The ABA-induced soybean ERF transcription factor gene GmERF75 plays a role in enhancing osmotic stress tolerance in Arabidopsis and soybean

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Abstract

Background: Ethylene-responsive factors (ERFs) play important roles in plant growth and development and the response to adverse environmental factors, including abiotic and biotic stresses.

Results: In the present study, we identified 160 soybean ERF genes distributed across 20 chromosomes that could be clustered into eight groups based on phylogenetic relationships. A highly ABA-responsive ERF gene, GmERF75, belonging to Group VII was further characterized. Subcellular localization analysis showed that the GmERF75 protein is localized in the nucleus, and qRT-PCR results showed that GmERF75 is responsive to multiple abiotic stresses and exogenous hormones. GmERF75-overexpressing Arabidopsis lines showed higher chlorophyll content compared to WT and mutants under osmotic stress. Two independent Arabidopsis mutations of AtERF71, a gene homologous to GmERF75, displayed shorter hypocotyls, and overexpression of GmERF75 in these mutants could rescue the short hypocotyl phenotypes. Overexpressing GmERF75 in soybean hairy roots improved root growth under exogenous ABA and salt stress.

Conclusions: These results suggested that GmERF75 is an important plant transcription factor that plays a critical role in enhancing osmotic tolerance in both Arabidopsis and soybean.

Keywords: Ethylene-responsive factor, Hypocotyl elongation, Root growth, Response mechanism, Osmotic tolerance, Soybean
ERF genes can also function in abiotic and/or biotic stress responsive pathways. TaERF1, a wheat ERF gene which could be induced by multiple environmental stresses including drought, salt, low temperature, and exogenous hormones such as ABA, ET, and salicylic acid (SA), was also identified as a defense gene against pathogen (Blumeria graminis f. sp. tritici). Overexpression of TaERF1 in Arabidopsis and tobacco could improve resistance to pathogens and enhance tolerance to multiple abiotic stresses [20]. Haynaldia villosa ERF1-V regulated the response to both powdery mildew and drought and salinity when overexpressed in wheat [21]. Similarly, TaAP1E1, a member of ERF family in wheat, enhanced resistance to Rhizoctonia cerealis and increased tolerance to freezing stress by activating defense- and stress-related genes that function downstream of the ET signaling pathway in wheat [22]. Therefore, ERF genes could encode multifunctional factors that respond to multiple stresses, integrate potentially various signal transduction pathways, and thus play dual roles in both abiotic and biotic stress responses in plants [14, 23].

Although ERFs have been found in diverse plants, many soybean ERFs have not been reported yet, which is one of the most economically important crop species. In addition, the functions of most ERF genes have yet to be determined. In this study, we searched for and integrated all non-redundant sets of soybean ERF genes. GmERF175, a highly ABA-induced ERF gene, was chosen for further expression and functional analysis. GmERF175 was up-regulated by multiple abiotic stresses and exogenous hormones, and overexpression of which could enhance osmotic tolerance in both Arabidopsis and soybean.

Results
Identification and physical locations of soybean ERFs
We used the Pfam [24] and SMART databases [25] as references for the identification of 160 non-redundant soybean ERFs (Additional file 1: Table S1). According to the soybean genome database, 160 soybean ERFs were distributed across 20 chromosomes (Fig. 1). The number of ERF genes on each chromosome differed considerably. There were 17 ERF genes distributed in chromosome 13, but only 3 in chromosome 12 (Fig. 1). Multiple alignments of full-length amino acid sequences were performed using MEGA 5.1 [26]. The ERF proteins could be clustered into eight groups (I to VIII) based on their phylogenetic relationships (Fig. 2). Almost one-fourth of the ERF proteins were clustered in Group I, while only nine were clustered in Group IV.

Expression profiles of soybean ERFs
To examine the expression patterns of ERFs, a map of soybean ERF gene expression in 14 soybean tissues and organs at different developmental stages was drawn based on the gene-chip data downloaded from the soybean genome database (Additional file 2: Figure S1; Additional file 3: Table S2). Soybean ERFs were expressed at the highest levels in the nodules of 21 days-old plants and at the lowest levels in seeds. A few soybean ERFs displayed different tissue-specific expression patterns. For example, eight ERFs were expressed in only one tissue, and nine ERFs were expressed in only two tissues. The expression levels for genes in different groups also differed. The expression levels of Group II genes were lower than those of genes in the other groups. The expression patterns of ERFs within the same group also varied. For example, GmERF127 transcripts reached the maximum level in flowers, whereas GmERF10 transcripts reached the highest level in roots. GmERF6, GmERF66, and GmERF84 were expressed at a low level, whereas GmERF52, GmERF112, GmERF122, and GmERF124 were expressed at an extremely high level. Interestingly, three-quarters of the extremely high-expressed ERF genes were clustered in Group VII. Therefore, Group VII was selected for further investigation.

