



Changes of Phenolic Acids Related Genes in *Taraxacum mongolicum* Hand.-Mazz. under Saline Stress

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Abstract

Dandelion (*Taraxacum mongolicum* Hand.-Mazz.) is rich in phenolic acids and has become popular in vegetable and medicine in China. Growing dandelion in saline-alkali land is considered to be an efficient strategy for the development of saline-alkali land. In order to screen candidate genes related to phenolic acids synthesis under saline stress, we evaluated phenolic acids accumulation from dandelion resource of A (*T. mongolicum* cv. dandelion cultivar “Binpu 2”) and B (*T. mongolicum* cv. a wild local dandelion “Tanghai”) under NaCl concentrations of 0, 0.3%, 0.5%, 0.7%, 0.9% and 1.2%. Result found that 4 main kinds of phenolic acids that caftaric acid, chlorogenic acid, caffeic acid and chicoric acid all showed the highest accumulations in treatment of 0.9% NaCl for the two dandelions. Thus we performed a transcriptome analysis of dandelion leaves at the NaCl concentration of 0.9%. Totally 2468 differentially expressed genes (DEGs) were detected from dandelion A, including 1456 up-regulated DEGs; and the total 3238 with 1369 up-regulated DEGs were found in dandelion B. GO annotation analysis showed that the functions of DEGs were mainly referred to phenylpropanoid biosynthesis process, secondary metabolite biosynthetic process, apoplast, etc. KEGG enrichment showed that DEGs were enriched in secondary metabolites biosynthesis, phenylpropanoid biosynthesis, plant hormone signal transduction, etc. We specially analyzed the DEGs of caffeic acid O-methyltransferase due to the highest content accumulated in dandelions, and found 4 DEGs related to O-methyltransferase 1 (OMT1), including 2 novel genes. We validated the expression profiles of the four candidate OMT1 genes by qRT-PCR, and found the results were consistent with the RNA-seq results.

Subject Areas

Plant Science

Keywords

Caffeic Acid, Dandelion, Differentially Expressed Genes, Saline Stress, Transcriptome

1. Introduction

Saline-alkali land is an important land resource with an area of ~100 million hectares in China, accounting for 78% of the existing cultivated land. Making full use of saline-alkali land resources is of great significance to the development of modern agriculture and the guarantee of food security (Wang *et al.*, 2019) [1]. The China government also proposed to make full use of saline-alkali land and continue to promote the transformation from the control of saline-alkali land to adapt crops to the selection of saline-alkali tolerant plants to adapt to saline-alkali land.

Dandelion (*Taraxacum mongolicum*) could tolerate saline stress of 1.5% NaCl, easily found in saline-alkali areas, and is also a medicinal herb. It is rich in caffeic acid, chicory acid and other phenolic acids, and has antibacterial and anti-inflammatory effects. It is widely used in medicine, health care and food industries (Wu *et al.*, 2022) [2]. However, at present, dandelion cultivars with high phenolic acid content were still few, leading to the insufficient supply of high quality raw dandelion materials, that limited the development of dandelion industry (Wu *et al.*, 2022) [3].

We created salt-tolerant callus mutant and bred the cultivar “Binpu 1” and “Binpu 2” with high yield and phenolic acids, and developed the cultivation technique in saline-alkali land (Wu *et al.*, 2022) [3]. We found that the proper salinity (<0.6%) could improve the yield and phenolic acids contents 5% - 10% higher than that in common conditions (Wu *et al.*, 2019) [4]. However, the molecular mechanism of response of phenolic acids accumulation in dandelion to saline stress was still unclear, and related reports were also few.

Transcriptome sequencing (RNA-seq) technology has been widely used in salt-tolerant research of wheat, maize, and cotton etc, and a large number of genes related to salt tolerance have been found (Nagai *et al.*, 2011) [5]. Nazanin *et al.* (2019) analyzed 2 wheat cultivars roots under treatments of 150 mM NaCl solution for 12 h, and found 5128 differentially expressed genes related to phenylpropanoid biosynthesis, transcription factors, glycosyltransferases, glutathione metabolism and plant hormone signal transduction (Amirbakhtiar *et al.*, 2019) [6]. Guo *et al.* (2015) compared the transcriptome changes of 2 salt-tolerant cotton cultivars in response to NaCl treatments, and identified 2857 differentially expressed probe sets responded to osmotic stress, hormone stimulus, secondary metabolism process (Guo *et al.*, 2015) [7]. Lin *et al.* (2022) reported high-quality genome assemblies of dandelion, which was important breakout for the development of molecular research in dandelion (Lin *et al.*, 2022) [8].

At present, the most researches on dandelion were focused on physiological

research (Chen *et al.*, 2021) [9], morphological research (Grauso *et al.*, 2019 [10]; Wang and Lu, 2019 [11]), medicinal research (Grauso *et al.*, 2019 [10]; Xie *et al.*, 2018 [12]) and rubber production related research (Lin *et al.*, 2017) [13], etc. However, the molecular mechanism of phenolic acids accumulation under saline stress was still few. Thus, in the current study, the salt-tolerant cultivar “Binpu 2” was mainly used to discover the differentially expressed genes in the leaves that responded to salt stress by RNA-seq technology. Through functional enrichment, the molecular regulation mechanism of dandelion that adapted to salt stress was analyzed, in order to lay a theoretical foundation for the cultivation of dandelion in saline-alkali land to improve the content of phenolic acid.

