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Identification and Bioinformatics Analysis of TCP Family Genes in Tree Peony

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Abstract The *TCP* (Teosinte branched1/Cincinnata/proliferating cell factor) family gene is a kind of plant specific transcription factor, which plays a significant role in regulating plant growth and development. In this study, 18 *TCP* genes were identified from the tree peony transcriptome data, the molecular weight was between 18 978.32 and 51 789.56 Da, the isoelectric points was between 5.81 and 9.45, and the subcellular localization prediction of TCP family members was in the nucleus. The classification of conserved amino acids in the tree peony TCP domain was similar to that of *Arabidopsis thaliana*. Phylogenetic analysis showed that the TCP proteins of tree peony were divided into two categories, Class I contained 10 TCP members, and Class Ⅱ contained 8 TCP members. MEME analysis results showed that 15 conserved domains were found in the tree peony TCP protein, Motif 1 was the TCP domain, and was found in all TCP members. Meanwhile, the transcription level of the tree peony *TCP* genes in bud, leaf, petal, piebaldness, stamen, pistil and seed were analyzed. This article systematically analyzed the tree peony *TCP* family genes, which provided a scientific basis for further research on functional genes and molecular breeding in tree peony.

Keywords Tree peony; TCP family gene; *TCP* domain

TCP family genes are plant-specific transcription factors, which are widely involved in regulating various stages of growth and development. Its name comes from the acronym of three genes, TEOSINTE BRANCHED1 (TB1) in *Zea mays*, CYCLOIDEA (CYC) in *Antirrhinum majus* and Proliferating Cell Factor (PCF) in rice (Cubas et al., 1999). The TCP family of proteins has an atypical bHLH conserved domain at the N-terminal, also known as the TCP domain, which contains 59 amino acids and is mainly involved in DNA binding, protein interaction and so on. Gene sequence analysis of TCP family in many plants showed that TCP family members could be divided into two major groups, Class I and Class II, or TCP-P and TCP-C. In contrast to Class II, Class I members have four amino acid deletions in the TCP domain (Martintrillo and Cubas, 2010). According to the characteristics of TCP domain, Class II members can be further divided into CIN and CYC subgroups (Lin et al., 2016).

TCP family members are common in higher plants, with 23 members in *Arabidopsis thaliana* (Yao et al., 2007), 16 members in *Phyllostachys edulis* (Liu et al., 2018) and 53 members in *Brassica juncea* (Li et al., 2019). 41 were found in *Panicum virgatum* (Zheng et al., 2019) and 37 were found in tea trees (Zhou et al., 2019). Studies have shown that the TCP family controls a variety of traits in plants, including branching, leaf and flower development, seed germination, circadian rhythm and hormonal pathways (Lin et al., 2016). A set of genes with redundant functions in *Arabidopsis*, including *AtTCP3*, *AtTCP4*, *AtTCP5*, *AtTCP10* and *AtTCP13*, regulate collateral formation (Koyama et al., 2010), while another set of genes, *AtTCP8*, *AtTCP15*, *AtTCP21*, *AtTCP22* and *AtTCP23* regulate the growth and proliferation of plants (Aguilar-Martinez and Sinha, 2013). SsCYC in *Sinningia speciosa* (Dong et al., 2018), LjCYC1, LjCYC2, LjCYC3 in *Lotus japonicus* (Wang et al., 2010), and GhCYC2 in Gerbera (Broholm et al., 2008) regulate floral organ development.

Paeonia suffruticosa Andr., as a famous ornamental flower in China, has a variety of flower types, which can be divided into single-petal type, lotus type, chrysanthemum type, rose type, melalea-type terrace, tugui type, gold ring type, crown type, hydrangea type and Louzi terrace type (Li et al., 2011). Compared with model plants, the molecular mechanism of flower development in tree peony is still in the preliminary stage, and the mechanism of flower type formation is still unclear. There are few reports about TCP gene in tree peony. Gao et al. (2011) cloned two fragments of *TCP* gene from 'Fengdan', which were 278 bp (*TCP1*) and 455 bp (*TCP2*) respectively by homologous gene cloning method. There is no systematic analysis of TCP family genes and detailed functional description of *TCP* genes. Since the complete tree peony genome has not been released yet, this study conducted the identification and analysis of TCP family genes based on tree peony transcriptome data. The results of this study will provide a scientific basis for further study of TCP family genes and the molecular mechanism of tree peony flower type regulation.

