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Genome Wide Identification, Characterization, and Expression Analysis of YABBY-Gene Family in Wheat (*Triticum aestivum* L.)

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Abstract: The small YABBY plant-specific transcription factor has a prominent role in regulating plant growth and developmental activities. However, little information is available about YABBY gene family in *Triticum aestivum* L. Herein, we identified 21 *TaYABBY* genes in the Wheat genome database. Then, we performed the conserved motif and domain analysis of *TaYABBY* proteins. The phylogeny of the *TaYABBY* was further sub-divided into 6 subfamilies (YABBY1/YABBY3, YABB2, YABBY5, CRC and INO) based on the structural similarities and functional diversities. The GO (Gene ontology) analysis of *TaYABBY* proteins showed that they are involved in numerous developmental processes and showed response against environmental stresses. The analysis of all identified genes in RNA-seq data showed that they are expressed in different tissues of wheat. Differential expression patterns were observed in not only control samples but also in stressed samples such as biotic stress (i.e., *Fusarium graminearum* (F.g), *septoria tritici* (STB), Stripe rust (Sr) and Powdery mildew (Pm), and abiotic stress (i.e., drought, heat, combined drought and heat and phosphorus deficiency), especially at different grain development stages. All identified *TaYABBY*-genes were localized in the nucleus which implies their participation in the regulatory mechanisms of various biological and cellular processes. In light of the above-mentioned outcomes, it has been deduced that *TaYABBY*-genes in the wheat genome play an important role in mediating various development, growth, and resistance mechanism, which could provide significant clues for future functional studies.

Keywords: wheat (*Triticum aestivum* L.); YABBY; expression profile

1. Introduction

As a sessile organism, plants are exposed to various environmental stresses throughout their life cycle, which impair biochemical and physiological processes [1]. Among several abiotic stresses, heat, drought and salt stresses cause a huge loss in total yield. Therefore, it is of significance importance to identify and understand the underpinning characteristics of new sources of defense biomarker in common crops such as wheat to overcome annual yield losses.

Plant Transcription factor (TFs) regulates gene expression in response to various abiotic stresses [2,3]. Several TFs are plant-specific. The small YABBY (TFs) is a plant specific gene family that consists of two highly conserved DNA-binding domains: a helix-loop helix domain (YABBY) and (C2C2) zinc finger-like domain [4]. Further, in plants, it has been reported for to make a significant contribution to lateral organ development, and in adaxial-abaxial polarity [5–8]. The Arabidopsis has

been subdivided into 6-YABBY subfamilies with regulation role during different processes [5,9–11]. FILAMENTIOUS FLOWER (FIL/YAB1), YAB2, YAB3, YAB5, was associated with specific floral organs development and formation of vegetative tissues; however, CRABS CLAW (CRC) and INNER NO OUTER (INO) mainly participated in the formation of floral organs. Similar functions of YABBY-genes family were documented in tomato, antirrhinum and cabbage [12,13]. However, in monocot plants, such as maize, YABBY genes were identified in association with the initiation of lateral organs instead of determining cell fate, which is in contrast with the previously reported Arabidopsis study [14]. Further, the rice *OsYABBY1* and *DROOPING LEAF* (DL) was not connected with lateral organ development. However, they share the same sub-group with CRC and YAB2, respectively [15–17]. The *OsYABBY4* gene from FIL/YAB1 member showed potential role in vascular tissues [18], and also regulates plant height, via facilitating the gibberellin pathway [19]. YABBY-like gene *Fasiated* (fas) in tomato regulates the fruit size, development and carpel number [20,21]. The *GmFILA* gene from soybean showed linkage with prolonged flowering time, development, growth and enhanced immune response against stresses [22].

Wheat is an important cereal that is the staple food for more than 2.5 billion people globally. Beyond its nutritional and health benefits, wheat contributes substantially to food security by providing 20% of dietary calories and protein worldwide [23]. The previous research on YABBY gene is mostly dominated by its role in lateral organ development and cell fate. However, no information is available about its function in wheat.

In this study, we systematically investigated the YABBY gene family in wheat at the whole genome level. The abiotic stress and biotic stress provide us with an insight into information of specific members of YABBY-gene family in resistance response. The expression analysis at different tissue provides us with knowledge about its regulation role in different processes.

2. Material and Methods

2.1. Identification of YABBY-Genes in Wheat

We retrieved the protein sequences of YABBY genes from the Arabidopsis [24], and wheat [25], using the Hidden Markov Model (HMM). The extracted *Triticum aestivum* L. protein sequences were analyzed by using CD-search NCBI (<http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi>, <http://www.ebi.ac.uk/interpro/search/sequence/>) and SMART (<http://smart.embl-heidelberg.de/>) databases. Proteins that do not exhibit YABBY domain were excluded. The chemical properties of *TaYABBY* proteins were examined by using the ExPasy online server (<http://web.expasy.org/protparam/>). The CELLO2GO [26], online server was used to predict the subcellular location of *TaYABBY* genes.

2.2. Phylogenetic Tree, Digital Expression and Motif Analysis

The maximum likelihood phylogenetic tree was developed by using Mega (version 7.0) [27]. The YABBY genes conserved motif was predicted by using online MEME server (latest Version 4.12.0) (<http://meme-suite.org/tools/meme>). The Expression levels were analyzed at different stages in all available tissue in response to biotic and abiotic stresses. The RNA-seq data retrieved in transcripts per million (TPM) retrieved from expVIP wheat Expression Browser (<http://www.wheat-expression.com/>) [28,29], The biotic stresses comprised of *Fusarium graminearum* (F.g), Stripe rust (Sr) and Powdery mildew (Pm) pathogen, while abiotic stress consists of drought, heat and a combination of heat and drought applications. The complete details with the used abbreviations of the treatments and materials are provided in Supplementary sheet 4. To determine the regulation patterns of a given gene subjected to a stress, the ratio of the expression value under a treatment to the control was calculated. Ratios under a given treatment that were greater than or less than 1.0 indicated that gene expression was altered by the stress treatment, while a ratio equal to 1.0 indicated the gene expression was unaltered by that treatment [28]. The Hemi 1.0 (<http://hemi.biocuckoo.org/faq.php>) software tool was used to construct heat-map on.

