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CLONING, SEQUENCE ANALYSIS, AND FUNCTIONAL STUDY OF THE *PEDOF-4* GENE IN RESPONSE TO DROUGHT STRESS

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Keywords: Passion fruit, Dof, Sequence analysis, Cloning, Drought

Abstract

DNA-binding with one finger (Dof) was a functionally important gene in plant stress tolerance processes. The cloned full-length (849 bp) passion fruit *PeDof-4* gene was sequenced, which encodes 282 amino acids with the molecular formula C1274H1983N375O408S14, molecular weight of 29529.87 u, and theoretical isoelectric point pI of 8.96. Evolutionary tree analysis showed that the *PeDof-4*-encoded proteins had a high degree of identity with Dof-encoded proteins in other plants. Blastp of the *PeDof*-4 encoded proteins revealed a closer affinity to the proteins encoded by the Dof of *Theobro ma cacao*. The relative expression of the *PeDof-4* gene was higher at 50% of the relative soil moisture content in the fluorescence qPCR experiments under different levels of drought stress. Tissue-specific analysis showed that the highest expression of this gene was found in the roots. Overexpression of GUS gene under the *PeDof-4 promoter* in *Arabidopsis thaliana* showed that *PeDof-4* could significantly respond to drought stress.

Introduction

The Dof (DNA-binding with one finger) gene family is recognized as an essential transcription factor within the plant biology (Shuichi *et al*. 2004). This family showcases a highly conserved Dof domain, located at the N-terminus, comprising roughly 52 amino acids (Wang *et al*. 2019). Research suggests that the Cys2/Cys2 type zinc finger within this domain binds uniquely to a conserved sequence, 5 ′-(T/A)AAAG-3′, present in the promoters of certain genes (Yanagisawa *et al*. 1999). The multifunctionality of the Dof domain is evident, as it supports DNA-protein interactions and aids in protein-protein interactions (Cheng *et al*. 2018). Initially discovered in maize, the first Dof gene was noted with a gene count of 18 (Li *et al*. 2016). Through genomics and transcriptomics analysis, an increasing number of Dof genes have been identified across various species, totaling 13 in passion fruit, 20 in *Chrysanthemum*, 30 in rice, 31 in wheat, 36 in Arabidopsis, 38 in pigeon pea, 41 in *Medicago truncatula*, 42 in banana, 74 in Chinese cabbage, and 76 in soybean (Chen 2023).

Transcription factors are critically involved in regulating plant growth and developmental processes (Lu *et al*. 2009). The pioneering discovery of the Dof gene, *ZmDof1*, revealed its function in modulating light-responsive gene expression, thus influencing light responses and nitrogen assimilation mechanisms (Yanagisawa and Sheen 1998). Subsequent research has uncovered the involvement of a multitude of Dof genes in a range of functions specific to plants, such as the regulation of seed maturation (Boccaccini *et al*. 2014, Santopolo *et al*. 2015), the

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ripening of fruits (Feng *et al*. 2016), adjustments in the timing of flowering (Liu *et al*. 2020) and hormonal signal pathways (Noguero *et al*. 2013). For instance, in rice, the *OsDof3* gene is crucial for gibberellin biosynthesis, while *OsDof12* and *OsDof23* are key regulators of flowering timing and seed gene expression, respectively (Li *et al*. 2009). Moreover, *SbDof* genes have been linked to responses to light, hormonal signals, and the activation of endosperm-specific genes (Kushwaha *et al*. 2011). Recent investigations have increasingly shown that Dof genes can also react to various abiotic stress conditions. Specifically, in tomatoes, the intensified expression of the Dof gene, *TDDF1,* has been associated with enhanced tolerance to drought and salt conditions (Ewas etal. 2017). Meanwhile, in rice, the repression of *OsDOF15* under salt stress in root systems and its overexpression led to decreased root sensitivity to salt by constraining ethylene production. This implies a role for *OsDOF15* in mitigating primary root growth inhibition under salt stress through ethical production control (Qin *et al*. 2019).

In the present investigation, the *PeDof-4* gene from *Passiflora eduli*s was successfully cloned, and its gene structure was analyzed using bioinformatics tools to predict its biological function. Furthermore, the functionality of *PeDof-4* in enhancing drought resistance in plants was validated through the utilization of the *Arabidopsis thaliana* transient transformation system.

