indicated that overexpression of *SlERF.J2* in WT plants triggered a constitutive photomorphogenic-like response under both dark and light conditions, and the resulting in shorter hypocotyls of *SlERF.J2*-OE lines seedlings.

Gene expression profiles in *SlERF.J2*-OE and WT tomato seedlings

To evaluate the role of *SlERF.J2* in controlling hypocotyl growth, we performed qRT-PCR analysis on WT and *SlERF.J2*-OE seedlings grown under light conditions. Aux/IAA mutants exhibit multiple auxin-related developmental phenotypes, including apical dominance, hypocotyl elongation, and leaf expansion (Tatematsu et al. 2004). In this study, expression of *IAA2*, *IAA3*, *IAA13*, *IAA19*, and *IAA23* were detected in seedlings of WT and *SlERF.J2*-OE lines (Fig. 3A). The expression levels of all genes were downregulated in the *SlERF.J2*-OE lines compared with WT. The basic leucine zipper (bZIP) transcription factor (*HY5*) is required to inhibit hypocotyl growth under light conditions.

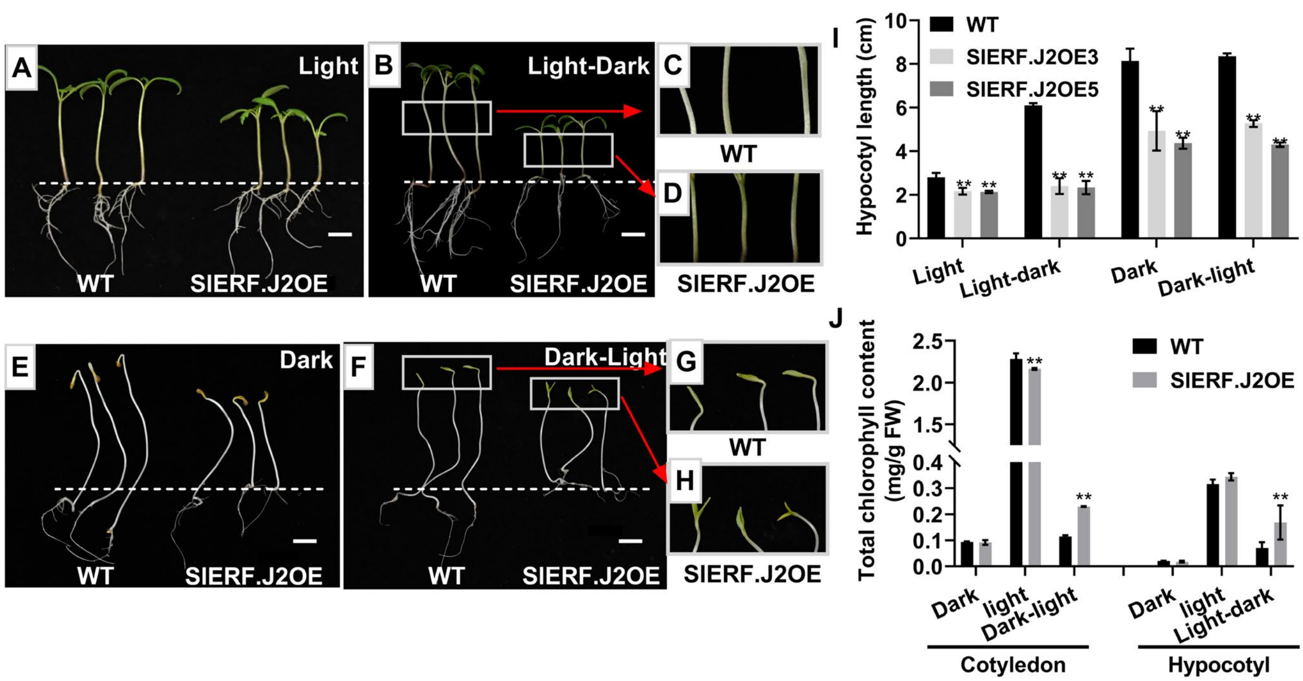

Fig. 2 Overexpression of *SlERF.J2* in tomato triggers a constitutive photomorphogenetic response. **A** WT and *SlERF.J2*-OE seedlings were grown under continuous light for 6 days. **B** Seedlings grown in A were transferred to dark conditions for 2 days. **C, D** The stem of the WT and *SlERF.J2*-OE seedling in B. **E** WT and *SlERF.J2*-OE seedlings were grown under continuous dark for 6 days. **F** Seedlings grown in (E) were transferred to light conditions for 2 days. **G, H** The cotyledon of the WT and *SlERF.J2*-OE seedling in (F). **I** Hypocotyl length of WT and *SlERF.J2*-OE seedlings in A, B, E, F. **J** Chlorophyll content in cotyledons and hypocotyls of WT and *SlERF.J2*-OE seedlings in A, B, E, F. Data are means (SD) of at least 20 seedlings. All data are means (±SE) of three independent biological replicates ($*P<0.05$, $**P<0.01$)

