Genomic identification and characterization of MYC family genes in wheat (Triticum aestivum L.)

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Abstract

Background: MYC transcriptional factors are members of the bHLH (basic helix-loop-helix) superfamily, and play important roles in plant growth and development. Recent studies have revealed that some MYCs are involved in the crosstalk between Jasmonic acid regulatory pathway and light signaling in Arabidopsis, but such kinds of studies are rare in wheat, especially in photo-thermo-sensitive genic male sterile (PTGMS) wheat line.

Results: 27 non-redundant MYC gene copies, which belonged to 11 TaMYC genes, were identified in the whole genome of wheat (Chinese Spring). These gene copies were distributed on 13 different chromosomes, respectively. Based on the results of phylogenetic analysis, 27 TaMYC gene copies were clustered into group I, group III, and group IV. The identified TaMYC genes copies contained different numbers of light, stress, and hormone-responsive regulatory elements in their 1500 base pair promoter regions. Besides, we found that TaMYC3 was expressed highly in stem, TaMYC5 and TaMYC9 were expressed specially in glume, and the rest of TaMYC genes were expressed in all tissues (root, stem, leaf, pistil, stamen, and glume) of the PTGMS line BS366. Moreover, we found that TaMYC3, TaMYC7, TaMYC9, and TaMYC10 were highly sensitive to methyl jasmonate (MeJA), and other TaMYC genes responded at different levels. Furthermore, we confirmed the expression profiles of TaMYC family members under different light quality and plant hormone stimuli, and abiotic stresses. Finally, we predicted the wheat microRNAs that could interact with TaMYC family members, and built up a network to show their integrative relationships.

Conclusions: This study analyzed the size and composition of the MYC gene family in wheat, and investigated stress-responsive and light quality induced expression profiles of each TaMYC gene in the PTGMS wheat line BS366. In conclusion, we obtained lots of important information of TaMYC family, and the results of this study was supposed to contribute novel insights and gene and microRNA resources for wheat breeding, especially for the improvement of PTGMS wheat lines.

Keywords: Wheat, MYC, Gene family, JA signaling, Light response, Male sterile

Background

The Jasmonic acid (JA) signaling pathway is complicated and is involved in several regulatory processes, such as plant growth and development, fertility regulation, and plant immunity [1, 2]. In Arabidopsis, components of JA signaling pathway include F-box protein CORONATINE INSENSITIVE1 (COI1), Jasmonate-ZIM (JAZ) domain repressor, and the bHLH transcription factor MYC2, which can regulate the expression patterns of JA-response genes [3]. JAZ proteins have been shown to block MYC2 activity in the absence of bioactive JAs by recruiting the general corepressors TOPLESS (TPL) and TPL-related proteins through the interaction with the adaptor protein novel interactor of JAZ (NINJA) [4]. In Arabidopsis, MYC2 was the first transcription factor (TF) found to be regulated by the JAZ proteins [3], and involved in defense regulation against insect herbivory via a partially redundant manner.

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with its homologs MYC3 and MYC4 [5, 6]. These three MYC TFs can form homo- and heterodimers to bind G-box (CAGCTG) elements or some variants of G-box elements [6]. However, these three MYC TFs play different roles in signaling pathways, despite they share the similar DNA binding sites. For instance, MYC3 and MYC4 are important for JA-mediated resistance to the herbivore Spodoptora littoralis, while the roles of MYC2, MYC3 and MYC4 are very weak in regulating JA-mediated inhibition of primary root growth. These differences might be due to their preferential production in root and shoot tissues [5, 6]. In addition to the JA signaling pathway, MYC2 is also involved in repressing primary root growth, anthocyanin biosynthesis, oxidative stress tolerance [7], blue light-mediated photomorphogenic growth, resistance to necrotrophic fungi, and biosynthesis of tryptophan and indole-glucosinolates [8]. Therefore, MYC2 acts as a key factor that connects many pathways.

Among environmental signals, light is an important influential factor modulating plant growth and development. Light is a source of energy for plant photosynthesis and acts as a signal in the coordination of plant adaptive responses to environmental changes [9]. Plant responses to light are often mediated by photoreceptors, which are sensitive to specific wavelengths of the solar spectrum. Phytochromes belong an important class of photoreceptors playing roles in light signaling. Phytochrome B (PHYB) is a positive regulator of photomorphogenesis [11]. Phytochromes proteins mainly include two types: the red light absorbing type (known as Pr) and the far-red light absorbing type (known as Pfr). They are interchangeable based on the R:FR ratios in environments [12]. Low R:FR ratio can reduce the levels of Pfr, and may be involved in shade-avoidance syndrome [11]. Recently, some studies have shown that components of JA signaling pathway, such as JAZ proteins, COIs and MYC2, are involved in several light-mediated responses. Robson et al. (2010) found that Arabidopsis mutations jin1 and myc2 are more sensitive to shade or FR light, and displayed an elongated hypocotyl phenotype under low R:FR ratio than wild type [13]. In addition, light-response related genes were upregulated under FR and blue light (BL) conditions in jin1/myc2 mutant [14]. MYC2 could interact with the Z-box and G-box light response elements and was thought as a negative regulator of blue light–mediated photomorphogenic growth [14]. Furthermore, MYC2 and SPA1 (suppressor of PHYA) may act redundantly in the dark and synergistically under light to suppress photomorphogenesis [15].

In addition, MYC2 also participates in the crosstalk among JAs and other plant hormones. In Arabidopsis, MYC2 was characterized as a transcriptional activator in ABA-inducible gene expression [16]. Song et al. (2014) demonstrated that MYC2 can interact with ethylene-stabilized transcription factor EIN3 and modulated JA and ET signal antagonism in Arabidopsis [17].

Wheat is one of the most important food crops. The fertility of the PTGMS wheat line BS366 is controlled by temperature and/or photoperiods [2]. The pollen of BS366 cannot be fully spilled out, due to the impaired anther dehiscence, which can be recovered by the application of MeJA in vitro [2]. In wheat JA signaling pathway, 8 COI genes and 14 JAZ genes have been identified [2, 18]. However, few studies have been reported about wheat MYC gene family, which is an important component of the JA signaling pathway. In the present study, the TaMYC gene family was characterized using the latest genome sequences. We analyzed gene structures, conserved motifs, chromosome localization, and the regulatory networks of the TaMYC gene family. Given the important roles of micro-RNAs, such as miR1120 and miR1130 are involved in the JA signaling pathway and participate in anther development in wheat PTGMS line [19], we also predicted the interactive relationships between TaMYC and micro-RNAs. In addition, the expression profiles of TaMYC genes in the PTGMS wheat line BS366 were detected using qRT-PCR. Results in this study are expected to support a basis for further investigations on the functions of TaMYC genes, and provide some gene resources for revealing the molecular mechanisms of male sterility in PTGMS wheat.