Conserved protein motifs and gene structures of soybean group VII ERFs
There are 12 ERF genes belonging to Group VII. To investigate the modular structure of the proteins encoded by these genes, DOG 2.0 was used to draw the domains in each protein. As shown in Additional file 4: Figure S2, each Group VII ERF protein had a typical AP2/ERF DNA-binding domain, which is highly conserved, consists of 57–61 amino acids, and contains three β-sheet regions and an α-helix. The key amino acid residues determining
Fig. 1 Distribution of ERF genes in the soybean genome. The blue bars represent the chromosomes (not drawn to scale), and the chromosome numbers are shown above the bars. Soybean ERFs were distributed on all 20 chromosomes. The numbers to the left of the chromosomes indicate the distances between the neighboring genes in megabases (Mb).
DNA-binding specificity are those at positions 14, Ala (A) and 19, Asp (D) [10].

Gene structure analysis was done to compare the distribution of introns and exons in each soybean ERF gene. Almost all the ERF genes contained one intron except for GmERF102, GmERF25, and GmERF78 which contained no intron (Additional file 5: Figure S3).

Expression pattern of GmERF75 under ABA treatment
ABA plays essential role in regulating seed germination, growth and development, and responses to environmental stresses in plants [10, 27, 28]. It has been reported that most drought-inducible and/or salt-inducible genes were also induced by exogenous ABA treatment in Arabidopsis [29], which suggested the existence of cross-talk between ABA and osmotic stress signaling pathways.

To investigate the expression levels of the 12 soybean ERFs after ABA treatment, quantitative real-time PCR (qRT-PCR) was conducted using cDNA obtained from hypocotyls and roots of ABA-treated soybean seedlings as a template. As shown in Fig. 3, almost all soybean ERFs were up-regulated to different extents in response to exogenous ABA treatment (Figs. 3a-l). Transcription level of GmERF75 was the highest up-regulated and
reached the highest level at 4 h after ABA treatment (Fig. 3g). Therefore, \textit{GmERF75} was selected for further study.

To investigate the expression pattern of \textit{GmERF75} in different soybean plant tissues, semi-quantitative PCR (semi-qPCR) was conducted. RNA was extracted from hypocotyls, roots, stems, and leaves of soybean seedlings. Parallel reactions amplifying Actin were performed to normalize the expression levels. This result showed that \textit{GmERF75} is predominantly expressed in hypocotyls and roots, with less expression observed in leaves (Additional file 6: Figure S4).

\textit{GmERF75} is localized in nucleus

The CDS of \textit{GmERF75} was acquired that contained complete 903 bp open reading frame (ORF), which encodes a putative protein of 300 amino acids (Additional file 7: Figure S5). The \textit{GmERF75} protein contains a putative basic amino acid region (KPVKRQRK) that potentially act as a nuclear localization sequence (NLS), and acidic amino acid regions, EKETEVEIAEEKNKVELESEE and EEEEVVVEE, in the C-terminal region that may act as transcriptional activation domains (Additional file 7: Figure S5).

To investigate whether the \textit{GmERF75} protein located in cell nucleus, the full-length ORF of \textit{GmERF75} was amplified and fused in frame with the hGFP gene under the control of the CaMV 35S promoter and then transferred into onion epidermal cells to observe fluorescence signal (Fig. 4). The result showed that \textit{GmERF75}:hGFP fusion protein fluorescence was predominantly observed in the nucleus. GFP fluorescence of the control one was distributed throughout the cell. These results indicated that the \textit{GmERF75} fusion protein was targeted to nucleus.

The \textit{GmERF75} promoter region contains diverse stress-responsive elements

To further investigate the transcriptional regulation of \textit{GmERF75}, 1809 bp promoter region of \textit{GmERF75} upstream of the ATG start codon was isolated. Putative \textit{cis}-acting elements in the promoter region were identified using the PLACE (http://www.dnaaffrc.go.jp/PLACE/) and PlantCARE (http://bioinformatics.psb.ugent.be/webtools/plantcare) databases. Several distinct regulatory motifs homologous to \textit{cis}-acting elements involved in responses to abiotic and biotic stresses and plant hormones were identified (Table 1).