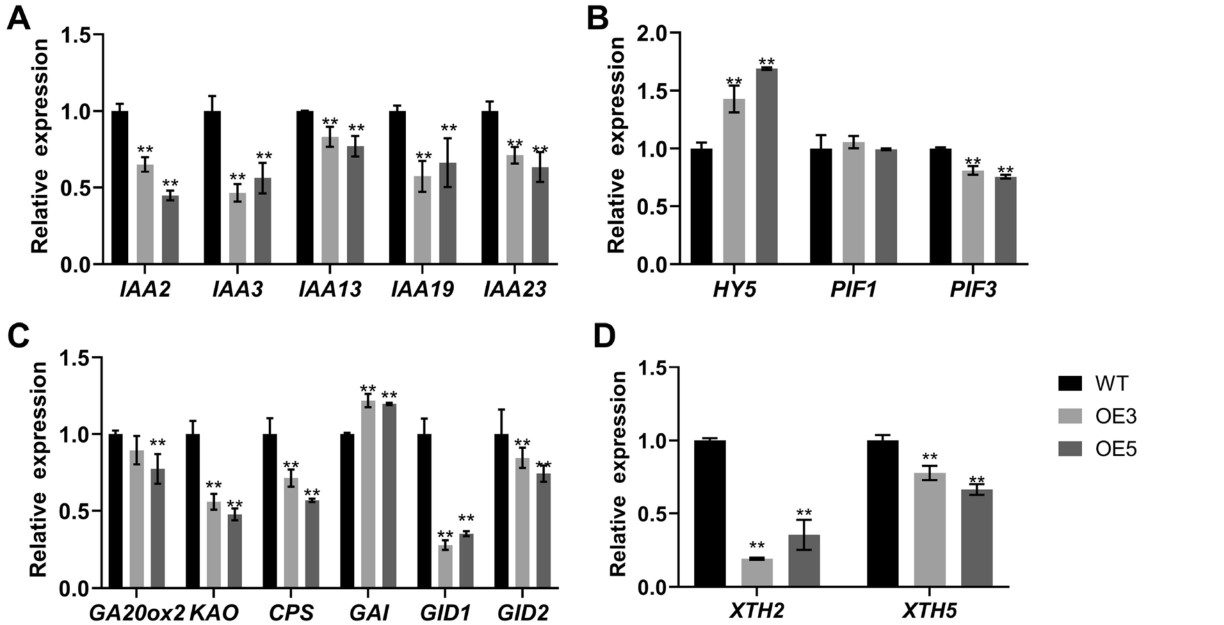

Fig. 3 Expression levels of genes related to auxin/gibberellin in wild-type and SlERF.J2-overexpressing seedlings. **A** Expression levels of *IAA2*, *IAA3*, *IAA13*, *IAA19* and *IAA23* in WT and *SlERF.J2*-OE seedlings. **B** Expression levels of *HY5*, *PIF1* and *PIF3* in WT and *SlERF.J2*-OE seedlings. **C** Expression levels of *GA20ox2*, *KAO*, *CPS*, *GAI*, *GID1* and *GID2* in WT and *SlERF.J2*-OE seedlings. **D** Expression levels of *XTH2* and *XTH5* in WT and *SlERF.J2*-OE seedlings. Expression values are relative to the *SlCAC* gene. All data are means (±SE) of three independent biological replicates (*$P<0.05$, **$P<0.01$)

PIF3 is a transcription factor that inhibits photomorphogenesis. In addition, the expression of light response-related genes *HY5* was significantly higher and *PIF3* was decreased in overexpression lines compared with WT.

Gibberellin (GA) and cell elongation-related genes were detected in seedlings of WT and *SlERF.J2*-OE lines. The expression of all tested GA important biosynthesis enzymes *GA20ox2*; two genes in the early steps of the GA biosynthetic pathway, *KAO* and *CPS*; and *GID1* and *GID2* encoding GA receptors were down-regulated in *SlERF.J2*-OE seedlings compared to wild type (Fig. 3C). The expression of *GAI*, encoding the DELLA protein as a repressor of GA signaling (Murase et al. 2008), was up-regulated in the *SlERF.J2*-OE lines. *XTH2* and *XTH5* play a role in cell expansion process (Saladie et al. 2006; Catala et al. 2001) and were significantly down-regulated in overexpressing lines.

SlERF.J2 affects tomato plant height

To gain further understanding of the function of *SlERF.J2* in tomato, we cultivated tomato seedlings of WT and *SlERF.J2*-OE lines under the same growth conditions. Four weeks after sowing, the plant height of the *SlERF.J2*-OE lines was significantly reduced compared with WT (Fig. 4A). From the top view of tomato seedlings, we observed that the leaves of *SlERF.J2*-OE plants were more compact than those of WT (Fig. 4B–E). This phenotype continued until the 12th week flowering and fruiting stage. Compared with WT, the *SlERF.J2*-OE lines had significantly lower plant height and also smaller internode lengths than WT plants (Fig. 4F). As shown in Fig. 4F, when the WT plants grew to 110 cm, the plant height of the *SlERF.J2*-OE lines was 42–60 cm, which was obviously about half lower than that of the WT plants. This demonstrates that the dwarf transgenic lines depicted the shortening of internodal length. To further confirm the role of *SlERF.J2* in plant development, We generated *slerf.j2* knockout mutants in tomatoes using the CRISPR/Cas9 system. The type of knockout is shown in Fig. S3. During tomato growth and development, we found that overexpression of *SlERF.J2* significantly suppressed plant height, while the *slerf.j2*^{ko} mutants had no obvious change compared with WT (Fig. 4J). This phenotype was maintained when the tomato was in the flowering stage (Fig. S4A–G). Statistical analysis of the plant height of WT, *SlERF.J2*-OE and *slerf.j2*^{ko} lines showed that the *SlERF.J2*-OE lines was significantly lower than WT, while the *slerf.j2*^{ko} lines had no significant change compared with WT (Fig. S4H). These results indicated that *SlERF.J2* affected the internodal length and height of tomato plants.