2.3. Chromosomal Location and Protein-Protein Interaction of YABBY Genes in ARABIDOPSIS

The Ensemble plants ([ftp://ftp.ensemblgenomes.org/pub/plants/release-31/fasta/triticum_aestivum/](http://ftp.ensemblgenomes.org/pub/plants/release-31/fasta/triticum_aestivum/)) were used to obtain chromosomal location of identified *TaYABBY*-genes [28]. Further, the MAPDraw was used to map the physical location of *TaYABBY*-genes and further by considering their chromosomal order, nomenclature was done. Protein-protein interactions of *Arabidopsis* were analyzed by using the STRING online server (<http://string.embl.de>) (version. 10).

2.4. Gene Structure and Conserved Motif Analysis

Genomic and CDS sequences of *TaYABBY*-genes were used to develop an exon/intron map in the Gene structure Display server program (<http://gsds.cbi.pku.edu.cn/>) [30]. The online server MEME 4.11.3 (<http://meme-suite.org/tools/meme>) was used to find the conserved motifs in the YABBY proteins [31].

2.5. Gene Ontology and Cis-Elements Analysis of YABBY Genes

The Ensemble Plants (http://plants.ensemble.org/Triticum_aestivum) database was used to retrieve 1.5 Kb genomic DNA sequences upstream of the start codon (ATG) of each identified *TaYABBY* gene. Cis-regulatory elements for all the YABBY genes were performed by using the online PlantCARE (<http://bioinformatics.psb.ugent.be/webtools/plantcare/html/>) database. The GO ontology analysis of *TaYABBY* protein sequences was obtained from the Blast2GO program Ver.2.7.2 (<http://www.blast2go.com>) and the groups of GO classification (molecular functions, biological process, and cellular component) were recorded.

3. Results

3.1. Identification and Analysis of *TaYABBY*

In present study, the 21 *TaYABBY* proteins from wheat were retrieved through Ensemble Plants (http://plants.ensemble.org/Triticum_aestivum) database. All the genes were named based on their chromosome location as *TaYABBY1* to *TaYABBY7* (Table 1). Further, we observed that all the *TaYABBY* genes are located in the nucleus. Different other characters of identified *TaYABBY* proteins were also summarized such as molecular weight, accession number, and chromosomal coordinates.

Table 1. The gene and protein features of *TaYABBY*-gene family.

Putative Gene Name	Accession ID	Subfamily	Protein Length	MW	pI	Gravy	Subcellular Location
TaYABBY1-1A	TraesCS1A02G176300.1	YaBBY2	297	31404.47	8.62	−0.349	N
TaYABBY1-1B	TraesCS1B02G203800.1	YaBBY2	297	31444.45	8.62	−0.353	N
TaYABBY1-1D	TraesCS1D02G162600.1	YaBBY2	296	31280.33	8.62	−0.328	N
TaYABBY2-2A	TraesCS2A02G197200.1	INO	166	17846.33	5.62	−0.352	N
TaYABBY2-2B	TraesCS2B02G224700.1	INO	168	18102.65	5.64	−0.376	N
TaYABBY2-2D	TraesCS2D02G205100.1	INO	164	17758.29	5.92	−0.347	N
TaYABBY3-2A	TraesCS2A02G386200.1	YaBY3/YABY1	262	28473.22	8.14	−0.423	N
TaYABBY3-2B	TraesCS2B02G403100.1	YaBY3/YABY1	268	28855.63	6.74	−0.302	N
TaYABBY3-2D	TraesCS2D02G382700.1	YaBY3/YABY1	269	28955.71	6.74	−0.323	N
TaYABBY4-4A	TraesCS4A02G058800.1	CRC	200	22304.67	8.98	−0.532	N
TaYABBY4-4B	TraesCS4B02G245900.1	CRC	200	22334.70	8.98	−0.545	N
TaYABBY4-4D	TraesCS4D02G245300.1	CRC	200	22318.70	8.98	−0.531	N
TaYABBY5-5A	TraesCS5A02G025900.1	YaBBY5	207	22915.81	8.97	−0.537	N
TaYABBY5-5B	TraesCS5B02G025100.1	YaBBY5	207	22663.48	9.13	−0.514	N
TaYABBY5-5D	TraesCS5D02G033700.1	YaBBY5	204	22376.21	9.28	−0.500	N
TaYABBY6-6A	TraesCS5A02G371500.1	YaBBY5	144	16610.89	9.35	−0.724	N
TaYABBY6-6B	TraesCS5B02G373600.1	YaBBY5	186	21052.01	9.30	−0.510	N
TaYABBY6-6D	TraesCS5D02G380900.1	YaBBY5	185	20968.88	9.30	−0.551	N
TaYABBY7-7A	TraesCS6A02G237700.1	YaBY3/YABY1	250	26684.33	8.13	−0.196	N
TaYABBY7-7B	TraesCS6B02G266200.1	YaBY3/YABY1	250	26652.34	8.13	−0.167	N
TaYABBY7-7D	TraesCS6D02G220400.1	YaBY3/YABY1	250	26684.33	8.13	−0.196	N

3.2. Evolutionary Relationship of TaYABBY

The construction of maximum likelihood phylogenetic tree provided more knowledge about the evolutionary history of YABBY proteins from both Arabidopsis and wheat. Further, according to their phylogenetic evolution, YABBY genes members were subdivided into six subfamilies based on their similarity with Arabidopsis. Enlisted as; (1) CRC accounting three genes; (2) YAB2 also accounting three genes; (3) YABBY1/YABBY3 (six members); (4) YABBY5 reported a maximum of six members, whereas there were three available genes in the INO-sub-family. Shown in (Figures 1 and 2).

