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Promoter Analysis and Expression Patterns of the YABBY Transcription Factor Family in Cassava (*Manihot esculenta*) under Various Environmental Conditions

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Abstract

The YABBY transcription factor (TF) family is a group of plant-specific proteins characterized by a unique structure comprised of a C2C2 zinc finger domain and a helix-loop-helix YABBY domain. These TFs play crucial roles in regulating various aspects of plant development, such as lateral organ formation and leaf polarity, as well as mediating responses to abiotic and biotic stresses. This study investigated the potential functions and expression profiles of 13 genes encoding the YABBY TF family in cassava (*Manihot esculenta*) under various stress conditions. Through a comprehensive analysis of promoter regions, we identified numerous *cis*-regulatory elements (CREs) associated with abiotic stress responses and phytohormone regulation. Specific CREs, such as low-temperature responsive elements and MYB recognize sites, were linked to cold and drought responses, respectively, suggesting their involvement in stress adaptation. RNA-Seq analysis under drought and PEG6000 treatments revealed significant transcriptional changes, with several YABBY genes being upregulated or downregulated, indicating their roles in drought tolerance and water use efficiency. Under biotic stress conditions, specifically cassava brown strike disease inoculation, YABBY genes exhibited diverse expression patterns, with notable downregulation of certain genes, suggesting their potential regulatory roles in stress responses. Taken together, these findings highlighted the diverse and critical functions of YABBY TFs in cassava's stress resilience and developmental processes.

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Keywords

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Introduction

Cassava, a starchy root crop native to South America, plays a crucial role in food security and agriculture, especially in tropical and subtropical regions (Olsen & Schaal, 1999; Guira *et al.*, 2017). It is a primary food source for over 800 million people globally, particularly in Africa, Asia, and Latin America, providing essential calories and nutrients (Li *et al.*, 2017; Malik *et al.*, 2020). Cassava cultivation is favored due to its remarkable ability to grow in poor soils and withstand harsh climatic conditions, including drought and low soil fertility (Gleadow *et al.*, 2016; Shan *et al.*, 2018). This resilience makes it a dependable staple crop in areas prone to adverse weather, contributing significantly to the livelihoods of smallholder farmers. Understanding the molecular mechanisms underlying cassava's stress responses is vital, as it can lead to improved breeding programs, enhance crop yields, and support sustainable agricultural practices (Okogbenin *et al.*, 2013; Turyagyenda *et al.*, 2013; Zhao *et al.*, 2015a). By studying these mechanisms, researchers can develop more resilient crop varieties, ensuring a more stable food supply and addressing food security challenges in regions vulnerable to climate change.

In higher plant species, the YABBY transcription factor (TF) is considered as a family of specific regulatory proteins characterized by a unique structure comprised of a C2C2 zinc finger domain and a helix-loop-helix YABBY domain (Finet *et al.*, 2016; Romanova *et al.*, 2021). These TFs have been reported to play crucial roles in regulating various aspects of plant development, including lateral organ development, leaf polarity, and reproductive organ formation (Shchennikova *et al.*, 2018; Zhang *et al.*, 2020). In addition to their developmental functions, YABBY TFs were also found to be involved in responding to environmental stresses (Liu *et al.*, 2022; Kong *et al.*, 2023; Hussain *et al.*, 2024). Recently, 13 members of the YABBY TF family, namely from MeYABBY01 to MeYABBY13, were surveyed in the recent cassava assembly (Vinh *et al.*, 2024). Investigating the expression levels of the YABBY TFs in cassava is essential to elucidate the molecular mechanisms underlying the plant's stress response. Understanding how YABBY genes are regulated under stress conditions can provide insights into cassava's resilience to adverse environmental factors, guiding the development of more robust and stress-tolerant cassava varieties through targeted breeding and genetic engineering efforts.

The aim of this study was to investigate the expression profiles of the genes encoding the YABBY TF family in cassava under adverse environmental conditions. We first analyzed the promoter regions to enrich the *cis*-regulatory elements (CREs). Next, three transcriptome databases were explored to access the expression patterns of genes encoding the YABBY TF family under abiotic and biotic stress conditions.

Materials and Methods

Data collection

Three types of sequences, encompassing coding DNA sequences, genomic DNA sequences, promoter sequences, and full-length protein sequences, of the 13 members of the YABBY TF family in cassava reported in the recent study (Vinh *et al*., 2024) were obtained from the newest cassava assembly (NCBI RefSeq assembly: GCF_001659605.2) (Bredeson *et al.*, 2016) available on Phytozome (Goodstein *et al.*, 2012) and NCBI.

