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Analysis of MYB Transcription Factor Family Based on Transcriptome Sequencing in Colored Potato

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Abstract MYB transcription factor family is one of the transcription factors with various functions and numerous quantities, which plays an important role in plant growth and metabolism regulation. In this study, based on the transcriptome sequencing data of color potato tubers, we screened MYB transcription factor genes during the development of color potato, and analyzed its conservative domain and subcellular localization; meanwhile, we analyzed the differential expression of R2R3 MYB transcription factor by TMEV software, and predicted the function of R2R3 MYB transcription factor with significant difference. The results showed that based on the transcriptome sequencing (RNA-Seq) data, 143 transcription factors of MYB family were annotated, selected, and divided into four categories (1R-MYB, R2R3-MYB, 3R-MYB and 4R-MYB) according to their structural characteristics. The result of the subcellular localization demonstrated that 138 MYB transcription factors were located in the nucleus, one MYB transcription factors were located in the cytoplasm, and four MYB transcription factors were located in the cell membrane. Conservative domain analysis showed that the conserved motifs of R2R3-MYB transcription factors are R2 and R3. Colored potato R2R3-MYB transcription factor gene was differentially expressed in different periods, among which 10 were up-regulated and 5 were down-regulated. According to the analysis of GO enrichment, 6 transcription factors of R2R3-MYB related to anthocyanin were annotated. This study will provide a reference for further study on the biological function and metabolic regulation mechanism of *MYB* gene related to anthocyanin synthesis in color potato.
Keywords Colored potato; RNA-seq; MYB family; Expression pattern

Colored potato (*Solanum tuberosum*) has rich color of skin or flesh, which is rich in anthocyanin (Brown et al., 2003) with high nutritional value. Anthocyanin is one of the flavonoids, and more than 20 species have been found (Jia et al., 2014). As a kind of dietary supplements and skin care products, anthocyanins occupy an important position in the market, with a variety of effects such as anti-tumor, anti-oxidation, and anti-aging (Xiao et al., 2020). The synthesis and metabolism of anthocyanins are regulated by transcription factors. At present, three kinds of transcription factors involved in anthocyanin metabolism have been identified, which are MYB family members, bHLH proteins and WD40 factors, among which R2R3-MYB is the most important transcription factor (Liu, 2016, Gansu Agricultural University, pp.161).

Plant MYB transcription factors play an important role in cell differentiation, hormone regulation, biotic and abiotic stress, plant secondary metabolism, flavonoid biosynthesis and so on. The structure of MYB transcription factors contains a conserved Myb domain, and the three conserved functional domains, namely, transactivation domain (TAD), negative regulatory domain (NRD) and DNA binding domain (DBD), are important components of plant MYB transcription factors (Frampton, 2004). The DNA binding domain consists of 1~3 negative repeated R. Each R is composed of 51~52 conserved amino acid residues, and there is one tryptophan residue every 18~19 amino acids. Its secondary structure is helix-corner-helix (HTH) (Chen et al., 2009). According to the number of R in DNA binding domain, MYB transcription factors are divided into four categories: (1) MYB transcription factor with one R, that is, 1R-MYB/MYB-related; (2) MYB transcription factor with two R, which accounts for the

largest number, namely R2R3-MYB; (3) MYB transcription factor with three R, namely 3R-MYB, which is relatively few in plants; (4) MYB transcription factor with four R, namely 4R-MYB, which is few at present.

In plants, R2R3-MYB has the largest number and multiple functions, which plays an important role in development and metabolism (Abe et al., 2003). *R2R3-MYB* genes of plants generally regulate anthocyanin biosynthesis induced by light and temperature (Takos et al., 2006). It was found that R2R3-MYB (FzMYB23) could promote the synthesis of flavonoids and increase the accumulation of anthocyanins in roots, stems, leaves and flowers of *Fagopyrum tataricum* (Wang et al., 2019). RhMYBs4-1 and RhMYBs6-1 in *Rosa chinensis* Jacq. encoded R2R3-MYB proteins of Sg4 and Sg6 subfamilies, respectively, and were expressed in petals of *Rosa chinensis*, which may be important regulatory genes for anthocyanin synthesis and petal color (Zhao et al., 2015). SlAN2-like in *Lycopersicon esculentum* Mill. regulated anthocyanin accumulation (Yan et al., 2020). It was found that the expression of SmMYB transcription factor was positively correlated with anthocyanin content in the study of eggplant (*Solanum melongena* L.) sepal (Zhou, 2016, Journal of Northeast Forestry University, pp.86). The expression of SmMYB18 in eggplant was positively correlated with the color of pericarp and the content of anthocyanin, while SmMYB19 was negatively correlated (Fu, 2017, Journal of South China Agricultural University, pp.61). SmNl isolated from purple potato B-5 was transferred into tobacco to obtain purple transgenic tobacco (Jia et al., 2019). Li (2018, Journal of Qinghai University, pp.88) predicted the function of potato MYB transcription factor, the results showed that potato R2R3-MYB protein was related to cell growth, development, secondary metabolism and response to abiotic stress.