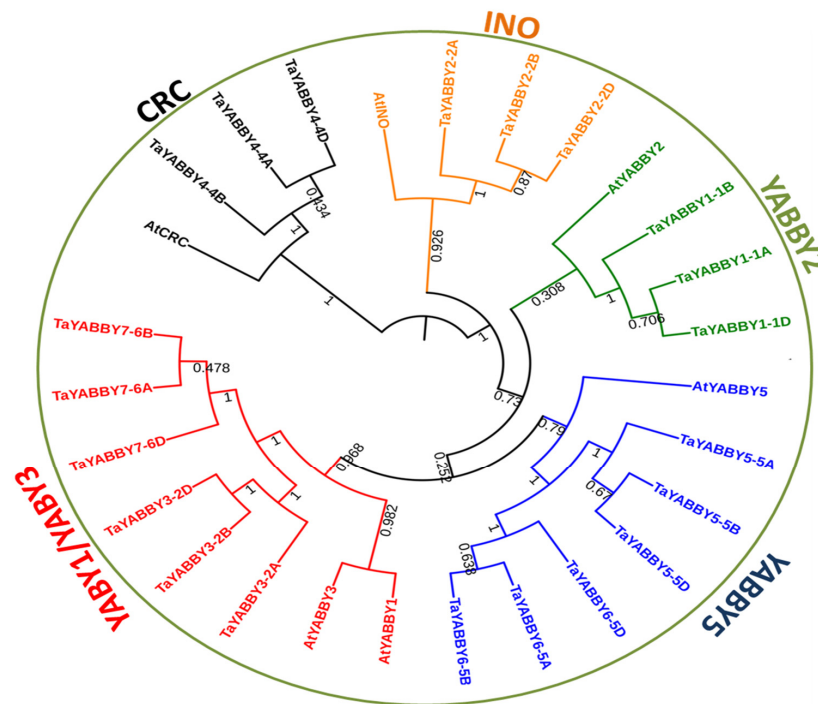


Figure 1. Phylogenetic tree of the YABBY genes between Arabidopsis and wheat based on characterized YABBY genes in Arabidopsis. Bootstrap values were calculated in 1000 replications by using MEGA 7.

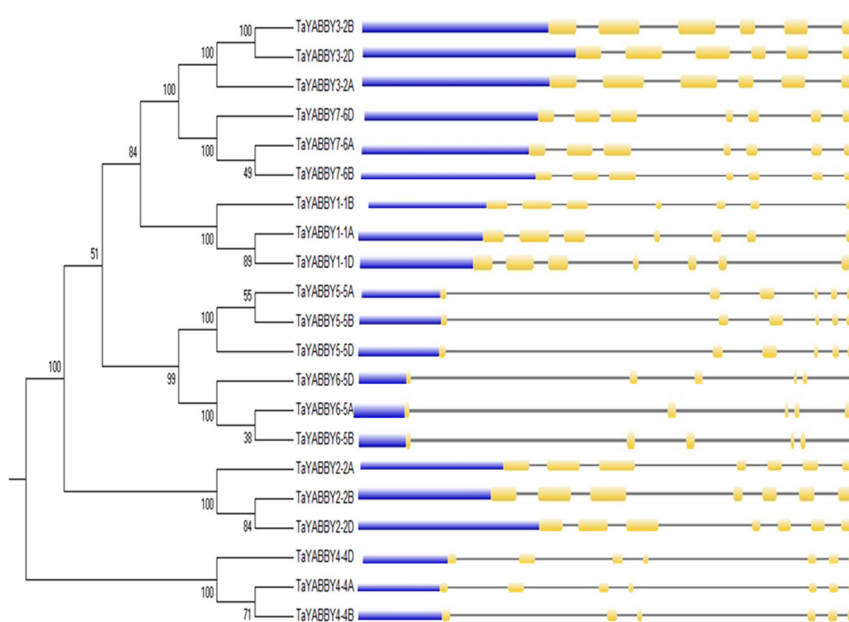


Figure 2. Phylogenetic relationships and gene structures of *TaYABBY* genes.

3.3. Conserved Motif Analysis, and Chromosomal Location of TaYABBY-Genes

Using MEME online server, ten conserved motifs were suited to explain the *TaYABBY* structure (Figure 3). Among the six subfamilies, YABBY5 and YABY1/YABY3 possessed more motifs than the other groups. The majority of the YABBY5 and YABY1/YABY3 members contain four or more motifs. The E-value was $b12$ for all identified *TaYABBY*-genes, given in (Table 2). *TaYABBY*-genes were distributed in hexaploid wheat across 1to 7 chromosomes. The maximum number of *TaYABBY* genes was six, mapped at chromosome 2 and 5, while chromosome 3 was missing. The chromosomes 1, 4, and 6 respectively reported same number of genes on homologue A, B and D chromosome (Figure 4). Further, we investigated the N-terminal zinc-finger-like C2C2 domain well known as DNA-binding domain and YABBY domain at the C terminal.

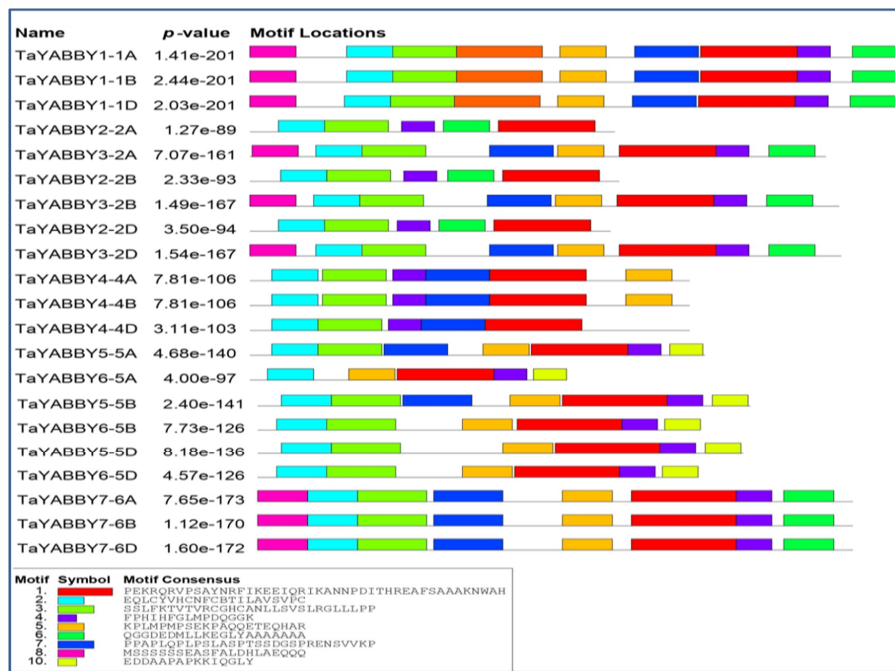


Figure 3. Schematic representation of the conserved motif of *TaYABBY*-genes.