Three RNA-seq datasets were obtained from GEO NCBI (Edgar *et al.*, 2002; Barrett *et al.*, 2013). These libraries included both biotic stress from cassava brown strike disease (CBSD) inoculation (GSE56467) (Patil *et al.*, 2015; Tomlinson *et al.*, 2018) as previously reported (Maruthi *et al.*, 2014) and abiotic stress conditions from a polyethylene glycol 6000 (PEG 6000) treatment (GSE93098) (Ding *et al.*, 2017) and drought stress (GSE98537) (Zhu *et al.*, 2020).

Promoter analysis

A 1000bp sequence upstream of the start codon was employed to identify the CREs as outlined in a previous study (Chu *et al.*, 2018). The PlantCARE website (Lescot *et al.*, 2002) was used to analyze the promoter regions of the genes. Several CREs were also manually

searched by using BioEDIT software (Hall, 1999). A list of two stress-responsive [LTRE (low-temperature responsive element) and MYBRS (MYB recognize site)] and six phytohormone-induced CREs [namely ABRE (abscisic acid-responsive element), TGACG-motif, P-box, TGA-box, TCA-element and CGTCA-motif] were explored as previously described (Abe *et al.*, 2003; Nakashima & Yamaguchi-Shinozaki, 2013; Chu *et al.*, 2018). The core sequences and putative functions of these CREs are provided in **Table 1**.

Transcriptomic analysis

We selected three microarray datasets available from GEO NCBI (Edgar *et al.*, 2002; Barrett *et al.*, 2013) to retrieve the transcriptional changes of the genes. Briefly, the GEO dataset GSE56467 explored the transcriptional response of cassava leaves infected with CBSD using an Illumina HiSeq 2000 (Maruthi *et al.*, 2014). The GEO dataset GSE93098 analyzed samples from different tissues (roots, folded leaves, fully expanded leaves, and bottom leaves) in response to a PEG 6000 treatment to simulate drought stress using an Illumina HiSeq 2000 (Ding *et al.*, 2017). The GEO dataset GSE98537 investigated the genetic regulation of drought-stress responses in cassava leaves using an Illumina HiSeq 2000 (Zhu *et al.*, 2020). The fold change was utilized to estimate the expression profile of the genes.

Data analysis

To estimate gene expression levels using fold-change in RNA-Seq, the fragments per kilobase of transcript per million mapped reads (FPKM) of each gene in the examined sample were explored. Differential expression analysis was performed using DESeq2 software (version 3.20) (Love *et al.*, 2014), which models the count data and estimates the fold change in gene expression between conditions. The fold change is calculated as the ratio of normalized expression levels (FPKM) between the two conditions. Significant differentially expressed genes were identified based on the fold-change and adjusted *P*-values, with upregulated genes showing a positive fold-change (fold-change ≥ 1.5) and downregulated genes showing a negative fold-change (fold-change ≤ -1.5).

Results and Discussion

Prediction of the *cis-regulatory* elements in the promoter regions of the YABBY transcription factor family

In order to investigate the potential function of the YABBY TF family in cassava, we performed a comprehensive analysis of the

Table 1. List of phytohormone-induced and stress-responsive *cis*-regulatory elements used in this study

#	Name of *cis*-regulatory element	Core sequence	Function	Reference
1	LTRE	CCGAAA	*Cis*-acting element involved in low-temperature responsiveness	(Abe *et al.*, 2003; Yamaguchi-Shinozaki & Shinozaki, 2005)
2	MYBRS	CAACTG or TAACTG	MYB binding site involved in drought-inducibility	(Maruyama *et al.*, 2012)
3	ABRE	CACGTG, ACGTG or TACGTG	*Cis*-acting element involved in ABA responsiveness	(Nakashima & Yamaguchi-Shinozaki, 2013)
4	TGACG-motif	TGACG	*Cis*-acting regulatory element involved in MeJA responsiveness	(Chu *et al.*, 2018)
5	P-box	GCCTTTTGAGT	Gibberellin responsive element	(Chu *et al.*, 2018)
6	TGA-box	TGACGTAA	Part of an auxin-responsive element	(Chu *et al.*, 2018)
7	TCA-element	CCATCTTTTT	*C*is-acting element involved in salicylic acid responsiveness	(Chu *et al.*, 2018)
8	CGTCA-motif	CGTCA	*Cis*-acting regulatory element involved in MeJA-responsiveness	(Chu *et al.*, 2018)

promoter regions based on various tools (Hall, 1999; Lescot *et al.*, 2002). As a result, a summary of the occurrences of CREs that were found in the promoter regions of genes encoding the YABBY TF family in cassava is provided in **Table 2**.