1 Results and Analysis

1.1 Physicochemical properties of tree peony TCP protein

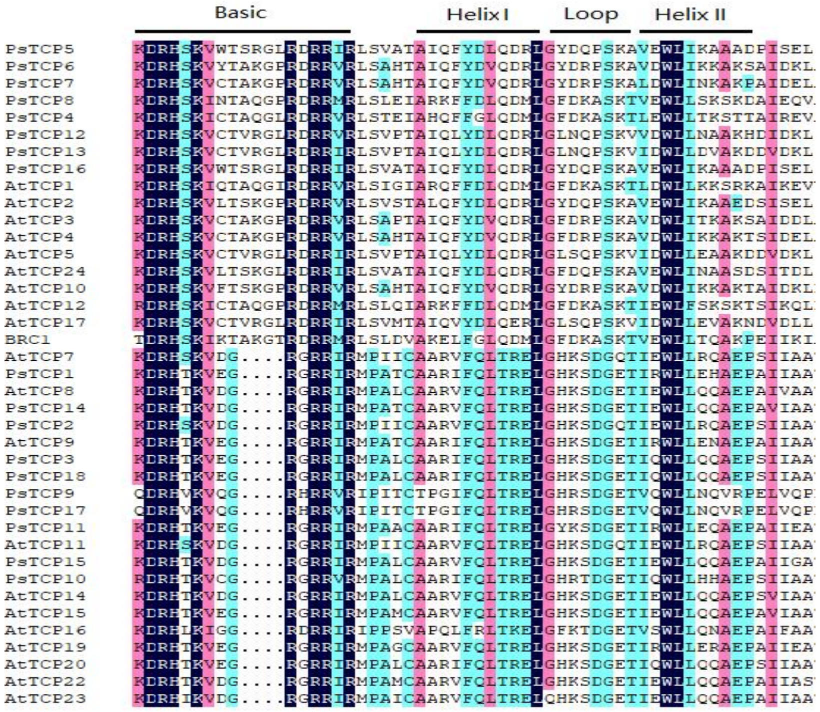
By searching the local database of tree peony gene, a total of 18 TCP family genes with complete coding boxes were obtained, named as *PSTCP1-PSTCP18*. Physical and chemical properties of 18 tree peony TCP proteins were analyzed (Table 1). The shortest amino acid sequence was PsTCP4, which contained 169 amino acids. The longest is PsTCP9, which contains 473 amino acids. The smallest molecular weight was PsTCP4, which was 18 978.32 Da. The molecular weight of PsTCP9 was 51 789.56 Da. PsTCP17 had the lowest isoelectric point (5.81) and PsTCP2 had the highest isoelectric point (9.45). The prediction result of subcellular localization was: 18 members subcellular localization were all in the nucleus.

Table 1 TCP deduced amino acid sequence characteristics and predicted subcellular location of genes

Gene name	Number of amino acids (aa)	Molecular weight (Da)	Theoretical pI	Subcellular localization
PsTCP1	346	37 276.98	7.84	Nucleus.
PsTCP2	261	27 421.64	9.45	Nucleus.
PsTCP3	308	33 149.81	9.02	Nucleus.
PsTCP4	169	18 978.32	8.71	Nucleus.
PsTCP5	461	50 083.64	7.14	Nucleus.
PsTCP6	325	36 425.28	6.89	Nucleus.
PsTCP7	380	41 129.21	6.50	Nucleus.
PsTCP8	330	37 024.59	8.49	Nucleus.
PSTCP9	473	51 789.56	5.92	Nucleus.
PsTCP10	210	22 562.48	7.70	Nucleus.
PsTCP11	315	33 410.80	8.60	Nucleus.
PsTCP12	355	39 352.60	6.90	Nucleus.
PsTCP13	378	42 084.36	9.20	Nucleus.
PsTCP14	356	38 311.34	7.82	Nucleus.
PsTCP15	360	38 428.41	7.92	Nucleus.
PsTCP16	464	50 231.76	7.12	Nucleus.
PsTCP17	456	49 926.54	5.81	Nucleus.
PSTCP18	309	33 247.92	8.68	Nucleus.