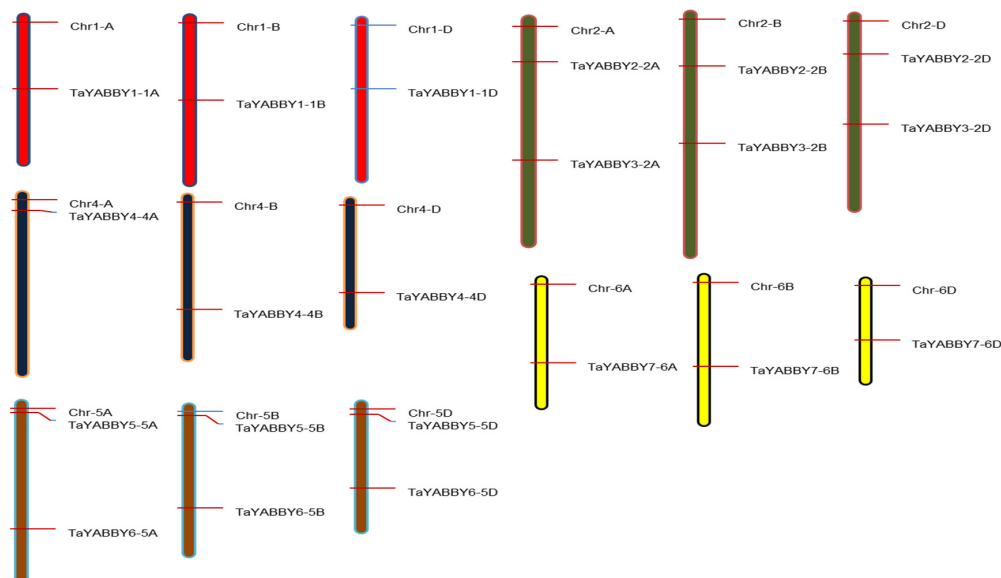


Figure 4. Chromosomal mapping of *TaYABBY* genes.

Table 2. Identified motif of *TaYABBY*-genes.

Motif	E-Value	Site	Width	Sequence	Motif-Logo
1	2.4e-783	21	44	PEKRQRVPSAYNRFIKEEIQRIKANNPDITHREAFSAAAKNWAH	
2	1.8e-305	21	21	EQLCYVHCNFCBTILAVSVPC	
3	6.4e-289	20	20	SSLFKTVTVRCGHCANLLSVSLRGLLLPP	
4	7.8e-116	21	21	FPHIHFGLMPDQGGK	
5	6.2e-065	17	17	KPLMPMPSEKPAQQETEQHAR	
6	3.3e-062	12	12	QGGDEDMLLKEGLYAAAAAAA	
7	1.3e-046	14	14	PPAPLQPLPLASPTSSDGSPRENSVVKP	
8	1.0e-042	9	9	MSSSSSEASFALDHLAEQQQ	
9	3.4e-028	3	3	TTTVAESAASAVTTTTSPPPAAAAHHGQFHYPSSLNL	
10	1.1e-020	6	6	EDDAAPAPKKIQGLY	

3.4. Gene Ontology of *YABBY*-Genes

We conducted gene ontology (GO) enrichment pathway analysis for the functional prediction of *TaYABBY*-genes. Three different types of functional predictions were done, namely: biological processes, molecular processes, and cellular processes (Figure 5). The in-silico biological prediction suggested that *TaYABBY*-genes are active in numerous biological processes such as response to environmental stimuli, developmental activities, metabolic activities, hormonal responses, and maturation. Additionally, the cellular prediction clarified that most of the *TaYABBY*-genes resided in the nucleus and could be involved in controlling many cellular activities. Meanwhile, the molecular prediction indicated that almost all the *TaYABBY*-genes have the DNA binding ability. Altogether, the obtained results clearly show that *TaYABBY* TFs are responsible for regulating plant growth by modulating the biological, molecular, and cellular activities.

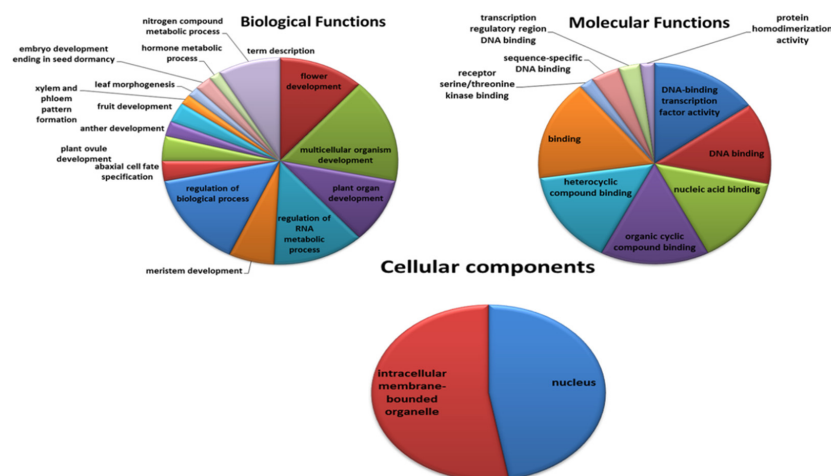


Figure 5. GO enrichment analysis of *TaYABBY* genes. The data represented as biological processes, cellular processes, and molecular processes.