Results

Identification of TaMYC gene family

After the removal of redundant gene, 27 non-redundant MYC gene copies, which belonged to 11 MYC genes, were identified. Firstly, we monitored the physical and chemical characteristics of these MYC gene copies. The coding sequence lengths of 27 MYC gene copies were ranged from 1332 bp to 2088 bp, and the deduced protein lengths were ranged from 443 to 695 amino acids (Table 1). The predicted molecular weights (MWs) of each MYC protein were ranged from 47.53 kDa to 75.62 kDa, and the corresponding isoelectric points (IPs) were changed from 4.96 to 8.73 (Table 1). Subcellular localization predictions revealed that MYC proteins were functioned in chloroplast, cytoplasmic, nuclear, or plasma membrane (Table 1). Different characteristics of TaMYC genes and proteins were obtained, and the results indicated that different TaMYC proteins might have different biological functions.

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Analysis of chromosomal locations and synteny
In order to understand the relative position of each TaMYC gene copy on wheat chromosomes, we marked their physical placements on wheat A, B, and D chromosomes. As shown in Figs. 1, 27 TaMYC gene copies were located on 13 chromosomes. 9, 10, and 8 TaMYC gene copies were located on chromosomes 1A-5A, 1B-4B, and 1D-4D, respectively (Fig. 1).

Gene and chromosomal segment duplication are the major forces of genome evolution in plants [20]. In the wheat genome, four tandem duplication events (TaMYC1-B1/TaMYC1-B2, TaMYC3-A1/TaMYC3-A2, TaMYC5-B1/TaMYC5-B2, and TaMYC11-A1/TaMYC11-A2) and 25 segmental duplication events were identified, which indicate that segmental duplication events were the main cause of the increase of MYC members in wheat (Additional file 1: Figure S1and Additional file 7: Table S4). Synteny analysis among TaMYCs and its ancestors were also analyzed. Nine members (TaMYC1-A, TaMYC3-A2, TaMYC4-A, TaMYC5-A, TaMYC5-B1/TaMYC5-B2, and TaMYC11-A1/TaMYC11-A2) of the TaMYC gene family have homology with genes of T. urartu and Ae. tauschii (Additional file 1: Figure S1).

### Table 1 Characteristics of TaMYC gene family members

| Gene name | Sequence ID | Locations | Protein/AA | Isoelectric point | Molecular weight of deduced protein/KD | Subcellular Localization |
|-----------|-------------|-----------|------------|------------------|----------------------------------------|-------------------------|
| TaMYC1-A  | TraesCS1A02G102400 | 1A:98584808:98591571:+ | 626 | 5.65 | 68.48 | Nuclear |
| TaMYC2-A  | TraesCS1A02G193200 | 1A:349338465:349360851:+ | 693 | 6.37 | 74.04 | Nuclear |
| TaMYC1-B1 | TraesCS1B02G112900 | 1B:131456949:131464291:+ | 631 | 5.84 | 69.22 | Nuclear |
| TaMYC1-B2 | TraesCS1B02G113100 | 1B:131775632:131785030:+ | 688 | 5.87 | 75.62 | Nuclear |
| TaMYC2-B  | TraesCS1B02G208000 | 1B:376071131:376073212:+ | 693 | 6.15 | 75.09 | Nuclear |
| TaMYC2-D  | TraesCS1D02G196900 | 1D:277092891:277094978:+ | 695 | 6.15 | 75.35 | Nuclear |
| TaMYC3-A1 | TraesCS2A02G409400 | 2A:667011017:667015600:+ | 568 | 5.37 | 62.65 | Nuclear |
| TaMYC3-A2 | TraesCS2A02G409600 | 2A:666746712:666752609:+ | 558 | 5.54 | 60.82 | Nuclear |
| TaMYC3-B  | TraesCS2B02G482000 | 2B:613532721:613536928:+ | 573 | 5.17 | 62.77 | Nuclear |
| TaMYC7-D  | TraesCS2D02G406800 | 2D:522323574:522329854:+ | 465 | 4.96 | 51.53 | Nuclear |
| TaMYC3-D  | TraesCS2D02G406900 | 2D:522521895:522526799:+ | 567 | 5.19 | 61.82 | Nuclear |
| TaMYC8-D  | TraesCS2D02G576000 | 2D:639529624:639535060:+ | 589 | 5.24 | 66.17 | Nuclear |
| TaMYC4-A  | TraesCS3A02G158600 | 3A:156267999:156270204:+ | 616 | 6.52 | 67.35 | Nuclear |
| TaMYC4-B  | TraesCS3B02G185400 | 3B:201339407:201341777:+ | 625 | 7.11 | 68.24 | Nuclear |
| TaMYC5-B1 | TraesCS3B02G288700 | 3B:463203072:463205129:+ | 443 | 8.47 | 47.53 | Nuclear |
| TaMYC5-B2 | TraesCS3B02G284800 | 3B:456323130:456324920:+ | 475 | 7.77 | 50.76 | Nuclear |
| TaMYC4-D  | TraesCS3D02G166300 | 3D:138192597:138194964:+ | 625 | 6.76 | 68.31 | Nuclear |
| TaMYC5-D  | TraesCS3D02G253700 | 3D:355318384:355320162:+ | 465 | 8.73 | 49.82 | Nuclear |
| TaMYC6-A  | TraesCS4A02G289000 | 4A:210635122:21065305:+ | 597 | 6.56 | 65.55 | Nuclear |
| TaMYC6-B  | TraesCS4B02G276900 | 4B:558578472:558580268:+ | 598 | 6.73 | 65.56 | Nuclear |
| TaMYC8-B  | TraesCS4B02G397400 | 4B:671703616:671707933:+ | 564 | 5.18 | 62.86 | Nuclear |
| TaMYC9-B  | TraesCS4B02G397800 | 4B:671764988:671776128:+ | 510 | 5.47 | 57.00 | Nuclear |
| TaMYC10-D | TraesCS4D02G224600 | 4D:38151243:381559778:+ | 557 | 6.49 | 61.40 | Nuclear |
| TaMYC6-D  | TraesCS4D02G275500 | 4D:46428380:446430176:+ | 598 | 6.56 | 65.99 | Nuclear |
| TaMYC11-A1| TraesCS4D02G489500 | 5A:659338425:659342323:+ | 570 | 5.31 | 63.15 | Nuclear |
| TaMYC11-A2| TraesCS5A02G558500 | 5A:709193171:709197273:+ | 585 | 5.26 | 64.93 | Nuclear |