In this study, based on transcriptome sequencing data of tubers at different developmental stages of color potato, MYB transcription factors with significant differences were screened for classification, subcellular localization prediction, and conserved domain analysis of potato R2R3-MYB protein. At the same time, the expression analysis and functional prediction of MYB genes differentially expressed at different developmental stages were carried out, which laid the foundation for the functional study of MYB genes related to anthocyanin in color potato.

1 Results and Analysis

1.1 Screening and classification of MYB transcription factor genes in color potato

Based on the transcriptome sequencing data, we screened 143 MYB transcription factors of color potato. The conserved domains of MYB transcription factors were analyzed. According to the classification method of Arabidopsis MYB genes (Dubos et al., 2010) and the number of SANT in the conserved domains, they were classified into 1R-MYB, R2R3-MYB, 3R-MYB and 4R-MYB transcription factors (Figure 1). Finally, we obtained 26 1R-MYB, 98 R2R3-MYB, 11 3R-MYB, and 8 4R-MYB transcription factors.

1.2 Subcellular localization prediction of MYB transcription factors in color potato

The results of the subcellular localization prediction (Figure 2) showed that there were 138 genes and 96 R2R3-MYB transcription factors in nuclear, accounting for 67.13% of the total genes. 1R-MYB and 3R-MYB transcription factors were also located in the nuclear. 4R-MYB transcription factors were identified in nuclear, cytomembrane and cytoplasm, respectively. Most of the R2R3-MYB transcription factors were involved in transcriptional regulation of nuclear genes. 1R-MYB and 3R-MYB may be involved in the transcriptional regulation of nuclear genes, while 4R-MYB transcription factors may be widely present in plant cells and participate in the transcriptional regulation of multiple genes.

1.3 Analysis of R2R3-MYB transcription factor domain in color potato

Alignment analysis of R2R3-MYB transcription factors in color potato (Figure 3) showed that the amino acid sequences of R2R3-MYB transcription factors were highly conserved and similar, which was consistent with the characteristics of the conservative domain of R2R3-MYB transcription factors. The two conserved motifs were R2 and R3, respectively.

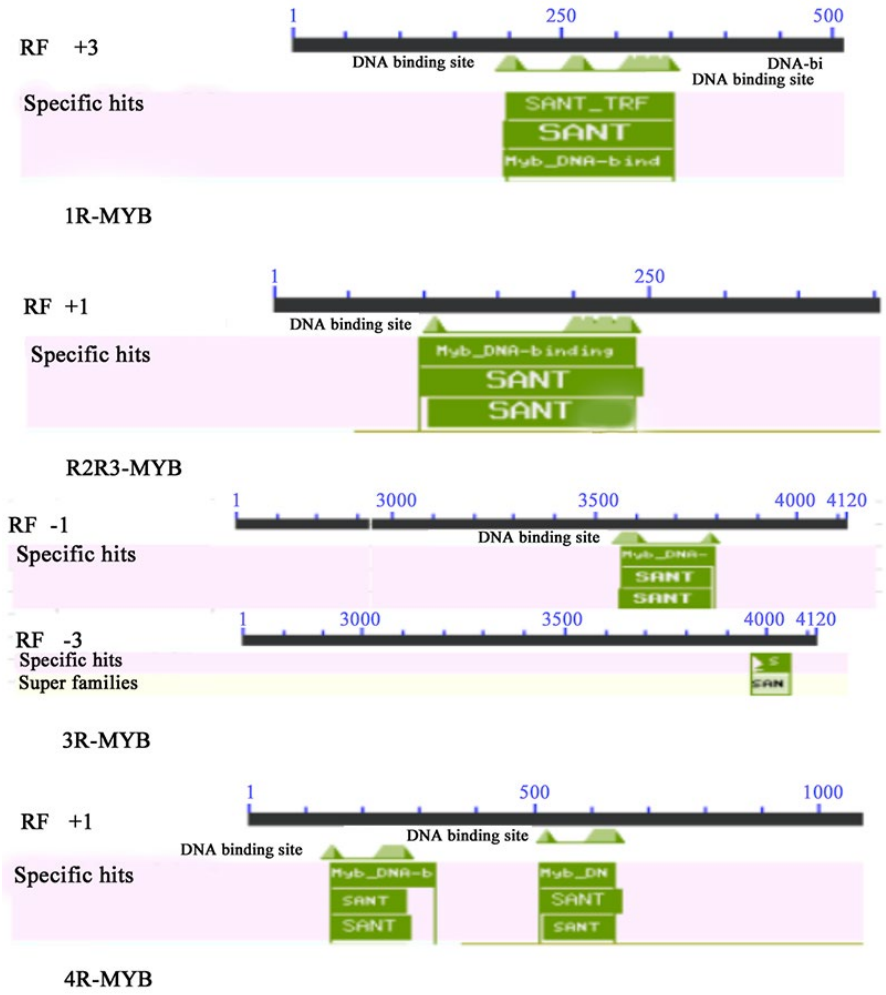

Figure 1 The number of MYB transcription factor DNA binding domains in colored potato