3.5. Protein-Protein Interaction of *AtYABBY*

The *AtYABBY* protein predicted analysis revealed an array of other proteins which co-regulate with YAB5 and INO sub-families (Figure 6). The KANADI (KAN), a key regulator of leaf growth, abaxial identity and meristem formation from GRAPY-family of TFs showed interaction with our reference gene. The putative bit-score of 0.918 indicated that KAN has the optimum interaction ability

with our reference protein YAB5, which is a member of AtYABBY. ASSEMETRIC LEAVE (AS1) protein contributes to the regulation of the formation of flat symmetrical leaves in combination with many other genes [32]. The interactive bit-score was 0.861 with YAB5, and INO-members. Furthermore, the YAB5 and INO-members possessed both heterodimer and homodimers activity by showing interaction with several other TFs. The details are given in Table 3.

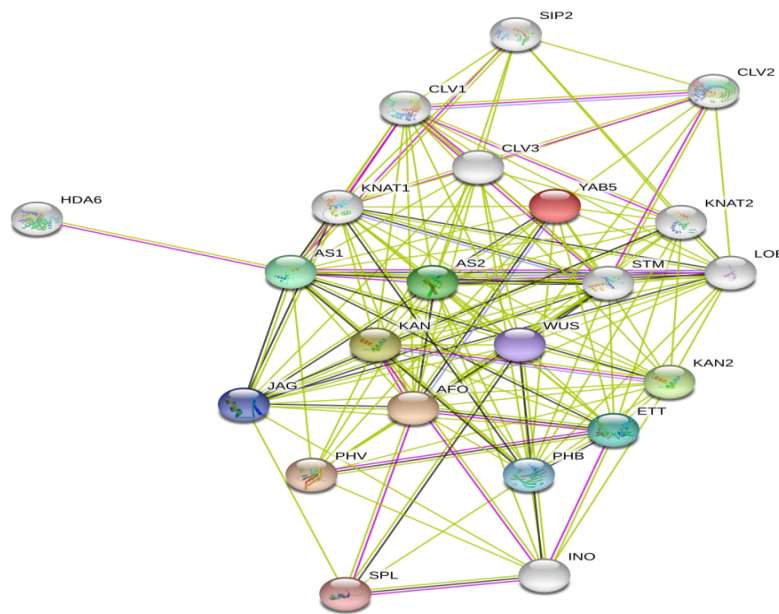


Figure 6. The prediction functional partners of AtYABBY-protein.

Table 3. Putative proteins from different families interacted with AtYABBY.

Protein Name	Gene Family	Putative Function
KANADI (KAN)	Homeodomin-like superfamily protein	Regulates organ polarity in Arabidopsis
ASYMMETRIC LEAVE (AS1)	ASYMMETRIC LEAVE Proteins	Transcription factor required for normal cell differentiation.
ARFs ETTIN (ETT)	B3 family protein	Auxin-responsible factor AUX/IAA-related
PHABULOSA (PHB)	Homeobox-leucine zipper family protein	Lipid-binding START domain-containing protein
JAGGED (JAG)	C2H2 and C2HC zinc fingers superfamily protein	Controls the morphogenesis of lateral organs
WUSCHEL (WUS)	Homeodomain-like superfamily protein	Transcription factor that plays a central role during early embryogenesis.
SPOROCTELESS (SPL)	Protein SPOROCTELESS	Transcription factor that plays a central role during embryogenesis
PHAVOLUTA (PHV)	Homeobox-leucine zipper family protein	Lipid-binding START domain-containing protein

3.6. Identified Cis-Regulatory Elements in TaYABBY Genes

The in-silico analyses of the TaYABBY-genes revealed that the upstream region of TaYABBY genes carried various hormonal, stress, and growth responsive cis-regulatory elements. In total, 49 cis acting elements, among them 12 cis-elements, were responsive to hormones and 38 were responsive to stress and growth related changes (Table 4). Hormonal responsive cis-elements such as TCA-element (Salicylic acid-responsive), AuxRR-core (involved in auxin responsiveness), ABRE (abscissic acid-responsive) and CGTCA-motif (MeJA responsive cis-element) were found in the majority of the TaYABBY-genes; meanwhile, a similar trend in P-box (gibberellin-responsive element)

and GARE-motif (gibberellin-responsive element) were also found in the upstream region of some genes. The MBS and ARE, which are drought-responsive, and anaerobic induction *cis*-elements were detected in almost all of the *TaYABBY*-genes followed by the ATCT-motif (Light responsive *cis*-regulatory elements), ACE, G-box and ATCT-motif, respectively. Some other growth and stress-responsive *cis*-regulatory elements namely TC-rich repeats (defense and stress responsive *cis*-element), CAT-box (Involved in meristem expression), were also recognized in the promoter region of *TaYABBY*-genes. The clustering of these *cis*-elements in the promoter region of *TaYABBY*-genes signifies their role in regulating gene expression under various environmental stimuli at different developmental stages.

Table 4. Types and number of *cis*-acting regulatory elements analysis involved in the growth, development, stress and hormonal response.

	Site Name	Function
Hormone	AuxRR-core	<i>cis</i> -acting regulatory element involved in auxin responsiveness
	ABRE	<i>cis</i> -acting element involved in the abscisic acid responsiveness
	P-box	gibberellin-responsive element
	TGA-element	auxin-responsive element
	CGTCA-motif	<i>cis</i> -acting regulatory element involved in the MeJA-responsiveness
	GARE-motif	gibberellin-responsive element
	TGACG-motif	<i>cis</i> -acting regulatory element involved in the MeJA-responsiveness
	TCA-element	<i>cis</i> -acting element involved in salicylic acid responsiveness
	CCAAT-box	MYBHv1 binding site
	GC-motif	enhancer-like element involved in anoxic specific inducibility
Stress and growth	AT1-motif	part of a light responsive module
	AE-box	part of a module for light response
	A-box	<i>cis</i> -acting regulatory element
	Box 4	part of a conserved DNA module involved in light responsiveness
	GCN4_motif	<i>cis</i> -regulatory element involved in endosperm expression
	I-box	part of a light responsive element
	MRE	MYB binding site involved in light responsiveness
	MSA-like	<i>cis</i> -acting element involved in cell cycle regulation
	Sp1	light responsive element
	ARE	<i>cis</i> -acting regulatory element essential for the anaerobic induction
	HD-Zip 1	element involved in differentiation of the palisade mesophyll cells
	MBSI	MYB binding site involved in flavonoid biosynthetic genes regulation
	CAAT-box	common <i>cis</i> -acting element in promoter and enhancer regions
	CAT-box	<i>cis</i> -acting regulatory element related to meristem expression
	chs-CMA2b	part of a light responsive element
	ATC-motif	part of a conserved DNA module involved in light responsiveness
	GATA-motif	part of a light responsive element
	ACE	<i>cis</i> -acting element involved in light responsiveness
	GA-motif	part of a light responsive element
	circadian	<i>cis</i> -acting regulatory element involved in circadian control
	TCCC-motif	part of a light responsive element
	TCT-motif	part of a light responsive element
	MBS	MYB binding site involved in drought-inducibility
	GT1-motif	light responsive element
	O2-site	<i>cis</i> -acting regulatory element involved in zein metabolism regulation