Phylogenetic analysis of TaMYC proteins
To reveal the functional information of TaMYC genes, a phylogenetic tree, which based on the compare among wheat, Arabidopsis, and rice, was constructed using N-J method. As shown in Fig. 2, MYC proteins of three species were clustered into four groups (I, II, III, and IV). TaMYCs were distributed in groups I, III and IV. Seven TaMYC proteins (16 copies) were clustered into group I,
while only TaMYC2 (three copies) was clustered into Group III. It was worth noting that three copies of TaMYC2 had a close homology with AtMYC2, AtMYC3 and AtMYC4, which are genes that have been demonstrated to play similar roles in plant development (Fig. 2).

**Structural analysis of TaMYC genes and proteins**

For understanding the structural features of TaMYC family members, firstly, the exon-intron structural features were revealed by aligning the predicted CDS against corresponding genomic sequences. As shown in Fig. 3, the intron–exon structures of different TaMYC genes were diverse, while copies of the same genes were similar or same, such as TaMYC6 (TaMYC6-A, TaMYC6-B and TaMYC6-D) and TaMYC11 (TaMYC11-A1 and TaMYC11-A2). It was notable that MYC genes of the same subgroup shared similar intron–exon structures, for instance, TaMYC4 and TaMYC6 were both in subgroup IV, and they only had one exon (Fig. 2 and Fig. 3).

Motifs in TaMYC proteins were also predicted in this study. Similar with the intron–exon structures of TaMYC genes, proteins of the same subgroup shared the same or similar motifs. Most copies of TaMYC proteins possessed six, seven or eight motifs (Fig. 3). TaMYC7-D only had five motifs (Fig. 3). As the member of bHLH superfamily, MYC family proteins contain a bHLH domain and a conserved bHLH-MYC_N domain [15, 21]. In this study, motifs 2, 3, 6 and 7 corresponded to bHLH-MYC_N domains, while motifs 1 and 4 corresponded to bHLH domains (Additional file 2: Fig. S2). The biological functions of other motifs remains unknown, but it could be predicted that some TaMYC proteins had unknown functions.

**Analysis of cis-regulatory elements of TaMYC genes**

The upstream promoter regions (1500 bp, Additional file 3: File S1) of TaMYC gene copies were retrieved from the wheat genome to identify cis-regulatory elements. Five light-responsiveness regulatory elements, including ACE, ATC-motif, Box 4, G-box and MRE were identified in all TaMYC promoter regions, indicating that TaMYCs might be involved in light signaling pathways (Fig. 4 and Additional file 5: Table S2). Eight hormone-responsive regulatory elements, including TGA-element, TCA-element, TATC-box, P-box, GARE-motif, CGTCA/TGACG-motif, AuxRR-core, and ABRE, which were associated with auxin, salicylic acid, gibberellin, MeJA, and ABA responses, were identified in the promoter region of TaMYC copies (Fig. 4 and Additional file 5: Table S2). Besides, six stress-responsive regulatory elements, WUN-motif, TC-rich repeats, MBS, LTR, GC-motif and ARE, which were associated with wound responsiveness,
defense and stress responsiveness, drought-inducibility, low-temperature responsiveness, anoxic specific inducibility and anaerobic induction, respectively, were identified (Fig. 4 and Additional file 5: Table S2). In addition, cis-regulatory elements for five regulators of development regulation and two regulators of biosynthesis regulation were identified. As shown in Additional file 5: Table S2, different types and numbers of regulatory elements were identified in the promoter regions of different TaMYC genes, indicating that TaMYC genes might have different functions in stress resistance, growth and development.

**Tissue/organ-specific expression profiles of TaMYC genes**

To study the tissue/organ-specific expression patterns of the 11 identified TaMYC genes, their expression patterns in root, stem, leaf, petal, pistil, stamen, and glume of the PTGMS wheat line BS366 were investigated by qRT-PCR. As shown in Figs. 5, 11 TaMYC genes showed different expression levels in different tissues. The expression levels of TaMYC5 and TaMYC9 in glume were higher than that in other tissues (Fig. 5). In addition, TaMYC1 and TaMYC2 had relatively high expression levels in pistil tissue, while TaMYC6, TaMYC10, and TaMYC11 had
relatively high expression in leaf tissue (Fig. 5). 

\textit{TaMYC4} was constitutively expressed in all six tissues (Fig. 5). Meanwhile, we noticed that \textit{TaMYC2}, \textit{TaMYC4}, \textit{TaMYC10}, and \textit{TaMYC11} displayed relatively high expression levels in stamen (Fig. 5).

\textbf{Effects of exogenetic MeJA treatment}

In order to investigate the functions of \textit{MYC}s in the JA signaling pathway at anther dehiscent stage, the expression profiles of \textit{TaMYC} genes in anthers, which treated with different concentrations of MeJA, were analyzed. As shown in Fig. 6, the expression of \textit{TaMYC3} was high under 2 mmol/L MeJA. The expression levels of \textit{TaMYC5}, \textit{TaMYC7}, \textit{TaMYC8}, \textit{TaMYC9}, and \textit{TaMYC10} in anther were induced by 4 mmol/L MeJA (Fig. 6). These results indicate that these \textit{TaMYC} genes could be strongly induced by MeJA and might be function on the JA signaling pathway in anther of the PTGMS wheat line BS366.