Many abiotic and biotic stress-related \textit{cis}-elements are distributed in the promoter region of \textit{GmERF75}. There are eight hormone-responsive elements including five ABA relative elements (i.e., an AERB, two MYBST1 core binding site sequences, a DPBF binding site, and a MYB binding site), a gibberellic acid responsive element (GARE), a SA responsive element (TCA element), and an auxin responsive element (TGA element). Pathogen related elements (a W-box, and a TC-rich repeat) were also found in the promoter region. Interestingly, the REα element (AACCAA), which is highly bound in etiolated plants but lowly bound in green plants, was found in the \textit{GmERF75} promoter region (Table 1). In addition, a
series of light-responsive elements such as Box-4, G-box, ACE, and ACGT-element were also found in the GmERF75 promoter region (Table 1). The presence of these cis-acting elements suggested that the expression level of GmERF75 could be regulated by multiple stresses, which in turn indicated that GmERF75 may participate in several signal transduction pathways.

Changes in GmERF75 expression in response to abiotic stresses and exogenous hormones
To investigate the expression level of GmERF75 under abiotic stresses including drought, salt, and high/low temperature, and in the presence of exogenous hormones, qRT-PCR was conducted using total RNA extracted from hypocotyls and roots of soybean seedlings.

Table 1  Analysis of putative cis-acting elements in the GmERF75 promoter

| GmERF75 | cis-acting elements | Core sequences | Functions |
|---------|---------------------|----------------|-----------|
| +       | W-box               | TTGACC         | fungal elicitor responsive element |
| +       | ACGT-element        | ACCT           | dehydration and dark-induced senescence |
| +       | core of MYBST1      | GGATA          | ABA and stress responsive element |
| +       | core of MYBST1      | GGATA          | ABA and stress responsive element |
| +       | ABRE                | ACGTG          | ABA responsive element |
| +       | DPBF binding site   | ACACNNNG       | ABA responsive element |
| +       | GARE                | TAACAAR        | gibberellin responsive element |
| +       | CAAT-box            | CCAATT         | common element in enhancer region |
| +       | Box-4               | ATTAAT         | light responsive element |
| +       | G-box               | CACGAC         | light responsive element |
| +       | G-box               | CACGTG/T       | light responsive element |
| +       | ACE                 | AAAACGTITTA    | light responsive element |
| +       | ACE                 | CTACGTAAT      | light responsive element |
| +       | TCA element         | GAGAAGATA      | salicylic acid responsive element |
| +       | TGA element         | AAGAC          | auxin responsive element |
| +       | TC-rich repeat      | ATTCCTAACC     | defense and stress responsive element |
| +       | MYB binding site    | WAACCA         | ABA and stress responsive element |
| +       | REA element         | AACCAC         | DNA binding activity is high in etiolated plants |
as a template. All of the treatments increased the expression level of GmERF75, particularly ET (about 75-fold increase). As shown in Fig. 5, GmERF75 was rapidly induced by ET, exhibiting the highest increase in expression which has a 75-fold change within 1 h after ET treatment, and then expression gradually declined to normal level observed before treatment. Upon high temperature treatment, GmERF75 expression peaked at 12 h (about 18-fold) and then declined to the initial level within 24 h. Low temperature could increase GmERF75 transcription level by 4 times after 2 h of treatment. Expression levels also increased in response to exogenous SA. These results suggest that GmERF75 may play a crucial role in numerous signal transduction pathways related to stress [30].

GmERF75 overexpression rescued two Arabidopsis erf71 mutants hypocotyl elongation

To investigate the function of GmERF75 in Arabidopsis, AtERF71 was identified as a homologous gene of GmERF75, which share 55.47% identity compare to GmERF75. Two Arabidopsis erf71 mutants (SALK_030459C, CS362782) were found to display shorter roots and hypocotyls compared with wild-type (WT) Arabidopsis [31] (Additional file 8: Figure S6). To assess whether GmERF75 could rescue the phenotype of erf71 mutants, GmERF75 was introduced into the two mutants under the control of the CaMV 35S promoter, and transgenic GmERF75::erf71 lines were obtained. T3 seeds of stable genetically inherited plants were used for further phenotypic analysis. Significant differences between WT and erf71 mutants hypocotyl length were observed. The erf71 mutants displayed shorter hypocotyls, while the GmERF75::erf71 lines shared the similar phenotype with WT (Additional file 8: Figure S6). This result indicated that GmERF75 could promote hypocotyl growth.