2. Materials and Methods

2.1. Plant Materials and Treatments

Dandelion seeds of BP (*T. mongolicum*. cv. “Binpu 2”) and TH (*T. mongolicum* cv. “Tanghai”) were collected from the Institute of Coastal Agriculture, Hebei Academy of Agriculture and Forestry Sciences in Hebei Province, China (North China, 39.23°N, 118.57°E). The seeds were sown in flower pots (32 cm high and 28 cm in diameter) in a soil mix of perlite, vermiculite, and peat and germinated at 25°C ± 2°C and 60% - 70% humidity in an experimental greenhouse. The pots were transferred to natural environment when dandelion seedlings were with 5 leaves and then irrigated 150 ml NaCl solutions of 0 (CK), 0.3%, 0.5%, 0.7%, 0.9% and 1.2% every two days. Four weeks later, the leaves were harvested and checked the contents of tartaric acid, chlorogenic acid, caffeic acid, and chicoric acid. Of which the fresh leaves samples from 0.9% NaCl were immediately placed in liquid nitrogen. Three biological replicates of 7 seedlings each were sampled in each NaCl treatment. The samples were stored in a -80°C freezer for further study.

2.2. Phenolic Compounds' Examination

The extraction and measurement method of dandelion phenolic acids were referred to our publications (Wu *et al.*, 2020) [14]. Dandelion leaves were dried at 80°C in oven, and then were extracted with 80% methanol for 30 min. The extract was checked by HPLC (HPLC 1200 series, Agilent Technologies Inc., USA) equipped with chromatographic column (Mars ODS-AQ (4.6 mm, 250 mm, 5 mm), Hming Technologies Co. Ltd, China) with the following conditions: injection volume, 0.5 ml; flow rate, 1 mL/min; methanol:0.2% phosphoric acid ratio, 40:60; detection wavelength, 327 nm; and detection time, 15 min.

2.3. RNA-Seq Analysis

RNA-Seq was performed by Biomarker Technologies Co., Ltd. (Beijing, China). Total RNA was extracted from fresh dandelion samples using the Tiangen RNA Pure kit for plants (Tiangen, Beijing, China). RNA integrity and concentration were assessed using an Agilent 2100 Bioanalyzer (Agilent Technologies, Inc., Santa Clara, CA, USA). The cDNA libraries were constructed according to the

manufacturer's instructions of the NEBNext Ultra RNA Library Prep Kit for Illumina (New England Biolabs, Ipswich, USA). The resulting dandelion libraries were sequenced on a flow cell of the Illumina HiSeq 2500 platform (Illumina, Inc., San Diego, USA).

The reference genome GWHBCHG00000000 (<https://ngdc.cncb.ac.cn/gwh/Assembly/19733>) was used to sequence alignment with HISAT2 method. FPKM (Fragments per kilobase of transcript per million fragments mapped) were used to standardize gene expression, and genes with $FC \geq 2$ and false discovery rate (FDR) < 0.01 were identified as differentially expressed genes (DEGs). Gene functional annotation and pathway analysis were performed based on seven databases: GO (Gene Ontology), KO (KEGG Ortholog database), KOG/COG (Clusters of Orthologous Groups of proteins), Nr (NCBI non-redundant protein sequences), Nt (NCBI non-redundant nucleotide sequences), Pfam (Protein family), and Swiss-Prot (a manually annotated and reviewed protein sequence database).

2.4. Quantitative Real-Time PCR (qRT-PCR) Analysis

Total RNA was extracted from dandelion samples according to the instructions of the Tiangen RNA Pure kit for plants (Tiangen, Beijing, China). The purity, concentration, and integrity of total RNA were measured on a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA). First-strand cDNA was synthesized using the PrimeScript RT reagent kit with gDNA Eraser (Takara Biotechnology Inc., Dalian, China). The qRT-PCR analysis was performed using TB Green Premix Ex Taq II (Cat. No. RR820A, Takara Biotechnology Inc., Dalian, China) on a CFX96 Real-Time System (BioRad Laboratories, Inc., Hercules, USA). The reaction protocol followed the manufacturer's instructions: 1 cycle at 98°C for 30 s; 38 cycles at 95°C for 5 s, 56°C for 30 s, and 72°C for 30 s; and 4°C until removal. The specific quantitative primers (**Table 1**) were designed using Primer Premier 5.0 (PREMIER Biosoft, CA, USA). The relative expression levels were calculated by the $2^{-\Delta\Delta CT}$ method using ZbUBA and ZbUBQ as internal standards.

2.5. Statistical Analysis

The experimental data from three independent biological replicates were

Table 1. Primers for qRT-PCR analysis of differentially expressed gene.

Gene name	ID*	Forward prime (5'-3')	Reverse prime (5'-3')	Product length/bp
<i>TmCOMT1</i>	TbA07G012370	TGTTTCAGTCTATCCCATCT	TTCTCCCACTCGTCCTTG	276
<i>TmCOMT2</i>	TbA04G072330	GTTGCTCACTAGCCATTC	ATTCACCATAGCGTTGTT	298
<i>TmCOMT3</i>	novel.13839	TGAGATAACAGAAGCGAAGC	AACATGAAACCCAACATACA	194
<i>TmCOMT4</i>	novel.13840	CGGTATGCCTAAGTCAAG	GAAGCCAAGTCTACGAAA	147

Note: here gene ID* was identified by the Metware Biotechnology Co. Ltd. (Wuhan, China).

analyzed by one-way analysis of variance (ANOVA) using SPSS 22.0 Statistics (SPSS Inc., Chicago, IL, USA). Tools related differentially expressed genes analysis such like Venn, Heat map etc. were constructed using online software with default value at <https://cloud.metware.cn>.

