Heterologous expression of ZmNF-YA12 confers tolerance to drought and salt stress in Arabidopsis

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Abstract
Drought and salinity are serious environmental factors limiting the growth and productivity of plants worldwide. Therefore, it is necessary to develop ways to improve drought and salinity stress tolerance in plants. In this study, a drought-responsive nuclear factor Y subunit A gene, ZmNF-YA12, was cloned from maize. qPCR revealed ZmNF-YA12 transcript in all vegetative and reproductive tissues, with higher levels in young roots. Expression analyses of maize revealed that ZmNF-YA12 was induced by abscisic acid (ABA), jasmonic acid (JA), and abiotic stresses, including dehydration, high salinity, cold, and polyethylene glycol (PEG) treatment. The heterologous expression of ZmNF-YA12 in Arabidopsis plants resulted in increased root length and better plant growth than in wild-type (WT) plants under conditions of mannitol, salt, and JA stress on 1/2 MS medium. Transgenic Arabidopsis showed improved tolerance to drought and salt stresses in soil, and higher proline content and lower malondialdehyde (MDA) content than WT controls. The transgenic plants also maintained higher peroxidase (POD) activities than WT plants under conditions of NaCl stress. A yeast two-hybrid experiment demonstrated that ZmNF-YA12 interacted with ZmNF-YC1 and ZmNF-YC15. Moreover, the transcript levels of stress-responsive genes (RD29A, RD29B, RAB18, and RD22) were markedly increased in transgenic lines under conditions of drought and salt stress. These observations suggested that the ZmNF-YA12 gene may confer drought and salt stress tolerance by regulating stress-related genes or interacting with ZmNF-YC1 and ZmNF-YC15, and has potential applications in molecular breeding with maintenance of production under conditions of stress.

Keywords Maize · Drought tolerance · Salt tolerance · NF-YA · Arabidopsis

Introduction
The crop yield of maize (Zea mays L.), the most widely grown cereal crop in the world, is considerably limited by a range of abiotic stress factors (Pechanova et al. 2013). Drought and increased soil salinity are projected to lead to a 50% loss of arable land by the year 2050, which will severely affect crop yields. Therefore, it is becoming increasingly important to improve water use efficiency and salt tolerance for agricultural production in the ever-decreasing area of arable land (Deinlein et al. 2014; Tiburcio et al. 2012). Transcription factors play important roles in abiotic stress responses in plants, and represent promising targets for the genetic engineering of plants with elevated stress resistance (Nowicka et al. 2018). Many plant genes are regulated in response to abiotic stresses, and the products of these genes have functions related to the stress responses and tolerance (Yamaguchi-Shinozaki and Shinozaki 2006).

Nuclear factor Y (NF-Y), also called CBF and CP1, consists of three different subunits (NF-YA, NF-YB, and NF-YC), and is a unique DNA-binding protein that interacts with the CCAAT motif, a common element present in the promoters of a number of mammalian genes (Maity and de Crombrugghe 1998). The core domains of the NF-YC/NF-YB proteins interact through histone fold motifs. This histone-like pair is closely related to the H2A/H2B and NC2α/NC2β families, both of which have features common
to this class of proteins and unique to NF-Y (Romier et al. 2003).

The plant NF-Y transcription factors have been reported to be key players in plant–microbe interactions, root development, and stress tolerance. Some members of the NF-Y gene families have been shown to be involved in responses to water and nutrient scarcity in mono- and dicotyledonous plants (Zanetti et al. 2017). AtNF-YB2 and AtNF-YB3 are both essential for the normal flowering induced by long days in Arabidopsis (Kumimoto et al. 2008). Transcription of OsNF-YA7 was shown to be induced by drought stress, and its overexpression in transgenic rice plants enhanced their drought tolerance (Lee et al. 2015). Overexpression of TaNF-YA10-1 in wheat conferred drought tolerance, with longer root length and better whole-plant growth under conditions of drought (Ma et al. 2015). Under 200 mM NaCl and 200 mM mannitol stresses, the expression of ShNF-YA1, 2, and 6 were upregulated (Maheshwari et al. 2019). Overexpression of GmNFYA5 in transgenic Arabidopsis and soybean resulted in increased drought tolerance (Ma et al. 2020). In potato, twelve SfNF-Y genes were upregulated and another two genes were downregulated under ABA, drought and salinity treatments (Xuanuyan et al. 2021). Transgenic tobacco plants overexpressing CsNF-YA5 showed superior growth and photosynthetic rates under both normal conditions and drought stress (Pereira et al. 2018). Overexpression ShNF-YB2 in sugarcane enhanced tolerance to drought and salinity stresses (Peter et al. 2020). CsNF-YAs had greater impacts than CsNF-YB and C under drought and ABA treatment (Wang et al. 2019). CmNF-YB8-RNAi transgenic chrysanthemum lines enhanced drought resistance, whereas lines overexpressing CmNF-YB8 were less tolerant to drought (Wang et al. 2021). PdNF-YB21 overexpression promoted root growth with highly lignified and enlarged xylem vessels in poplar, resulting in increased drought resistance (Zhou et al. 2020). However, the biological roles of many members of the NF-Y family in maize are not clear.