We found that one CRE involved in low-temperature responsiveness, namely LTTRE, was localized in the promoter regions of three genes, *MeYABBY03*, *MeYABBY05*, and *MeYABBY08*. Meanwhile, MYBRS (CRE involved in drought-inducibility) was recorded in the promoter regions of two genes, *MeYABBY03* and *MeYABBY06*. Our analysis suggested that these genes might be involved in cold and drought conditions.

Next, to hypothesize which genes encoding the YABBY TF family in cassava were regulated by phytohormones, the phytohormone-induced CREs were enriched. As expected, ABRE was found in the promoter regions of three genes, namely *MeYABBY05*, *MeYABBY06*, and *MeYABBY12*. Two CREs involved in the MeJA responsiveness, the TGACG-motif and CGTCA-motif, were found in the promoter regions of six genes, namely *MeYABBY01*, *MeYABBY02*, *MeYABBY06*, *MeYABBY08*, *MeYABBY10*, and *MeYABBY11*. Additionally, the P-box and TGA-box, two CREs involved in gibberellin and auxin responsiveness, were found in the promoter regions of *MeYABBY04* and *MeYABBY10*, respectively. A CRE involved in salicylic acid responsiveness, namely the TCA-element, was recorded in the promoter regions of four genes, namely *MeYABBY08*, *MeYABBY09*, *MeYABBY10*, and *MeYABBY13*.

Previously, the enrichment of stress-responsive and phytohormone-induced CREs was reported in the promoter regions of genes encoding YABBY TF families in higher plant species. In carrots, various CREs with distinct physiological and biological roles were identified in the promoter regions of genes encoding the YABBY TF family (Hussain *et al.*, 2024). Notably, ABRE was found in four YABBY genes, while five YABBY genes contained the TGACG element (Hussain *et al.*, 2024). Only one YABBY gene had the TCA-element associated with salicylic acid response, and another gene showed TC-rich repeats, indicating involvement in stress and defense, while MYBRS, responsive to drought, was present in three YABBY genes, and two YABBY genes contained LTRE, which responds to low

Table 2. Summary of the phytohormone-induced and stress-responsive *cis*-regulatory elements found in the promoter regions of the YABBY transcription factor family in cassava

#	Gene name	Stress-responsive *cis*-regulatory elements		Phytohormone-induced *cis*-regulatory elements					
		LTRE	MYBRS	ABRE	TGACG-motif	CGTCA-motif	P-box	TGA-box	TCA-element
1	*MeYABBY01*					+			
2	*MeYABBY02*					+			
3	*MeYABBY03*	+	+						
4	*MeYABBY04*						+		
5	*MeYABBY05*	+		+					
6	*MeYABBY06*		+	+	+				
7	*MeYABBY07*								
8	*MeYABBY08*	+			+	+			+
9	*MeYABBY09*								+
10	*MeYABBY10*				+			+	+
11	*MeYABBY11*					+			
12	*MeYABBY12*			+					
13	*MeYABBY13*								+

temperatures (Hussain *et al.*, 2024). Five YABBY genes showed the CGTCA motif, also involved in methyl jasmonic acid responsiveness, while the P-box, TATC box, and TCA element, related to gibberellin and salicylic acid responses, were each found in one YABBY gene (Hussain *et al.*, 2024). To explore the potential functions of YABBY genes in *Juglans regia* and *J. mandshurica*, the CREs in their upstream promoter regions were also examined (Liu *et al.*, 2022). The analysis identified the stress response elements of MBS, associated with drought stress, and LTR, related to low-temperature stress (Liu *et al.*, 2022). These findings indicated that YABBY genes may be involved in plant development, stress responses, and phytohormone responses in *J. regia* and *J. mandshurica* (Liu *et al.*, 2022). Furthermore, the promoter regions of the YABBY genes in *Platycodon grandiflorus* included various CREs (Kong *et al.*, 2023). Each YABBY gene featured light-responsive CREs, which were the most abundant, followed by several hormonal CREs (Kong *et al.*, 2023). Among them, *PgYABBY1* had the highest diversity of CREs, with 11 different types related to defense and stress responses, zein metabolism regulation, and endosperm expression (Kong *et al.*, 2023). *PgYABBY4* featured four types of CREs, with the occurrences of ABRE, while *PgYABBY5* and *PgYABBY6* each contained three CREs, including both light-responsive CREs and ABRE (Kong *et al.*, 2023).