3. Results

3.1. Growth and Phenolic Acids Content Analysis

We compared 4 kinds of main phenolic acids content in dandelion under different NaCl treatments, and results found that two dandelion cultivars expressed different ability to response NaCl stress, of which “BP” performed better than “TH” in the growth and phenolic acids accumulation (**Figure 1**). Caffeic acid

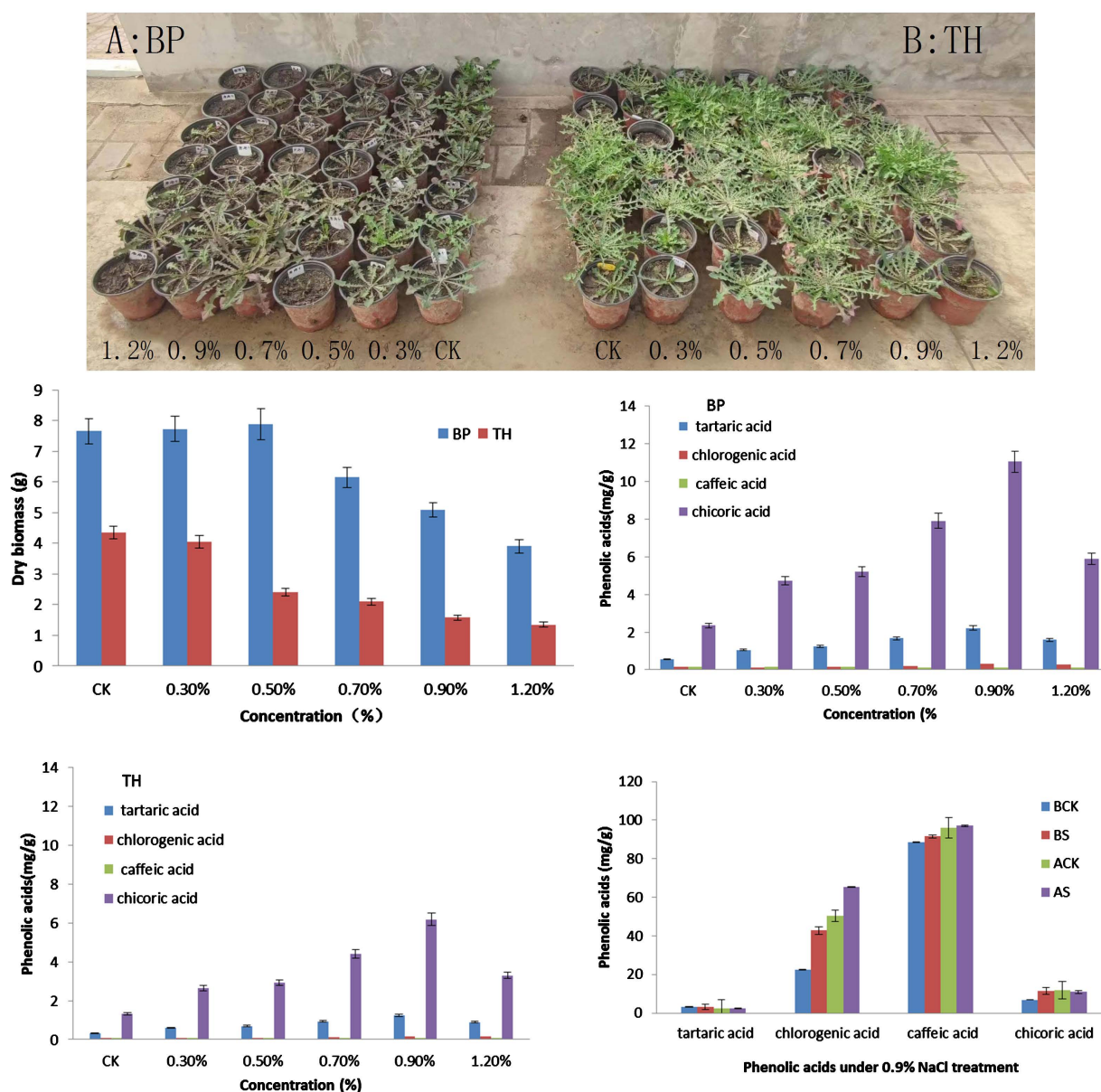


Figure 1. Two cultivars “BP” (A) and “TH” (B) performance under different NaCl treatment.

content was the highest among the all treatments. Especially, 4 kinds of phenolic acids contents accumulated significantly under treatment of 0.9% NaCl. Hence, the fresh leaves samples from 0.9% NaCl treatment were further carried out transcriptome analysis.

3.2. RNA-Seq Quality Control

RNA-seq result of 12 samples obtained raw reads and clean reads containing over 6.8 G clean base, as shown in **Table 2**. Q20 values all exceed 97%, suggesting that the sequence data was reliable and could be subjected to further analysis. The mapped data to the reference genome GWHBCHG00000000 (<https://ngdc.cncb.ac.cn/gwh/Assembly/19733>) all exceed 70%, indicating that the sequencing data could be used for the analysis of differentially expressed genes. From the mapped data comparison of two dandelion cultivars, “TH” (B) was more closed to reference genome than that of “BP” (A), partly confirming the differences of mutant cultivar “BP” in gene level (Wu *et al.*, 2022.) [3].

3.3. Analysis of Differentially Expressed Genes

RNA sequencing was performed on 12 samples to investigate the molecular regulation of phenolic acids synthesis under saline stress (**Figure 2**). In dandelion resources, the larger number of DEGs were identified in BCK vs. BS (3238, up-regulate 1369), followed by ACK vs. AS (2468, up-regulate 1456). In saline stress treatment, the largest number of DEGs were identified in AS vs. BS (10,148, up-regulate 4403), followed by ACK vs. BCK (9354, up-regulate 4591). In addition, 673 and 6413 DEGs were identified in dandelion resources and saline stress treatment. Above results revealed that dandelion resource A (TH) was more sensitive to saline stress than that of dandelion B (BP). From the gene

Table 2. Sequencing reads quality assessment.