3.7. Digital Expression Profiling of TaYABBY-Genes in Various Tissues in Normal and in Response to Stresses, at Different Tissues

3.7.1. Reproductive and Vegetative Growth

Overall, all identified TaYABBY-genes were expressed in all the tested tissues which comprised of spikes, stem, roots, leaves, stems, spikes and grains (Figure 7 and Supplementary sheet 3). The one or three of the five tissues from total 25 investigated tissues and stages showed optimum expression level. For instance, the INO-members TaYABBY2-2B, and TaYABBY2-2A showed dominant transcript level in selected DTCS-tissues; however, low expression was recorded in GTE-tissues at 12 DPA (Days Post Anthesis). The total, six YABBY1/YABBY3 members showed varied expression at 12 DPA. For example, TaYABBY3-2D, TaYABBY7-6A, TaYABBY7-6B and TaYABBY7-6D expressed highly during grain development process (Figure 7). Other genes presented either low or no expression in any of the studied tissues. The CRC and YABBY5 members showed similar trends in GTE-tissues, but TaYABBY4-4A, TaYABBY4-4D, TaYABBY6-5A and TaYABBY6-5B displayed high expression level in GTE-tissues. However, all of the other genes were identified in relatively low or medium expression level.

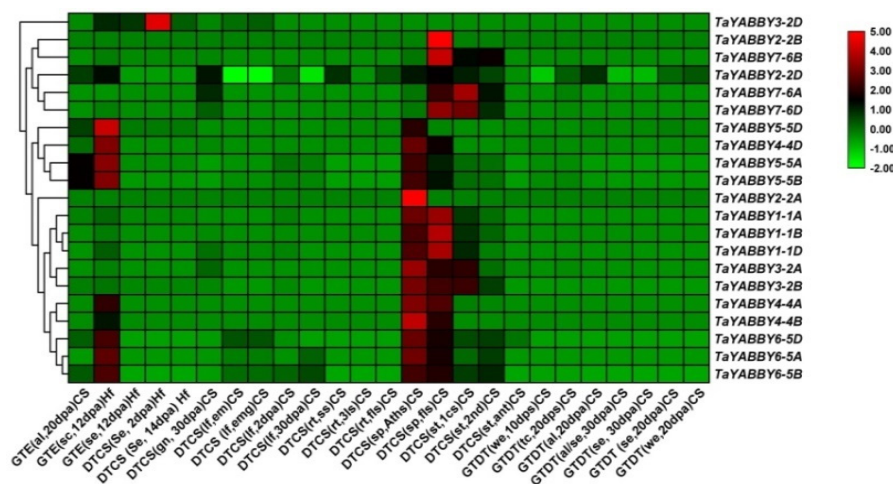


Figure 7. Heatmap of expression profiles for TaYABBY-genes in different tissue and stages. The color scale above represents expression values. Green and Red indicated the expression values increased and decreased, respectively, black indicated the expression was unregulated, GTE (Grain tissue specific expression) dpa (days post anthesis, DTC (Developmental time-course of Chinese Spring), GTDT (Grain tissue-specific developmental time-course). For further detail see supplementary sheet 4.

3.7.2. Biotic Stress

Plant treated with pathogens including Pm, Sr, and F. g were selected for expression analysis. Detail is given in Figure 8 and Supplementary sheet 2. We observed significant differences in the expression of control and stressed samples. For instance, the INO-member TaYABBY2-2B induced to a maximum of four-fold under FHB (Spk, fgi4d) in spikes, whereas TaYABBY2-2A increased three-fold in FHB (mi3h and mi50h). The YABBY2 members such as TaYABBY1-1A, TaYABBY1-1B, TaYABBY1-1D, and YABBY1/YABBY3-members such as TaYABBY3-2A, TaYABBY3-2B, and TaYABBY3-2D expression was unaffected in all the tested tissues under all the treatments (Figure 8). A similar trend was shown by TaYABBY7-6B and TaYABBY7-6D. Other genes either showed low or no fold-change in the majority of the studied tissues. All nine CRC and YABBY5 members displayed varied fold-change in the GTE tissues. In addition, in TaYABBY4-4A, TaYABBY4-4D, TaYABBY6-5A and TaYABBY6-5B, expression reached a maximum of five-fold in GTE-tissues. All the remaining genes plummeted significantly in grains and spikelet's tissue (Figure 8). Under FHB, almost all the genes were deduced except TaYABBY4-4B, TaYABBY4-4D and TaYABBY5-5D (Figure 8). Furthermore, under Sr and Pm, all the TaYABBY genes exhibited a down-regulated expression trend.