Previously, we reported that ZmNF-YA12 (GRMZM5G857944) could respond to abiotic stress (Zhang et al. 2016). To investigate the molecular biology function of ZmNF-YA12, its tissue-specific expression, gene expression patterns under different exogenous stresses, heterologous expression in Arabidopsis, and yeast two-hybrid experiment were performed. Transgenic Arabidopsis lines expressing ZmNF-YA12 showed improved drought and NaCl tolerance. ZmNF-YA12 interacts with ZmNF-YC1 and ZmNF-YC15. Our data suggest that ZmNF-YA12 may represent an important mechanism underlying the function of NF-Y under NaCl and drought stress.

Materials and methods

Isolation of ZmNF-YA12

Total RNA was isolated from maize seedlings using TRIzol reagent (CW Biotech, Beijing, China) and reverse-transcribed to complementary DNA (cDNA) using HiScript II Q RT SuperMIX (Vazyme, Nanjing, China). The full ZmNF-YA12 cDNA was amplified by PCR using the forward primer (FP) 5’-ATGCTTCTTCCCTTCTTCTT-3’ and reserve primer (RP) 5’-TCATCTCATACTGGAA CCT-3’. Conserved Domains (https://www.ncbi.nlm.nih.gov/Structure/cdd/docs/cdd_search.html) was used to retrieve the protein structure of ZmNF-YA12. PlantCARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/) was used to analyze the ZmNF-YA12 promoter.

Plant materials, growth conditions, and treatments

For tissue-specific analysis, leaves, stems, and roots were harvested from three-leaf seedlings grown in a greenhouse (28 °C, 16/8 h day/night cycle). Mature leaves, roots, silks, tassels, and embryos were harvested at the grain-filling stage from plants grown in the field. All harvested materials were frozen immediately in liquid nitrogen and stored at −80 °C.

To determine the ZmNF-YA12 expression patterns under various stress conditions, maize seedlings were grown in 12-cm hydroponic barrels containing nutrient solution. Three-leaf maize seedlings were subjected to dehydration, NaCl, polyethylene glycol (PEG), cold, abscisic acid (ABA), and jasmonic acid (JA) treatments. For dehydration treatment, the whole seedling was removed, washed, and placed on an experimental table for natural dehydration at room temperature (25 °C). For salt and PEG treatments, the roots of the seedlings were immersed in solutions containing 200 mM NaCl and 20% PEG, respectively. For cold treatment, seedlings were kept at 4 °C. For each of the above four treatments, the shoots and roots were collected at 0, 1, 2, 5, 10, and 24 h after treatment. For the ABA and JA treatments, the leaves of the seedlings were sprayed with solutions containing 100 μM ABA or 100 μM JA and covered with plastic film. The leaves were then collected at 0, 1, 2, 5, and 10 h after treatment. The samples were immediately frozen with liquid nitrogen for isolation of RNA.

Arabidopsis thaliana ecotype Columbia (Col-0) was used for transformation in this study. After vernalization treatment, seeds were surface-sterilized in a solution of 0.5% NaClO for 10 min, and washed five times with sterile...
distilled water. Following this treatment, the seeds were germinated and grown on half-strength Murashige and Skoog (1/2 MS) medium (pH 5.8–6.0). The plates were transferred to a growth chamber at 22 °C for germination.