Sample	Raw Reads	Clean Reads	Clean Base(G)	Q20 (%)	GC Content (%)	Mapped reads in total (%)
ACK1	46,634,100	45,519,664	6.83	97.36	43.82	35,333,803 (77.62%)
ACK2	46,666,044	45,859,138	6.88	97.36	43.52	35,779,557 (78.02%)
ACK3	48,739,982	47,425,492	7.11	97.5	43.72	36,750,108 (77.49%)
AS1	46,836,758	46,011,050	6.9	97.43	43.65	36,100,849 (78.46%)
AS2	47,611,414	46,228,226	6.93	97.37	43.34	36,246,433 (78.41%)
AS3	47,712,324	46,610,646	6.99	97.2	43.47	36,458,224 (78.22%)
BCK1	49,256,148	47,700,136	7.16	97.42	43.29	41,008,312 (85.97%)
BCK2	52,091,904	50,973,832	7.65	97.34	44.37	44,122,179 (86.56%)
BCK3	49,824,296	47,912,786	7.19	97.4	43.77	41,245,251 (86.08%)
BS1	48,258,700	46,752,226	7.01	97.27	44.67	40,032,929 (85.63%)
BS2	48,078,506	46,995,656	7.05	97.51	44.35	40,385,849 (85.94%)
BS3	49,603,488	48,295,998	7.24	97.24	44.53	41,384,923 (85.69%)

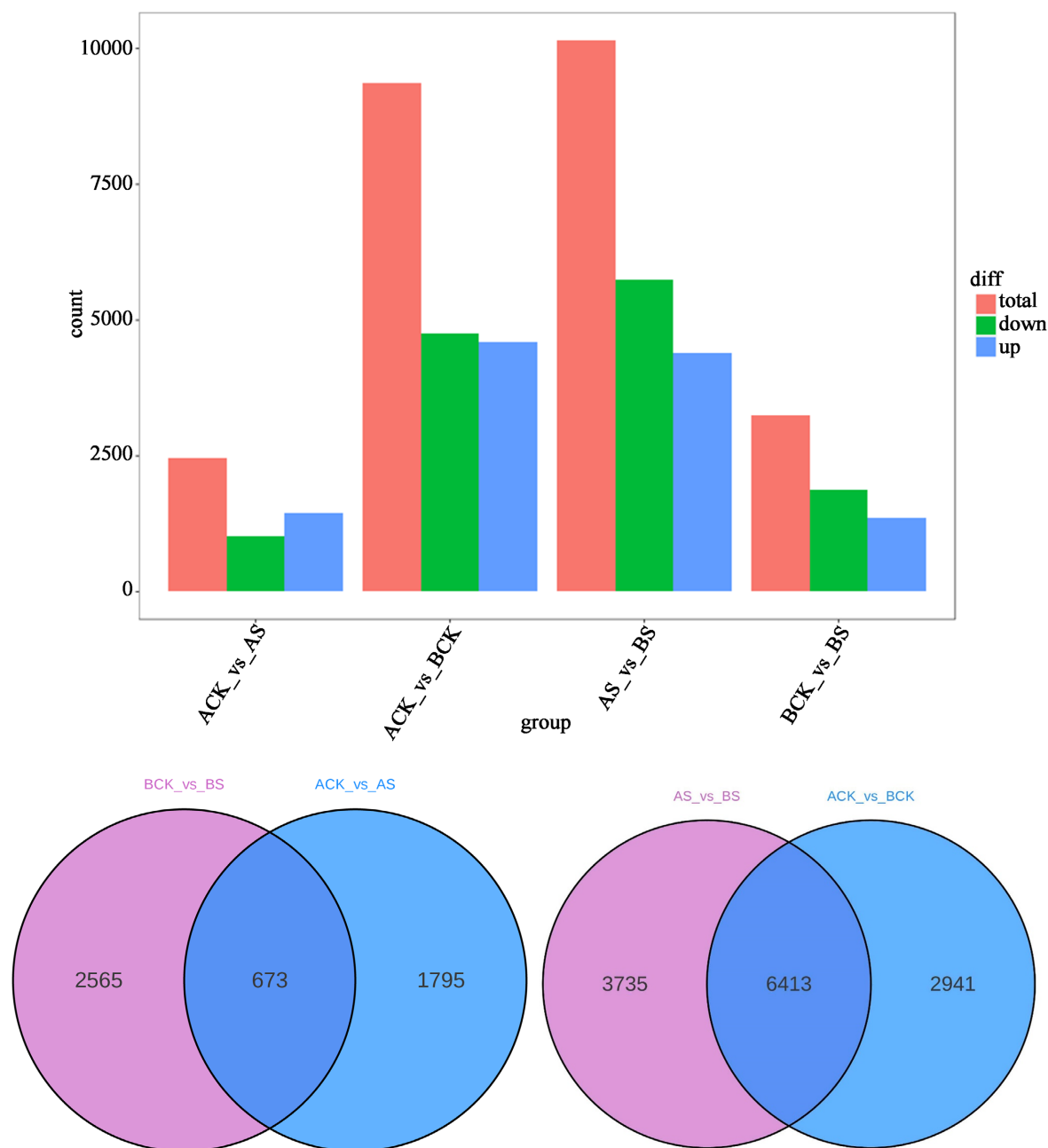


Figure 2. DEGs analysis of two cultivars “BP” (A) and “TH” (B).

regulated mode (ACK vs. AS and BCK vs BS), the two dandelion resource has different or even opposite response mechanism.