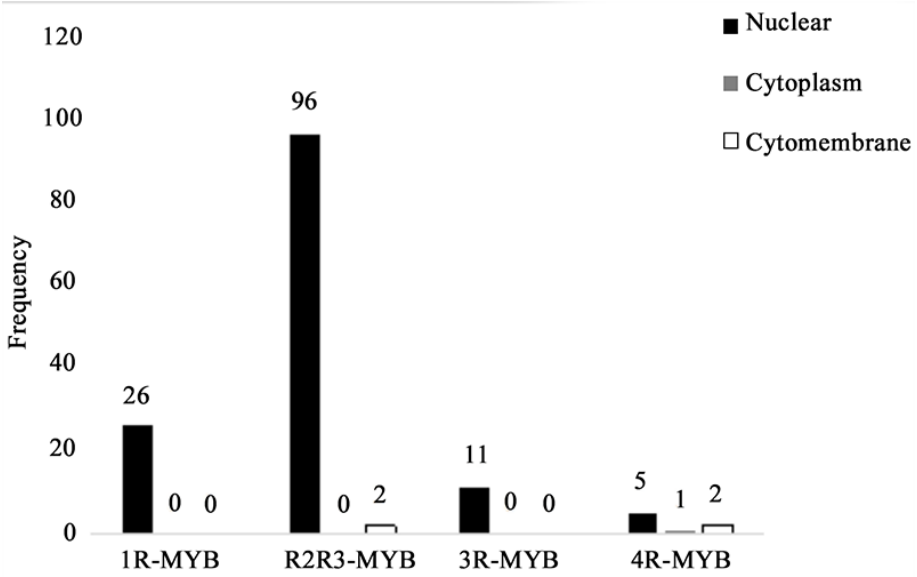

Figure 2 Frequency distribution of MYB transcription factor subcellular localization in colored potato

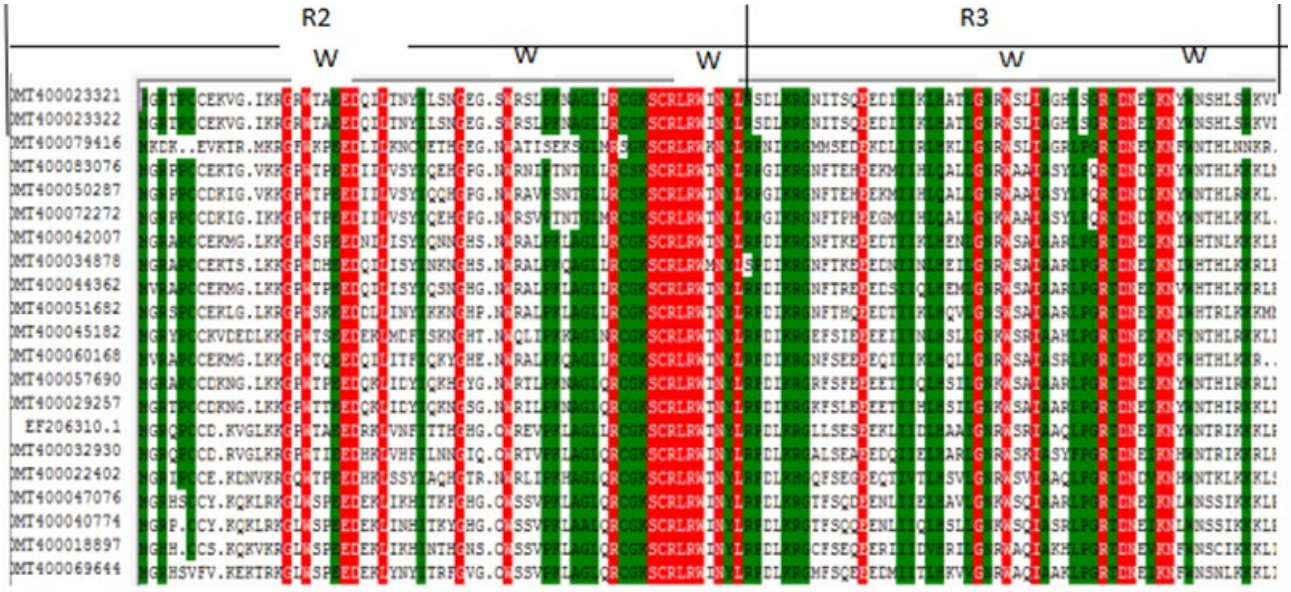

Figure 3 Alignment of colored potato part R2R3-MYB domain protein sequences

In the two conserved domains of colored potato R2R3-MYB, the R2 MYB motif contained about 60 amino acid residues and three extremely conserved tryptophan residues (W), which were separated by 20 and 19 amino acids, respectively. While the R3 MYB motif contained about 57 amino acid residues and two extremely conserved tryptophan residues (W), and the second tryptophan residue was replaced by valine (V) (Figure 4). In addition to the extremely conserved tryptophan residues, there were glycine (G), arginine (R), proline (P), cysteine (C), lysine (K), glutamic acid (E), aspartic acid (D), leucine (L) and tryptophan (W) in R2 and R3 motifs to maintain the structure of R2R3-MYB transcription factors and play specific functions.