**Gene expression analysis using qPCR**

cDNA samples were obtained as described above. qPCR was performed in a CFX Connect Real-time PCR system (Bio-Rad, Hercules, CA, USA) using a Super Real PreMix (SYBR Green) kit (Tsingke Biotech, Beijing, China) according to the manufacturer’s instructions. The primers used for qPCR were designed according to the ZmNF-YA12 cDNA sequence (FP: 5′-AGCAACCTCCATTGGCAGTCA-3′ and RP: 5′-GGCTGCCCACAATCTCTCAGAT-3′). Each reaction was performed in triplicate, and the results are expressed relative to the expression levels of Actin (FP: 5′-GTTGCTAGTGGTG-3′ and RP: 5′-AACGACCTT AATCTCAGTCTGC-3′) and GAPDH (FP: 5′-CCCTTATCAACACCGACTAC-3′ and RP: 5′-AACCTCTGGAC ACCACCCT-3′) in each sample using the 2^{−ΔΔCT} method.

**Vector construction and transformation of Arabidopsis**

The ZmNF-YA12 cDNA was cloned into the pCAMBIA-3301 vector driven by the cauliflower mosaic virus (CaMV) 35S promoter (Supplementary Fig. 1), as confirmed by sequencing. The resulting construct was transformed into Arabidopsis Col-0 by the floral dip method using Agrobacterium tumefaciens GV3101. The first generation (T₀) seeds of transgenic Arabidopsis were screened on 1/2 MS medium containing 50 mg/L kanamycin, and transgenic plants were confirmed by PCR and qPCR (FP: 5′-AACCTCATCTGGCG TGTGGG-3′ and RP: 5′-GTATAATGCGGAGCTCT AATC-3′; and FP: 5′-AGCAACCTCCATTGGCAGTCA -3′ and RP: 5′-GGCTGCCCACAATCTCTCAGAT -3′, respectively). Homozygous plants of the T₃ generation were used for further analysis.

**Root growth assay**

For root growth assay, transgenic and wild-type (WT) seeds were placed on 1/2 MS agar plates for germination. Seven days later, five germinated seedlings of the same size from each line were carefully transferred to 1/2 MS agar plates supplemented with 150 mM NaCl, 150 mM mannitol, 50 mM JA, or 10 μM ABA. Seedling root lengths were measured using ImageJ software (NIH, Bethesda, MD, USA) after 8 days of upright growth in treatment medium.

**Drought and NaCl treatment of transgenic Arabidopsis**

Drought and NaCl tolerance assays were performed on seedlings grown in pots in a greenhouse. Transgenic and WT seeds were germinated on 1/2 MS medium. One-week-old seedlings were planted in 7-cm pots containing mixed soil (vermiculite: humus = 1:1) of equal quality and well-watered for 3 weeks. For drought stress treatment, the seedlings were subsequently cultured without watering for 3 weeks and then re-watered for 2 days. For NaCl stress treatment, the plants were irrigated with a solution containing 450 mM NaCl for 1 week. Drought and NaCl tolerance experiments were performed in triplicate. Samples of Arabidopsis leaves were collected after the seedlings exhibited distinct phenotypes under drought and salt treatments. The peroxidase (POD) activity, proline, malondialdehyde (MDA), and chlorophyll contents were measured using a commercial assay kit (Solarbio, Beijing, China) according to the manufacturer’s instructions. The sixth from last rosette leave was used to measure chlorophyll contents and all leaves were measured to calculate the rate of green leaves.

**Yeast two-hybrid assays**

For yeast two-hybrid analysis, the ZmNF-YA12 cDNA was cloned into the bait plasmid pGBK7 (pGBK7-ZmNF- YA12). Eight proteins were predicted to interact with ZmNF-YA12 using STRING database (https://cn.string-db.org/) and six of them were related to abiotic stress. The full-length cDNAs of ZmNF-YB7 (GRMZM2G169884_ T01), ZmNF-YC1 (GRMZM2G089812_T01), ZmNF- YC15 (GRMZM2G124421_T01), ZmNF-YC17 (GRMZM2G311316_T01), ZmCOI1 (GRMZM2G151536), and ZmMYC2 (GRMZM2G049229) were separately cloned into the target pGADT7 plasmid. The bait and target plasmids to be tested for interactions were co-transformed into the yeast strain AH109 and plated on synthetic defined (SD) medium lacking leucine and tryptophan (SD/-LT) for screening transformants. The independent transformed colonies were then grown on SD medium lacking leucine, tryptophan, adenine, and histidine (SD/-AHLT). Survival of the yeast colonies on SD/-AHLT medium indicated that the target gene can interact with ZmNF-YA12.