Materials and Methods

Young leaves of passion fruit "Tainong" were selected, washed with sterile water, and immediately snap frozen with liquid nitrogen and kept in a refrigerator at -80 ℃ as a reserve. The materials were obtained from the Chinese Academy of Tropical Agricultural Sciences (CAATS). The cloning vector pMD19-T was purchased from TaKaRa, and the *E. coli* strain JM109 was maintained in the laboratory. The high-fidelity enzyme PrimeS-TAR® Max DNA Polymerase, Ex Taq was purchased from TaKaRa; the plasmid extraction kit and DNA recovery kit were purchased from AXY-GEN, and the DNA marker was purchased from Beijing Zhongke Ruitai Company. Other chemicals were of analytical grade.

The young leaves of passion fruit "Tainong" were ground with liquid nitrogen and followed the instructions of the Trizol Total RNA Extraction Kit (BioWorks kit SK1312). 1.5% agarose, 1×TAE electrophoresis buffer, and the pictures were observed and preserved in the gel imaging system. Total RNA was reverse transcribed into cDNA using a Thermo Fisher (K1622) kit and stored at -80°C in a refrigerator.

A Dof family gene, *PeDof-4*, was obtained from the Passiflora genome database, and primers were designed according to its sequence using the NCBI Primer-BLAST tool, The primer sequences were *PeDof-4*F: 5'-ATGGCAAAGGATGTGGGAGACAGCAG-3'; *PeDof-4*R: 5'-CTAAACAGTTG GGTTGCTCCTGAAG-3'. The designed primers were used to amplify the full-length *PeDof-4* gene. The PCR amplification procedure was as follows: pre-denaturation at 95°C for 3 min; 95°C for 40 s, 55°C for 40 s, 72°C for 50 s for a total of 35 cycles, and inactivation at 72°C for 10 min. PCR products were purified and recovered. The PCR products were purified and recovered, connected to the cloning vector pMD19-T, and transformed into *E. coli* JM109 competent cells, and PCR identification of monoclonal colonies was carried out. A few PCR-positive clones were selected and sent to Shanghai Bioengineering for sequencing analysis.

PeDof-4 molecular mass and pI were predicted using Protparam online software; *PeDof-4* protein hydrophilic-hydrophobicity was analyzed by using ExPasy-ProtScale. The deduced *PeDof-4* was analyzed by the Motif Search tool (http://www.genome.jp/tools/motif/) for the amino acid sequences for biologically significant sites. *PeDof-4* was analyzed by SOPMA online software. Clustering analysis of *PeDof-4* with Dof from other plants was carried out by using DNAMAN, and the amino acid sequences encoded by *PeDof-4* were compared with the amino

acid sequences of Dof gene from other plants by using the software Clustal X and MEGA3 for generating phylogenetic trees.

A 2000-bp DNA sequence before the start codon of *PeDof-4* gene was amplified by PCR and cloned into the pMD19-T vector. The promoter of *PeDof-4* was assessed by DNAMAN. Expression vectors were constructed to examine whether *PeDof-4* responds to drought stress. The *PeDof-4* promoter PCR fragment was cloned into the pCAMBIA1304 vector digested with NcoI/HinIII, and termed as pCAMBIA1304-*PeDof-4*p. The vector was transferred into the EHA105 strain of *Agrobacterium tumefacians*.

Agrobacterium tumefaciens transformed with pCAMBIA1304-*PeDof-4*p was grown in YEB medium containing Kan and Rif antibiotics at 28°C and resuspended into 1/2 MS solution to OD 600 = 0.8-1.0. Inflorescence impregnation method was used to transform *Arabidopsis thaliana*. Transgenic *Arabidopsis* seeds were germinated in MS medium as well as MS medium supplemented with 200 mM mannitol (to simulate drought stress), and 7-day-old seedlings were used for the test.

We froze the samples, and the total RNA was extracted from samples of the roots, stems, leaves, flower, and fruit of the passion fruit, using the plant RNA isolation kit (Fuji, China, Chengdu) with three biological replicates. The cDNA was used for qRT-PCR. Primer sequences were designed using the Primer 5.0 tool. The expression of *PeDof-4* was detected by quantitative real-time polymerase chain reaction (qRT-PCR) analysis using SYBR ® Premix Ex Taq™ (TaKaRa, Japan, Tokyo) chemistry on Lightcycle-480 (Roche). Relative expression levels were calculated using the $2^{-\Delta\Delta Ct}$ method.