\textbf{Photochromic conversion-induced expression profiles of \textit{TaMYC} genes}

Many studies have suggested that MYC may be involved in the cross-talk between the JA signaling pathway and
light signaling pathway (R:FR ratio mediated Pfr/Pr conversion) [12]. To investigate photochromic conversion-induced expression profiles of TaMYC genes, different R:FR ration light treatments were performed on BS366 seedlings. As shown in Fig. 7, TaMYC1, TaMYC2, TaMYC6, TaMYC7, TaMYC8, TaMYC9 and TaMYC11 were upregulated in R and FR light-enriched conditions compared to white light conditions. In addition, TaMYC4 was downregulated by far-red light, and TaMYC5 and TaMYC10 were inhibited under R light condition (Fig. 7).

Expression profiles of TaMYC genes under phytohormone treatments
The expression profiles of TaMYC genes in the leaf tissues of the PTGMS line BS366 under plant hormones treatments were analyzed to determine the responsive profiles. Under ABA treatment, the expression levels of TaMYC2, TaMYC8, and TaMYC9 were upregulated at 4 h post-treatment, then downregulated at 12 h post-treatment (Fig. 8). TaMYC4, TaMYC5 and TaMYC6 were induced after ABA treatment. TaMYC1, TaMYC3, TaMYC7, TaMYC10 and TaMYC11 showed negative responses to ABA treatment (Fig. 8). Under GA treatment, the expression of TaMYC7, TaMYC8, TaMYC9, and TaMYC10 were inhibited, while the expression of TaMYC2, TaMYC4, TaMYC5, and TaMYC6 were promoted (Fig. 8). The transcript profiles of TaMYC3 and TaMYC11 were slightly upregulated and peaked at 4 h post-treatment. TaMYC1 was downregulated at 4 h post-treatment, but showed an increase profile at 12 h post-treatment (Fig. 8). Under IAA treatment, the expressions of all TaMYC genes were downregulated (Fig. 8).

Abiotic stress-induced expression profiles of TaMYC genes
The transcriptional profiles of TaMYC genes under abiotic stresses were monitored in this study. As shown in Fig. 9, the expressions of TaMYC1, TaMYC2, TaMYC3, TaMYC4, TaMYC5, TaMYC6, TaMYC8, TaMYC10, and TaMYC11 were upregulated under low temperature treatment. The expression levels of TaMYC7 and TaMYC9 were decreased at 4 h post-treatment, and recovered at 12 h post-treatment (Fig. 9). Under high salinity conditions, TaMYC1, TaMYC2, TaMYC3, TaMYC6, TaMYC7, TaMYC8, TaMYC9, TaMYC10, and TaMYC11 were downregulated. Only TaMYC4 and TaMYC5 were promoted after saline treatment (Fig. 9). Under drought stress, TaMYC5 and TaMYC8 were upregulated, while the rest of TaMYCs were downregulated (Fig. 9).

microRNA targeting prediction of TaMYC genes
In order to uncover the interactions between microRNAs (miRNAs) and their MYC targets, we predicted the potential networks using online tool (Additional file 6: Table S3). As shown in Fig. 10, seven TaMYC genes, including TaMYC3, TaMYC5, TaMYC6, TaMYC7, TaMYC8, TaMYC10, TaMYC11, were regulated by 12 miRNAs (taemiR1127b-3p, taemiR9657a-3p, taemiR9676-5p, taemiR1138, taemiR167b, taemiR5384-3p, taemiR9773, taemiR1128, taemiR164,
taemiR9657c-3p, taemiR9675-3p, and taemiR9677a). We speculated these miRNAs could inhibit the expression levels of target TaMYCs at the transcriptional or translational level. One TaMYC gene might be targeted by multiple miRNAs, while several TaMYC genes might be regulated by the same miRNA (Fig. 10). In order to understand the potential functions, we pointed out the response model of each target TaMYC gene under different stresses or treatments. TaMYC3, TaMYC5, TaMYC6, and TaMYC8 were responded to cold stress, TaMYC7 was mainly responded to salinity, and TaMYC10 and TaMYC11 were thought to show a close relationship with drought stress (Fig. 10). Only TaMYC3 showed a clear response to 2 mmol/L MeJA treatment, and the rest of 6 TaMYCs were promoted at 4 mmol/L MeJA treatment (Fig. 10). TaMYC7-D was sensitive to red light stimulus, while others were more sensitive to far red light (Fig. 10). Besides, we found that TaMYC3 and TaMYC8 could response to GA, and TaMYC7, TaMYC10, and TaMYC11 were mainly regulated by IAA (Fig. 10). Although the precise functions of most miRNAs in this study were unknown, some miRNAs (such as taemiR167 and taemiR1127b-3p) had already identified as factors involved in the regulation of male sterility in wheat [2, 19]. Based on the network shown in Fig. 10, we thought that TaMYC3, TaMYC5, TaMYC6, and TaMYC8 maintained high possibilities on the regulation of temperature-induced male sterility in wheat PTGMS line BS366.

**Discussion**

The JA signaling pathway is involved in plant growth and development, and it can regulate the plant fertility [22], anthocyanin accumulation [23] and leaf senescence [24]. MYC is an important component of the COI1/JAZ/MYC2 complex and can mediate JA and various hormone signaling pathways, and the light signaling
However, there are few reports regarding the function of MYC in crop plants. In the present study, aiming to understand the roles of MYC genes in wheat, 27 candidate TaMYC copies were isolated (Fig. 1 and Table 1) and clustered into 11 MYC genes (Fig. 2). These TaMYC genes were classified into 3 subgroups based on phylogenetic analysis and shared relatively close homology with MYCs of Arabidopsis and rice (Fig. 2). Furthermore, phylogenetic analysis revealed that TaMYC2 had close homology with AtMYC2, AtMYC3 and AtMYC4, indicating that TaMYC2 may have similar roles in regulating wheat development (Fig. 2).

Cis-regulatory sequences, such as enhancers and promoters, can control development and physiology by regulating gene expression [25]. Cis-regulatory elements, acting as important molecular switches, are involved in the regulation of gene transcription under external stimuli [26]. To clarify the functions of TaMYC genes, cis-regulatory elements in the promoter regions of TaMYC genes, and their expression profiles under various stresses were analyzed. It was found that six stress-responsive elements, five light-responsive elements, and eight hormone-responsive elements were identified in TaMYC promoter regions (Fig. 4 and Additional file 6: Table S3). The 11 TaMYCs contained different types and numbers of cis-acting regulatory elements in each promoter region, indicating that these genes had different regulatory functions that responded to different stress and hormone treatments. Furthermore, we evaluated the expression profiles of TaMYC genes in PTGMS wheat line BS366 seedlings under different stress conditions and hormone treatments. Inducible expression analyses revealed that both TaMYC4 and TaMYC6, with similar
protein structures (Fig. 3), were up-regulated by treatments of ABA, GA, low temperatures, and drought (Fig. 8 and Fig. 9). Similar expression profile trends also exited in TaMYC1 and TaMYC2 under treatment with low temperature and salinity treatments (Fig. 9).