GmERF75 improved osmotic stress tolerance in transgenic Arabidopsis plants

The GmERF75 gene was strongly induced by various abiotic stresses (Fig. 5). To evaluate the contribution of the GmERF75 gene to abiotic stress tolerance, two GmERF75-overexpressing Arabidopsis lines were grown under PEG, NaCl, and dark conditions. The GmERF75-overexpressing lines displayed longer hypocotyls under different abiotic stresses than WT Arabidopsis plants (Fig. 6a). The largest differences in hypocotyl length between the 35S::GmERF75 lines and WT were observed after 5 days of treatment with 75 mM salt and 6% PEG (Fig. 6c).

To test the tolerance to salt and drought in late stage of Arabidopsis, three-week-old seedlings were treated with 250 mM NaCl for 2 weeks or not watered for 1 week and then re-watered (Fig. 6b). The chlorophyll content of each line were recorded (Fig. 6d). The result showed that the chlorophyll content of transgenic plants under salt treatment was increased by 20.11 and 39.66% compared to WT and the mutants, respectively. For drought treatment, the chlorophyll content of transgenic plants was increased by 29.70% compared to WT, Taken together, these results suggest that GmERF75 has a role in improving tolerance to osmotic stress in Arabidopsis.
GmERF75 improved tolerance to salt stress and exogenous ABA in transgenic soybean hairy roots

To further investigate the function of GmERF75 in stress tolerance in soybean, a pGFPGUSPlus vector designed to express pGFPGUSPlus-GmERF75 was constructed and then transformed into Cucumopine-type Agrobacterium rhizogene strain K599, which was injected into Superroot of Lotus corniculatus. The positive transgenic hairy roots cultured on 1/2 Murashige and Skoog (MS) medium containing PEG, NaCl, or dark condition, respectively. The higher dry weights of transgenic hairy roots also supported this conclusion (Fig. 7b). As shown in Fig. 7b, transgenic hairy roots transformed with pGFPGUSPlus-GmERF75 exhibited more growth than those transformed with the empty vector control under different concentrations of NaCl and ABA. Extremely significant differences between the transgenic and control hairy roots were observed under 85 and 120 mM NaCl treatment, and significant differences were also observed under 50 and 100 μM ABA. However, there was no obvious difference between transgenic and vector control hairy roots under the PEG condition (data not shown). These results suggested that GmERF75 could improve salinity and exogenous ABA tolerance in soybean.

Discussion

Transcription factors function as either activators or repressors that up-regulate or down-regulate, respectively, a whole array of target genes, overexpression of which can modulate stress tolerance in plants [32]. Numerous transcription factors have been reported involving in defense against multiple abiotic and biotic stimulus in plants, such as WRKY [33, 34], MYB [35], NAC [36], and ERF [30, 37]. Therefore, the identification and functional analysis of new transcription factor genes is of great importance for understanding the molecular mechanisms of stress tolerance in plants, which may aid efforts to improve crop productivity. ERF transcription factors have been shown to be involved in the response
to environmental stresses [5]. In this study, a comprehensive set of 160 soybean ERFs was identified and characterized. To better understand ERF-mediated stress responses, a highly ABA-induced soybean ERF, *GmERF75*, was isolated and its involvement in stress signal transduction pathways was investigated.

**GmERF75 may integrate the SA and ET/JA pathways**

The signal transduction pathways under abiotic stress were extremely complicated and complex in higher plants [38]. Hormones signaling transduction pathways were associated with different environmental stresses when plants resist various stresses, such as drought, salt, cold. It has been verified that there is an antagonistic effect between SA and JA pathways and between the JA/ET and ABA pathways which could precisely regulated the stress-related gene expression [39–41]. Accordingly, the expression levels of some plant defense genes are impacted via multiple signaling pathways during defense responses [42].