Expression profiles of the YABBY transcription factor family under abiotic stress conditions

Cassava is recognized for its remarkable tolerance to abiotic stresses (Gleadow *et al.*, 2016; Shan *et al.*, 2018). Its resilience to drought, poor soil fertility, and high temperatures is attributed to several physiological and molecular mechanisms. Of interest to us, we expected that several YABBY genes would exhibit differential expression levels under drought stress. To assess the expression levels of genes encoding the YABBY TF family under water limitation in cassava, we analyzed two sets of RNA-Seq data related to drought (Zhu *et al.*, 2020) and PEG6000 treatments (Ding *et al.*, 2017).

Under drought conditions, genes encoding the YABBY TF family exhibited great transcriptional changes in treated leaf samples (**Figure 1**). Specifically, four genes, namely *MeYABBY05*, *MeYABBY06*, *MeYABBY09*, and *MeYABBY10*, were not responsive to the drought stress in leaf tissues (fold-change < 1.5-fold). We found that six genes, namely *MeYABBY01*, *MeYABBY03*, *MeYABBY04*, *MeYABBY08*, *MeYABBY11*, and *MeYABBY13*, were reduced (fold-change ≤ -1.5-fold) in drought-treated leaves. Among them, *MeYABBY03*, *MeYABBY11*, and *MeYABBY13* were noted to be strongly down-regulated in leaf samples under the drought treatment by -43.96, -35.49, and -262.66-fold, respectively. The significant reduction of these YABBY genes in drought-treated cassava leaves highlights their potential role in the plant's response to drought stress, suggesting their involvement in pathways that modulate adaptation to water scarcity. This dramatic downregulation could be a protective mechanism to reduce growth and conserve energy during drought conditions (Okogbenin *et al.*, 2013; Zhao *et al.*, 2015b). In contrast, our analysis proposed three up-regulated genes (fold-change ≥ 1.5-fold), namely *MeYABBY02*, *MeYABBY07*, and *MeYABBY12*. Among them, *MeYABBY02* and *MeYABBY12* were recorded to be highly induced in drought-treated leaves by 21.38 and 7.14-fold, respectively. The induction of certain YABBY genes in drought-treated cassava leaves indicated their potential involvement in the plant's adaptive response to water deficit. Upregulation of these genes suggested they may enhance drought tolerance by maintaining cellular homeostasis, activating protective mechanisms, and improving water use efficiency under drought conditions (Okogbenin *et al.*, 2013; Zhao *et al.*, 2015b).

Under the PEG 6000 treatment, genes encoding the YABBY TF family exhibited variable expression patterns in examined tissue samples (**Figure 2**). In root tissues, we found that only one gene, namely *MeYABBY01*, was reduced (-1.71-fold) in this sample at 24h after the treatment of PEG 6000. This gene was also down-regulated in bottom leaf tissues at 24h after the PEG treatment (-1.97-fold) and in PEG 6000-treated fully expanded leaves. *MeYABBY03* was

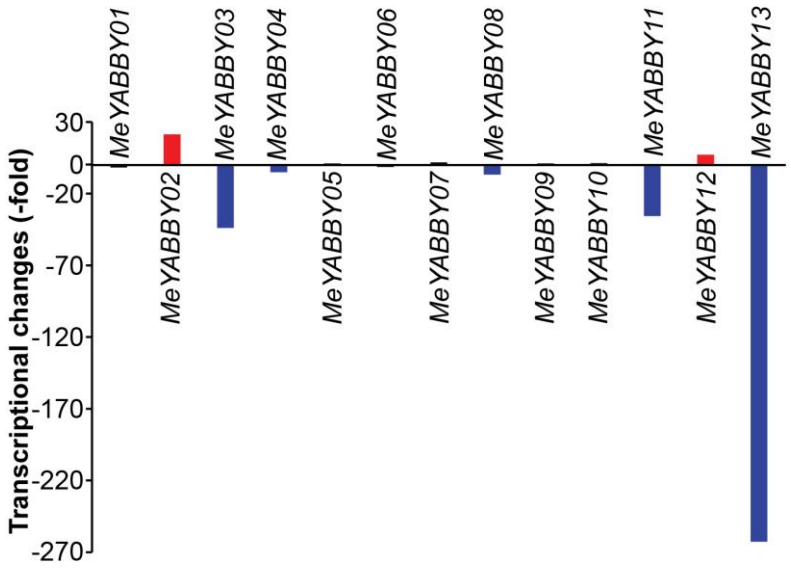

Figure 1. Transcriptional changes of genes encoding the YABBY transcription factor family in drought-treated leaves in cassava