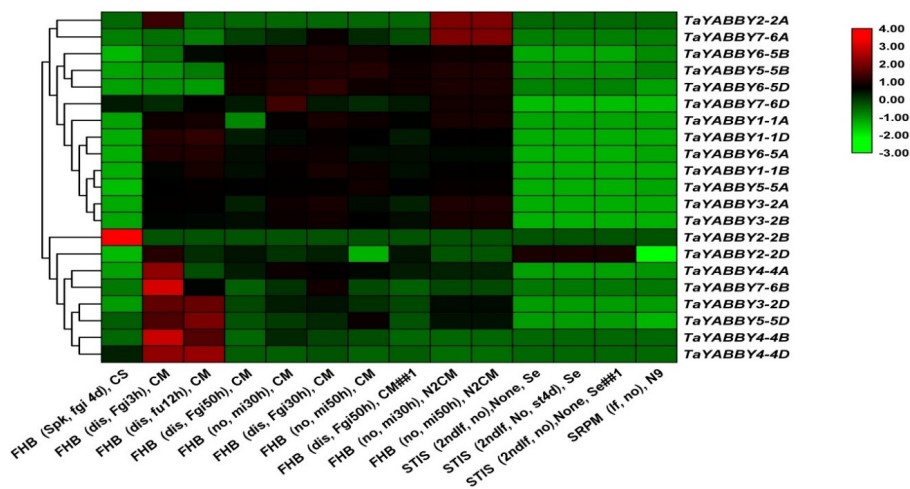


Figure 8. Heatmap of expression profiles for *TaYABBY*-genes under biotic stresses. The color scale above represents expression values. Green and Red indicated the expression values increased and decreased, respectively, black indicated the expression was unregulated. FHB (Fusarium head blight) inoculation at different time point, STS (Septoria tritici infected Seedlings), SRPM (If, no), N9 (Stripe rust and powdery mildew time course of infection in Seedlings) respectively. Further detail given in supplementary sheet 4.

3.7.3. Abiotic Stress

The expression of *TaYABBY*-genes under abiotic stresses such as drought (DH), and phosphorus deficiency (PS) at different stages and tissues were investigated (Figure 9 and Supplementary sheet 1). For example, the transcript levels of *TaYABBY2-2D*, *TaYABBY3-2D*, *TaYABBY4-4D*, *TaYABBY7-6B*, *TaYABBY3-2A*, and *TaYABBY4-4B* induced four-fold under DH-condition in 14 days seedlings. The same trend was shown by *TaYABBY6-5A*, *TaYABBY6-5D*, *TaYABBY2-2B*, and *TaYABBY3-2B* after 6 h under DH-stress in Chinese spring wheat (Figure 9). The expression values of *TaYABBY5-5A* and *TaYABBY5-5B* was one to six times lower than those of the controls in response to PS the expression values of *TaYABBY3-2D* was 2.50, respectively. For a total of 18 *TaYABBY*-genes, we observed down-regulated expression under DH and PS stresses (Figure 9).

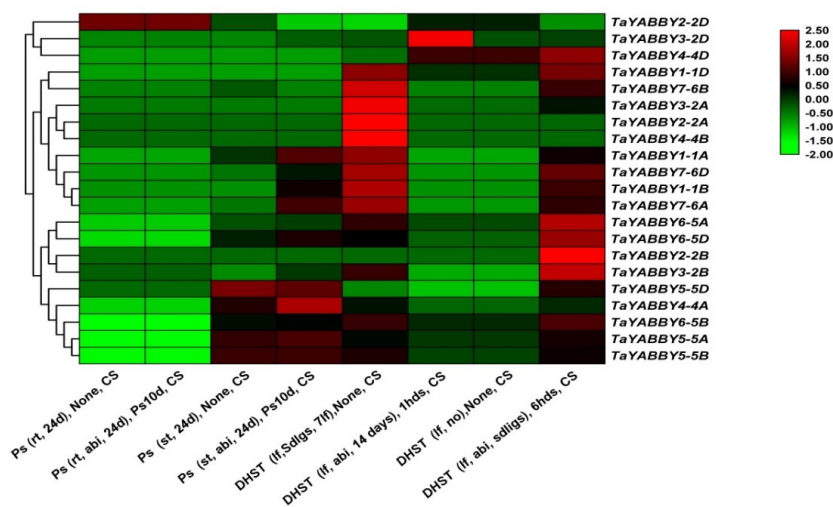


Figure 9. Heatmap of expression profiles for *TaYABBY*-genes under abiotic stresses. The color scale above represents expression values. Green and Red indicated the expression values increased and decreased, respectively, black indicated the expression was unregulated. PS (Phosphate starvation in Roots and shoots), DHST (Drought and heat stress time-course in Seedlings). Further detail given in supplementary sheet 4.

4. Discussion

Plants are sessile in nature and counter several kinds of environmental conditions throughout their life cycle, which could disturb their developmental processes. To cope with adverse conditions, they have developed a well-organized mechanism of stress-specific responses in specific tissues at specific stages [1]. The YABBY gene family is a plant specific transcription factor involved in flowering, seed developments, leaf and shoots development. Their response under different environmental stresses has been widely studied in rice, cotton, tomato, pineapple, Chinese cabbage and soybean [12,15,33–36]. However, relatively few studies have been conducted about YABBY genes in main cereal crops. In our present study, we performed a comprehensive analysis of YABBY genes in wheat. Our study will help to advance the knowledge and understanding of their functional characters in future studies.

4.1. YABBY Genes Are Widely Distributed in Wheat

The hexaploid wheat is an ideal example to study allopolyploidization evolution, developed through hybridization of two species, *Triticum* and *Aegilops* [37]. The genome-wide analysis of the YABBY-gene family revealed the presence of eight members in AtYABBY-genes (detail given in Supplementary sheet 5) and 21 TaYABBY-genes (Supplementary sheet 5). In comparison to most expanded group of YABBY genes observed in typical allotetraploid upland cotton [38], relatively fewer 17-genes were identified in soybean [2]. This is further given as 8, 12, 13 and 6 in rice, Pak-Choi, maize and Arabidopsis [9,15,39,40], respectively.