3.4. Go Enrichment Analysis of DEGs

In GO annotation analysis of 2 dandelions under saline stress, most DEGs were annotated in cellular process and metabolic process in the category of biological process, and cellular anatomical entity in the category of cellular component, and binding and catalytic activity in the category of molecular function (**Figure 3**). Further, we carried out the analysis for 50 significantly enriched GO-Terms,

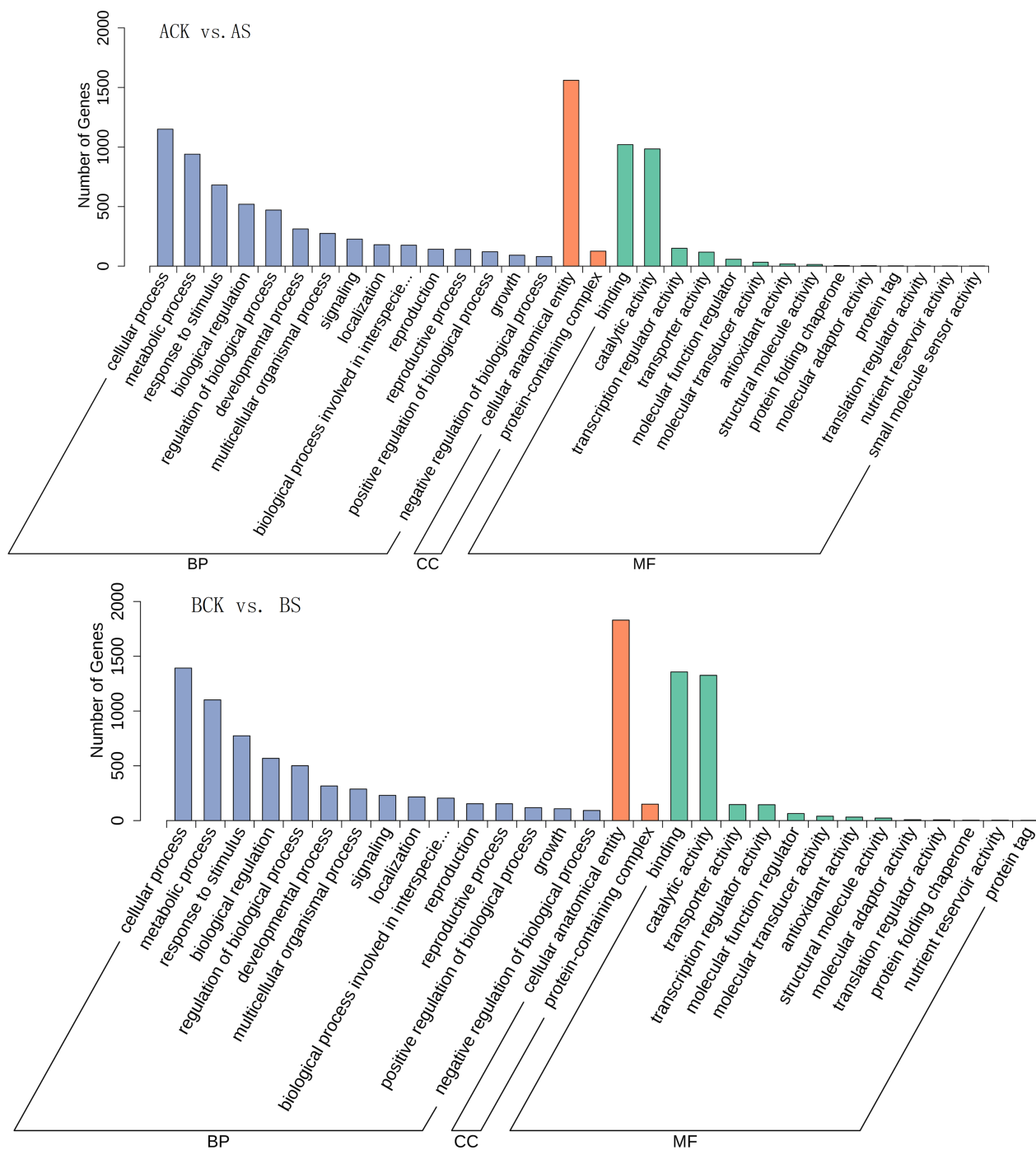


Figure 3. Go enrichment analysis of DEGs for two cultivars.

results showed that the biological process terms phenylpropanoid metabolic process (GO: 0009698), response to extracellular stimulus (GO: 0009991), response to ethylene (GO: 0009723), and secondary metabolite biosynthetic process (GO: 0044550), the cellular component terms apoplast (GO: 0048046), and the molecular function terms hydrolase activity (GO: 0004553), monooxygenase activity (GO: 0004497), and calmodulin binding (GO: 0005516) were among the most highly enriched terms (Figure 4).