Phytohormone crosstalk involves a very complex signaling regulative network, is universally available in plants, and plays a very important role in plant regulation of growth and development as the role of in JA signaling pathway [27]. TaMYC genes were found to contain different numbers of hormone-responsive elements, especially ABA (ABRE) and MeJA (CGTCA/TGACG-motif) (Additional file 5: Table S2). ABA is a "stress hormone" that can regulate plant growth, stress tolerance, seed germination, and tissue/organ senescence [18]. In Arabidopsis, MYC2 functions in ABA signaling pathways [16]. In this study, TaMYC2, 4, 5, 6, and 8 were upregulated under ABA treatment (Fig. 8). It is known that MeJA may play a positive regulatory role in anther dehiscence and glume opening [2, 28]. As an important component of the JA signaling pathway, TaMYCs were also regulated by MeJA. For example, the promoter region of TaMYC3 was rich in CGTCA/TGACG-motifs (numbers of motifs were 2, 1, and 3 for TaMYC3a-A, TaMYC3b-A, and TaMYC3-B, respectively) (Fig. 4 and Additional file 5: Table S2), and they displayed very high expression levels after MeJA treatment (Fig. 6). Meanwhile, the transcriptional levels of the rest of TaMYC were significantly induced by different concentrations of MeJA (Fig. 6), although there were no CGTCA/TGACG-motifs in the promoter region of TaMYC4, 5 and 10. This indicated that the gene expression level under different treatments was not only dependent on the presence of relevant cis-acting regulatory elements, but also might be regulated by other physiological pathways in wheat.

A growing body of evidences indicate that the JA response is modulated by the ecological context of the plant, especially light, which is emerging as a critical regulator of JA signaling [29]. In Arabidopsis, MYC2 can
interact with SPA1 (suppressor of PHYA) redundantly in the dark and synergistically in the light to suppress photomorphogenesis by binding to the G-box (found in the promoter of SPA1) [21]. In this study, we also found that most of TaMYC genes were rich in G-box cis-acting regulatory elements. For example, TaMYC1, TaMYC5, TaMYC6, and TaMYC11 contained at least 4 G-box motifs, which are involved in light responsiveness (Fig. 4 and Additional file 5: Table S2). The state of conversion between Pfr and Pr is involved in detecting the quality of light by monitoring R:FR ratios [30]. Some evidences show that FR light-enriched environments could inactivate PHYB and promote the shade avoidance syndrome [30]. To investigate the possible functions of TaMYCs in light signaling, we utilized the R:FR ratio-based Pfr/Pr conversion experiment. The results showed that all TaMYCs were induced by R and FR, such as the expression of TaMYC1, 2, 3, 6, 7, 8, 9 and 11, which were up-regulated under both low and high R:FR ratios in the dark (Fig. 7). Here, the expression of TaMYC4 was down-regulated under low R:FR ratios (far-red light-enriched environment), and expression of TaMYC5 was down-regulated under high R:FR ratios (red light-enriched environment), indicating that these two genes might be regulated by other crosstalk pathways in wheat line BS366. In coi1 mutants, the expressions of JA biosynthetic gene (e.g.  

![Figure 8](image_url)  
**Fig. 8** Relative expression of TaMYC genes under phytohormone treatments. The error bars indicate the standard deviation obtained from three replications. Wheat actin gene is used as the inner reference.

![Figure 9](image_url)  
**Fig. 9** Relative expression of TaMYC genes under abiotic stresses. The error bars indicate the standard deviation obtained from three replications. Wheat actin gene is used as the inner reference.
AOC1), signaling gene (JAZ1 and MYC2), and wound response (VSP1) genes were attenuated, suggesting that FR light is a positive regulator of JA-responsive gene expression [13]. In this study, TaMYC genes showed different expression patterns under FR or R light-enriched environments, indicating they might differentially regulate different branches of the JA signaling pathway.

Many recent studies have indicated that miRNAs are involved in anther development and male sterility [19]. To further understand the roles of TaMYCs, the interaction relationship between TaMYCs and wheat miRNAs were predicted. Totally, seven TaMYCs were targeted by 12 tae-miRNAs, including taemiR164 and taemiR167, which play important roles in plant growth and development (Fig. 10). In plants, miR164 targeted genes participate in various physiological and biochemical processes during plant development and in response to biotic/abiotic stress [31, 32]. For example, miR164 is involved in age-dependent cell death in Arabidopsis leaves by cleaving ORE (A NAM transcription factor) [33]. Plants with mutated miR164-CUC1 and miR164-CUC2 exhibit multiple phenotypes, such as leaf shape and polarity defects, extra petals, missing sepals, and reduced fertility [34, 35]. In addition, miR164 can also be regulated by light, and its expression was up-regulated under UV-B radiation treatment in maize [36]. In the present study, TaMYC6 responded to red/far-red light stimulation, hormone treatment, low temperatures stress, and drought stress, and might be targeted by miR164 (Fig. 10). In Arabidopsis, miR167 targeting Auxin Response Factor 6 (ARF6), and ARF8, which regulates jasmonate biosynthesis by inhibiting downstream genes, regulates pollen development [37]. Wang et al. (2019) demonstrate that tae-miR167, can induce male sterility and reduce the expression levels of AtARF6 and AtARF8 as well as reduce the content of JA and IAA in transgenic Arabidopsis [38]. One study shows that miR167 expression is upregulated in the light and downregulated in darkness, suggesting that miR167 may be regulated by light or the circadian clock [39]. Here, the results indicate that miR167 may interact with TaMYC3 (Fig. 10). With an experiment under MeJA treatment (Fig. 6), it was speculated that TaMYC3 might be a core factor in JA-light crosstalk, which needs to be verified by further experiments.