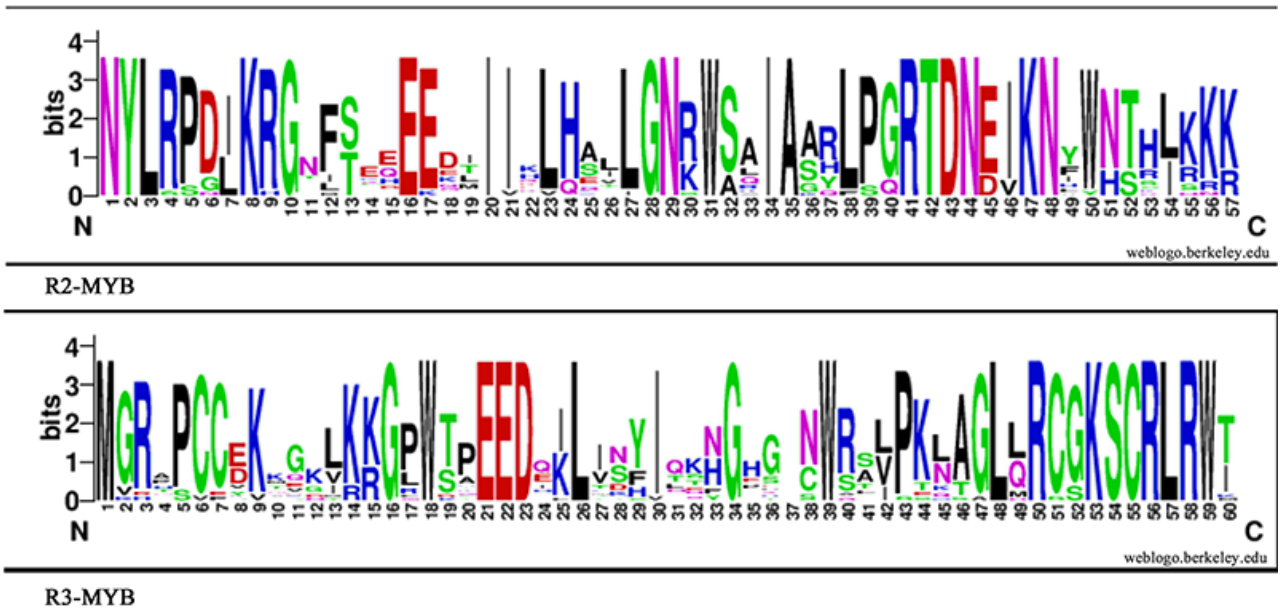

Figure 4 DNA binding domain of colored potato R2R3-MYB transcription factors

1.4 Analysis of expression pattern of R2R3-MYB transcription factor gene in different stages of color potato

The differential expression of the same gene in different periods can be visually displayed by drawing the differential gene heat map (Figure 5). The expression of 37 differentially expressed R2R3-MYB in potato tuber formation stage (S11, S12, S13), tuber growth stage (S21, S22, S23) and tuber maturation stage (S31, S32, S33) were analyzed. The results showed that with the development and maturity of potato, the expression of each MYB

gene was different. During the whole growth period, 11 MYB transcription factors were expressed, such as PGSC0003DMT400072258, PGSC0003DMT400070549, PGSC0003DMT400080428. 10 MYB transcription factors were down-regulated, of which 4 genes were up-regulated during tuber formation and growth, and down-regulated at maturity, such as PGSC0003DMT400078151, PGSC0003DMT400034878. While 6 MYB transcription factors were down-regulated from the growth period of tubers such as PGSC0003DMT400018896, PGSC0003DMT400036281. With the development of potato tubers, five MYB transcription factors began to up-regulate in potato tuber growth period such as PGSC0003DMT400003796, PGSC0003DMT400034371, PGSC0003DMT400000903. The expression of 11 MYB transcription factors decreased first and then increased from tuber formation to tuber growth and maturity such as PGSC0003DMT400042007, PGSC0003DMT400020635.