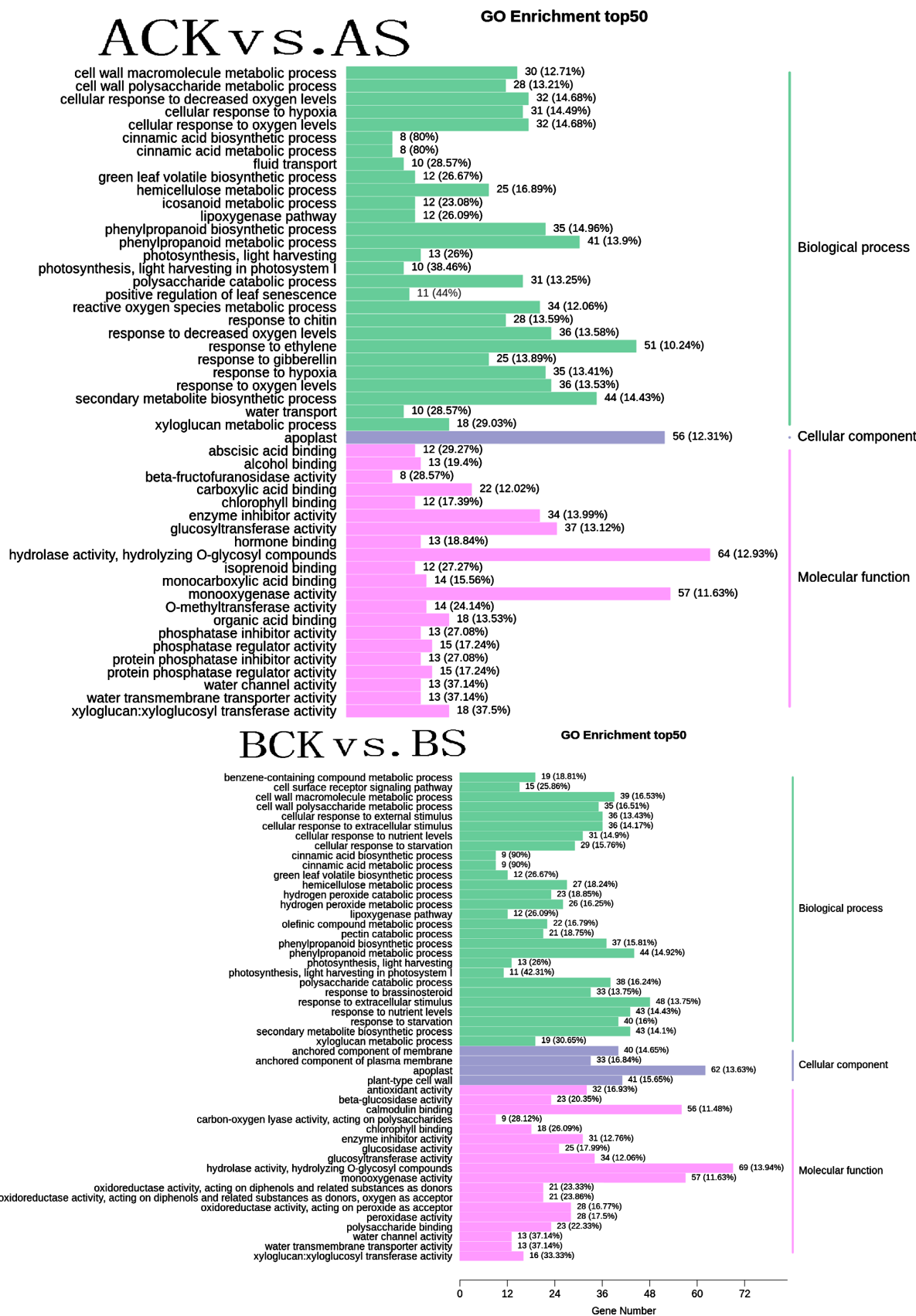


Figure 4. Go enrichment analysis of DEGs for two cultivars.

3.5. KEGG Enrichment Analysis of DEGs

For further analysis of gene functions, the top 20 enriched metabolic pathways were presented in the form of a bubble diagram (Figure 5). During saline stress,