**Conclusions**

In this study, a comprehensive overview of the MYC gene family in wheat, including gene structures, phylogenetic relationships, and expression profiles, was provided. The roles of TaMYCs in response to abiotic stresses and light quality conversion were preliminary revealed. Moreover, our results provided insights into the crosstalk between MeJA signaling and light signaling in PTGMS wheat line BS366.

**Methods**

**Plant materials, growth conditions, and sample collection**
Wheat PTGMS line BS366 (winter wheat) were planted in the experimental fields in Beijing (China, N 39°54′, E 116°18′) and managed conventionally.

For tissue-specific expression analysis, wheat seedlings were grown until reaching the heading stage in experimental fields. Root, stem, leaf, petal, pistil, stamen, and glume of wheat were collected for tissue-specific expression analysis. For abiotic stresses, two-week-old wheat seedlings were cultured in the thermostatic artificial climate chamber (CLC-BIV-M/CLC404-TV, MMM, Germany) (20 °C, 12 h day/12 h night cycle). For low temperatures stress, seedlings were placed in an incubator at 10 °C (12 h day/12 h night cycle). For salinity and drought stresses, seedlings were treated with 200 mmol/L NaCl solution and 20%...
PEG 6000 (~ 0.5 MPa), respectively. For hormone treatments, seedlings were sprayed with 100 mmol/L ABA, 50 mmol/L IAA, or 100 mmol/L GA, with water as the control. Leaf tissue was collected from seedlings after 0, 4 and 12 h of stress treatment.

For effect of exogenous MeJA analysis, anthers of seedlings planted in experimental fields were treated with 0, 2 and 4 mmol/L MeJA solution at the heading stage. This experiment was carried out at the same time point within 5 days. Then collected at the anthers to investigate the effect of exogenous MeJA on the expression patterns of MYCs.

For effect of light quality conversation, four-leaf stage seedlings cultured in experimental fields were transferred into an artificial climate incubator with a 12-h photoperiod at a light intensity of 600 μmol/(m²*s) using fluorescent lamps. Night broken was performed at middle night (ZT = 18 h) using red (λ = 660 nm, 50 μmol/(m²*s)) and far-red light (λ = 731 nm, 40 μmol/(m²*s)) for ten days. Anthers were collected to determine the effect of conversion between red and far red lights on TaMYCs expression patterns. All samples were rapidly frozen in liquid nitrogen and stored at −80°C.

Identification of the MYC gene family in wheat

The genome sequence data and the annotation information of wheat (Chinese spring) were obtained from the Ensembl Plants database (http://plant.ensembl.org/index.html). MYC protein data of Arabidopsis thaliana (At) and Oryza sativa (Os) were downloaded from TIAR (http://www.Arabidopsis.org/) and TIGR (http://www.jcvi.org/). The hidden Markov models (HMM) of MYC protein (Pfam accessions: PF14215 and PF00010) were downloaded from the Pfam database (http://pfam.xfam.org/) [40], and were used as queries to search for potential MYC proteins in the wheat protein data sets by using HHMER3.0 [41] with an E-value cutoff of 1.0E-05. Subsequently, the nucleotide and genomic sequences of each TaMYC gene copy was confirmed based on the database accession number of protein. In order to confirm conserved domains of MYC, candidate protein sequences were subjected to online domain analysis program NCBI–CDD (https://www.ncbi.nlm.nih.gov/cdd/), and SMART (http://smart.embl-heidelberg.de/).

Naming scheme of wheat MYC gene family

MYC gene copies isolated in this study were defined as TaMYC. The different copies of same TaMYC gene in A, B, and D sub-genomes were clustered based on the phylogenetic results. The order of each TaMYC gene was decided based on their locations on A, B, and D wheat chromosomes and the clustering relationship on the cladogram.

Chromosomal locations and synteny analysis

Positional information of TaMYC genes were collected based on the genome annotation information. The synteny analysis of TaMYC genes was performed by using the whole genome synteny block data, which was available in the Plant Genome Duplication Database (http://chibba.agtec.uga.edu/duplication/) [42]. The visualization of chromosomal locations of TaMYC gene family was carried out by using Circos-0.69 (http://circos.ca/) [43].

Physicochemical characteristics and cis-elements analysis

Protein sequence length, theoretical isoelectric point and molecular weight of TaMYC proteins were predicted by using the ExPaSy online tool (http://www.expasy.org/). Subcellular localization were predicted by using the WoLEPSORT online tool (http://www.genscript.com/wolf-psort.html). To investigate putative cis–acting regulatory elements in the promoter regions of TaMYC genes, 1500 base pair genomic DNA sequences upstream of the initiation codon were retrieved and screened against the Plant CARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/) [44].

Structural analysis of TaMYC genes and proteins

The full-length coding sequences (CDS) and genomic sequences of the TaMYC genes were collected from wheat reference genome database (IWGSC; https://www.wheatgenome.org/). The structure analysis of TaMYC genes were performed via GSDS2.0 (http://gsds.cbi.pku.edu.cn/) [45]. Conserved motifs of TaMYC proteins were analyzed using the online program MEME [46].

Multiple sequence alignment and phylogenetic tree construction

Multiple alignment of MYC protein sequences of wheat and other species (O. sativa and A. thaliana) was performed by using DNAMAN (ver. 6.0) with default parameters. An unrooted phylogenetic tree was constructed by using MEGA7.0 [47] with the neighbor–joining (NJ) method (1000 bootstrap trials, the Poisson model) based on the results of multiple alignment.

Expression analysis of TaMYC genes

Total RNA extraction, first-strand cDNA synthesis and Quantitative real-time PCR (qRT-PCR) was performed according to Bai et al. (2018) [2]. The data were analyzed using the 2−ΔΔCt method [48]. Each experiments were replicated three times. The primers used in this study were listed in Additional file 4: Table S1. Wheat actin gene (Genbank: AB181991) was used as the inner reference.

miRNA targeting prediction of the TaMYC gene family

To investigate whether miRNA interacts with TaMYC genes, the known and studied miRNA sequences of...
wheat were collected from miRbase and subjected to online psRNATarget.

Supplementary information
Supplementary information accompanies this article at https://doi.org/10.1186/s12864-019-6373-y.