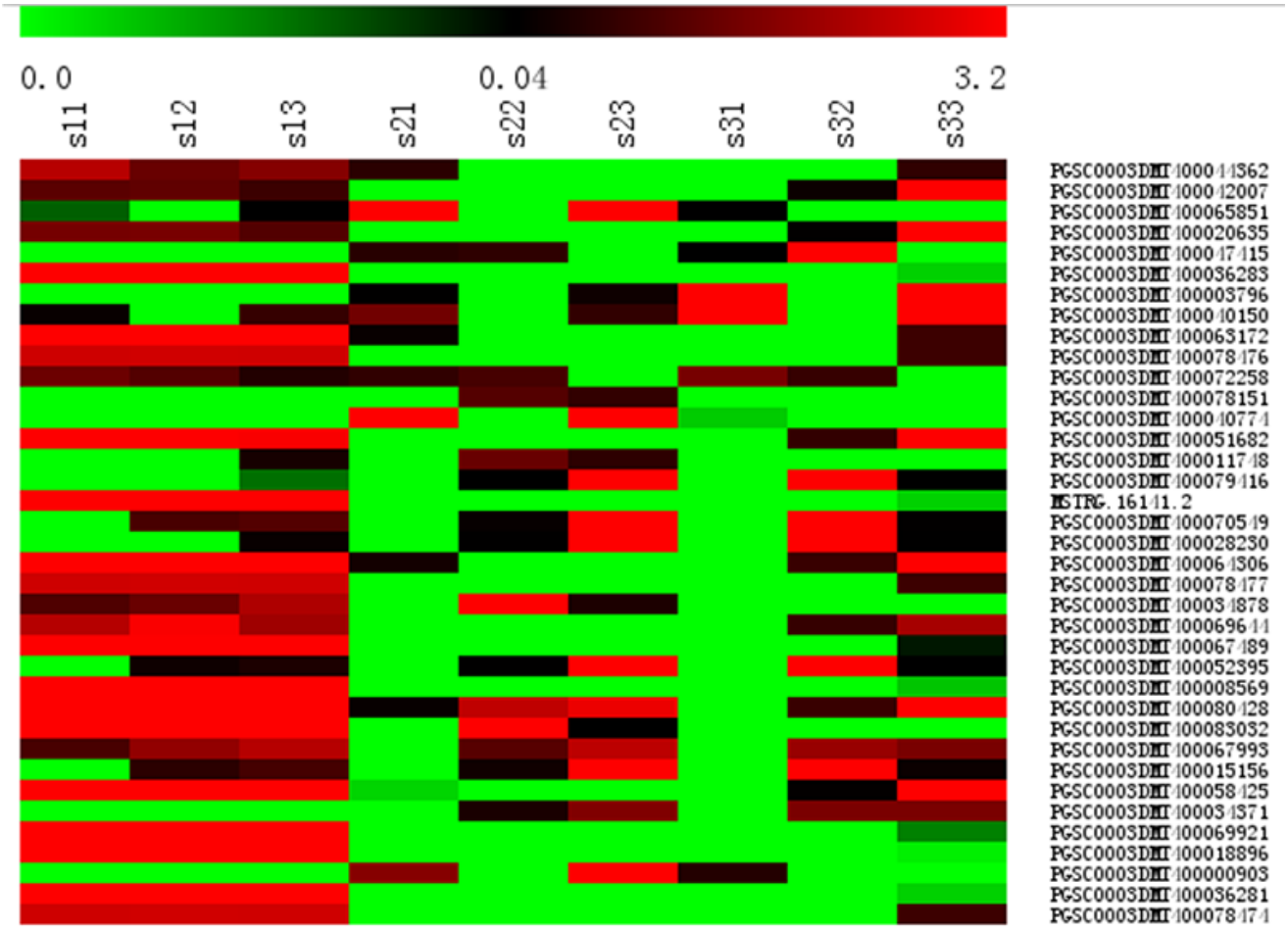

Figure 5 The pattern of expression of R2R3-MYB family in different development period of colored potato
Note: Different colors show different gene expression; Red: High expression quantity; Green: Low expression quantity

1.5 Functional prediction of R2R3-MYB transcription gene in color potato

The expression and function of genes are closely related. The enrichment analysis of GO in the differentially expressed R2R3-MYB transcription factor gene in transcriptome data showed that the six genes annotated by GO:0031540 and GO:0009718 were MSTRG.16141.2, PGSC0003DMT400036283, PGSC0003DMT400036281, PGSC0003DMT400078477, PGSC0003DMT400078476 and PGSC0003DMT400078474, respectively, which were involved in the biosynthesis of anthocyanins in color potato (Table 1).

Table 1 Prediction of genes related to anthocyanin in colored potato

GO ID	GO term	GO function classification	Gene name of GO annotation
GO:0031540	Regulation of anthocyanin biosynthetic process	Biological process	MSTRG.16141.2; PGSC0003DMT400036283; PGSC0003DMT400036281
GO:0009718	Anthocyanin-containing compound biosynthetic process	Biological process	PGSC0003DMT400078477; PGSC0003DMT400078476; PGSC0003DMT400078474

1.6 Sequence analysis of six R2R3-MYB transcription factors related to anthocyanin synthesis

The molecular formulas of six R2R3-MYB transcription factors MSTRG.16141.2, PGSC0003DMT400036283, PGSC0003DMT400036281, PGSC0003DMT400078477, PGSC0003DMT400078476 and PGSC0003DMT400078474 in color potato were $C_{1267}H_{1991}N_{373}O_{384}S_{14}$, $C_{476}H_{766}N_{142}O_{124}S_{6}$, $C_{1011}H_{1585}N_{287}O_{323}S_{15}$, $C_{904}H_{1441}N_{273}O_{266}S_{10}$, $C_{630}H_{983}N_{173}O_{193}S_{7}$, and $C_{769}H_{1204}N_{220}O_{222}S_{7}$, respectively. Of which the maximum molecular weight was 29 041.85 Da and the minimum was 10 654.65 Da; the theoretical isoelectric point was between 4.92 and 9.59, and the hydrophilic coefficient was -0.480~-0.822, indicating a strong hydrophilicity.

