



Genome-wide analysis of the WRKY gene family in physic nut (*Jatropha curcas* L.)



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ABSTRACT

The WRKY proteins, which contain highly conserved WRKYGQK amino acid sequences and zinc-finger-like motifs, constitute a large family of transcription factors in plants. They participate in diverse physiological and developmental processes. WRKY genes have been identified and characterized in a number of plant species. We identified a total of 58 WRKY genes (*JcWRKY*) in the genome of the physic nut (*Jatropha curcas* L.). On the basis of their conserved WRKY domain sequences, all of the *JcWRKY* proteins could be assigned to one of the previously defined groups, I–III. Phylogenetic analysis of *JcWRKY* genes with *Arabidopsis* and rice WRKY genes, and separately with castor bean WRKY genes, revealed no evidence of recent gene duplication in *JcWRKY* gene family. Analysis of transcript abundance of *JcWRKY* gene products were tested in different tissues under normal growth condition. In addition, 47 WRKY genes responded to at least one abiotic stress (drought, salinity, phosphate starvation and nitrogen starvation) in individual tissues (leaf, root and/or shoot cortex). Our study provides a useful reference data set as the basis for cloning and functional analysis of physic nut WRKY genes.

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1. Introduction

The WRKY transcription factors contain one or two WRKYGQK sequence domains followed by a zinc finger motif, which can bind to the W box of target genes, thus regulating their expression (Eulgem et al., 2000; Sun et al., 2003). The first WRKY gene to be identified, *SPF1*, which was found in sweet potato, was considered to play a potential negative role in the regulation of sucrose induced genes (Ishiguro and Nakamura, 1994). Since then, increasing numbers of WRKY genes have been recognized in plants. In the *Arabidopsis* genome, 72 WRKY genes have been predicted and they can be divided into three groups on the basis of the WRKY domain sequence (Eulgem et al., 2000). There are 109 WRKY genes in rice (*Oryza sativa* L.) (Ross et al., 2007), 57 in cucumber (*Cucumis sativus* var. *sativus* L.) (Ling et al., 2011), and 105 in poplar (*Populus trichocarpa*) (He et al., 2012).

WRKYs play important roles in development and stress responses. Firstly, WRKYs have been proved to be involved in the processes of lateral root formation (Devaiah et al., 2007; Zhang et al., 2008), seed

development (Gonzalez et al., 2009; Luo et al., 2005) and leaf senescence (Besseau et al., 2012). Additionally, members of the WRKY protein are central to the innate immune systems of plants, such as the pathogen associated molecular pattern (PAMP) and effector-triggered immunity (ETI) based defense pathways and systemic resistance (Eulgem and Somssich, 2007). In *Arabidopsis* and rice, many WRKY genes have been shown to participate in responses to various abiotic stresses, such as threshold temperatures, cold, salinity, drought and low inorganic phosphate (Chen et al., 2009; Jiang and Deyholos, 2009; Li et al., 2011; Qiu and Yu, 2008; Wu et al., 2009).

The physic nut (*Jatropha curcas* L.) is a small perennial tree or large shrub, which belongs to the *Euphorbiaceae* family. Physic nut is a drought-resistant, non-food oilseed plant that could meet many of the requirements for commercial biodiesel production. It is well-adapted to semiarid and barren soil environments that are not suitable for cultivation of most crops (Makkar et al., 1997). Following the recent sequencing of the physic nut genome and the development of expressed sequence tag (EST) libraries by our group and others (Natarajan and Parani, 2011; Sato et al., 2011), it is now a useful model for studying the members of different families of transcription factor genes and their evolution. In this study, we searched the genome sequences in order to identify the WRKY genes in physic nut (*JcWRKY*). Subsequently, we characterized the motifs and exon–intron organization of these genes and subjected them to phylogenetic analysis. Finally, we analyzed the expression of the *JcWRKY* genes under normal growth conditions and under various abiotic stresses.

Abbreviations: ERK, extracellular signal-regulated protein; EST, expression sequence tag; ETI, effector-triggered immunity; LRR, leucine-rich repeat; MAP, mitogen-activated protein; NBS, nucleotide binding site; NJ, Neighbor-joining; PAMP, pathogen associated molecular pattern; PCR, polymerase chain reaction; RT-PCR, reverse transcriptase polymerase chain reaction; TPM, transcripts per million; UTR, untranslated region; WD, WRKY domain.

