Cloning and Expression Analysis of the WD40 Transcription Factor Gene DcWD40-1 from Dracaena cambodiana Postprint

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Abstract

Dracaena cambodiana is the main source plant of domestic dragon' s blood resin, whose primary chemical constituents are flavonoid compounds. Current research on dragon' s blood resin has focused on chemical composition and pharmacological activity analysis, while the molecular mechanism underlying its formation remains poorly understood. WD40 transcription factors play important regulatory roles in flavonoid accumulation. Based on transcriptome data of Dracaena cambodiana, this study cloned a WD40 gene, DcWD40-1, from Dracaena cambodiana using RT-PCR. The gene contains a 1,353 bp open reading frame, encoding 450 amino acids, with a protein molecular weight of 50.77 kD and a theoretical isoelectric point of 5.71. Bioinformatics analysis revealed that DcWD40-1 belongs to the WD40 protein family, possesses five conserved WD40 domains, and exhibits high homology and strong conservation with WD40 proteins from other plants. Using the Genome Walking method, a 1,503 bp promoter sequence of DcWD40-1 was isolated. This region exhibits typical structural characteristics of eukaryotic promoters and contains multiple response elements responsive to hormones and stress. Expression analysis demonstrated that dragon' s blood resin inducers could induce DcWD40-1 expression, and changes in DcWD40-1 were positively correlated with dragon' s blood resin formation and flavonoid accumulation. Furthermore, DcWD40-1 also responded positively to methyl jasmonate, cytokinin, brassinolide, and UV-B treatments. These results lay a foundation for further investigation into the potential function and mechanism of DcWD40-1 in flavonoid biosynthesis.

Full Text

Cloning and Expression Analysis of the WD40 Transcription Factor Gene DcWD40-1 from Dracaena cambodiana

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Abstract

Hainan dragon' s blood tree (*Dracaena cambodiana*) is the primary botanical source of dragon' s blood in China, with flavonoids constituting its main chemical components. While previous research has focused on chemical composition and pharmacological activity analyses, the molecular mechanisms underlying dragon' s blood formation remain poorly understood. WD40 transcription factors play crucial regulatory roles in flavonoid accumulation. In this study, we cloned a WD40 gene designated *DcWD40-1* from *Dracaena cambodiana* based on transcriptome data using RT-PCR technology. The gene contains a 1,353 bp open reading frame encoding 450 amino acids, with a predicted molecular weight of 50.77 kD and theoretical isoelectric point of 5.71. Bioinformatic analysis revealed that DcWD40-1 belongs to the WD40 protein family, possesses five conserved WD40 domains, and shows high homology and strong conservation with WD40 proteins from other plants. Using genome walking, we isolated a 1,503 bp promoter sequence of *DcWD40-1* that exhibits typical eukaryotic promoter structural characteristics and contains multiple hormone- and stress-responsive elements. Expression analysis demonstrated that dragon' s blood inducers can induce *DcWD40-1* expression, with changes in DcWD40-1 positively correlating with dragon' s blood formation and flavonoid accumulation. Additionally, *DcWD40-1* responded positively to methyl jasmonate, cytokinin, brassinosteroid, and UV-B treatments. These results establish a foundation for further investigation of the potential functions and mechanisms of DcWD40-1 in flavonoid biosynthesis.

Keywords: *Dracaena cambodiana*, dragon' s blood, flavonoids, WD40 transcription factor, gene expression

Introduction

Dragon' s blood is a traditional precious Chinese medicine with therapeutic effects including blood circulation promotion, anti-inflammation, analgesia, hemostasis, and tissue regeneration (Gupta et al, 2008; Wang et al, 2011).

Dracaena cambodiana serves as the botanical source of domestic dragon' s blood in China (Zheng et al, 2009; Wang et al, 2013). Previous studies have shown that flavonoid compounds constitute the main chemical components of dragon' s blood from *D. cambodiana* (Chen et al, 2012; Zheng et al, 2012; Wang et al, 2017). These flavonoids exhibit diverse biological activities, including anticancer, antitumor, anti-inflammatory, antifungal, thrombin inhibition, and antiproliferative properties (Luo et al, 2011; Mei et al, 2013; Wang et al, 2017). While considerable research has focused on the chemical constituents, pharmacological activities, and clinical applications of dragon' s blood, the mechanisms underlying flavonoid accumulation and dragon' s blood formation remain unclear (Zhu et al, 2016).