1.2 Comparison and analysis of TCP domain sequences

In order to analyze the sequence characteristics of TCP domain in tree peony TCP family members, the amino acid sequences of TCP domain in Tree peony and *Arabidopsis thaliana* were compared and analyzed (Figure 1). The 18 TCP family members of tree peony all contain a complete TCP (atypical bHLH) domain, and the basic domain contains 15 or 19 amino acids. A total of 11 highly conserved amino acids were found in the TCP domain, including 8 in basic and 3 in HLH. The distribution of conserved amino acids in the TCP domain was similar in *Arabidopsis thaliana* and tree peony, which also proved that the TCP domain was highly conserved in tree peony and *Arabidopsis thaliana*. In addition, we found that 11 genes in *Arabidopsis thaliana* and 10 genes in tree peony were missing 4 amino acids in the basic region of the TCP domain. They may belong to Class I, and the rest of the genes may belong to Class II.



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                Basic                     Helix I    Loop    Helix II
PsTCP5   KDRHSKVWTSRGLRDRRIRLSVATAIQFYDLQDRLGYDQPSKAVEWLIKAAADPISEL
PsTCP6   KDRHSKVYTAKGPRDRRVRLSAHTAIQFYDVQDRLGYDRPSKAVDWLIKKAKSAIDKL
PsTCP7   KDRHSKVCTAKGPRDRRVRLSAHTAIQFYDVQDRLGYDRPSKALDWLINKAKPAIDEL
PsTCP8   KDRHSKINTAQGPRDRRMRLSLEIARKFFDLQDMLGFDKASKTVEWLLSKSKDAIEQV
PsTCP4   KDRHSKICTAQGLRDRRVRLSTEIAHQFFGLQDMLGFDKASKTLEWLLTKSTTAIREV
PsTCP12  KDRHSKVCTVRGLRDRRVRLSVPTAIQLYDLQDRLGLNQPSKVVDWLLNAAKHDIDKL
PsTCP13  KDRHSKVCTVRGLRDRRIRLSVPTAIQLYDLQDRLGLNQPSKVIDWLLDVAKDDVDKL
PsTCP16  KDRHSKVWTSRGLRDRRIRLSVATAIQFYDLQDRLGYDQPSKAVEWLIKAAADPISEL
AtTCP1   KDRHSKIQTAQGIRDRRVRLSIGIARQFFDLQDMLGFDKASKTLDWLLKKSRKAIKEV
AtTCP2   KDRHSKVLTSKGPRDRRVRLSVSTALQFYDLQDRLGYDQPSKAVEWLIKAAEDSISEL
AtTCP3   KDRHSKVCTAKGPRDRRVRLSAPTAIQFYDVQDRLGFDRPSKAVDWLITKAKSAIDDL
AtTCP4   KDRHSKVCTAKGPRDRRVRLSAHTAIQFYDVQDRLGFDRPSKAVDWLIKKAKTSIDEL
AtTCP5   KDRHSKVCTVRGLRDRRIRLSVPTAIQLYDLQDRLGLSQPSKVIDWLLEAAKDDVDKL
AtTCP24  KDRHSKVLTSKGLRDRRIRLSVATAIQFYDLQDRLGFDQPSKAVEWLINAASDSITDL
AtTCP10  KDRHSKVFTSKGPRDRRVRLSAHTAIQFYDVQDRLGYDRPSKAVDWLIKKAKTAIDKL
AtTCP12  RDRHSKICTAQGPRDRRMRLSLQIARKFFDLQDMLGFDKASKTIEWLFSKSKTSIKQL
AtTCP17  KDRHSKVCTVRGLRDRRIRLSVMTAIQVYDLQERLGLSQPSKVIDWLLEVAKNDVDLL
BRC1     TDRHSKIKTAKGTRDRRMRLSLDVAKELFGLQDMLGFDKASKTVEWLLTQAKPEIIKI