It is known that certain ERF transcription factors are targets of different signaling pathways [5]. For example, ERF1 can be activated rapidly by ET or JA or synergistically activated by both [43, 44]. *AERF4*, which acts as a transcriptional repressor, can be induced by both ET and JA [13, 45]. Meanwhile, the SA signal transduction pathway can act antagonistically with the ET/JA pathway [46, 47]. However, in this study, the *GmERF75* gene could be induced by exogenous SA, JA, and ET, which indicates that the transcription of *GmERF75* can be activated by both the SA and JA/ET pathways (Fig. 5) [48]. These results indicate that *GmERF75* may integrate signals from the SA and ET/JA pathways but does not contribute to the antagonistic interplay between them during the soybean seedling stage.

**The role of GmERF75 in enhancing hypocotyl length**

Hypocotyl elongation is regulated by a combination of extrinsic and intrinsic signals, including light and plant hormones [49–51]. Plants have evolved a complicated network of photoreceptors and numerous downstream signaling factors that enable them to respond and adapt to the ambient light environment [52]. vonArnim et al. found that *Arabidopsis* seedlings grown under light...
displayed short hypocotyls and open cotyledons with functional chloroplasts via photomorphogenesis, while dark-grown plants exhibit long hypocotyls and closed cotyledons and develop etioplasts via a process termed etiolation or skotomorphogenesis [53]. It was reported that light is closely related to hypocotyl cell elongation [54, 55], and that photoreceptors can modulate downstream transcription factors, such as ELONGATED HYOCOTYL5 (HY5) [56]. HY5 can indirectly affect the transduction of many hormone signal transduction pathways, such as ABA, ET, and JA [57]. In this study, GmERF75 was mainly expressed in hypocotyls (Additional file 6: Figure S4) and could be induced by exogenous ABA, ET, and JA (Fig. 5), which suggested GmERF75 functions downstream of these hormone signaling pathways. The erf71 mutants displayed shorter hypocotyls, while the hypocotyls of GmERF75:erf71 lines were not significantly different in length to WT hypocotyls (Additional file 7: Figure S5). These results implied that GmERF75 may be involved in the light-photoreceptor-HY5-ABA/ET/JA signal transduction pathway to modulate hypocotyl growth. In addition, promoter analysis showed there are six light-responsive cis-elements in the promoter region of GmERF75, which suggested that this gene may be directly regulated by light. Taken together, these results suggested that GmERF75 may regulate hypocotyl elongation through light-related signaling pathways. GmERF75 may be an essential factor in diverse abiotic signaling pathways

It is well known that there are complex connections among various hormones and stress signaling pathways in plants, and a single gene may play roles in many different signaling pathways at same time. Overexpression of JcDREB2, a physic nut AP2/ERF gene, in rice can suppress the expression of some gibberellic acid biosynthetic genes and induce salt tolerance-related genes to regulate salt stress response [58]. AhDREB1 is an important member of the AP2/ERF family in peanut. Arabidopsis plants overexpressing AhDREB1 had higher ABA sensitivity compared with WT and the expression levels of downstream drought stress-related genes were altered, which demonstrated that overexpression of AhDREB1 could improve tolerance to drought by affecting the ABA-dependent pathway [59]. Similarly, transgenic tobacco plants expressing GmERF9 had enhanced tolerance to drought and cold stresses and increased expression levels of PR genes such as PR1 and PR2 [60]. In this study, both transgenic Arabidopsis plants and soybean hairy roots expressing GmERF75 showed high salt stress tolerance and lower ABA sensitivity. These results suggested that GmERF75 may be involved in salt- and ABA-related signaling pathways. Based on these findings, we conclude that GmERF75 encodes a transcription factor that is likely to be an important determinant of osmotic stress signal transduction pathways in Arabidopsis and soybean.

Conclusion GmERF75, protein localized in the nucleus, is responsive to multiple abiotic stresses and exogenous hormones. Two independent Arabidopsis mutations of AtERF71, a gene homologous to GmERF75, displayed shorter hypocotyls, and overexpression of GmERF75 in these mutants could rescue the short hypocotyl phenotypes. GmERF75-overexpressing Arabidopsis lines showed higher chlorophyll content under drought and salt stress. Overexpressing GmERF75 in soybean hairy roots improved root growth under exogenous ABA and salt stress. GmERF75 is an important plant transcription factor that plays a critical role in enhancing osmotic tolerance in both Arabidopsis and soybean.

Methods Database searches and the chromosomal distribution of ERF genes in the soybean genome

The whole genome sequence and repeat information for soybean were obtained from the JGI Glyma1.0 annotation (http://www.phytozome.net/index.php) [61]. The gene chip data for soybean were obtained from SoyBase (http://www.soybase.org/) [62]. The chromosomal distribution was determined using the chromosome locus information from Phytozome. The MapInspect program was used to draw the chromosomal distribution map.