The transgenic *Arabidopsis* with pCAMBIA1304-*PeDof-4*p under normal and drought stress were GUS stained. For GUS staining, seedlings were incubated in X-Gluc solution for 24 hrs at 37°C (Jefferson *et al*. 1987; Song *et al*. 2022). GUS enzyme activity was determined by 4-methylumbel ureylglucuronide fluorometry (Xu *et al*. 2020).

Results and Discussion

Using the cDNA of young leaves of passion fruit "Tainong" as template, full length, *PeDof-4* gene *(849bp)* was amplified by PCR using *PeDof-4*F and *PeDof-4*R primers (Fig. 1).

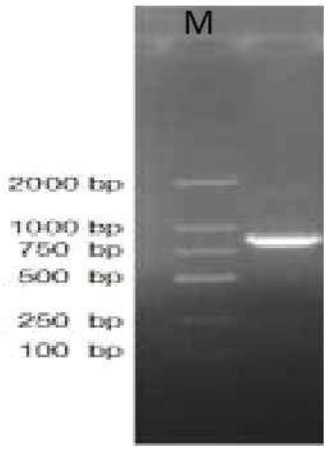

Fig.1. The result of PCR in *PeDof-4* cloning.
Notes: M: D2000 plus DNA Marker.

The physicochemical properties of *PeDof-4* encoded proteins were analyzed using Protparam online software. The *PeDof-4* gene-encoded proteins were 282 amino acids, with molecular formula of C1274H1983N375O408S14, molecular weight 29592.87 u, and theoretical isoelectric point pI of 8.96. Meanwhile, the *PeDof-4* proteins were analyzed using Protparam online software. The amino acid composition of *PeDof-4* protein was analyzed, in which the highest percentage was Serine (Ser. S) at 14.9%, followed by Glycine (Gly, G) at 13.8%, and the lowest percentage of Histidine (Hist, H) at 1. 1% (Table 1).

Table 1. Amino acid composition.

Amino acid	Quantity	Percentage (%)
Ala (A)	21	7.4
Arg (R)	15	5.3
Asn (N)	15	5.3
Asp (D)	8	2.8
Cys (C)	8	2.8
Gln (Q)	15	5.3
Glu (E)	9	3.2
Gly (G)	39	13.8
His (H)	3	1.1
Ile (I)	8	2.8
Leu (L)	25	8.9
Lys (K)	8	2.8
Met (M)	6	2.1
Phe (F)	13	4.6
Pro (P)	18	6.4
Ser (S)	42	14.9
Thr (T)	13	4.6
Trp (W)	4	1.4
Tyr (Y)	6	2.1
Val (V)	6	2.1

Notes: Ala: Alanine; Arg: Arginine; Asn: Asparagine; Asp: Asparticacid; Cys: Cysteine; Gln: Glutamine; Glu: Gluta micacid; Gly: Glycine; His: Histidine; Ile: Isoleucine; Leu: Leucine; Lys: Lysine; Met: Methionine; Phe: Phenylalanine; Pro: Proline; Ser: Serine; Thr: Threonine; Trp: Tryptophan; Tyr: Tyrosine; Val: Valine.

The results of hydrophilic-hydrophobicity analysis of *PeDof-4* protein using ExPasy-ProtScale revealed that 20 standard amino acids are present in *PeDof-4*. The total number of non-polar (hydrophobic) amino acids (A, V, L, I, P, F, W, M) in *PeDof-4* protein was 101, and the hydrophobic amino acids accounted for 35.8% of the total amino acids; the total number of polar amino acids (G, S, Y, C, T, N, Q) was 138; the total number of basic amino acids (K, R, H) was 26; and the total number of acidic amino acids (D, E) was 17. The hydrophilicity and hydrophobicity analysis of *PeDof-4* protein showed that there were more hydrophobic amino acids than hydrophilic amino acids (including polar amino acids, acidic amino acids and basic amino acids) (Fig. 2), among which arginine (R) had the lowest score of -4.500, and isoleucine (I) had the highest score of 4.500, according to the rule that the lower the amino acid score was the more

hydrophilic, and the higher the score was the more hydrophobic. According to the rule, the lower the score, the more hydrophilic the amino acid is; and the higher the score, the more hydrophobic the amino acid is.