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JeWRKY07N	DGYN	WRKYGQK	QVKGSE	NPRS	YKCT	YP	---	NC	PTKKK	VEKS	-	LDGQ	ITE	IVYK	GS	HNH																																					
JeWRKY08N	DGYN	WRKYGQK	QVKGSE	NPRS	YKCT	FP	---	NC	PTKKK	VERS	-	LDGQ	ITE	IVYK	GS	HNH																																					
JeWRKY04N	DGYN	WRKYGQK	QVKGSE	YPRS	YKCT	HP	---	NC	PVKKK	VERS	-	LDGQ	IAE	IVYK	GE	HNH																																					
JeWRKY05N	DGYN	WRKYGQK	QVKGSE	FPRS	YKCT	HP	---	NC	PVKKK	VERS	-	LDGQ	VTE	I	IYK	GQ	HNH																																				
JeWRKY06N	DGYN	WRKYGQK	PIKGS	EYPRS	YKCT	HP	---	NC	PVKKK	VERS	-	SDGQ	ITE	I	IYK	GL	HNH																																				
JeWRKY10N	DGYN	WRKYGQK	QVKGSE	YPRS	YKCT	HP	---	NC	QVKKK	IERS	-	HDGQ	ITE	I	IYK	GA	HNH																																				
JeWRKY11N	DGYN	WRKYGQK	QVKGSE	YPRS	YKCT	HP	---	NC	L	VKKK	VERS	-	HEGH	ITE	I	IYK	GA	HNH																																			
JeWRKY09N	DGYN	WRKYGQK	HVKGSE	FPRS	YKCT	HP	---	NC	E	VKKL	FERS	-	HDGQ	ITE	I	IYK	GT	HDH																																			
JeWRKY01N	DGYH	WRKYGQK	L	VKGNE	F	IRS	YKCT	HP	---	NC	QVKK	QLERS	-	HDGQ	IAD	IVY	F	GQ	HDH																																		
JeWRKY02N	DGYN	WRKYGQK	QVKS	P	KGS	S	RS	YKCT	YS	---	DC	CAK	-	IECAD	HS	GH	VI	E	IVN	KGT	HS	H																															
JeWRKY03N	DGNS	WRKYGQK	QVKG	S	K	S	S	RS	YKCT	SHS	---	NC	HAKKK	V	QRC	D	H	S	GR	I	D	V	V	Y	I	G	H	DH																									
JeWRKY05C	DGYR	WRKYGQK	VVKGN	P	YPRS	YKCT	TP	---	GC	K	V	R	K	H	V	E	R	A	A	D	P	K	A	V	I	T	T	Y	E	G	K	H	NH																				
JeWRKY06C	DGYR	WRKYGQK	VVKGN	P	H	P	RS	YKCT	ST	---	GC	N	V	R	K	H	V	E	R	A	A	A	D	P	K	A	V	I	T	T	Y	E	G	K	H	NH																	
JeWRKY07C	DGYR	WRKYGQK	VVKGN	P	N	P	RS	YKCT	HP	---	GC	P	V	R	K	H	V	E	R	A	S	H	D	L	R	A	V	I	T	T	Y	E	G	K	H	DH																	
JeWRKY08C	DGYR	WRKYGQK	VVKGN	P	N	P	RS	YKCT	S	I	---	GC	P	V	R	K	H	V	E	R	A	S	H	D	L	R	A	V	I	T	T	Y	E	G	K	H	NH																
JeWRKY10C	DGYR	WRKYGQK	VVKGN	P	N	P	RS	YKCT	S	A	---	GC	S	V	R	K	H	V	E	R	A	S	H	N	L	K	V	I	T	T	Y	E	G	K	H	NH																	
JeWRKY11C	DGYR	WRKYGQK	VVKGN	P	N	P	RS	YKCT	N	A	---	GC	T	V	R	K	H	V	E	R	A	S	H	D	L	K	S	V	I	T	T	Y	E	G	K	H	NH																
JeWRKY09C	DGYR	WRKYGQK	VVRGN	P	N	P	RS	YKCT	N	A	---	GC	P	V	R	K	H	V	E	R	A	S	H	D	P	K	A	V	I	T	T	Y	E	G	K	H	NH																
JeWRKY04C	DGFR	WRKYGQK	VVKGN	P	YPRS	YKCT	GL	---	K	N	V	R	K	H	V	E	R	V	S	D	D	P	G	A	F	I	T	T	Y	E	G	K	H	NH																			
JeWRKY01C	DGYR	WRKYGQK	L	V	K	G	N	P	N	P	RS	YKCT	S	P	---	GC	P	V	K	K	H	V	E	R	A	S	H	D	P	K	V	V	I	T	S	Y	E	G	H	DH													