Alignment and phylogenetic analysis

We used the Pfam [24] (http://pfam.sanger.ac.uk/) and SMART databases [25] (http://smart.embl-heidelberg.de/) as references for the identification of 160 non-redundant soybean ERFs (Additional file 1: Table S1). Amino acid sequence alignments were performed using ClustalX and were manually corrected. Neighbor-joining method was used to construct the phylogenetic tree of soybean ERFs by MEGA 5.1 [26].

Expression profiles and gene structure analysis

Expression analysis was conducted using soybean GeneChip expression data for different tissues and developmental stages. The genomic DNA sequences and corresponding coding sequences of the 12 soybean ERF genes were submitted to the Gene Structure Display Server (GSDS) website (http://gsds.cbi.pku.edu.cn/) to visualize the gene structures [63]. The conserved motifs were analyzed using multiple EM for motif elicitation (MEME) software. The sequences were aligned using DNAMan software.
Protein domain and homology modeling
The amino acid sequences of the 12 Group VII ERF genes were submitted to the Protein Fold Recognition Server (PHYRE2) (http://www.sbg.bio.ic.ac.uk/phyre2/html/page.cgi?id=index) for structural homology modeling. DOG 2.0 was used to draw the protein domains.

Plant materials and stress treatments
Soybean seedlings (Glycine max cv. Tiefeng 8) grown in soil at 25 °C for 14 days were subjected to various abiotic stress and exogenous hormone treatments. To investigate the effects of exogenous ABA on ERF transcript family, the soybean seedlings were incubated in 100 μM ABA for 0, 0.5, 1, 2, 4, 8, or 12 h [64]. To investigate the effects of abiotic stresses on ERF transcript family, seedlings were subjected to stress for 0, 0.5, 1, 2, 5, 12, or 24 h. For rapid induction of drought stress, seedlings were exposed to air on filter paper [65]. For cold stress, seedlings were placed in a 4 °C chamber [66]. For high-temperature treatment, seedlings were placed in a 42 °C oven, and for salt stress, seedlings were incubated in 200 mM NaCl [35]. To investigate the effects of the exogenous hormones SA and JA on physiological and molecular responses, seedlings were subjected to stress for 0, 0.5, 1, 2, 5, 12, or 24 h. 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Three-week-old seedlings were supplied with 250 mM NaCl 2 weeks for salt treatment. Three-week-old seedlings normally grown in soil were not watered for drought treatment. A week later, different phenotypes were observed. The Arabidopsis plants were re-watered and recovered for 1 week, and the leaves of each line were collected. Plants normally watered were used as a control. Three independent replicates were performed for each treatment. In order to quantify the phenotype of Arabidopsis response to salt and drought, the chlorophyll content of each line were determined according to the protocol (Cominbio, China). Take 0.1 g of Arabidopsis leaves of each line and wash them with distilled water. Add 1 mL of 80% acetone, mix well and leaching overnight until the leaves are completely white. Add 80% acetone to 1 mL cuvette and zero the cuvette. The absorbance values of the samples at 663 nm and 645 nm were measured and recorded as A663 and A645. Total chlorophyll content (mg/g FW) = (20.21*A645 + 8.02*A663)*1 mL/0.05 g/1000.

Soybean hairy root induction and stress treatments
Seedling growth, rooting, hairy root induction, and hairy root transformation were performed as described by Chen et al. [74, 75]. Chlorine gas-sterilized soybean seeds were germinated in B5 medium. The cotyledons of 4-day-old seedlings as explant were harvested and wounded with a scalpel with K599 carrying the pGFPGUSPlus-GmERF75 binary vector for 5 days growth, which was used to transform Superroot-derived L. corniculatus plants for about 11 days to observe the hairy roots. The positive transgenic hairy roots were verified via fluorescence GFP. Then the transgenic hairy roots and the control were supplied with different concentrations of NaCl treatment for 1 week then the root elongation was measured. Three independent replicates were performed for each treatment.

Statistical analysis
For experiments with single time point, three biological repetitions were performed. For experiment with multiple time points, three independent biological repetitions and three technical repetitions were performed. The data was shown as the means ± SD of all of the replicates. Asterisks indicate significant difference or extremely significant difference from the control at *P < 0.05 or **P < 0.01, which was determined by Student's t test.