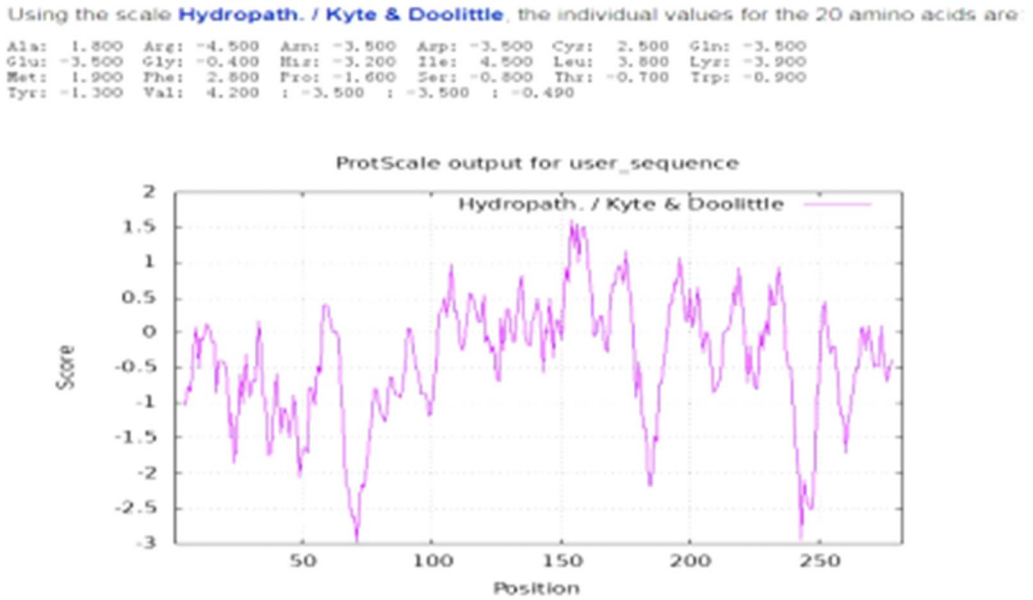

Fig. 2. Hydrophilic and hydrophobic analysis of protein products encoded by *PeDof-4*.

Biologically significant site analysis of the deduced *PeDof-4* amino acid sequence using the Motif Search tool (http://www.genome.jp/tools/motif/) predicted a Dof structural domain between sites 16 and 71 (Fig. 3).

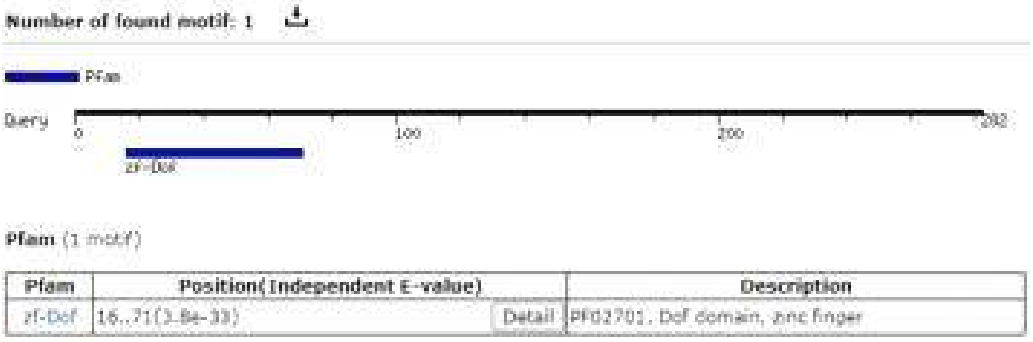

Fig. 3. Motif prediction from the deduced amino acid sequence of *PeDof-4*.

Comparison of the amino acid sequences deduced from *PeDof-4* with the Dof amino acid sequences of other higher plants, which have been registered in NCBI for homology (Fig. 4), showed that the amino acid sequences encoded by *PeDof-4* in different plants showed a high degree of homology, which was more than 60%.BLASTX analysis showed that the amino acid

sequences encoded by *PeDof-4* showed 62.86%, 62.61%, 62.57% and 60.5% homology with those encoded by *TmDof (Theobroma cacao)*, *MeDof (Manihot esculenta)*, *HbDof (Herraniaum bratica)* and *JcDof (Jatropha curcas)*, respectively.