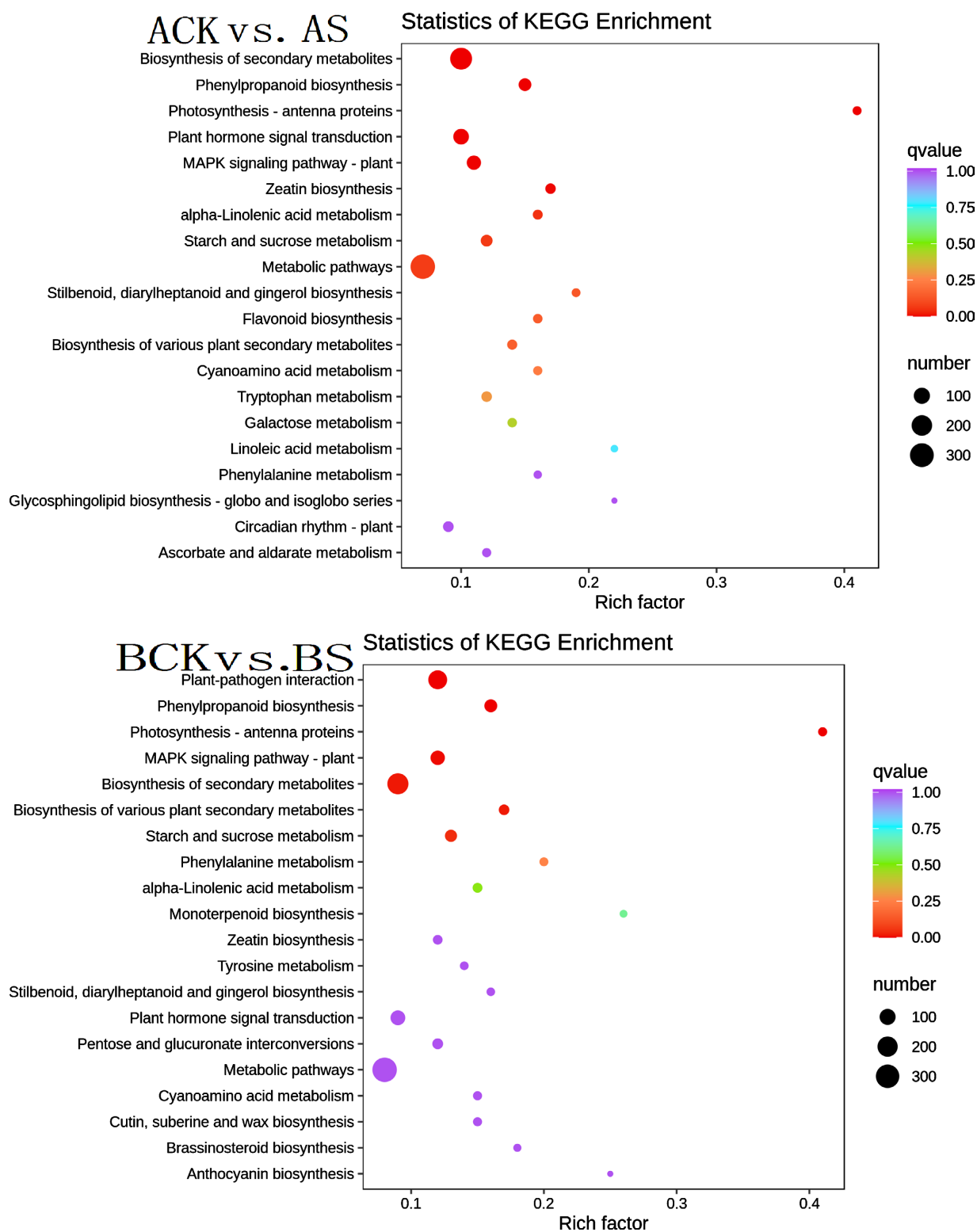


Figure 5. KEGG enrichment analysis of DEGs for two cultivars.

the DEGs were enriched mainly in biosynthesis of secondary metabolites (ko01110), phenylpropanoid biosynthesis (ko00940), plant hormone signal transduction (ko04075), MAPK signaling pathway (ko04016), and metabolic pathways (ko01100). Biosynthesis of secondary metabolites (ko01110) was strongly enriched in both cultivars, followed by phenylpropanoid biosynthesis (ko00940).

3.6. Phenolic acids Related DEGs Analysis and qRT-PCR Validation

According to GO and KEGG analysis, we found DEGs of two dandelion resources were both enriched in biosynthesis of secondary metabolites, phenylpropanoid biosynthesis, and plant hormone signal transduction. Phenolic acids like tartaric acid, chlorogenic acid, caffeic acid, and chicoric acid were secondary metabolites in plant and belonged to phenylpropanoid biosynthesis. Of which, the caffeic acid showed the highest accumulation under 0.9% NaCl treatment (**Figure 1**). Hence, we constructed a pathway diagram showing the DEGs related to caffeic acid biosynthesis according to phenylpropanoid biosynthesis (ko00940) (**Figure 6**). In total, 22 structural genes were mapped to this pathway. Caffeic acid is synthesized from phenylalanine through the phenylpropanoid pathway, in which PAL, 4CL, CYP73A, HCT, C3'H and CSE are the key rate-limiting enzymes. It is then transformed into ferulic acid by COMT, another key rate-limiting enzyme. We found 4 COMT genes, of which one gene was up-regulated in dandelion A (BP, cv. "Binpu 2"). In addition, the caffeic acid content was higher in dandelion A than that of dandelion B (TH, cv. "Tanghai"). Hence, we inferred that this gene maybe regulated the accumulation of caffeic acid in dandelion, but it needs to be further verified. Last, we selected the 4 COMT genes to be validated the expression patterns (**Figure 7** and **Table 1**). Their relative expression levels in qRT-PCR were consistent with their FPKM values in the transcriptomic data, confirming the accuracy of the transcriptome

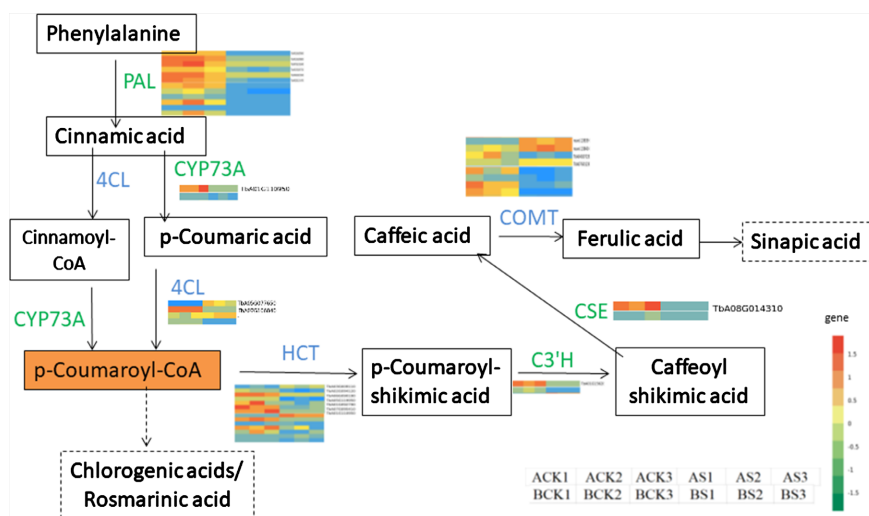


Figure 6. Caffeic acid biosynthesis pathway. Genes with green was down-regulated, blue was mixed regulated.