Additional file 1: Figure S1. Chromosomal localizations and syntenic relationships among TaMYC genes in Triticum aestivum, T. urartu and Ae. Tauchii. Lines in grey indicate tandem duplication. Lines in blue, green and orange indicate segmental duplication

Additional file 2: Figure. S2. Consensus sequence and logos of motifs from wheat MYC proteins

Additional file 3: File S1. Promoter sequences of MYC gene copies

Additional file 4: Table S1. The primers used in this study

Additional file 5: Table S1. Numbers of cis-regulatory elements in the upstream promoter regions of TaMYC genes

Additional file 6: Table S4. miRNA targeting prediction of TaMYC gene family

Additional file 7: Table S4. Segmental duplication of TaMYC genes

Abbreviations
ABA: Abscisic acid; GA: Gibberellin; IAA: Indole-3-acetic acid; MeJA: Methyl jasmonate; PTGMS: Photoperiod-Temperature sensitive Genic Male Sterile

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Authors’ contributions
JB, YY, LZ and CZ designed the study. YY, LG and JB performed the experiments, analyzed the data, and drafted the manuscript. ZL, HG, XG and WD assisted with bioinformatics analysis and aided in writing the manuscript. SY, HG, XG and FZ aided in performing the experiments.

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Availability of data and materials
The data sets supporting the results of this article are included within the article and its additional files.

Ethics approval and consent to participate
PTGMS wheat line BS366 seeds were provided by Beijing Engineering and Technology Research Center for Hybrid Wheat.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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References
1. Schweizer F, Fernández-CP, Zander M, Díez-Díaz M, Fonseca S, Glauser G, Lewsey MG, Ecker JR, Solano R, Raymond P. Arabidopsis basic helix-loop-helix transcription factors MYC2, MYC3, and MYC4 regulate glucosinolate biosynthesis, insect performance, and feeding behavior. Plant Cell. 2013; 25(9):3117–32.
2. Bai JF, Wang YK, Wang P, Yuan SH, Gao JG, Duan WJ, Wang N, Zhang FT, Zhang WJ, Qin MY, et al. Genome-wide identification and analysis of the COI gene family in wheat (Triticum aestivum L.). BMC genomics. 2018;19(1):754.
3. Chini A, Boter M, Solano R. Plant oxylipins: COI1/JAZ5/MYC2 as the core jasmonic acid-signalling module. FEBS J. 2009;276(17):4682–92.
4. Pauwels L, Barbero GF, Geerinck J, Tilleman S, Grunewald W, Perez AC, Chico JM, Bossche RV, Sewell J, Gil E, et al. NINJA connects the co-repressor TOPLESS to jasmonate signalling. Nature. 2010;464(7289):788–91.
5. Cheng Z, Sun L, Qi T, Zhang B, Peng W, Liu Y, Xie D. The bHLH transcription factor MYC3 interacts with the jasmonate ZIM-domain proteins to mediate jasmonate response in Arabidopsis. Mol Plant. 2011;4(2):279–88.
6. Fernandez-Calvo P, Chini A, Fernandez-Barbera G, Chico JM, Gómez-Ibáñez S, Geerinck J, Eeckhoudt D, Schweizer F, Godoy M, Franco-Zorrilla JM. The Arabidopsis bHLH transcription factors MYC3 and MYC4 are targets of JAZ repressors and act additively with MYC2 in the activation of jasmonate responses. Plant Cell. 2011;23(2):701.
7. Lorenzo O, Chico JM, Sanchez-Serrano JJ, Solano R. JASMONATE-INSENSITIVE1 encodes a MYC transcription factor essential to discriminate between different jasmonate-regulated defense responses in Arabidopsis. Plant Cell. 2004;16(7):1938–50.
8. Dombrecht B, Xue GP, Sprague SJ, Kirkegaard JA, Ross JJ, Reid JB, Pitt GP, Sewelam N, Schenk PM, Manners JM, et al. MYC2 differentially modulates diverse jasmonate-dependent functions in Arabidopsis. Plant Cell. 2007;19(7):2225–45.
9. Chico J, Fernández-Barbera G, Chini A, Fernández-Calvo P, Díez-Díaz M, Solano R. Repression of jasmonate-dependent defenses by shade involves differential regulation of protein stability of MYC transcription factors and their JAZ repressors in Arabidopsis. Plant Cell. 2014;26(5):1967–80.
10. Foita KM, Marunich SA. Green light: a signal to slow down or stop. J Exp Bot. 2007;58(12):3099.
11. Martínez-García JF, Galstyan A, Salla-Martret M, Cifuentes-Esquível N, Galleni M, Bou-Torrent J. Regulatory components of shade avoidance syndrome. Adv Bot Res. 2010;53:65–116.
12. Kazan K, Manners JM. The interplay between light and jasmonate signalling during defence and development. J Exp Bot. 2011;62(12):4087–100.
13. Robson F, Okamoto H, Patrick E, Harris SR, Wasternack C, Breakley C, Turner JG. Jasmonate and phytochrome a signalling in Arabidopsis wound and shade responses are integrated through JAZ2 stability. Plant Cell. 2010;22(4):1143–60.
14. Yadav V, Mallappa C, Gangappa SN, Bhata S, Chattopadhyay S. A basic helix-loop-helix transcription factor in Arabidopsis, MYC2, acts as a repressor of blue light-mediated photomorphogenic growth. Plant Cell. 2005;17(7):1953–66.
15. Gangappa SN, Chattopadhyay S, MYC2, a bHLH transcription factor, modulates the adult phenotype of SPA1. Plant Signal Behav. 2010;5(12):1650–2.
16. Abe H, Usao T, Ito T, Seki M, Shinozaki K, Yamaguchi-Shinozaki K. Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signalling. Plant Cell. 2003;15(3):63–78.
17. Song S, Huang H, Gao H, Wang J, Wu D, Liu X, Yang S, Zhao Q, Li C, Qi T, et al. Interaction between MYC2 and ETHYLENE INSENSITIVE3 modulates antagonism between jasmonate and ethylene signaling in Arabidopsis. Plant Cell. 2010;22(4):1143–60.
18. Wang Y, Qiao L, Bai J, Wang P, Duan W, Yuan S, Yuan G, Zhang F, Zhang L, Zhao C. Genome-wide characterization of JASMONATE-ZIM DOMAIN transcription repressors in wheat (Triticum aestivum L.). BMC Genomics. 2017;18(1):152.
19. Bai JF, Wang YK, Wang P, Duan WJ, Yuan SH, Sun H, Yuan GL, Ma JX, Wang N, Zhang FT, et al. Uncovering male fertility transition responsive miRNA in a wheat photo-thermosensitive genic male sterile line by deep sequencing and degradation analysis. Front Plant Sci. 2017;8:1370.
20. Wu Y, Zhe Z, Ma L, Chen M. The preferential retention of starch synthesis genes reveals the impact of whole-genome duplication on grass evolution. Mol Biol Evol. 2008;25(6):1003–6.
21. Gangappa SN, Prasad VB, Chattopadhyay S. Functional interconnection of MYC2 and SPA1 in the photomorphogenic seedling development of Arabidopsis. Plant Physiol. 2009;154(3):1210–9.