4.2. The Evolution of YABBY Proteins in Wheat

There are eight AtYABBY and 21 TaYABBY proteins, named AtYABBY1–AtYABBY8 and TaYABBY1 to TaYABBY7. To obtain an overall picture of the TaYABBY proteins and their relationships with those of AtYABBY, a phylogenetic tree was constructed, which divided all of the 21 TaYABBY-genes into six sub-families. Most of the sub-families contained different numbers of TaYABBY and AtYABBY-genes, indicating the large extent of conservation among the TaYABBY, and AtYABBY-genes. Two YABBY1/YABBY3 sub-family members were exhibited in AtYABBY-genes, and six TaYABBY-genes resided in this common clade, according to evolutionary relation suggesting that the proteins in these sub-families shared a last common ancestor. In this study, only YAB5 and Yab1/YAB3 sub-family members containing maximum numbers of TaYABBY protein grouped together with AtYABBY-genes. It seems that the YAB5 and YAB1/YAB3 subfamily has maximum sequence conservation among TaYABBY, and AtYABBY, which may be related to their conserved functions in different species. To further strengthen our knowledge about the presence of TaYABBY-genes, chromosomal mapping was done. The putative 21 TaYABBY genes were mapped at seven homologous chromosomes of wheat (Figure 4), TaYABBY3-2A, TaYABBY3-2B, and TaYABBY3-2D were reported at homologous chromosome 2. A similar trend was shown by TaYABBY6-5A, TaYABBY6-5B, and TaYABBY6-5D at chromosome 5.

According to this study, TaYABBY-proteins could be characterized as single light responsive called AT1-*cis*-element, and several other potential hem-binding sites. Our *cis*-regulatory elements analysis indicated that these putative regulators are able to make a contribution toward developmental and growth mechanisms, and are also identified in growth and stress responsive responses (Table 4) when combined with expression analyses (Figures 7–9).

4.3. TaYABBY-Genes Digital Expression Profiling under Normal and Stresses during Developmental Processes of *Triticum aestivum* L.

Previously available public transcription data and qRT-PCR analysis suggested that the YABBY gene family could make a significant contribution to regulating dynamic developmental programs, such as maintenance meristem organization in the spikelets, abaxial cell fate, and lamina expansion [2,41,42]. Here we presented a compressive investigation of TaYABBY gene expression levels at different tissue, and stages in wheat.

4.3.1. TaYABBY-Genes Crucially Regulated the Wheat Growth and Developmental Activities

FIL/YAB1 members reported as important regulator in cell fate, and abaxial domain of lateral organs [36,43–45]. Our findings are consistent with these results. For example, *TaYABBY1-1A*, *TaYABBY1-1B*, *TaYABBY1-1D*, members of YAB/YAB3 are highly expressed in selected DTCS (rt, rep, fls), CS and DTCS (sp, rep, fls), CS (Chinese spring wheat) in specific tissues of root and spikes during their reproductive period (Figure 7, Supplementary sheets 3 and 4). The YABBY2-members have been identified to specific differentiation of certain cell types in rice [15]. A similar trend was reported in our current study for *TaYABBY2-2A*, and *TaYABBY2-2B* showed maximum expression under selected DTCS (sp, rep, fls), CS (Figure 7). Previous studies have indicated the significant contribution of YAB3-members in leaf and petal tissues. Further, due to YAB3-member loss, its function resulted in narrow leaf [34,44], which signifies its role in modulating the organ structures.

4.3.2. Biotic Stresses

Biotic stresses such as FHB caused major devastation of wheat yield and quality by accumulating mycotoxins. The resistance mechanism in wheat against FHB is governed by cumulating effect of several genes [46]. We found that certain members of CRC, and YAB1/YAB3 such as “*TaYABBY2-2A*, *TaYABBY2-2B*, *TaYABBY7-6B* and *TaYABBY4-4B*” could be part of that resistance mechanism, as shown in Figure 8 and supplementary sheet 4. However, in other sub-families such as YABY1/YAB3 and YABBY5, members did not show clear fold-change against FHB stress. All genes expression was unaffected in response to powdery mildew inoculation, as seen in (Figure 8).

4.3.3. Abiotic Stresses

The understanding of the influence of changing climatic conditions has been a predominant avenue toward modern research advances. The underlying mechanism in systematic variation under combined influence of heat and drought is a complex and difficult processes. The current study utilized transcriptomic data of different tissues at different stages, as seen in Figure 9. The CRC-member of YABBY protein plays a key role in the most crucial and important phase of carpels developmental in a plant’s life cycle [42]. In this study, a maximum of four-fold induction in the transcript level of *TaYABBY4-4A*, *TaYABBY4-4B* and *TaYABBY4-4D* in leaves and root tissues under drought and heat stress. These results are concurrent with the previous findings of [10]. Thus, all these finding significantly provide important and crucial information for the role of *TaYABBY*-genes which could be used in further functional analysis of cereal crops. The widely available RNA-seq data in several studies collected by using next-generation sequencing technology could be used on non-model crops. The validation of RNA-Seq data by qRT-PCR has been done in plethora of previous experiments [7,47]. Furthermore, the well-known public transcriptomic database expVIP, which we used as a data source, contains RNA-seq data that has been validated by qRT-PCR [29,48–50].

5. Conclusions

A total of 21 *TaYABBY* family TFs were recognized and distributed into 6 subfamilies based on their domain and structural characteristics. Additionally, heat map analysis showed the expression of *TaYABBY* in different tissues. The expression under various abiotic stresses and biotic stress implied the potential role of *TaYABBY* genes in mediating the resistance of wheat. Moreover, the regulation of stress is a complex mechanism. Here, the in-silico analysis provided useful information for future functional studies in stress biology. Therefore, further research work is needed to elucidate the regulation and pathway mechanism of *TaYABBY* TFs in wheat.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4395/10/8/1189/s1>, sheet 1: Expression of wheat YABBY genes in response to abiotic stresses, sheet 2: Expression of wheat YABBY genes in response to biotic stresses, sheet 3: Expression patterns of wheat YABBY genes in normal conditions. Sheet 4: The details of the materials and treatments for the retrieved expression values (extracted from <http://www.wheat-expression.com/>), sheet 5: The YABBY gene IDs of Arabidopsis, and Wheat. The following are

available at supplementary detail (sheet 1–5): the (tpm) values of extracted data from wheatEXP online database and *Arabidopsis thaliana* gene ID with nomenclature name (Sheet 5) used in this study.

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