AtTCP7   KDRHSKVDG....RGRRIRMPIICAARVFQLTRELGHKSDGQTIEWLLRQAEPSIIAA
PsTCP1   KDRHTKVEG....RGRRIRMPATCAARIFQLTRELGHKSDGETIRWLLEHAEPAIIAA
AtTCP8   KDRHTKVDG....RGRRIRMPALCAARVFQLTRELGHKSDGETIEWLLQQAEPAIVAA
PsTCP14  KDRHTKVDG....RGRRIRMPATCAARVFQLTRELGHKSDGETIEWLLQQAEPAVIAA
PsTCP2   KDRHSKVDG....RGRRIRMPIICAARVFQLTRELGHKSDGQTIEWLLRQAEPSIIAA
AtTCP9   KDRHTKVEG....RGRRIRMPATCAARIFQLTRELGHKSDGETIRWLLENAEPAIIAA
PsTCP3   KDRHTKVEG....RGRRIRMPALCAARIFQLTRELGHKSDGETIQWLLQQAEPSIIAA
PsTCP18  KDRHTKVEG....RGRRIRMPALCAARIFQLTRELGHKSDGETIQWLLQQAEPSIIAA
PsTCP9   QDRHVKVQG....RHRRVRIPITCTPGIFQLTRELGHRSDGETVQWLLNQVRPELVQP
PsTCP17  QDRHVKVQG....RHRRVRIPITCTPGIFQLTRELGHRSDGETVQWLLNQVRPELVQP
PsTCP11  KDRHTKVEG....RGRRIRMPAACAARIFQLTRELGYKSDGETIRWLLEQAEPAIIEA
AtTCP11  KDRHSKVDG....RGRRIRMPIICAARVFQLTRELGHKSDGQTIEWLLRQAEPSIIAA
PsTCP15  KDRHTKVDG....RGRRIRMPALCAARVFQLTRELGHKSDGETIEWLLQQAEPAIIGA
PsTCP10  RDRHTKVCG....RGRRVRMPALCAARIFQLTRELGHRTDGETIQWLLHHAEPSIIAA
AtTCP14  KDRHTKVDG....RGRRIRMPALCAARVFQLTRELGHKSDGETIEWLLQQAEPSVIAA
AtTCP15  KDRHTKVEG....RGRRIRMPAMCAARVFQLTRELGHKSDGETIEWLLQQAEPAVIAA
AtTCP16  KDRHLKIGG....RDRRIRIPPSVAPQLFRLTKELGFKTDGETVSWLLQNAEPAIFAA
AtTCP19  KDRHTKVEG....RGRRIRMPAGCAARVFQLTRELGHKSDGETIRWLLERAEPAIIEA
AtTCP20  KDRHTKVEG....RGRRIRMPALCAARIFQLTRELGHKSDGETIQWLLQQAEPSIIAA
AtTCP22  KDRHTKVDG....RGRRIRMPAMCAARVFQLTRELGHKSDGETIEWLLQQAEPAIIAS
AtTCP23  KDRHIKVDG....RGRRIRMPAICAARVFQLTRELQHKSDGETIEWLLQQAEPAIIAA
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Figure 1 Sequence alignment of TCP domain in tree peony and Arabidopsis

1.3 Phylogenetic analysis of TCP family proteins in tree peony

Phylogenetic trees were constructed using TCP domains of tree peony and Arabidopsis (Figure 2). In general, TCP members can be divided into Class I and Class II. Class I contains 10 tree peony TCP members and 11 Arabidopsis TCP members. Class II contains 8 tree peony TCP members and 10 Arabidopsis TCP members. The classification results of TCP family members in Arabidopsis were consistent with previous studies (Yao et al., 2007). AtTCP16 is relatively independent from Class I in the phylogenetic tree. According to Figure 1, the amino acids of Class I member at the 24th and 30th positions in the TCP domain are C and Q, respectively, while AtTCP16 is V and R, respectively. This may be the reason why AtTCP16 is relatively independent in phylogenetic analysis.