Flavonoid biosynthesis in plants is primarily controlled by structural genes (encoding various enzymes in the flavonoid biosynthetic pathway) and regulatory genes (transcription factors) (Tohge et al, 2017). WD40 transcription factors interact with MYB and bHLH transcription factors to form MBW complexes that coordinately regulate the expression of multiple structural genes involved in flavonoid biosynthesis (Xu et al, 2015). WD40 proteins represent a ubiquitous protein family in eukaryotes that are highly conserved during evolution, typically containing multiple WD40 repeat motifs composed of 40-60 amino acid residues (Xu & Min, 2011). WD40 genes associated with flavonoid synthesis have been isolated and identified in various plants, including *Arabidopsis TTG1* (Baudry et al, 2004), apple *MdTTG1* (An et al, 2012), Chinese bayberry *MrWD40-1* (Liu et al, 2013), persimmon *DkWDR1* (Naval et al, 2016), pomegranate *PgWD40* (Bensimhon et al, 2011), tartary buckwheat *FtWD40* (Yao et al, 2017), and tomato *SlAN11* (Gao et al, 2018). However, no WD40-like transcription factors have been reported in *D. cambodiana* to date.

In our previous research, we employed the patented "inorganic salt inducer infusion method"to induce dragon's blood formation in *D. cambodiana*, analyzed its chemical composition, and examined transcriptome data before and after induction. This work led to the derivation of the flavonoid biosynthetic pathway and the identification of a WD40-encoding gene predicted to play a regulatory role in flavonoid biosynthesis (Zhu et al, 2016). Building upon these findings, the present study clones this gene and analyzes its spatiotemporal expression characteristics to establish a foundation for investigating its potential functions and mechanisms in flavonoid biosynthesis.

Materials and Methods

1.1 Plant Materials *Dracaena cambodiana* plants used in this study were cultivated at the Institute of Tropical Biosciences and Biotechnology, Chinese Academy of Tropical Agricultural Sciences. Dragon' s blood induction was performed by injecting 10% inorganic salt inducer solution into the stems using the infusion method. Samples were collected at 0, 3, and 6 days post-treatment as

previously described (Zhu et al, 2016). For stress treatments, uniform tissue culture seedlings were transferred to liquid medium for 7 days before exposure to UV-B radiation or foliar spraying with 200 $M \cdot L^{-1}$ methyl jasmonate (MeJA), abscisic acid (ABA), cytokinin (CTK), or brassinosteroid (BR). Samples were collected at 0, 3, 12, and 24 hours post-treatment. All samples were immediately frozen in liquid nitrogen and stored at -80°C.

1.2 Nucleic Acid Extraction and cDNA Synthesis Total RNA and genomic DNA were extracted using the Plant Total RNA Isolation Kit and Plant DNA Isolation Kit from FOREGENE (Chengdu, China), respectively. Total RNA was reverse-transcribed into cDNA using the All-in-One First-Strand Synthesis MasterMix (with DNase I) from NOVA® Yugong Biolabs (Jiangsu, China) according to the manufacturer' s protocol.

1.3 Cloning of DcWD40-1 Gene and Promoter Based on the WD40 EST sequence obtained from the *D. cambodiana* transcriptome database, specific primers were designed for full-length amplification: WD40F (5 -CTACAAATTCATGTGAGCGG-3) and WD40R (5 -CGGCAGCTCAGCTGCCTACAG-3). The *DcWD40-1* gene was amplified from cDNA template, and the PCR product was identified by agarose gel electrophoresis. The target band was recovered, ligated into the pMD19-T vector, and transformed into *E. coli* DH5α. Positive clones were identified by colony PCR and sequenced by Nuosai Gene Company. The amino acid composition, molecular formula, molecular weight, and isoelectric point were predicted using ExPASy online software (https://www.expasy.org/). Subcellular localization was predicted using PSORT (http://psort1.hgc.jp/form.html), and amino acid sequence alignment was performed using DNAMAN software.

The promoter region of *DcWD40-1* was cloned using the Universal Genome Walker 2.0 Kit (Clontech). Genomic DNA was digested with four restriction enzymes (EcoRV, StuI, PvuII, and DraI) and ligated to adaptors using T4 DNA ligase. Using the ligation product as template, two rounds of PCR were performed with adaptor primers (AP1 and AP2, provided in the kit) and gene-specific primers (PWD: 5 -TGGAGGTGGTGGGTATTTCG-3 ; PWD2: 5 -GATACTCGTTGCTGGATTATAGGA-3). The amplified product was identified by agarose gel electrophoresis, recovered, ligated into pMD19-T vector, transformed into *E. coli* DH5α, and sequenced. Promoter element analysis was conducted using the online tool PlantCARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/).