The secondary structures of R2R3-MYB transcription factors showed that the secondary structures of the six MYB transcription factor proteins mainly contained α-helix, random coil and β-turn (Figure 6). In the secondary structure of each transcription factor protein, it was mainly composed of α-helix and β-turn structures, which were arranged in intervals to form a stable structure. The tertiary structure of R2R3-MYB transcription factors showed that these six transcription factors were predicted to be matched to MYB proteins. The three-dimensional configuration characteristics of MYB proteins showed that they all contained helix-turn-helix (HTH) structure, but there were certain differences in each MYB transcription factor (Figure 7).

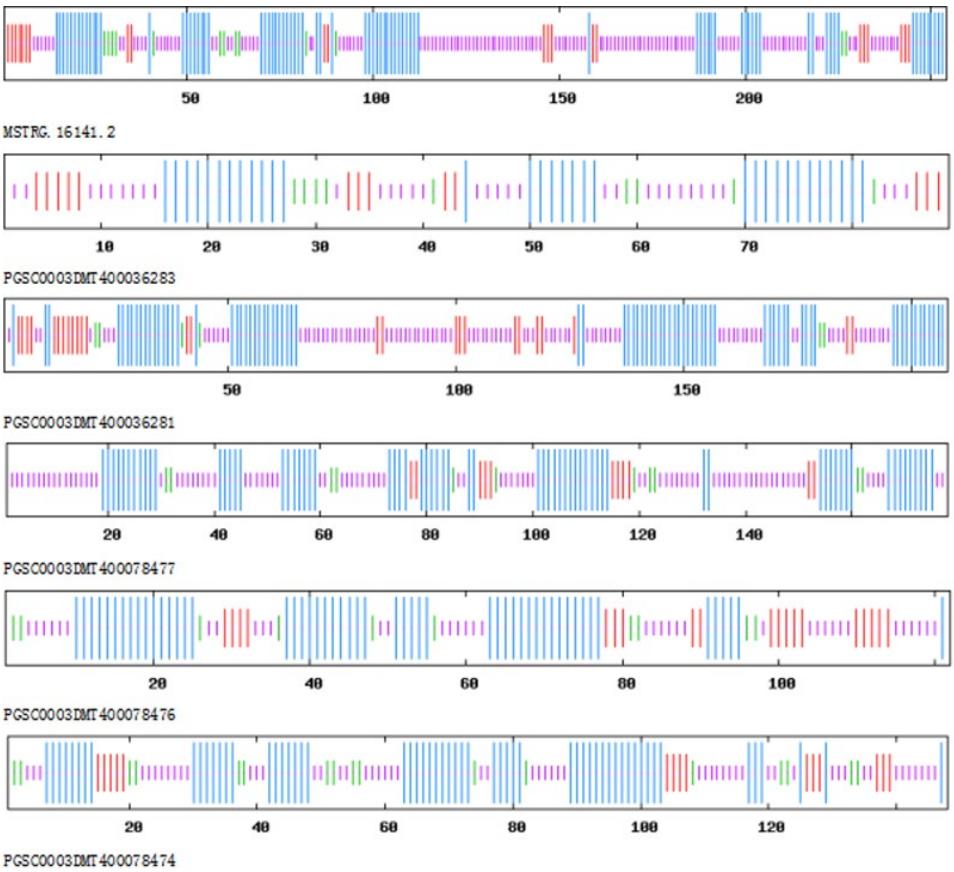

Figure 6 The secondary structure of six MYB transcription factors related to anthocyanin in colored potato

Note: Blue: Alpha helix; Purple: Random coil; Red: Extended strand; Green: Beta turn