Overexpression of *SlERF.J2* affects auxin signaling

Auxin has long been considered a major regulator of plant growth and development (Zouine et al. 2014). In

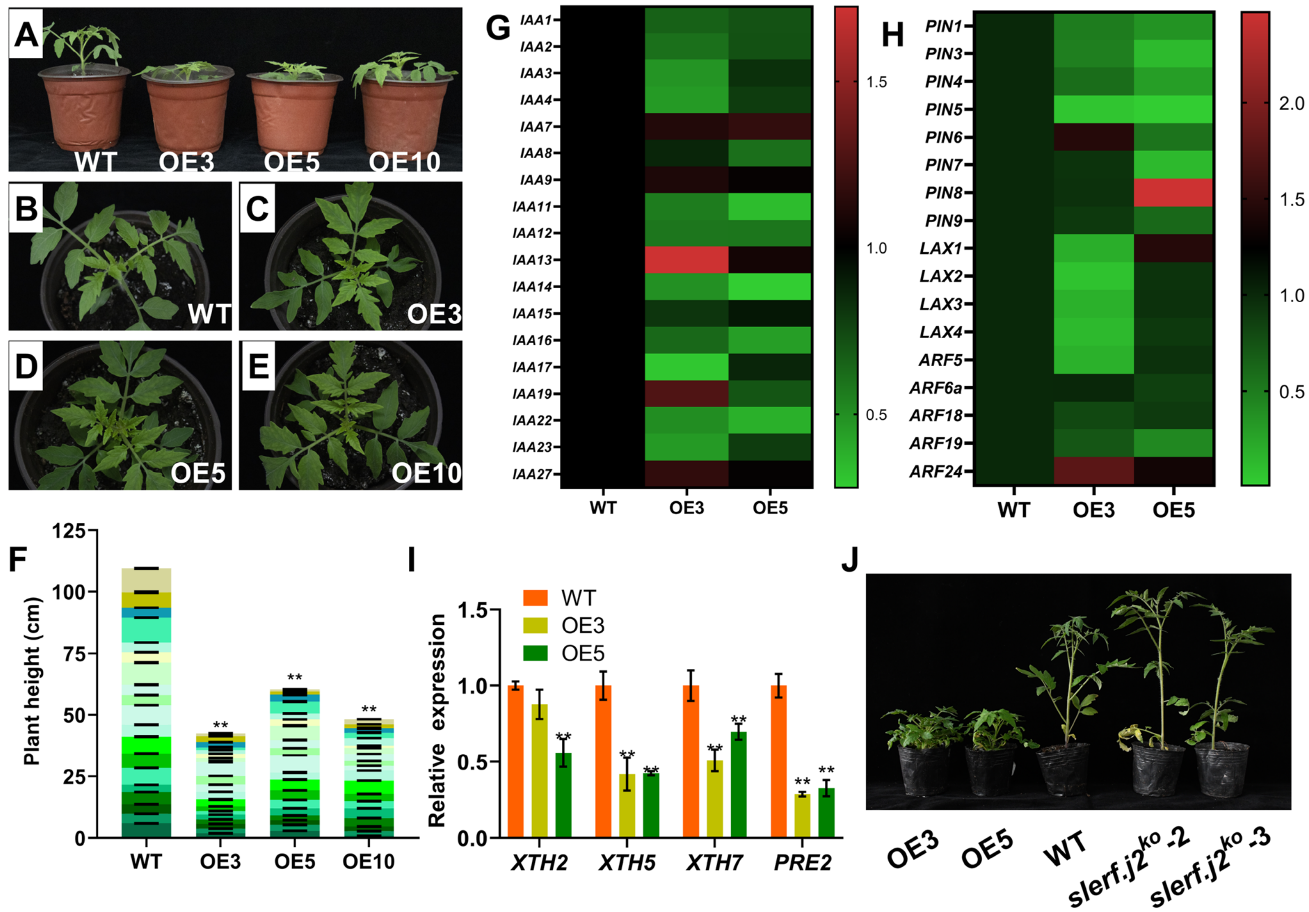

Fig. 4 *SlERF.J2* affects plant growth and the expression levels of growth-related genes. **A** Plant height phenotypes of WT and *SlERF.J2*-OE lines. **B–E** Top view of plants in (A). **F** Height of WT and *SlERF.J2*-OE tomato plants at 12 weeks. **G, H** qRT-PCR analysis of auxin-related genes *IAA1*, *IAA2*, *IAA3*, *IAA4*, *IAA7*, *IAA8*, *IAA9*, *IAA11*, *IAA12*, *IAA13*, *IAA14*, *IAA15*, *IAA16*, *IAA17*, *IAA19*, *IAA22*, *IAA23*, *IAA27*, *PIN1*, *PIN3*, *PIN4*, *PIN5*, *PIN6*, *PIN7*, *PIN8*, *PIN9*, *LAX1*, *LAX2*, *LAX3*, *LAX4*, *ARF5*, *ARF6a*, *ARF18*, *ARF19*, and *ARF24* expression level. **I** Expression levels of leaves cell development-related genes *XTH2*, *XTH5*, *XTH7*, and *PRE2*. Expression values are relative to the *SlCAC* gene. The relative expression of each gene in WT leaves was normalized to 1. **J** Plant height phenotypes of *SlERF.J2*-OE lines, WT and *slerf.j*^{2ko} lines. All data are means (±SE) of three independent biological replicates (*$P<0.05$, **$P<0.01$)