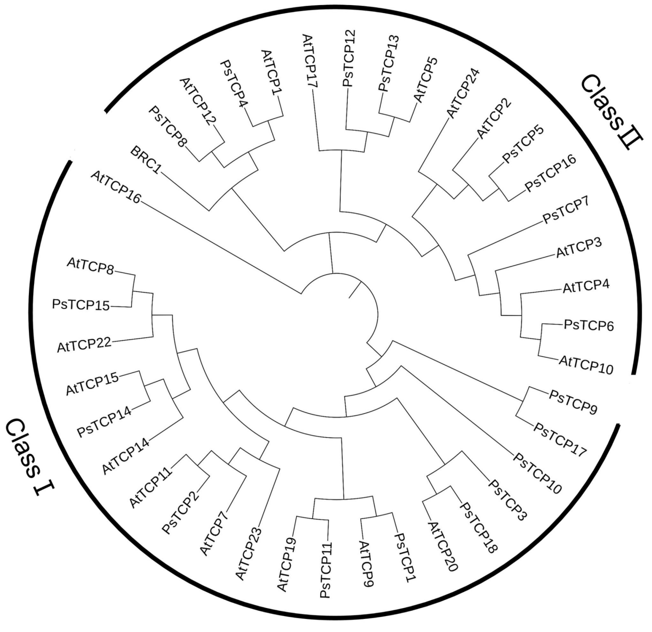

Figure 2 Phylogenetic tree analysis of TCP gene family in tree peony

1.4 Conservative domain analysis

The conserved domain analysis of TCP proteins in 18 tree peonies was performed using MEME online tool. Results showed that a total of 15 conserved domains Motif 1-Motif 15 were found (Figure 3). Among them, Motif 1 is the TCP domain, which exists in all TCP members, Motif 5 exists in 11 genes, Motif 4 exists in 8 genes. Motif3, Motif6, Motif8, Motif13 only appear in TCP9 and TCP17, Motif11, Motif12, Motif14 only appear in TCP3 and TCP18, Motif7, Motif10, Motif15 only appear in TCP5 and TCP16. Motif2 and Motif9 occur only in TCP5, TCP9, TCP16 and TCP17.