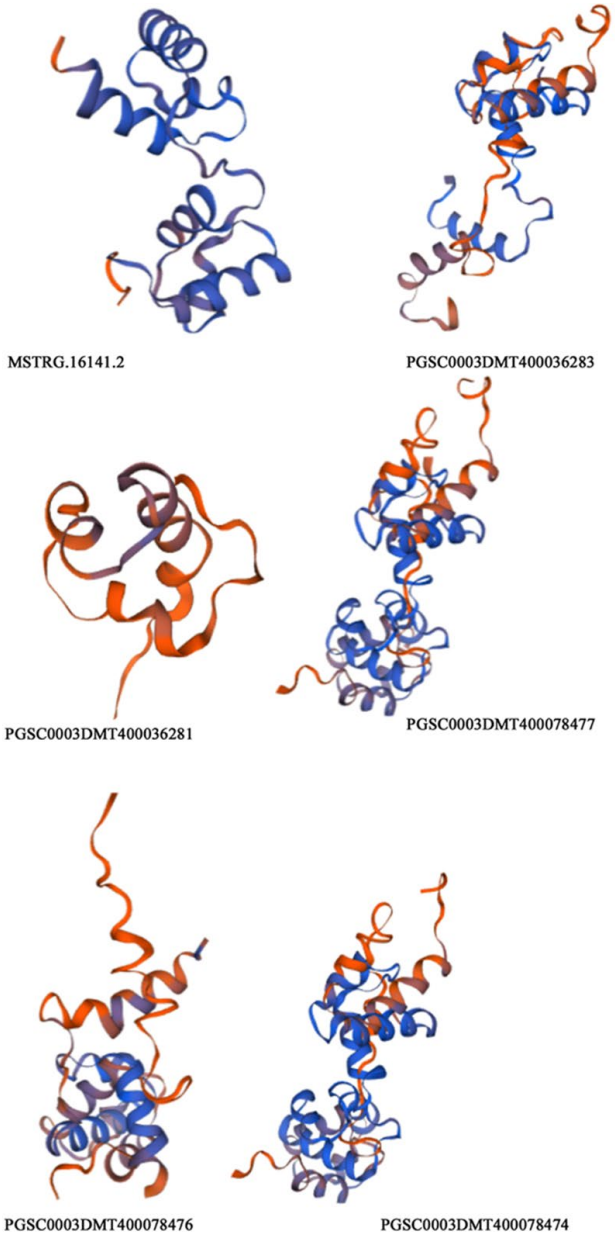

Figure 7 The tertiary structure of six MYB transcription factors related to anthocyanin in colored potato

2 Discussion

The conserved domains of R2R3-MYB transcription factors in color potato are R2 and R3. There are three conserved tryptophan residues in the R2 motif, which are separated by 20 and 19 amino acid residues, respectively. The interval between tryptophan residues in R2 is more active. The analysis of the conserved domain of potato R2R3-MYB showed that there were differences among each species. The interval of tomato R2R3-MYB transcription factors was 1~2 amino acid residues more than that of color potato (Liu, 2012, Journal of Zhejiang Normal University, pp.78). Compared with Liu et al. (2019), the interval of tryptophan residues in the conserved domain motif of potato was 10 amino acids less. Therefore, the R2 motif may be the functional activation region of color potato R2R3-MYB transcription factors, prone to insertion or deletion of amino acid residues. The two tryptophan residues in R3 motif of color potato MYB gene were separated by 18 amino acids, and the second tryptophan residue was replaced by valine (V). There is a base substitution in the R3 motif of color potato, which is the same as that described by Yan et al. (2017) in *Lycium barbarum* Murr. and Matus et al. (2008) in *Oryza sativa* L. R3 is also a highly conserved region of MYB transcription factors.

The function of gene is closely related to the expression. Among six R2R3-MYB transcription factors related to anthocyanin synthesis in color potato, the expression of MSTRG.16141.2, PGSC0003DMT400036283, PGSC0003DMT400036281 transcription factor decreases with the maturity of potato, which may be negatively correlated with anthocyanin synthesis. PGSC0003DMT400078477, PGSC0003DMT400078476, PGSC0003DMT400078474 transcription factors decreased first and then increased with potato tuber formation stage to tuber growth stage and mature stage, which may have a complex expression mechanism. The analysis of physical and chemical properties showed that it had strong hydrophilicity. It was speculated that ABA could promote the accumulation of anthocyanin under drought stress, which was consistent with the study of Shi (2019, Journal of Shanxi Agricultural University, pp.88) that drought stress promotes anthocyanin accumulation in *Ipomoea batatas* Lam. Among the secondary and tertiary structures of six MYB transcription factors related to anthocyanins in color potato, the main structures are α-helix and β-turn structures, forming a stable helix-turn-helix (HTH) structure, which is similar to the MYB structure of *Agropyron mongolicum* Keng analyzed by Ma et al. (2019).

In this study, the conserved domain of R2R3-MYB transcription factors was analyzed to lay a foundation for the study of the function of R2R3-MYB transcription factors in color potato. At the same time, it provides a theoretical basis for the biological function and metabolic regulation mechanism of MYB genes related to anthocyanin biosynthesis in color potato.