**Statistical analysis**

The experiments were repeated three times and the data are presented as the mean ± SEM. The significance of the differences in the data was determined using SPSS statistical analysis.
software (v. 25.0; SPSS Inc., Chicago, IL, USA). In all analyses, \( p < 0.05 \) was taken to indicate statistical significance.

**Results**

**Isolation and characterization of ZmNF-YA12**

The full-length ZmNF-YA12 cDNA is 816 bp in length and encodes 271 amino acid residues with a predicted molecular mass of 29.3 kDa and isoelectric point (pI) of 10.96. Protein structure alignment showed that the ZmNF-YA12 sequence included an NF-Y transcription factor conserved domain (Fig. 1a). The results indicated that ZmNF-YA12 is a member of the NF-YA transcription factor family. The deduced amino acid sequence of ZmNF-YA12 was further compared to other NF-YA proteins from various organisms by phylogenetic analysis (Fig. 1b). The results indicated that ZmNF-YA12 is closely related to OsHAP2E. Analysis of the ZmNF-YA12 promoter using the PlantCARE database revealed a series of light-related and hormone stress response elements, including CAT-box, G-box, and CGTCA motif (Supplementary Fig. 2). The results suggest that ZmNF-YA12 may play important roles in responses to environmental stresses and regulation of plant growth and development.

**Expression pattern of maize ZmNF-YA12**

The expression levels of ZmNF-YA12 in different tissues under various stresses were determined by qPCR. The
results showed that ZmNF-YA12 was expressed at higher levels in young roots than in other tissues (Fig. 2), and the expression levels of ZmNF-YA12 in shoots and roots were upregulated by dehydration treatments (Fig. 3a). For PEG treatment, the expression of ZmNF-YA12 was significantly upregulated in roots and increased rapidly at 1 h and then declined in shoots (Fig. 3b). Under conditions of cold and NaCl treatment, the expression of ZmNF-YA12 was markedly induced in roots but not in shoots (Fig. 3c, d). As shown in Fig. 3e, the ZmNF-YA12 transcript level was downregulated at 1, 3, and 5 h, and upregulated at 10 h, with ABA treatment. With JA treatment, the expression of ZmNF-YA12 first decreased and then increased, peaking at 3 h (Fig. 3f).

**Tolerance of transgenic Arabidopsis plants to salt, mannitol, JA, and ABA stress**

To assess the effects of ZmNF-YA12 in responses to abiotic stresses, ZmNF-YA12 transgenic Arabidopsis plants (L-1, L-2, L-3) and WT seedlings were grown on 1/2 MS medium with different treatments. WT and transgenic plants showed similar root lengths under normal and 10 μM ABA conditions. However, the roots of transgenic lines were much longer than those of WT plants in the presence of 150 mM NaCl, 150 mM mannitol, or 50 μM JA (Fig. 4; Supplementary Figs. 3–6).

**Heterologous expression of ZmNF-YA12 confers enhanced drought and salt tolerance in Arabidopsis**

Under control conditions, both WT and ZmNF-YA12 transgenic plants exhibited a similarly normal growth phenotype. Drought and salt stress significantly inhibited the growth of WT plants, which exhibited more wilted and smaller leaves (Fig. 5a and Fig. 6a). However, ZmNF-YA12 transgenic Arabidopsis plants showed less wilted leaves and more green and larger leaves (Fig. 5b and Fig. 6b). For drought treatment, after re-watering for 2 days, the ZmNF-YA12 transgenic lines recovered more quickly, grew more green leaves and appeared to be healthier than WT plants (Fig. 5c).

To further characterize the function of ZmNF-YA12, we examined the MDA, proline, chlorophyll contents and POD activity under drought and salt stress treatment in transgenic lines and WT plants. As shown in Fig. 5d, MDA content was lower in the transgenic plants than WT controls under drought stress. As expected, the proline content was much higher in the transgenic lines than in WT plants (Fig. 5e). Under NaCl treatment, the activities of POD in the transgenic lines were much higher than in WT plants (Fig. 6c). However, there were no significant differences in chlorophyll contents and POD activity between WT and transgenic plants with drought treatment (Fig. 5f and g) and in chlorophyll, MDA and proline contents with salt treatment (Fig. 6d, e and f). These results suggested that the heterologous expression of ZmNF-YA12 improves drought and salt tolerance in Arabidopsis.