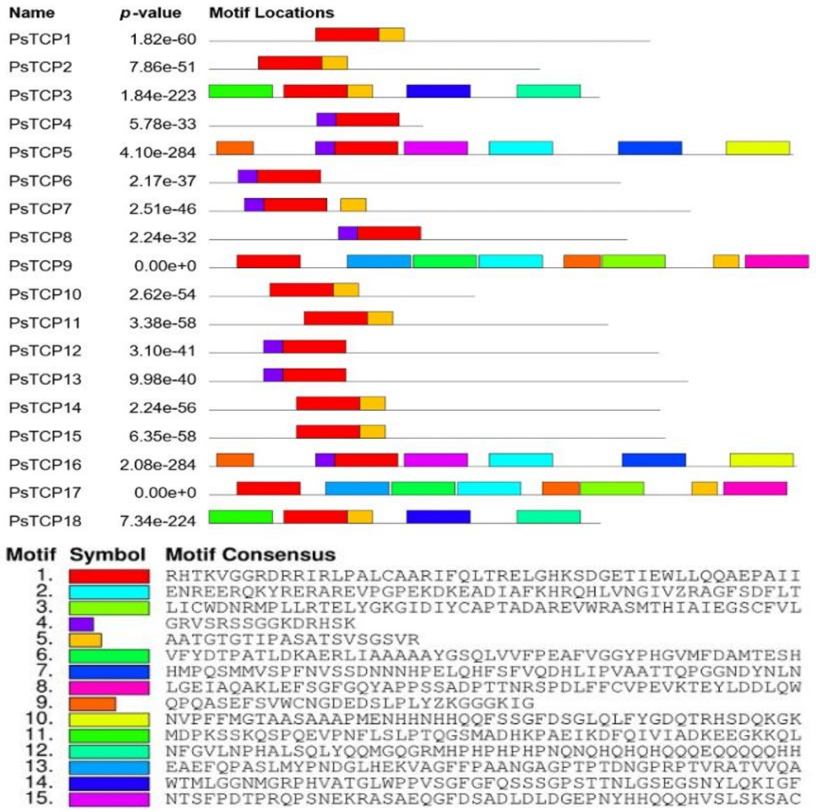

Figure 3 Conserved domain analysis of the Tree Peony TCP proteins

1.5 Transcriptional level analysis of TCP family genes in different tissues

FPKM values in transcriptome sequencing were used to represent gene transcription levels, and the transcription levels of 18 tree peony *TCP* genes in different tissues were analyzed (Table 2). Twelve genes were transcribed in all tissues, six genes were transcribed in some tissues, of which *PsTCP8* was transcribed only in buds and pistils, and *PsTCP4* was transcribed only in buds, leaves and flower spots. The transcriptional level of *PsTCP7* was the highest in leaves, petals and buds, followed by *PsTCP5* and *PsTCP2*. *PsTCP2*, *PsTCP14* and *PsTCP15* were the genes with the highest transcription level in the pistil. *PsTCP10*, *PsTCP18* and *PsTCP2* were among the seeds. *PsTCP12* and *PsTCP2* in the Mosaic. Stamens are *PsTCP11* and *PsTCP10*.

2 Discussion

TCP family transcription factors exist widely in plants and are also important regulatory factors. Through the mining of woody plant genome information, it was found that the number of TCP genes varies significantly among different species, for example, there are 16 TCP genes in *Phyllostachys edulis* (Liu et al., 2018), 37 TCP genes in tea tree (Zhou et al., 2019), and 53 TCP genes in *Brassica juncea* (Li et al., 2019). In this study, a total of 18 *TCP* genes were identified based on transcriptome data of tree peony. Compared with other woody plants, fewer *TCP* genes were reported in this study, probably because a few TCP genes were not detected due to spatio-temporal specific transcription in transcriptome sequencing experiments.

Table 2 FPKM values of *TCP* family genes in different tissues of tree peony

Gene name	Shoot	Leaf	Petal	Petal spot	Stamen	Pistil	Seed
PsTCP1	3.65	6.87	16.5	6.36	0.86	4.48	0.25
PsTCP2	43.81	42.57	43.02	36.14	2.84	30.85	5.93
PsTCP3	0.7	1.04	1.35	1.36	0.46	1.64	1.44
PsTCP4	10.73	7.04	0	0.08	0	0	0
PsTCP5	60.27	53.23	59.06	10.16	0.75	24.66	3.39
PsTCP6	5.29	4.72	6.27	4.56	0.31	1.65	0.71
PsTCP7	135.32	155.58	173.98	18.18	0.75	15.44	2.57
PsTCP8	0.21	0	0	0	0	1.45	0
PsTCP9	2.82	2.27	0.29	0.18	0.27	2.32	1.81
PsTCP10	4.09	1.04	11.03	12.28	4.67	15.66	11.23
PsTCP11	5.06	2.87	2.87	0.91	5.74	3.17	0.37
PsTCP12	15.2	20.09	55.39	39.49	3.68	3.39	0
PsTCP13	2.02	3.8	0.27	0	0	0.26	0
PsTCP14	24.7	21.82	1.23	4.19	0.37	27.49	0.5
PsTCP15	19.79	19.51	3.38	3.87	0.44	25.58	2.33
PsTCP16	26.26	33.54	43.65	8.81	0.78	10.77	1.86
PsTCP17	3.98	1.41	0	0.21	0.52	3.63	3.81
PSTCP18	3.32	3.46	0.87	6.38	0.72	8.67	6.51

By analyzing the TCP sequences of tree peony and *Arabidopsis thaliana*, we found that TCP members could be classified into Class I and Class II, and 11 amino acid sequences in the TCP domain were identical. These results indicated that the TCP family members were relatively conserved in the process of gene evolution, and the role of the TCP family members in the growth and development of tree peony could be inferred from the function of the *TCP* gene in model plants. For example, *AtTCP14* and *AtTCP15* regulate the shape and size of flowers in *Arabidopsis thaliana* (Koyama et al., 2011). *PsTCP14* and *AtTCP14* are clustered together in the phylogenetic tree, and we speculated that *PsTCP14* may play an important role in the formation of tree peony flower type. In the process of studying members of the TCP family, it was found that some members were functionally redundant, such as some members of Class I in *Arabidopsis thaliana*, and mutations of a single gene could not cause phenotypic changes (Martintrillo and Cubas, 2010). In the process of analyzing the conserved domain of tree peony TCP protein, it was also found that some members had some common domain, for example, Motif11, Motif12 and Motif14 only appeared in TCP3 and TCP18. We speculated that TCP3 and TCP18 retained similar gene functions in the process of evolution.