this study, we analyzed the transcript accumulation of auxin-related genes in leaves of WT and *SlERF.J2*-OE lines, including eighteen Aux/IAA transcription factor genes (*IAA1*, *IAA2*, *IAA3*, *IAA4*, *IAA7*, *IAA8*, *IAA9*, *IAA11*, *IAA12*, *IAA13*, *IAA14*, *IAA15*, *IAA16*, *IAA17*, *IAA19*, *IAA22*, *IAA23*, *IAA27*) (Audran-Delalande et al. 2012), eight encoding PIN auxin efflux transport protein (*PIN1*, *PIN3*, *PIN4*, *PIN5*, *PIN6*, *PIN7*, *PIN8*, *PIN9*) (Pattison and Catala 2012), four auxin transporter genes (*LAX1*, *LAX2*, *LAX3*, *LAX4*) (Pattison and Catala 2012) and five auxin response genes (*ARF5*, *ARF6a*, *ARF18*, *ARF19*, *ARF24*) (Fig. 4G, H) (Zouine et al. 2014). Compared with WT, the expression levels of all other genes were down-regulated except for *IAA7*, *IAA13*, *IAA19*, *IAA27*, *PIN8* and *ARF24* which were up-regulated in *SlERF.J2*-OE lines. These results suggested that auxin homeostasis may be disrupted in the *SlERF.J2*-overexpressing plants.

In addition, the expression levels of genes related to plant cell expansion and cell division, *XTH2*, *XTH5*, *XTH7*, and *PRE2*, showed significant changes in overexpression lines compared with WT (Fig. 4I). According to previous reports, *XTH2*, *XTH5* and *XTH7* play roles in cell wall reorganization and cell expansion process (Catala et al. 2001; Saladie et al. 2006). *PRE2* plays a role in the regulation of cell size (Zhu et al. 2019). These genes were down-regulated in the *SlERF.J2*-OE lines, suggesting that *SlERF.J2* may affect cell development to affect plant height.

The role of *SlERF.J2* in gibberellin-dependent growth and development

Gibberellin (GA) is an important hormone that regulates plant growth (Depuydt and Hardtke 2011). Given that overexpression of *SlERF.J2* caused a dwarf phenotype,

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we sought to further explore the role of GA in the *SlERF.J2*-OE lines. Here, we tested the response of WT and *SlERF.J2*-OE lines to GA treatment. We first sprayed 50 μM GA3 or aqueous solution as the control to 4-week-old plant leaves every 2 days for 8 days. Thereby, these plants were divided into two groups: CK-0 d and CK-8 d (Fig. 5A, C); GA3-0 d and GA3-8 d (Fig. 5B, D). The WT plants were significantly taller than *SlERF.J2*-OE plants before GA3 treatment (Fig. 5A, B). In the GA3 treatment experiment, WT plants in the control group were still significantly higher than *SlERF.J2*-OE plants (Fig. 5C); after exogenous spraying of GA3, both WT and *SlERF.J2*-OE plants grew significantly taller, but WT plants were a slightly taller than the *SlERF.J2*-OE plants (Fig. 5D). Plant heights of transgenic and WT plants were measured as shown in Fig. 5E, F, and showed that after GA3 treatment, WT plants were about 7 cm longer than the control group, while *SlERF.J2*-OE plants were 11–15 cm longer than the control group. These results suggested that the dwarf phenotype of *SlERF.J2*-OE lines could be partly rescued by GA3 application, and that *SlERF.J2*-OE plants were more sensitive to exogenous GA3 stimulation.

We further speculated that overexpression of *SlERF.J2* might change the sensitivity of the transgenic lines to GA3, so the sensitivity of tomato seedlings to GA3 was performed (Fig. S5A). To examine the response of seedlings to GA3, we transferred the germinated seeds to MS medium without or with GA3. After GA3 treatment, the hypocotyl lengths of WT and *SlERF.J2*-OE lines were obviously promoted, but the hypocotyls of the seedlings of *SlERF.J2*-OE lines were promoted by 66–70%, and the hypocotyls of WT seedlings were promoted by 61% (Fig. S5B), suggesting that the *SlERF.J2*-OE seedlings were more sensitive to GA3.

Overexpression of *SlERF.J2* regulates the transcripts accumulation of gibberellins-related genes

To further explore the possibility of *SlERF.J2*-mediated GA pathway change, we examined the expression levels of GA-related genes in tomato leaves of WT and *SlERF.J2*-OE lines before and after GA treatment. Except for *CPS*, the expression of all tested GA biosynthetic genes *KS*, and *KAO* was down-regulated, while the GA catabolism gene *GA2ox2* was up-regulated (Fig. 6E) in *SlERF.*