**ZmNF-YA12 interacts with ZmNF-YC1 and ZmNF-YC15**

To investigate the mechanisms underlying the involvement of ZmNF-YA12 in stress regulation, yeast two-hybrid assay was performed to identify proteins interacting with ZmNF-YA12. The results showed that ZmNF-YA12 has no self-transcriptional activation activity. All the transformed yeast cells grew well on SD/-LT medium, and the yeast cells transformed with both pGBKT7-ZmNF-YA12+pGADT7-ZmNF-YC1 and pGBKT7-ZmNF-YA12+pGADT7-ZmNF-YC15 grew well on SD/-AHLT medium, indicating that ZmNF-YA12 interacts with ZmNF-YC1 and ZmNF-YC15 (Fig. 8).

**Discussion**

The growth, development, and productivity of maize are seriously affected by abiotic stresses, such as drought, salinity, high and low temperatures, and by biotic stresses, such as fungi, viruses, and pests (Gong et al. 2014). The NF-Y transcription factors are important regulators of plant...
development and responses to environmental stress (Petroni et al. 2012). The maize genome includes 50 ZmNF-Y genes (14 ZmNF-YA, 18 ZmNF-YB, and 18 ZmNF-YC) (Zhang et al. 2016). In this study, we identified and characterized a gene, ZmNF-YA12, related to stress tolerance. ZmNF-YA12 transcript levels were significantly induced by dehydration, PEG, cold, NaCl, ABA, and JA treatments (Fig. 3). The expression of ZmNF-YA12 in shoots was induced at 1 h and then declined, similar result was also observed in other previously reported gene, such as GmNF-YA3 (Ni et al. 2013). However, the expression of ZmNF-YA12 was significantly induced in roots but not in shoots with cold and NaCl treatments, which may be related to its tissue-specific expression (Fig. 2).

Several studies have indicated that NF-Y genes are involved in stress responses. OsHAP2E, a homolog of ZmNF-YA12, confers biotic and abiotic resistance, and increased photosynthesis and tiller numbers in rice (Alam et al. 2015). Overexpression of SiNF-YA1 in transgenic tobacco lines enhanced drought and salt tolerance (Feng et al. 2015). Transgenic Arabidopsis plants overexpressing

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**Fig. 3** Expression of ZmNF-YA12 in response to abiotic and hormone stress in maize. **a–f** ZmNF-YA12 expression under conditions of dehydration, PEG, cold, NaCl, ABA, and JA stress. GAPDH was used as an internal control. Data are shown as the mean ± SEM (n = 3)
AhNF-YC showed increased seedling sensitivity to ABA, and influenced the expression of several genes associated with secondary metabolism, development, and ABA-related responses (Palmeros-Suárez et al. 2015). Heterologous expression of MsNF-YB21 in Arabidopsis led to a longer root length and conferred improved osmotic and salt tolerance (Feng et al. 2021). Our data showed that transgenic Arabidopsis seedlings expressing ZmNF-YA12 had longer roots than WT plants when grown on 1/2 MS medium under mannitol, NaCl, and JA treatments (Fig. 4). Furthermore, seedlings of ZmNF-YA12 transgenic plants grown in soil under drought and high NaCl conditions showed enhanced tolerance in comparison to WT plants (Fig. 5a and Fig. 6a). Several physiological and biochemical factors, such as
a

WT  L-1  L-2  L-3
Control

WT  L-1  L-2  L-3
Drought

WT  L-1  L-2  L-3
Re-water

b

Drought

The rate of green leaves (%)

WT  L-1  L-2  L-3

c

Re-water

The rate of green leaves (%)

WT  L-1  L-2  L-3

d

WT  L-1  L-2  L-3
Control  Drought

MDA content (umol)

e

WT  L-1  L-2  L-3
Control  Drought

Purine content (mg/g)

f

WT  L-1  L-2  L-3
Control  Drought

POD activity (U/mg)

g

WT  L-1  L-2  L-3
Control  Drought

Chlorophyll content (mg/g)
MDA, proline, chlorophyll contents, and POD activity, play essential roles in plant tolerance to abiotic stresses. Proline plays a role as a compatible solute under conditions of environmental stress and contributes to the redox balance of the cell (Lehmann et al. 2010). MDA is the most frequently measured biomarker of oxidative stress, i.e., lipid oxidation, which indicates the extent of membrane damage. Fig. 5 shows improved drought tolerance in transgenic Arabidopsis plants expressing ZmNF-YA12. Healthy WT and 35S-ZmNF-YA12 plants were grown for 20 days with or without (control) water deficit, followed by re-watering for 2 days. The rates of green leaves in WT and transgenic lines under drought and re-watering treatments were measured. Measurements of MDA and proline contents in transgenic lines and WT plants are also shown. *p < 0.05; **p < 0.01 compared to the corresponding controls.