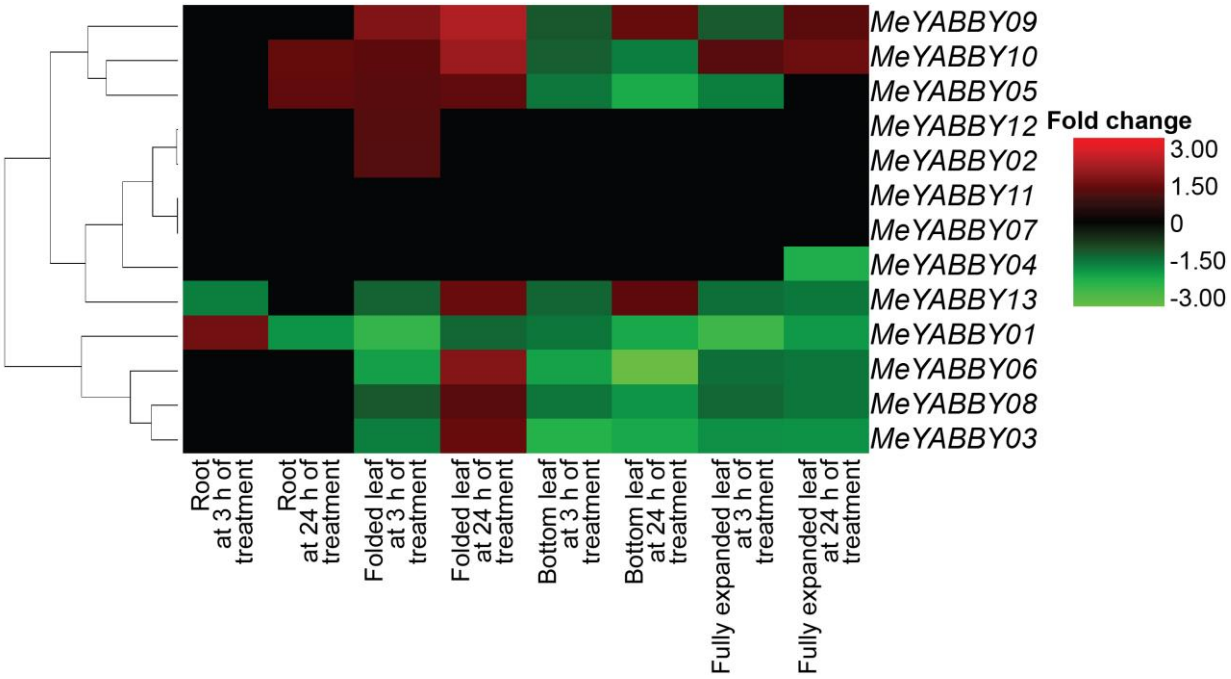

Figure 2. Transcriptional changes of genes encoding the YABBY transcription factor family in PEG 6000-treated root and leaf samples in cassava

reduced in both the treated bottom leaf and fully expanded leaf samples by -1.96-fold and -1.71-fold at 24h after the treatment, respectively, while two genes, *MeYABBY04* and *MeYABBY05*, were down-regulated in fully expanded leaves and bottom leaves by -2.05-fold and -1.98-fold, respectively. *MeYABBY08* was down-regulated in the PEG 6000-treated bottom leaves (-1.73-fold), whereas two genes, *MeYABBY09* and *MeYABBY10*, were up-regulated in the PEG 6000-treated folded leaves by 2.09-fold and 1.84-fold at 24h after the treatment, respectively. One gene, namely *MeYABBY06*, was reduced (-1.85-fold) but induced (1.58-fold) in folded leaves at 3h and 24h after the treatment, respectively. Interestingly, this gene was also down-regulated

in bottom leaf samples by -1.89-fold and -3.39-fold at 3h and 24h after the treatment of PEG 6000, respectively.