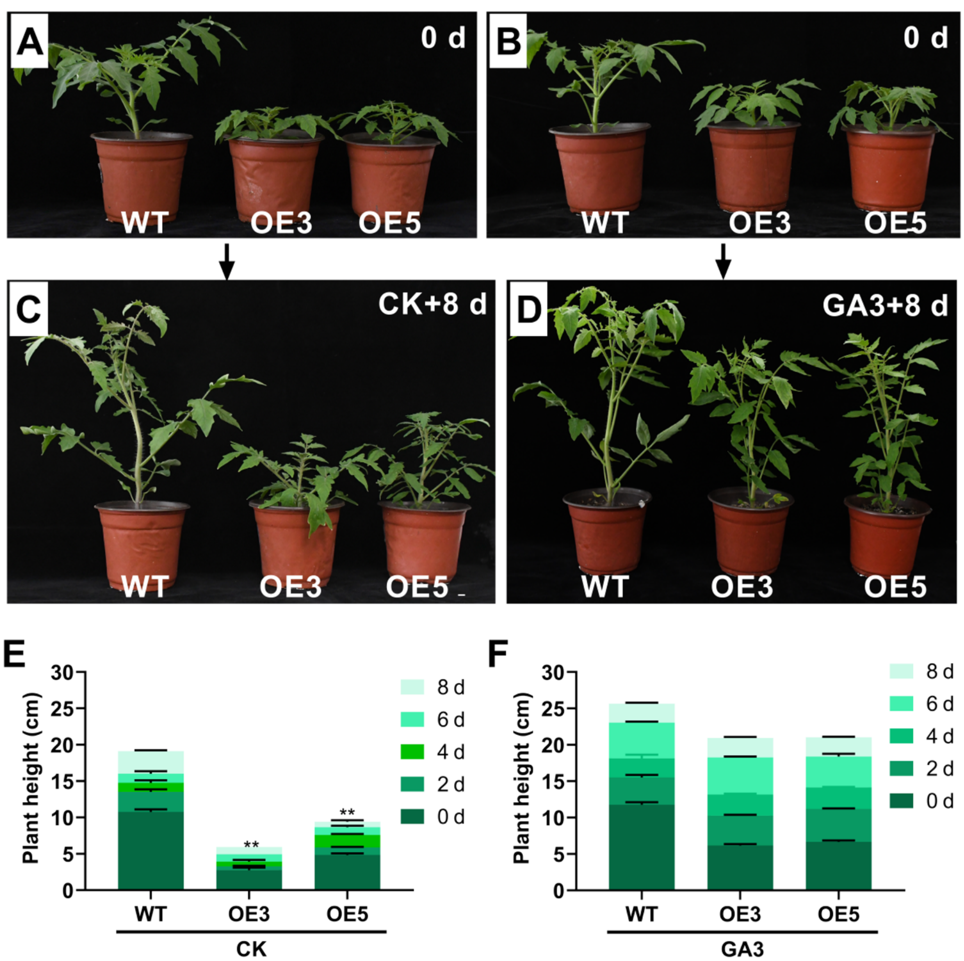

Fig. 5 The phenotype of WT and *SlERF.J2*-OE transgenic tomato plants under control and GA3 treatments. **A, B** Growth characteristics of wild-type and transgenic tomato plants before treatment. **C** Growth characteristics of control wild-type and transgenic tomato plants. **D** Growth characteristics of wild-type and transgenic tomato plants after 8 days of GA3 treatment. **E, F** Height of WT and *SlERF.J2*-OE tomato plants after control and GA3 treatment. All data are means (±SE) of three independent biological replicates (*$P<0.05$, **$P<0.01$)