3 Materials and Methods

3.1 Material cultivation and sampling

The experimental material was purple potato (*Solanum tuberosum*) 'Huasong 66', which was provided by Inner Mongolia Huasong Agricultural Technology Co., Ltd. On May 1, 2018, the seeds were sown in the farm of the Agronomy College, Inner Mongolia Agricultural University (40°46′N, 110°45′E), and regularly fertilized, watered and weeded. From July 29, 2018, selected plants with good growth every 7 days and took samples of potato tubers under the ground during the potato tuber formation period (s1, s2), tuber growth period (s3, s4), starch accumulation period (s5; 2/3 of the aboveground stems and leaves wither and yellow), and tuber maturity period (s6; all the aboveground parts wither and yellow). The potato tuber samples were taken 6 times in the whole growth and maturity period, and three repeated samples were taken in each period. After quick freezing in liquid nitrogen, the potato tuber samples were placed in the refrigerator at -80℃ for further use.

The color potato tuber samples were sent to Hangzhou LC Biotech Co., Ltd for transcriptional sequencing. The subsequent analysis is based on the sequencing result data.

3.2 Total RNA extraction and transcriptome sequencing of color potato

TRK-1002RNA purification kit (product#TPK-1002; LC Sciences, Hangzhou, China) was used for total RNA extraction of potato. 50 mg of the sample was fully ground in liquid nitrogen, and then 600 μL lysate was added to grind until dissolved. Transferred homogenate to centrifuge tube, 12 000 rpm, then centrifuged at room temperature for 2 min. Took the supernatant, added double 70% ethanol, vortex blending. 600 μL water phase containing ethanol was used on the column and centrifuged at room temperature for 1 min at 12 000 rpm. The supernatant was discarded, 400 μL scrubbing solution was added to the column and centrifuged at 12 000 rpm for 1 min at room temperature. Discard the supernatant and repeat this step twice. Transferred the column to a 1.5 mL collecting tube, added 50 μL RNA eluent to the column, centrifuged for 2 min at 8 000 rpm, centrifuged at room temperature for 1 min at 12 000 rpm, and turned the column around at room temperature for 1 min at 12 000 rpm.

The *OD* value of the extracted product was measured by Nanodrop, and RNA integrity was detected by 1% formaldehyde denaturing agarose gel electrophoresis. During the construction of transcriptome library, the mixed treatment of RNA extracted from each period was performed. s1 and s2 treatment was S1 (tuber formation stage), s3, s4 and s5 treatment was S2 (tuber growth stage), s6 treatment was S3 (mature stage), each treatment was repeated three times. The samples were sent to Hangzhou LC Biotech Co., Ltd for transcriptional sequencing.

3.3 Screening of MYB transcription factors in color potato

In transcriptome sequencing database, genes with significant differences were screened, and *MYB* genes were screened by annotation information. The MYB transcription factor related genes were compared by NCBI BLAST one by one, and the Structure Home was used to predict the domain.

3.4 Subcellular localization and conserved motif analysis of MYB transcription factor in color potato

The amino acid sequences of selected MYB transcription factors were input into Cell-PLoc 2.0 online analysis software one by one for subcellular localization prediction and classification. Multiple sequence alignment software Clustal X 1.83 was used to compare the amino acid sequence of the screened R2R3-MYB transcription factor, remove the gap in the sequence and complete alignment. The multi-series alignment results of Clustal X 1.83 software were imported into DNAMan software, and the multi-sequence alignment diagram was drawn after removing redundant amino acids. Weblogo (http://weblogo.berkeley.edu/) was used to analyze the conserved domain of amino acid sequence alignment results without redundant sequences.

3.5 Expression analysis of MYB transcription factor in color potato

TMEV software was used to analyze the gene expression of some R2R3-MYB transcription factors with significant differences. The FPKM values of each gene were processed by $\log_2$, and the average and standard deviation were calculated and converted to Z values (Z sample-i=[(log2(Signal sample-i)-Mean (Log_2(Signal) of all samples)][Standard deviation (Log_2(Signal) of all samples)]). Differential expression of transcription factor genes at different developmental stages was analyzed by drawing the expression heat map of differential genes.

3.6 Functional prediction of R2R3-MYB transcription factor in color potato

Based on Genome, mRNA, Gene Orthology (GO) and KEGG database, the annotation information of genes was obtained. The GO enrichment analysis of selected R2R3-MYB transcription factors with significant differences was carried out, and the function of MYB transcription factors was preliminarily predicted by GO annotation information.

3.7 MYB transcription factor analysis related to anthocyanin in color potato

The ProtParam tool (https://web.expasy.org/protparam/) of online analysis software ExPASy was used to analyze the physicochemical properties of the six predicted R2R3-MYB transcription factors related to anthocyanin. In addition, SOMPA (http://npsa-pbil.ibcp.fr/cgi-bin.age=npsa_sopma.html) and SWISS-MODEL (https://swissmodel.expasy.org/interactive) were used for secondary and tertiary structure prediction of six anthocyanin-related R2R3-MYB transcription factor proteins in color potato.

Authors' Contributions

WXJ, FBB and ZNQ are the experimental designers and executors of this study, completing data analysis and writing the first draft of the paper. CYF and SCH participated in the experimental design and analyzed the experimental results. MYH and YZ are the designers and directors of the project, guiding experimental design, data analysis, paper writing and revision. All authors read and approved the final manuscript.

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