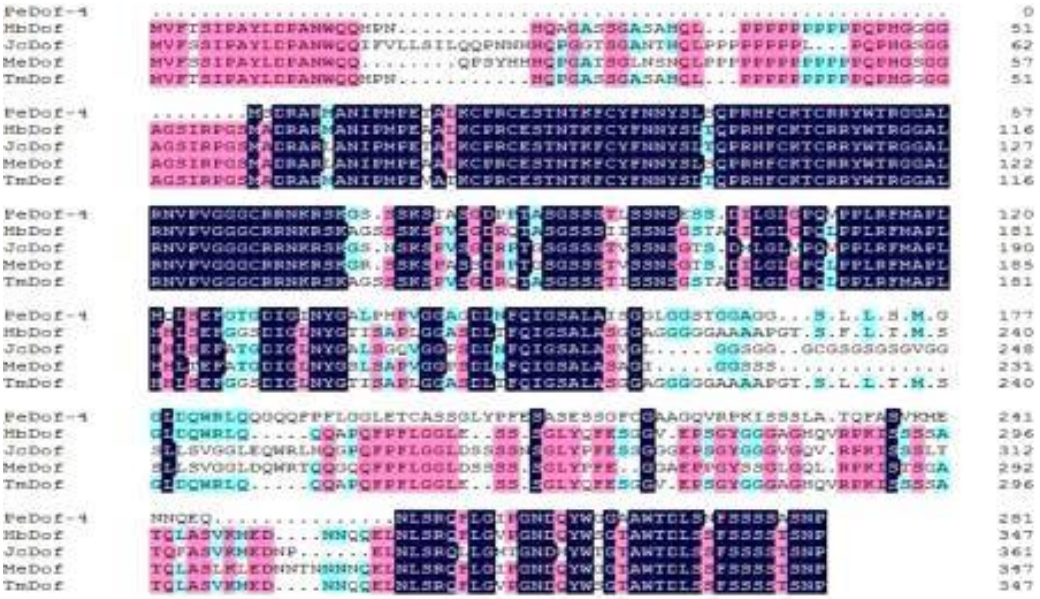

Fig. 4. Prediction of *PeDof-4* protein tertiary structure.

The amino acid sequence encoded by *PeDof-4* was analyzed against the amino acid sequences of Dof in other plants in a phylogenetic tree using Clustal X and MEGA3 software. The results showed that passion fruit *PeDof-4* was homologous to *Hevea brasiliensis*, *Manihot esculenta*, *Jatropha curcas*, *Mercurialis annua*, *Carica papaya*, *Citrus sinensis* and other homologous genes had close homology, and the specific relationship evolution diagram (Fig. 5).

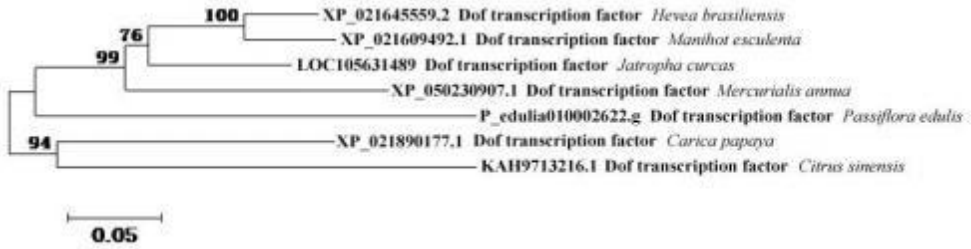

Fig.5. Phylogenetic relationships of Dof in plants.

The promoter elements of *PeDof-4* gene were analyzed using PlantCARE software, and the results showed that the fragment contained multiple TATA-box and CAAT-box core cis-acting elements, and the rest of the functional elements mainly included abscisic acid-responsive elements (ABRE), light-responsive elements (TCT-motif, Box 4, G- Box, AE-box, MRE), etc. (Fig. 6). This analysis suggests that the function of the genes may be related to abiotic stress and plant development.