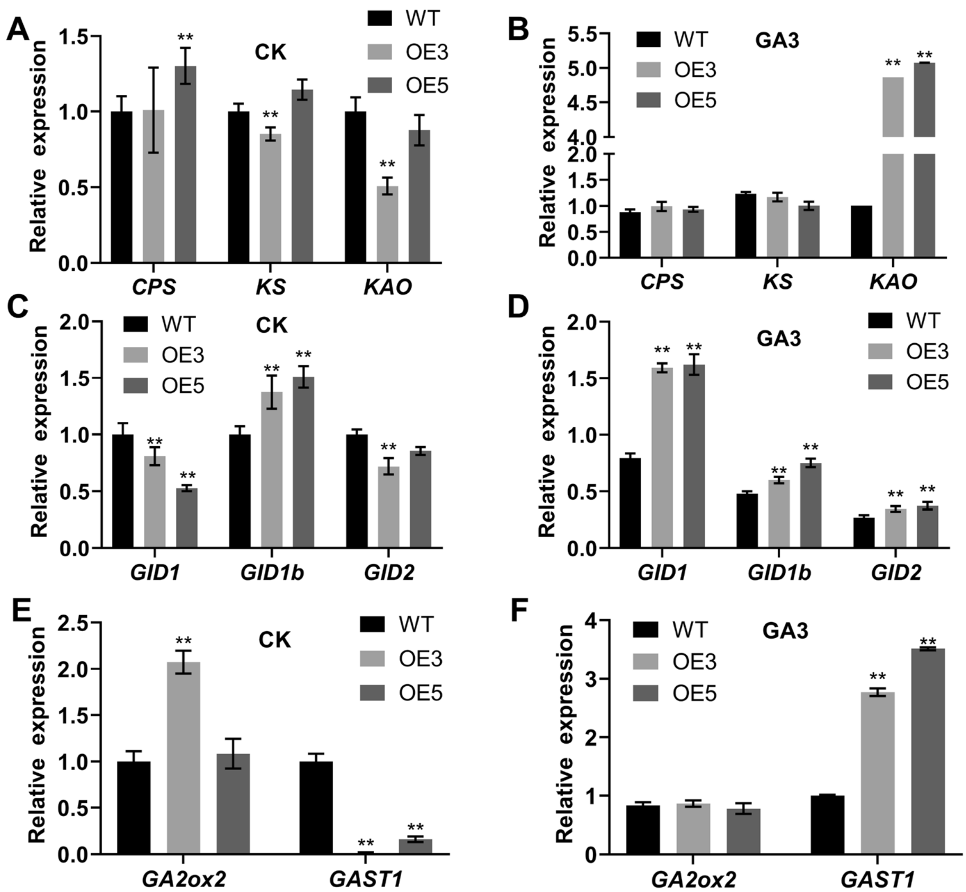

Fig. 6 Expression levels of GA-related genes in WT and *SlERF.J2*-OE transgenic plants under control and GA3 treatments. **A, C, E** The expression of *CPS*, *KS*, *KAO*, *GID1*, *GID1b*, *GID2*, *GA2ox2* and *GAST1* genes was analyzed by qRT-PCR under control conditions. **B, D, F** The expression of *CPS*, *KS*, *KAO*, *GID1*, *GID1b*, *GID2*, *GA2ox2* and *GAST1* genes was analyzed by qRT-PCR under GA3 treatments conditions. All data are means (± SE) of three independent biological replicates (**P* < 0.05, ***P* < 0.01)

J2-OE tomato leaves. In addition, the GA receptor genes *GID1* and *GID2* were down-regulated (Voegele et al. 2011) (Fig. 6C), while the expression of *GID1b* was up-regulated (Fig. 6C). Meanwhile, the expression of the gibberellin-inducible gene *GAST1* (Shi and Olszewski 1998) was significantly down-regulated (Fig. 6E). These results indicated that the overexpression of *SlERF.J2* could affect gibberellin metabolism and signal strength in leaf development.

We identified the responsiveness of *SlERF.J2*-OE and WT plants to GA3. With the 8 days application of GA3, these plants showed the response in plant height increment, and GA-related genes were further detected using qRT-PCR. After GA3 treatment, the expression levels of the GA biosynthetic genes *CPS* and *KS* genes did not change compared with WT, while the *KAO* gene was significantly up-regulated (Fig. 6B) in the *SlERF.J2*-OE lines. GA receptor genes (*GID1*, *GID1b*, *GID2*) were also up-regulated (Fig. 6D). The GA catabolism gene *GA2ox2* was unchanged, while the gibberellin-inducible gene *GAST1* was significantly up-regulated (Fig. 6F). These results suggested that GA3 treatment increases the expression of GA-related genes in *SlERF.J2*-OE lines in tomato.

SlERF.J2 directly targets the auxin transcription factor *IAA23* gene

Given that overexpression of *SlERF.J2* suppressed tomato seedling hypocotyl length and plant height, among the differentially expressed genes, the sequence analysis of IAA-related genes showed that *IAA23* and *IAA27* promoter sequences contained DRE (dehydration response element) elements (Fig. S6). It was previously reported that Sl-ERF.B3 regulates the expression of *Sl-IAA27* by directly binding to its promoter (Liu et al. 2018). In addition, qRT-PCR analysis results revealed that the gene expression levels of *IAA23* and *IAA27* were down-regulated in the *SlERF.J2*-OE lines compared with WT (Fig. 4G). To investigate whether SlERF.J2 can regulate the activity of the *IAA23* and *IAA27* promoters, a transient transactivation assays was performed in *N. benthamiana* leaves. The promoters of *IAA23* and *IAA27* genes were, respectively, cloned into pGreen II 0800-LUC vector, and then co-transformed into tobacco leaves with the effector 35S::SlERF.J2 or empty vector (Fig. 7A). As shown in Fig. 7B, the LUC/REN ratio of IAA23pro was inhibited by approximately 40% in the presence of SlERF.J2 compared to the control (empty vector). As shown in Fig. 7C, the