22. Turner TG, Ellis C, Devoto A. The jasmonate signal pathway. Plant Cell. 2002;14(14 Suppl):S153.

23. Shan X, Zhang Y, Peng W, Wang Z, Xie D. Molecular mechanism for jasmonate-induction of anthocyanin accumulation in Arabidopsis. J Exp Bot. 2009;60(13):3849–60.

24. Reinbothe C, Springer A, Samol I, Reinbothe S. Plant oxylipins: role of jasmonic acid during programmed cell death, defense and leaf senescence. FEBS J. J. E. Special Issue. 2010;276(17):4666–81.

25. Winkopp PJ, Kalya G. Cis-regulatory elements: molecular mechanisms and evolutionary processes underlying divergence. Nat Rev Genet. 2012;13(1):59–69.

26. Nakashima K, Ito Y, Yamaguchi-Shinozaki K. Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. Plant Physiol. 2009;149(1):88–95.

27. Kazan K, Manners JM. JAZ repressors and the orchestration of phytohormone crosstalk. Trends Plant Sci. 2012;17(1):22–31.

28. Liu SY, Qin ZL, Zhang FT, Zhao CP, Qing MA. Hormonal regulation of glume size control in Arabidopsis meristems. Development. 2004;19(1):4311–16.

29. Radhika V, Kost C, Mithofer A, Boland W. Regulation of extrafloral nectar secretion by jasmonates in lima bean is light dependent. Proc Natl Acad Sci U S A. 2010;107(40):17228–33.

30. Martinez-Garcia, J F, Gallstyan A, Salla-Martret M, Cifuentes-Esquivel N, Galleni M, Bou-Torrent J. Regulatory components of shade avoidance syndrome. Adv Bot Res. 2010;53:66–116.

31. Zheng L, Zhang X, Zhang H, Gu Y, Huang X, Liu H, Zhang J, Hu Y, Li Y, Yu G, Liu Y, Lawson SS, Huang Y. The miR164-dependent regulatory pathway in developing maize seed. Molecular genetics and genomics : MGG. 2019;294(2):501–17.

32. Fang Y, Xie K, Xiong L. Conserved miR164-targeted NAC genes negatively regulate drought resistance in rice. J Exp Bot. 2014;65(8):2119–30.

33. Kim JH, Woo HR, Kim J, Lim PO, Lee IC, Choi SH, Hwang D, Nam HG. Trifurcate feed-forward regulation of age-dependent cell death involving miR164 in Arabidopsis. Science. 2009;323(5917):1053–7.

34. Laufs P. MicroRNA regulation of the CUC genes is required for boundary size control in Arabidopsis meristems. Development. 2004;131(1):431–22.

35. Mallory AC, Dugas DV, Bartel DP, Bartel B. MicroRNA regulation of NAC-domain targets is required for proper formation and separation of adjacent embryonic, vegetative, and floral organs. Curr Biol. 2004;14(12):1035–46.

36. Nakashima K, Ito Y, Yamaguchi-Shinozaki K. Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. Plant Physiol. 2009;149(1):88–95.

37. Kazan K, Manners JM. JAZ repressors and the orchestration of phytohormone crosstalk. Trends Plant Sci. 2012;17(1):22–31.

38. Liu SY, Qin ZL, Zhang FT, Zhao CP, Qing MA. Hormonal regulation of glume size control in Arabidopsis meristems. Development. 2004;19(1):4311–16.

39. Radhika V, Kost C, Mithofer A, Boland W. Regulation of extrafloral nectar secretion by jasmonates in lima bean is light dependent. Proc Natl Acad Sci U S A. 2010;107(40):17228–33.

40. Martinez-Garcia, J F, Gallstyan A, Salla-Martret M, Cifuentes-Esquivel N, Galleni M, Bou-Torrent J. Regulatory components of shade avoidance syndrome. Adv Bot Res. 2010;53:66–116.

41. Zheng L, Zhang X, Zhang H, Gu Y, Huang X, Huang H, Liu H, Zhang J, Hu Y, Li Y, Yu G, Liu Y, Lawson SS, Huang Y. The miR164-dependent regulatory pathway in developing maize seed. Molecular genetics and genomics : MGG. 2019;294(2):501–17.

42. Fang Y, Xie K, Xiong L. Conserved miR164-targeted NAC genes negatively regulate drought resistance in rice. J Exp Bot. 2014;65(8):2119–30.

43. Kim JH, Woo HR, Kim J, Lim PO, Lee IC, Choi SH, Hwang D, Nam HG. Trifurcate feed-forward regulation of age-dependent cell death involving miR164 in Arabidopsis. Science. 2009;323(5917):1053–7.

44. Laufs P. MicroRNA regulation of the CUC genes is required for boundary size control in Arabidopsis meristems. Development. 2004;131(1):431–22.

45. Mallory AC, Dugas DV, Bartel DP, Bartel B. MicroRNA regulation of NAC-domain targets is required for proper formation and separation of adjacent embryonic, vegetative, and floral organs. Curr Biol. 2004;14(12):1035–46.

46. Casati P. Analysis of UV-B regulated miRNAs and their targets in maize leaves. Plant Signal Behav. 2013;8(10):e26758.

47. Krzywinski M, Schein J, Birol I, Connors J, Gascoyne R, Horsman D, Jones SJ, Marra MA. Circos: an information aesthetic for comparative genomics. Genome Res. 2009;19(9):1639–45.

48. Livak KJ, Schmittgen TD. Analysis of relative gene expression data using real-time quantitative PCR and the 2−(−ΔΔCT) Method. 2001;8(4):503–12.

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