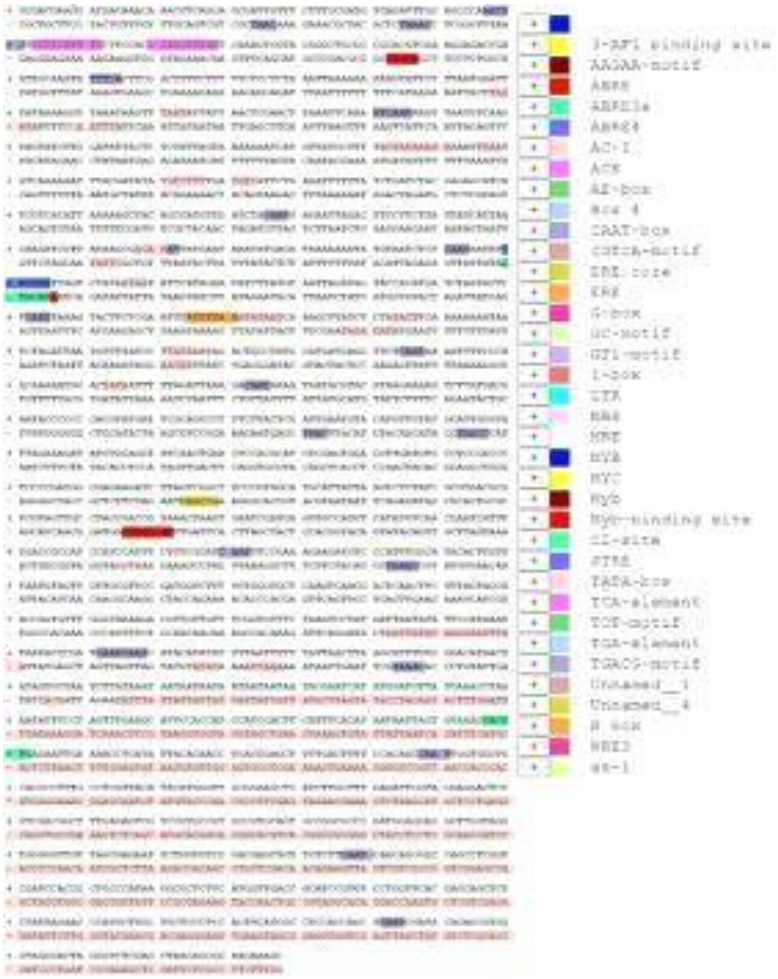

Fig. 6. Cis-acting element of *PeDof-4*.

The results of tissue-specific expression showed that *PeDof-4* was expressed in all tissues of passion fruit, with the highest expression in the roots (Fig. 7).

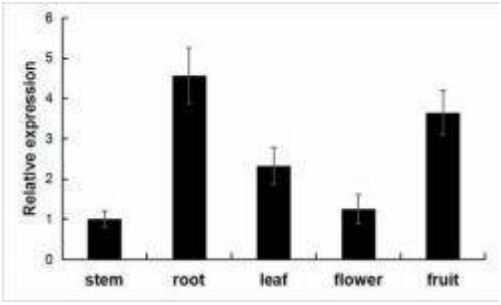

Fig. 7. Expression patterns of *PeDof-4* in different tissues of passion fruit.

When transgenic seedlings were grown for 7 days in MS medium supplemented with 200 mM mannitol, GUS staining showed that their leaves were deeper than the control, suggesting that expression of the gene was induced by drought stress. Meanwhile, the GUS enzyme activity of seedlings under drought stress was higher than that of the control (Fig. 8).

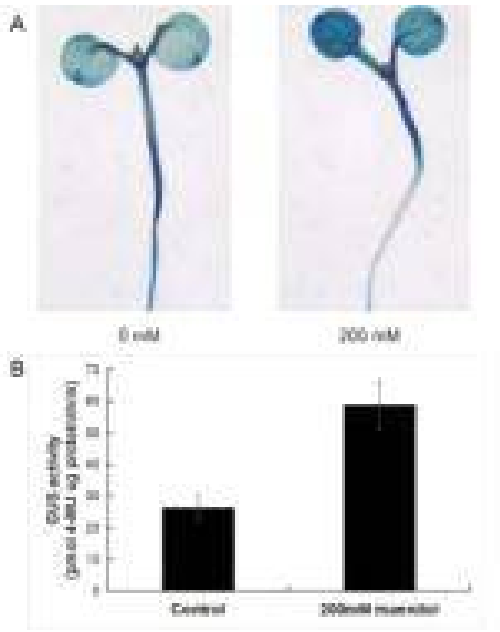

Fig. 8. Induction and expression pattern of *PeDof-4* under drought stress. (A) GUS staining of overexpressing Arabidopsis strains. (B) GUS activity quantitative analysis of overexpressing Arabidopsis.