Expression profiles of the YABBY transcription factor family under biotic stress conditions

To access the expression levels of genes encoding the YABBY TF family under biotic stress conditions in cassava, we explored the previous RNA-Seq data related to the CBSD-inoculated leaves of cassava plants (Maruthi *et al.*, 2014). As a result, the transcriptional changes of the 13 genes encoding the YABBY TF family are provided in **Figure 3**.

We found that all the genes encoding the YABBY TF family exhibited divergent expression levels in CBSD-treated leaf tissues. Particularly, the expression levels of six genes, namely *MeYABBY02*, *MeYABBY04*, *MeYABBY07*, *MeYABBY11*, *MeYABBY12*, and MeYABBY13, were not detected in inoculated leaf samples. Meanwhile, *MeYABBY03*, *MeYABBY09*, and *MeYABBY10* were not significantly induced (fold-change ≥ 1.5-fold) and *MeYABBY01*, *MeYABBY05*, and *MeYABBY08* were not significantly reduced (fold-change ≤ -1.5-fold) in treated leaves. Interestingly, we found that *MeYABBY06* was strongly reduced in CBSD-inoculated leaf tissues by approximately -49.23-fold. This evidence suggested that *MeYABBY06* might be a negative regulator in leaf tissues under the CBSD treatment.

Previously, the expression levels of genes encoding the YABBY TF family in plant species under biotic stress conditions were reported (Zhang *et al.*, 2020). For example, to explore the roles of YABBY genes in the stress responses of *J. regia*, their expression patterns in different walnut varieties subjected to biotic stress were analyzed (Liu *et al.*, 2022). The study showed that YABBY gene expression levels were higher in anthracnose-resistant cultivars compared to anthracnose-susceptible cultivars, indicating a potential role for YABBY genes in conferring anthracnose resistance (Liu *et al.*, 2022). Among them, YABBY genes exhibited low expression levels in the early-stage susceptible cultivars (Liu *et al.*, 2022). However, three genes, namely *YABBY02*, *YABBY04*, and *YABBY10*, were highly expressed in the early-stage resistant cultivars, highlighting the significant roles of YABBY genes in early-stage biotic stress defense (Liu *et al.*, 2022).

Conclusions

Our analysis of the promoter regions of genes encoding the YABBY transcription factor family in cassava identified numerous *cis*-regulatory elements linked to abiotic stress

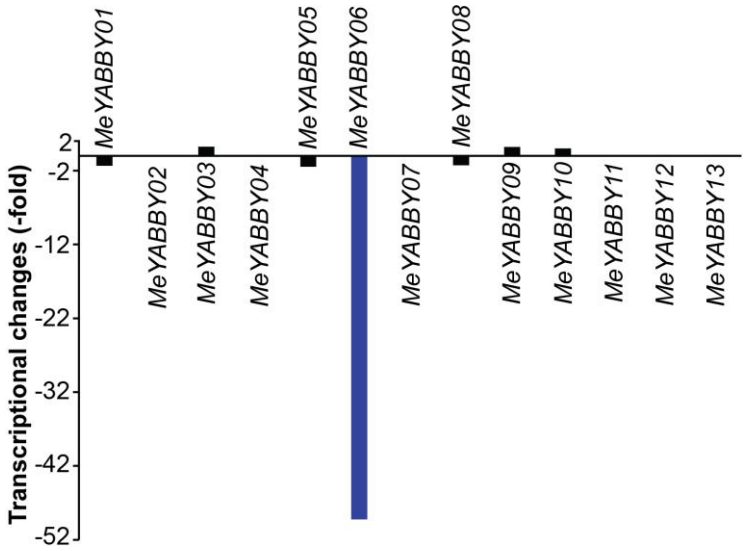

Figure 3. Transcriptional changes of genes encoding the YABBY transcription factor family in cassava brown strike disease-inoculated leaves in cassava

responses, phytohormone regulation, and plant development. Key elements, such as LTRE and MYBRS, were associated with cold and drought responses, while ABRE, the TGACG-motif, and TCA-element suggested roles in hormonal regulation. Expression profiling revealed significant up- or downregulation of *MeYABBY* genes under drought, polyethylene glycol 6000, and cassava brown strike disease inoculation, highlighting their potential roles in stress tolerance and adaptation. These findings emphasize the diverse functions of YABBY TFs in cassava's responses to environmental stresses and development.

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