Fig. 6 shows enhanced salt tolerance of transgenic plants expressing ZmNF-YA12. Phenotypes of WT and transgenic seedlings in soil with or without (control) 450 mM NaCl treatment are shown. Four-week-old transgenic and WT plants were irrigated with NaCl solution. Photographs were taken 7 days after treatment. Statistical analysis of green leaves of 35S-ZmNF-YA12 and WT plants shows POD activity and chlorophyll content were measured in transgenic and WT plants. *p < 0.05; **p < 0.01 compared to the corresponding controls.
Fig. 7  RD29A, RD29B, RAB18, and RD22 transcript levels in WT and ZmNF-YA12 transgenic plants under three growth conditions. Actin2 was used as an internal control. Data represent the mean ± SEM (n = 3). *p < 0.05; **p < 0.01

Fig. 8  Protein interaction assays between ZmNF-YA12 and candidate genes
peroxidation (Tsikas 2017). With drought treatment, transgenic ZmNF-YA12 plants showed lower MDA content and higher proline content than WT controls (Fig. 5d, e). Therefore, we concluded that ZmNF-YA12 transgenic plants have enhanced drought tolerance. Peroxiredoxins are thiol PODs with a variety of functions in the oxidation resistance and redox signaling networks of the cell (Liebthal et al. 2018). Leaf chlorophyll content represents the photosynthetic capacity, and high oxidative stress inhibits its synthesis and accumulation (Agathokleous et al. 2020). The levels of POD activity in 35S:ZmNF-YA12 Arabidopsis were much higher than in WT plants under high NaCl conditions (Fig. 6c). These results indicated that ZmNF-YA12 has a positive effect on salinity, osmotic, and drought stress responses in plants.

To investigate the mechanisms of action of ZmNF-YA12 in stress responses, we examined the expression levels of stress-responsive genes. Previous studies showed that RD29A and RD29B can be induced by drought and salt stress, and responded to dehydration and ABA treatments (Mianne et al. 2011; Nakashima et al. 2006). In addition, RD22 and RAB18 are marker genes for ABA-induced gene expression and key nodes in ABA-responsive signaling networks (Rushton et al. 2012; Yao et al. 2020). In the present study, these four stress-related genes showed significantly elevated expression levels in the transgenic ZmNF-YA12 compared to WT plants under drought and high NaCl treatments (Fig. 7a, b, c, d). These results indicated that ZmNF-YA12 improves salt and drought tolerance by inducing the expression of stress-related genes in Arabidopsis.

Proteins interact with other proteins in complex network systems to perform their diverse and targeted functions (Bhardwaj et al. 2016). A previous study showed that the maize NF-Y family gene NF-YA3 could interact with the JA activator MYC4 to improve drought and heat tolerance (Su et al. 2018). PwNF-YB3 can interact with PwHAP5, and heterologous expression PwNF-YB3 in Arabidopsis can induce the expression of drought response genes (Zhang et al. 2015). There have been no previous reports regarding the interactions of ZmNF-YA12 proteins in maize. In the present study, yeast two-hybrid experiments showed that ZmNF-YA12 interacted with ZmNF-YC1 and ZmNF-YC15. Our previous study showed that ZmNF-YC15 was induced by drought stress (Zhang et al. 2016). Therefore, ZmNF-YA12 may respond to stress by interacting with ZmNF-YC15.

In conclusion, we cloned and characterized the NF-Y gene ZmNF-YA12 from Zea mays. ZmNF-YA12 was expressed at high levels in young roots and induced by abiotic stresses. Its heterologous expression conferred enhanced tolerance to drought and salt stress by regulating the expression of stress-related genes. The gene may also perform its diverse and targeted functions by interacting with ZmNF-YC1 and ZmNF-YC15. These results will be helpful to understand the roles of NF-Y in abiotic stress responses.

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Author contributions ZZ, RY and ZW: conceived and designed the experiments; TZ, DZ and CZ: performed the experiments and analyzed the data; TZ: wrote the manuscript and ZZ, RY and ZW: revised and approved the publication.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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