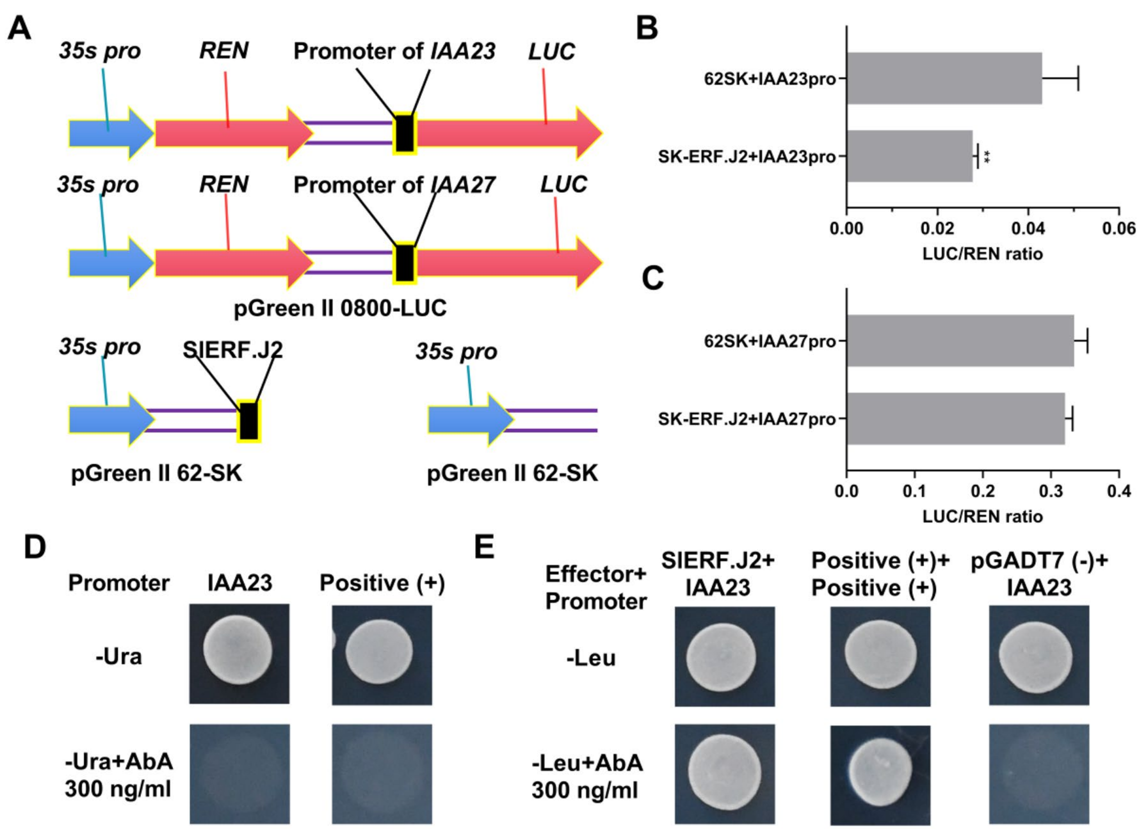

Fig. 7 SlERF.J2 interacts with XI and PLA8 and regulates the activity of the *IAA23* promoter. **A** Schematic map of the transient expression vectors pGreenII-0800-LUC and pGreenII-62-SK. *REN* renilla luciferase, *LUC* firefly luciferase. **B, C** Transcriptional regulation of *IAA23* and *IAA27* promoters by SlERF.J2. All data are means (± SE) of three independent biological replicates (*$P < 0.05$, **$P < 0.01$). **D** The IAA23 promoter and the positive control in yeast grown on SD/-Ura medium containing aureobasidin A (− Ura + AbA) did not detect the auto-activation ability. **E** The interaction between SlERF.J2 and the IAA23 promoter was determined by the yeast one-hybrid assay. The interactions were determined on SD/-Leu medium in the presence of AbA (− Leu + AbA)

LUC/REN ratio of IAA27pro did not change significantly in the presence of SlERF.J2 compared to the control (empty vector). To further determine whether *IAA23* was the direct target of SlERF.J2, we examined the ability of SlERF.J2 to directly bind to the *IAA23* promoter using a yeast one-hybrid (Y1H) assay (Fig. 7D, E). The results showed that the promoter of *IAA23* could be recognized by SlERF.J2. Taken together, these results indicated that SlERF.J2 can directly target the auxin transcription factor *IAA23* and that the activity of the *IAA23* promoter was negatively regulated by SlERF.J2 in vivo.

Discussion

The AP2/ERF transcription factor family is involved in many growth and developmental processes in plants (Xie et al. 2019). It has been reported that *CBF1*, an AP2/ERF family transcription factor, increases the protein abundance of PIF4 and PIF5 and promotes hypocotyl growth under ambient temperatures in *Arabidopsis* (Dong et al. 2020). Two independent *Arabidopsis* mutations of *AtERF71* and *GmERF75* showed shorter hypocotyls, and overexpression of *GmERF75* rescued the short hypocotyl phenotypes in these mutants (Zhao et al. 2019). Members of the plant-specific transcriptional regulator group-VII ERF (ERF-VII) family were involved in the regulation of shoot elongation and photomorphogenesis (Gibbs et al. 2014). Here, we report that *SlERF.J2* was a negative regulator of hypocotyl elongation and plant height in tomato. In this study, expression of *SlERF.J2* was up-regulated during light-to-dark transition (Fig. 1H), and the hypocotyl length of the seedlings of the *SlERF.J2*-OE lines was shorter than that of the WT under both light and dark conditions (Fig. 2A, E). When the light-treated seedlings were transferred to dark conditions, the hypocotyl length of the WT seedlings increased significantly, whereas the hypocotyl length of the *SlERF.J2-OE* lines was unchanged (Fig. 2B, I). In addition, the expression of *SlERF.J2* was induced under dark conditions, further indicating that overexpression of *SlERF.J2* could inhibit the length of hypocotyl.

The phytochrome-interacting factor *pif3* mutants have been reported to exhibit a short hypocotyls under red light (Job and Datta 2021). In addition, *PIF3* is a positive regulator of chloroplast development, and the *pif1pif3* double mutant showed elevated protochlorophyllide levels, decreased hypocotyl elongation and increased cotyledon opening in the dark (Stephenson et al. 2009). Here, we examined the expression levels of *PIF1* and *PIF3* in WT and *SlERF.J2*-OE plant seedlings. Compared with WT tomato plants, the expression level of *PIF1* did not change significantly, while the expression level of *PIF3* was down-regulated in *SlERF.J2*-OE plants. After dark-to-light culture, the cotyledons of *SlERF.J2*-OE seedlings were opened compared with WT seedlings (Fig. 2G, H), and the chlorophyll content of *SlERF.J2*-OE seedlings was found to be higher in cotyledons (Fig. 2J), indicating that *SlERF.J2*-OE seedlings accumulated more protochlorophyllide in the dark, which is similar to the phenotype of *pif3* mutants. This result indicated that overexpression of *SlERF.J2* affected the expression of *PIF3*, and the transgenic seedlings maintained photomorphogenic properties. We speculate that *SlERF.J2* may be involved in light signaling and plastid development, thereby affecting hypocotyl elongation.