1.4 Gene Expression Analysis Quantitative real-time PCR (qPCR) was performed using SYBR® Select Master Mix on an Mx3005P Real-Time PCR System. The *Actin* gene served as internal control with primers qDcACT-F (5 -ACCGAGAGAGGGTACTCATT-3) and qDcACT-R (5 -CCAGCTCCTGCTCGTAATC-3). Target gene primers were

qWD1-F (5 -GAATGGAGGTGGTGGGTATTT-3) and qWD1-R (5 -TTTGTTTGATGGAGGAGAGAGA-3). The 20 L qPCR reaction contained 10 L 2×SYBR mix, 1 L each of forward and reverse primers (10 $M \cdot L^{-1}$), 1 L cDNA template, and 7 L ddH_2O. Cycling conditions were: 95°C for 10 min; 40 cycles of 95°C for 15 s, 60°C for 30 s, 72°C for 30 s. Relative gene expression was analyzed using the 2^(-ΔΔCt) method.

Results

2.1 Cloning of DcWD40-1 Based on the WD40 gene EST sequence from the *D. cambodiana* transcriptome database, specific primers were designed to amplify the full-length sequence, yielding a specific band of approximately 1,500 bp. The target fragment was ligated into the T-vector and sequenced, confirming consistency with the transcriptome sequencing result. This gene was designated *DcWD40-1*. The full-length *DcWD40-1* gene obtained in this study is 1,550 bp, containing a complete 1,353 bp open reading frame.

2.2 Molecular Characteristics of DcWD40-1 The DcWD40-1-encoded protein consists of 450 amino acids, with glycine (Gly) and serine (Ser) being the most abundant residues (40 each, accounting for 8.9%). The molecular formula of DcWD40-1 protein is $C_{2238}H_{3412}N_{634}O_{689}S_{17}$, with a predicted molecular weight of 50.77 kD and theoretical isoelectric point of 5.71. Subcellular localization prediction indicated highest probability (71.4%) of localization in microbodies. Amino acid sequence analysis revealed that DcWD40-1 possesses the structural features of plant WD40 transcription factors, including five WD40 repeat motifs. The amino acid sequence of DcWD40-1 showed 77.1%, 76.9%, 75.6%, and 74.9% homology with corresponding WD40 sequences from date palm (*Phoenix dactylifera*), oil palm (*Elaeis guineensis*), *Apostasia shenzhenica*, and *Dendrobium catenatum*, respectively.

[Figure 1: see original paper] *Alignment of DcWD40-1 and other WD40 proteins from various plants. Note: The conserved WD40 domains are underlined.*

2.3 Cloning and Sequence Analysis of DcWD40-1 Promoter Using the genome walking method, we isolated a 1,503 bp promoter region of *DcWD40-1*. This region exhibits typical eukaryotic promoter structural characteristics, containing multiple basic elements such as TATA-box and CAAT-box. Additionally, the promoter sequence harbors various hormone-responsive elements including cytokinin response elements (CMRs), abscisic acid response elements (ABRE), auxin response elements (TGA-box), salicylic acid response elements (TCA-element), and jasmonic acid response elements (CGTCA-motif). It also contains defense and stress-responsive elements such as TC-rich repeats, anaerobic induction elements (ARE), heat shock elements (HSE), low temperature response elements (LTR), and numerous light-responsive elements including 3-AF1 binding site, ATCC-motif, ATCT-motif, Box I, GA-motif, G-box SP1, and

GT1-motif. These findings suggest that these hormones and stress factors may influence the transcriptional level of *DcWD40-1*.

[Figure 2: see original paper] *Promoter sequence of DcWD40-1 and main regulatory elements.*

2.4 Expression of DcWD40-1 Under Dragon' s Blood Inducer Treatment Inorganic salts can induce dragon' s blood production and upregulate the expression of genes related to flavonoid accumulation. Therefore, we examined the expression patterns of *DcWD40-1* under inorganic salt treatment. Quantitative PCR results showed that *DcWD40-1* expression was upregulated by 1.6-fold and 2.5-fold at 3 and 6 days post-induction, respectively [Figure 3: see original paper]A. In previous transcriptome data, the FPKM values of *DcWD40-1* increased by 3.6-fold and 6.8-fold compared to the control at 3 and 6 days post-induction [Figure 3: see original paper]B. These results demonstrate that dragon' s blood inducers can induce *DcWD40-1* expression.