Transcriptional abundance of 18 tree peony TCP genes in different tissues was analyzed. *PsTCP2*, *PsTCP5* and *PsTCP7* maintained high transcriptional levels in all tissues of tree peony, which may play an important role in organ development and morphological maintenance. The trace transcription of *PsTCP4* and *PsTCP8* was only detected in some tissues, suggesting that the two genes were specifically transcribed at specific stages of growth and development or began to be transcribed after receiving specific signals. In this study, *PsTCP5* and *PsTCP16* were identified as homologous genes of *AtTCP2* (Figure 2). *PsTCP10*, *PsTCP3*, and *PsTCP18* are homologous genes of *AtTCP20* (Figure 2). In this study, *PsTCP5* and *PsTCP16* were found to have the highest expression levels in petals and also in other tissues. Previous studies have shown that *AtTCP2* is only expressed in flowers, but not in other tissues (Yao et al., 2007).

Therefore, it is speculated that *PsTCP5* and *PsTCP16* may be involved in the specific transcription of the growth and development stage of tree peony petals. In this study, tissue-specific expression of *PsTCP10*, *PsTCP3* and *PsTCP18* were found to have the highest expression levels in pistil. Previous studies have shown that *AtTCP20* may be involved in regulating cell amplification, division and differentiation (Hervé et al., 2009). Therefore, *PsTCP10*, *PsTCP3* and *PsTCP18* in tree peony may be related to the proliferation, division and differentiation of pistil cells. The results showed that these different *TCP* genes might be involved in different biological processes. The analysis of transcription level will provide reference for further prediction of *TCP* gene function and selection of research objects.

In summary, 18 *TCP* family genes were identified and systematically analyzed from tree peony in this study. These results provide a basis for the study of gene function and molecular breeding of tree peony TCP family.

3 Materials and Methods

3.1 Identification of members of tree peony TCP family

Transcriptome sequencing and assembly of 7 tissues including bud, leaf, petal, flower spot, stamen, pistil and seed were carried out in the laboratory in the early stage, and the TCP family genes of tree peony were studied on this basis. The candidate tree peony *TCP* gene was obtained by comparing Unigene with PlantTFDB by HMMER program. TCP domains of candidate genes were analyzed one by one by SMART, and genes with complete TCP domains and coding frames were selected for analysis.

3.2 Sequence analysis of TCP protein

ExPASy proteomics server (https://www.expasy.org/) was used to calculate the protein molecular weight and theoretical isoelectric points of tree peony TCP. Using the wolf PSORT (https://wolfpsort.hgc.jp/) to predict the subcellular localization of tree peony TCP. DNAman software was used for sequence alignment analysis. Phylogenetic analysis was performed using Mega 5.0, Neighbor Joining method and 1 000 bootstrap tests. The phylogenetic tree was processed by iTOL. The conserved domain in tree peony TCP protein was analyzed by MEME online tool (http://meme-suite.org/), and the threshold was set to 1e-10.

3.3 Calculation of TCP gene transcription level in tree peony

The raw data of transcriptome sequencing in different tissues of tree peony were downloaded from Genome Sequence Archive (http://bigd.big.ac.cn/gsa) of CNCB-NGDC, with accession number of CRA001327. Clean reads were compared to Unigene using Bowtie2 (Langmead and Salzberg, 2012), and then gene expression levels of each sample were calculated using RSEM (Li and Dewey, 2011). Transcriptional abundance of genes in different tissues was expressed by fragments per kb per million reads (FPKM) (Mortazavi et al., 2008).

Authors' contributions

ZYZ and LX are the experimental design and executor of this study. LHY, DXJ and ZY completed data analysis and wrote the first draft of the paper; LHY, DXJ and ZY participated in experimental design and analysis of experimental results; ZYZ and LHY are the architects and principals of the project, guiding experimental design, data analysis, paper writing and revision. All authors read and approved the final manuscript.

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