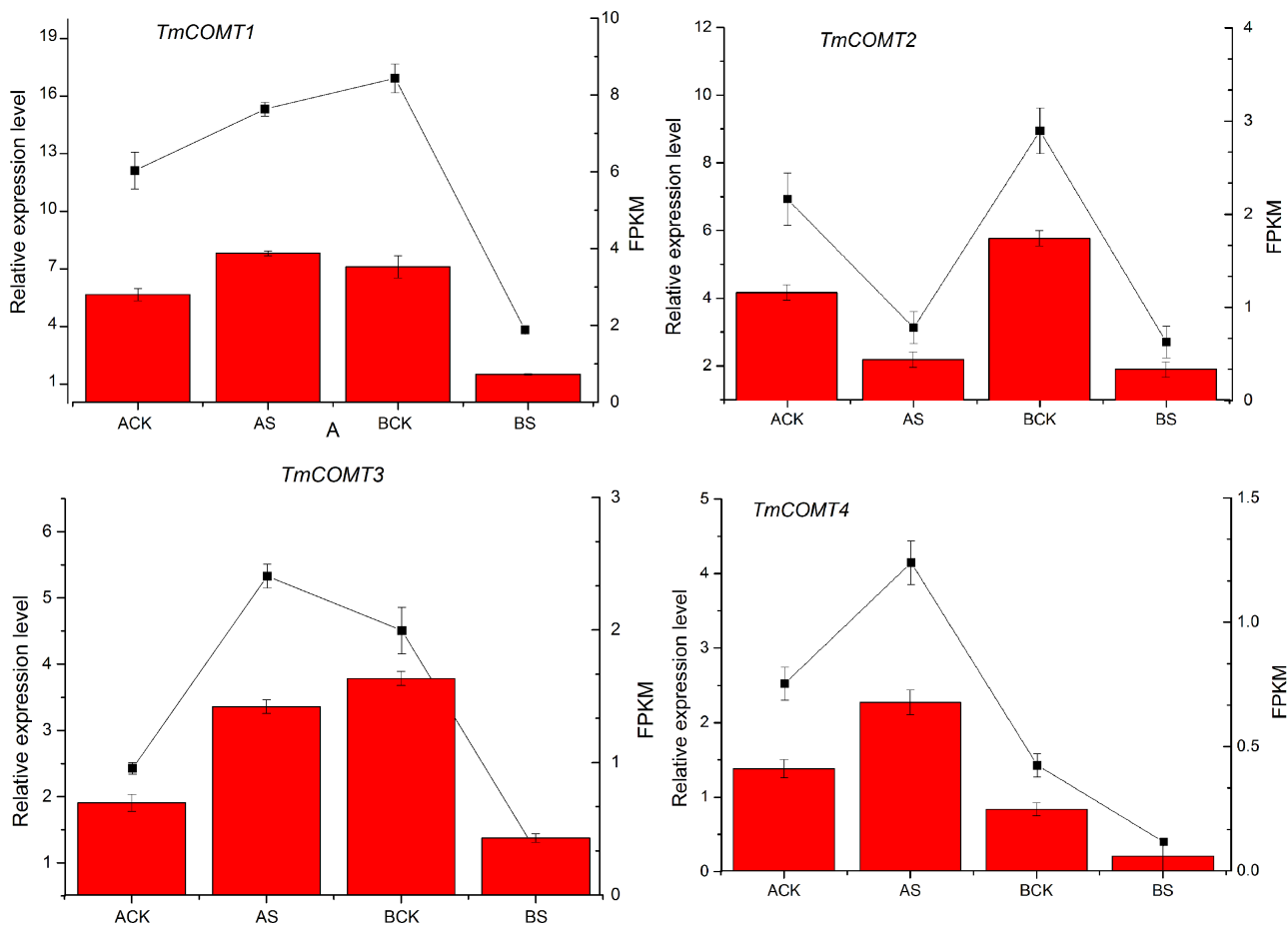


Figure 7. qRT-PCR validation of the expression patterns of candidate genes that participated in the synthesis of caffeic acid. The bar graphs present the results of the qRT-PCR, and the line graphs present the RNA-seq results. The scale on the left axis represents the relative expression level and the scale on the right axis represents the FPKM value. Data are means \pm SD of the three biological replicates.

data and repeatability of the expression patterns.

4. Discussion

Saline stress is a common abiotic stress because of the existence of large area of saline-alkali land in the world. Plant under saline stress will produce a series of secondary metabolites against the injury. Dandelion is rich in phenolic acids, like caffeic acid, chlorogenic acid and cichoric acid etc. These compounds were often found in the pathway of phenylpropanoid biosynthesis in higher plants. Combining the GO and KEGG analysis for DEGs of dandelion under saline stress, we found most DEGs were enriched in metabolites related pathway, of which phenylpropanoid biosynthesis was both enriched in the two dandelion resources. In addition, pathway or GO-term of plant hormone signal transduction/response to ethylene was also enriched. Some researchers also indicated that plant exogenous hormones like ethylene or ABA has important functions on the metabolites regulation of plant under saline stress to against the salt injury. Thus we could guess that saline stress could promote dandelion produce some plant

hormones including ethylene, that in further caused some genes expression to promote dandelion to produce secondary metabolites including phenolic acids to against saline stress. However, it needs to be further verified.

We constructed the caffeic acid biosynthesis pathway based on DEGs and pathway of phenylpropanoid biosynthesis. However, from this pathway, phenylalanine was transformed to p-coumaroyl-CoA through enzymes of PAL, 4CL, and CYP73A, and then continued to be transformed to caffeic acid through enzymes of HCT, C3'H and CSE. This was different from common phenylpropanoid biosynthesis in plant. We guess that dandelion under saline stress would enhance this pathway. However, we should investigate the metabolites changes and related genes in this pathway for further verify the caffeic acid biosynthesis pathway of dandelion under saline stress.

5. Conclusion

We mainly investigated the changes of phenolic acids related genes in dandelion under saline stress and constructed the caffeic acid biosynthesis pathway. In total, we identified 22 structural genes in this pathway and found 4 candidate COMT genes closely related to caffeic acid accumulations. Results provided the basis for the molecular mechanism of COMT on the regulation of caffeic acid biosynthesis under saline stress in future.

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Conflicts of Interest

The authors declare no conflicts of interest.

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