Passiflora edulis, belonging to the Passiflora family (Passifloraceae), is a perennial evergreen vine that produces passion fruits renowned for their aromatic pulp derived from over 100 fruit species. Native to central and northern South America, passion fruit cultivation is predominantly observed in Central and South America, Australia, and Africa. The *Passiflora* genus comprises approximately 520 species, with only around 60 species deemed suitable for fresh consumption. Currently, major passion fruit cultivation regions include Brazil, Colombia, Ecuador, Australia, Vietnam, and China, encompassing a total plantation area of approximately 5 million mu with a production value of around 40 billion yuan.

Characterized by a shallow root system spanning 4-5 meters horizontally, passion fruit plants necessitate adequate water supply throughout their reproductive phase. Water requirement escalates during budding, tasseling, flowering, and fruiting stages, with drought posing a growth inhibition threat. Optimal growth conditions entail an annual rainfall of 1500-2000 mm, evenly distributed. Enhancing passion fruit's resilience to drought stress and reducing water resource dependence are crucial for the sustainable advancement of the industry. Addressing these challenges is paramount for industry progression, making the investigation of passion fruit responses to drought stress a primary scientific endeavor.

Transcription factors are critical in managing plant development, and recent research has highlighted the response of plant Dof genes to abiotic stresses like drought, enhancing the stress resistance capabilities of the plants. Specifically, in tomatoes, the *SlCDF15* genes were activated

due to osmotic, salt, heat, and cold stress conditions. Enhanced expression of *SlCDF1* or *SlCDF3* in Arabidopsis has demonstrated improved drought and salt tolerance (Corrales *et al*. 2014). According to Corrales *et al*. (2014), all *SlCDF* genes in the tomato, which belong to the Dof gene family, are influenced by drought, suggesting these genes may serve as primary regulators in drought response pathways, potentially influencing various stress-regulated target genes (Corrales *et al*. 2014).

In Chinese cabbage, a significant number of Dof genes rapidly increased expression under salts, drought, heat, and cold stresses (Ma *et al*. 2015). Further, research discovered an interaction between ABA1 and *CsDof-22*. This interaction underscored the critical role of ABA1 in the biosynthesis of abscisic acid (ABA) according to STRING data, hinting that *CsDof-22* might contribute similarly in ABA production. Experimentally, it has been shown that ABA is essential for osmotic and drought stress resistance (Zhou *et al*. 2014). In the case of banana, numerous MaDof genes exhibited reduced expression under drought and salt stress (Dong *et al*. 2016). The current research on the *PeDof-4* gene from *Passiflora edulis* reveals that it is inducible under different drought stress conditions and was also transiently expressed in tobacco. This induction under various drought stress timelines suggests that the gene is responsive to such environmental challenges.

The analysis of amino acids in the proteins sequenced showed a high content of alanine (Ala,A). Using the Motif Search tool to inspect the sequence's biological significance, it was found that *PeDof-4* possesses a Dof structural domain typical to the Dof gene's amino acid composition, aligning with the characteristic structure of the Dof gene family. Phylogenetic tree construction illustrated that *PeDof-4* shares the closest genetic ties with species such as Mercurialis annua, Jatropha curcas, Manihot esculenta, and Hevea brasiliensis, highlighting its strong genetic relatedness with these species (Wang *et al*. 2008). Examination of the promoter elements indicated the presence of sequences responsive to low temperature, abscisic acid, growth hormones, and light within the *PeDof-4* gene's promoter, pointing to a potential role of this gene in responding to abiotic stress and influencing plant growth and developmental mechanisms. Promoters are crucial for kickstarting the transcription process and the spatial and temporal regulation of gene activity (Potenza *et al*. 2004). Thus, choosing promoters that can be induced is a strategic approach to effectively manage gene expression.

In this study, the *PeDof-4* sequence was cloned from passion fruit. Using bioinformatics methods, we investigated the gene and its protein sequence and speculated on its possible biological roles through multiple sequence comparisons, phylogenetic analysis, and promoter element analysis. In addition, this study investigated the expression of *PeDof-4* under drought conditions, and the results indicated that the gene is induced to express itself by drought stress. Transgenic *Arabidopsis thaliana* was able to respond to drought stress. These preliminary results provide a basis for future studies on the functional analysis and regulation of Dof gene expression.

Acknowledgments

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