Supplementary information
Supplementary information accompanies this paper at https://doi.org/10.1186/s12870-019-2666-6.

Additional file 1: Table S1. Genetic information for soybean ERFs.
Additional file 2: Figure S1. Analysis of soybean ERF expression in different organs and developmental stages. Normalized expression data for the soybean ERFs were collected from SoyBase (http://www.soybase.org/) (Additional file 3: Table S2). The expression levels (vertical coordinates) are reported in transcripts per million (TPM). The different tissues and developmental stages are shown under the horizontal ordinate. The different colors indicate the expression levels of soybean ERFs.
Additional file 3: Table S2. Expression data during different organs and development periods of soybean ERFs.
Additional file 4: Figure S2. Protein domains in the 12 soybean ERF proteins. DOG 2.0 was used to draw the domains in each protein. The conserved AP2/ERF domain is indicated by blue boxes.
Additional file 5: Figure S3. Intron-exons of the 12 soybean ERF genes. The diagrams of intron-exon structure were generated using the GSDS online tool. The exons, introns, and untranslated regions (UTRs) are indicated by yellow boxes, black lines, and blue boxes, respectively.
Additional file 6: Figure S4. GmERF75 expression in specific tissues of soybean plants under normal growth conditions. RNA was extracted from hypocotyls, roots, stems, and leaves of soybean seedlings. Parallel reactions amplifying Actin were performed to normalize the expression levels.
Additional file 7: Figure S5. Nucleotide and deduced amino acid sequences of the GmERF75 gene. Untranslated regions (UTRs) and intron sequences are indicated by lowercase letters. The deduced amino acid sequence is shown below the DNA sequence. The AP2/ERF domain is underlined. Basic amino acid regions that potentially act as nuclear localization signals are outlined by boxes, and an acidic amino acid region that may act as a transcriptional activation domain is shown in bold italics. A potential N-linked glycosylation site is indicated by a dotted line.
Additional file 8: Figure S6. GmERF75 rescued the short hypocotyl length phenotype of two erf71 mutants. (A) The erf71 mutants displayed shorter hypocotyls than the WT. (B) Overexpression of GmERF75 in the mutants partially rescued the short hypocotyl length phenotype. The histogram on the right shows the distribution of hypocotyl lengths for at least 30 seedlings.
Additional file 9: Table S3. Primers used for qRT-PCR of soybean ERFs in Group VII.

Abbreviations
ABA: Abscisic acid; ACC: 1-aminoacyclopropane-1-carboxylic acid; AD: Activation domain; AP2: APETALA2; CaMV: Cauliflower mosaic virus; DSBP: DO promoter-binding factors; DRE/CRT: Dehydration-responsive element/C-repeat; EREBP: Ethylene-responsive element binding protein; ERF: Ethylene-responsive factor; ET: Ethylene; GFP: Green fluorescent protein; GUS: β-glucuronidase; JA: Jasmonic acid; qRT-PCR: quantitative real-time PCR; RT-PCR: Reverse transcription PCR; SA: Salicylic acid; WT: Wild type

Acknowledgments
We thank Dr. Ryo Akashi for providing the Superroot culture of L. corniculatus; Peter Gresshoff for providing A. thaliana strain K599 and the binary vector pGFPGUSPlus; and Dr. Wen-Sheng Hou for providing plant material preparation, technical assistance and soybean seeds.
Authors' contributions

ZSX coordinated the project, conceived and designed experiments, and edited the manuscript; MZ and LJY conducted bioinformatics analysis, performed experiments and wrote the first draft; MJ and YL conducted bioinformatics analysis; JCG, JHL, and JDF contributed valuable discussion and substantively revised it; M; provided analytical tools and analyzed the data; YZM coordinated the project and edited the manuscript. All authors have read and approved the final manuscript.

Funding

The design and data collection of this study was supported by the National Natural Science Foundation of China (31871624). Analysis and interpretation of data in this research was supported by the National Transgenic Key Project of the Ministry of Agriculture (2018ZX08009009B). The manuscript was written with financial support from the Talents Introduced Fund of Anhui Science and Technology University (NXYJ201604).

Availability of data and materials

The datasets using for the present study are available in the JGI Glyma1.0 repository, https://phytozome.jgi.doe.gov/pz/portal.html.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 29 June 2019 Accepted: 2 October 2019

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