Plant growth and development was coordinated by a complex network of interacting hormones. Sl-ERF.B3 inhibits the expression of *Sl-IAA27* by directly binding to its promoter. Ectopic expression of *Sl-ERF.B3* leads to impaired sensitivity to auxin, resulting in shortened hypocotyls and dwarfing plants (Liu et al. 2018). *AtERF109* mediates cross-talk between JA signaling and auxin biosynthesis, thereby regulating lateral root formation (Cai et al. 2014). In this study, we further cultivated tomato seedlings and found that overexpression of *SlERF.J2* resulted in a dwarf phenotype (Fig. 4A). The *slerf.j2* knockout mutant did not affect plant height (Fig. 4J). In this study, we found that knocking out the mutant *slerf.j2* had no effect on plant height, possibly due to the low background expression level of the *SlERF.J2* gene in tomato tissues, and the expression of *SlERF.J2* gene may not be needed during the growth and development of tomato, on the contrary, overexpression of *SlERF.J2* gene will inhibit the elongation of tomato hypocotyl and plant height. This phenotype was further verified by detecting the expression of auxin and GA-related genes (Figs. 4G, H; 6A, C, E). First, we demonstrated that overexpression of *SlERF.J2* altered the mRNA accumulation of some auxin-related genes by qRT-PCR analysis. The results showed that the expression of most auxin-related genes was down-regulated in the *SlERF.J2*-OE lines compared to WT. Subsequently, it was demonstrated that SlERF.J2 could bind to the promoter of *IAA23* and inhibit its expression by a dual-luciferase reporter system (Fig. 7). These results suggested that overexpression of *SlERF.J2* may lead to impaired sensitivity to auxin, resulting in shortened hypocotyl and dwarfing plants. In addition, GA also plays an important role in regulating cell expansion and plant height (Schomburg et al. 2003). We found that the dwarf phenotype of *SlERF.J2*-OE lines could be partly rescued by exogenous application of GA3, and *SlERF.J2*-OE plants were more sensitive to exogenous GA3 stimulation. By detecting GA-related genes, it was found that the expression of gibberellin-inducible gene (*GAST1*) genes was down-regulated in *SlERF.J2*-OE lines compared with WT. These results suggested that overexpression of *SlERF.J2* may inhibit gibberellin synthesis by inhibiting gibberellin-inducible genes, resulting in a dwarf phenotype. However, exogenous application of GA3 partially rescued the dwarf phenotype.

In short, we report an ethylene transcription factor, *SlERF.J2*. We demonstrate that overexpression of *SlERF.J2* affects hypocotyl elongation and plant height from

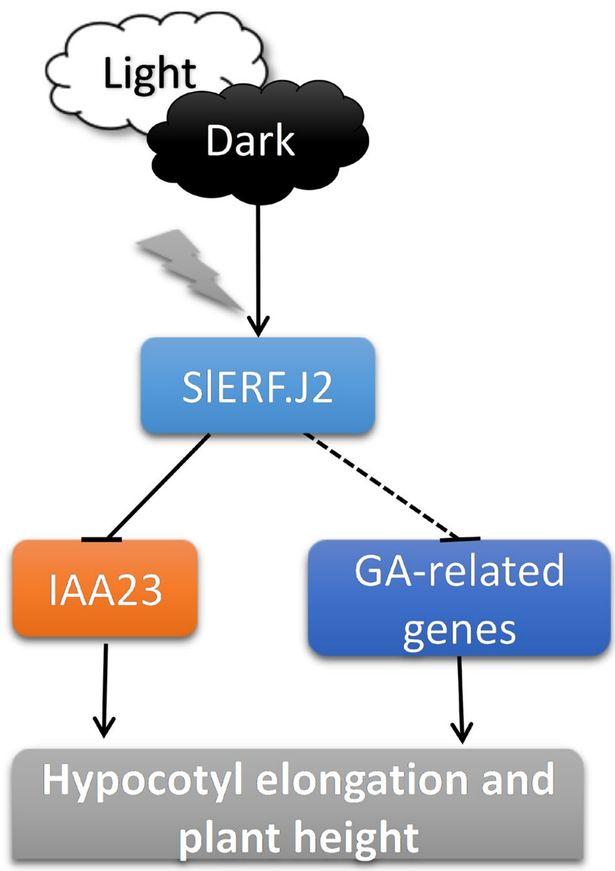

Fig. 8 A proposed model illustrates the regulatory role of SlERF.J2 in the hypocotyl and plant high. Under the alternation of darkness and light condition, the expression of *SlERF.J2* can be induced; SlERF.J2 can regulate the promoter activity of *IAA23* and inhibit its expression; overexpression of *SlERF.J2* may inhibits the expression of GA-related genes. In conclusion, overexpression of *SlERF.J2* inhibited hypocotyl length and plant height, and played an important role in the regulation of light, auxin, and gibberellin signaling

phenotypic analysis and related gene expression levels. In addition, SlERF.J2 directly binds to the promoter of *IAA23* to inhibit its activity, thereby suppressing the plant height of the *SlERF.J2*-OE lines. We propose a model to elucidate the potential function of *SlERF.J2* in tomato hypocotyl and plant height (Fig. 8), and provide a molecular mechanism for studies on how to decipher crosstalk between different hormones to control plant growth and development in the future.

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Author contributions ZH and QX designed and managed the research work and improved the manuscript. YC, HY designed the experiments and analyzed the data. YC, BT, FL, GC performed the experiments. YC wrote the manuscript.

Data availability All data supporting the findings of this study are available within the paper and within its supplementary materials published online.

Declarations

Conflict of interest All authors have read and approved this version of the article, and due care has been taken to ensure the integrity of this work. All the authors have declared no conflict of interest.

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