[Figure 3: see original paper] *Expressions of DcWD40-1 in response to the inducer of dragon' s blood. Note: A. Expression analysis based on qPCR; B. Expression analysis based on FPKM values.*

2.5 Expression of DcWD40-1 Under Stress Treatments Plant hormones and light play important regulatory roles in flavonoid secondary metabolite formation. Therefore, we investigated the response characteristics of *DcWD40-1* to hormones (MeJA, CTK, ABA, and BR) and UV-B stress. qPCR results showed that, except for ABA [Figure 4: see original paper]C, all five treatments induced *DcWD40-1* expression. Under MeJA and BR treatments, expression peaked at 24 hours post-treatment, reaching 2.1-fold and 6.5-fold of normal levels, respectively [Figure 4: see original paper]A, D. Under CTK treatment, maximum expression occurred at 12 hours post-treatment, with a 6.2-fold upregulation [Figure 4: see original paper]B. *DcWD40-1* showed a strong response to UV-B, with expression reaching 74.5-fold of the control at 3 hours post-treatment [Figure 4: see original paper]E.

[Figure 4: see original paper] *Expressions of DcWD40-1 under different stress treatments. Note: A. MeJA treatment; B. CTK treatment; C. ABA treatment; D. BR treatment; E. UV-B treatment.*

Discussion

WD40 repeat proteins represent an ancient and highly conserved protein family that participates extensively in plant growth and development processes, including signal transduction, cell division, gene expression regulation, protein ubiquitination, histone methylation, genome stability, and cell cycle control (Xu & Min, 2011). Previous studies have demonstrated that WD40 proteins are closely associated with flavonoid accumulation in plants (Xu et al, 2015).

The first WD40 gene identified in flavonoid metabolism regulation was *PhAN11* from petunia (De et al, 1997), and subsequent studies have identified WD40-like transcription factors related to flavonoid synthesis in multiple plant species. WD40 proteins typically interact with MYB and bHLH transcription factors to form MBW complexes that coordinately regulate flavonoid biosynthesis. In the MBW transcriptional complex, MYB and bHLH members possess DNA-binding properties, while WD40 transcription factors generally lack recognizable cis-acting elements or catalytic activity, functioning instead to stabilize protein interactions and enhance partner gene activity (Xu et al, 2014; Xu et al, 2015). Although WD40 transcription factors cannot directly regulate the expression of flavonoid biosynthetic structural genes, overexpression of WD40 genes has been shown to significantly increase flavonoid content in transgenic plants across multiple species (Yao et al, 2017; Gao et al, 2018), demonstrating their important regulatory role in flavonoid accumulation.

In this study, we isolated *DcWD40-1*, a gene encoding a WD40 transcription factor from *D. cambodiana*. The encoded protein exhibits typical structural features of plant WD40 proteins, containing five WD40 repeat motifs. Both FPKM values and qPCR analysis demonstrated that inorganic salt inducers can upregulate *DcWD40-1* expression in *D. cambodiana*, with changes in DcWD40-1 positively correlating with dragon's blood formation and flavonoid accumulation (Zhu et al, 2016), suggesting its potential importance in flavonoid biosynthesis. Flavonoid compounds have long been recognized as protective chemicals against UV damage in plant tissues, and light, particularly UV radiation, can induce flavonoid accumulation and related gene expression (Petrussa et al, 2013). Plant hormones including jasmonic acid, abscisic acid, cytokinin, and brassinosteroid have been confirmed to play significant regulatory roles in flavonoid biosynthesis (De et al, 2012; Yun et al, 2015; Xin et al, 2017; Koyama et al, 2018). 6-benzylaminopurine (6-BA), a synthetic cytokinin, promotes dragon' s blood formation and induces expression of flavonoid biosynthesis-related genes in *D. cambodiana* tissue culture seedlings (Yang et al, 2009; Wang et al, 2015). We identified one jasmonic acid response element (CGTCA-motif), four cytokinin response elements (CMR), and numerous light response elements (including 3-AF1 binding site, ATCC-motif, ATCT-motif, Box I, GA-motif, G-box SP1, GT1-motif) in the *DcWD40-1* promoter region. Expression analysis further confirmed that MeJA, CTK, BR, and UV-B significantly upregulate *DcWD40-1* expression, indicating that DcWD40-1 may participate in flavonoid biosynthesis regulation through MeJA, CTK, BR, and UV-B signaling pathways. Future research will further investigate the functional and regulatory characteristics of *DcWD40-1* to establish a basis for increasing flavonoid content in *D. cambodiana* through transgenic approaches or hormonal and chemical regulation.

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Note: Figure translations are in progress. See original paper for figures.