JeWRKY02C	DGYR	WRKYGQK	M	V	K	G	N	P	H	P	R	N	Y	Y	CT	S	A	---	GC	P	V	R	K	H	I	E	T	A	V	D	N	T	N	A	V	I	T	Y	K	I	H	DH											
JeWRKY03C	DGYR	WRKYGQK	M	V	K	G	N	S	R	L	R	S	Y	Y	CT	S	A	---	GC	P	S	R	K	H	V	E	R	N	T	D	D	A	T	T	A	T	I	T	Y	E	G	K	H	DH									
JeWRKY27	DGYQ	WRKYGQK	V	T	R	D	N	P	S	P	R	A	Y	F	K	C	S	F	A	P	---	S	C	P	V	K	K	V	Q	R	S	I	E	D	Q	S	V	L	V	A	T	Y	E	G	E	H	NH						
JeWRKY28	DGYQ	WRKYGQK	V	T	R	D	N	P	C	P	R	A	Y	F	K	C	S	F	A	P	---	S	C	P	V	K	K	V	Q	R	S	A	E	D	P	S	V	L	V	A	T	Y	E	G	E	H	NH						
JeWRKY29	DGYQ	WRKYGQK	V	T	K	D	N	P	S	P	R	A	Y	F	R	C	S	M	A	P	P	V	G	C	P	V	K	K	V	Q	R	C	V	E	D	K	S	L	L	V	A	T	Y	E	G	E	H	NH					
JeWRKY36	DGCQ	WRKYGQK	I	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	V	A	P	---	T	C	P	V	R	K	Q	V	Q	R	C	A	E	D	M	S	I	L	I	T	T	Y	E	G	T	H	NH					
JeWRKY37	DGCQ	WRKYGQK	I	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	V	A	P	---	A	C	P	V	R	K	Q	V	Q	R	C	A	E	D	M	S	I	L	I	T	T	Y	E	G	T	H	NH					
JeWRKY34	DGCQ	WRKYGQK	I	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	V	S	P	---	T	C	P	V	R	K	Q	V	Q	R	C	I	E	D	M	S	I	L	I	T	T	Y	E	G	T	H	NH					
JeWRKY35	DGCQ	WRKYGQK	I	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	V	A	P	---	GC	P	V	R	K	Q	V	Q	R	C	L	E	D	M	S	I	L	I	T	T	Y	E	G	T	H	NH						
JeWRKY31	DGCQ	WRKYGQK	M	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	M	A	V	---	GC	P	V	R	K	Q	V	Q	R	C	A	E	D	R	T	I	L	I	T	T	Y	E	G	N	H	NH						
JeWRKY32	DGCQ	WRKYGQK	M	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	M	A	A	---	GC	P	V	R	K	Q	V	Q	R	C	A	E	D	R	T	I	L	I	T	T	Y	E	G	N	H	NH						
JeWRKY30	DGCQ	WRKYGQK	M	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	M	A	V	---	GC	P	V	R	K	Q	V	Q	R	C	A	E	D	K	T	I	L	I	T	T	Y	E	G	N	H	NH						
JeWRKY33	DGCQ	WRKYGQK	M	A	K	G	N	P	C	P	R	A	Y	Y	R	C	T	M	A	S	---	GC	P	V	R	K	O	V	O	R	S	A	E	N	K	A	I	L	V	T	T	Y	E	G	Y	H	S	H					
JeWRKY38	DGYK	WRKYGQK	S	I	K	N	S	Q	N	P	R	S	Y	Y	R	C	T	N	P	---	R	C	S	A	K	K	Q	V	E	R	S	S	E	D	Q	D	T	L	I	I	T	Y	E	G	L	H	L	H					
JeWRKY26	DGYR	WRKYGQK	A	V	K	N	S	P	Y	P	R	S	Y	Y	R	C	T	T	Q	---	K	C	T	V	K	K	R	V	E	R	S	F	Q	D	P	S	I	V	I	T	T	Y	E	G	H	NH							
JeWRKY25	DGYR	WRKYGQK	A	V	K	N	S	P	Y	P	R	S	Y	Y	R	C	T	S	Q	---	K	C	R	V	K	K	R	I	E	K	S	V	E	D	P	S	I	V	I	T	T	Y	E	G	H	NH							
JeWRKY24	DGYR	WRKYGQK	A	V	K	N	S	P	F	P	R	S	Y	Y	R	C	T	N	S	---	K	C	T	V	K	K	R	V	E	R	S	S	D	D	P	S	I	V	I	T	T	Y	E	G	H	C	H						
JeWRKY23	DGYR	WRKYGQK	A	V	K	N	S	P	Y	P	R	S	Y	Y	R	C	T	S	A	---	GC	G	V	K	K	R	V	E	R	S	S	E	D	P	T	I	V	V	T	T	Y	E	G	H	T	H							
JeWRKY18	DGYR	WRKYGQK	A	V	K	N	S	P	F	P	R	S	Y	Y	R	C	T	S	A	---	S	C	N	V	K	K	R	V	E	R	S	Y	S	D	P	S	I	V	V	T	T	Y	E	G	Q	T	H						
JeWRKY17	DGYR	WRKYGQK	A	V	K	N	N	K	F	P	R	S	Y	Y	R	C	T	H	Q	---	GC	N	V	K	K	Q	V	Q	R	L	T	K	D	E	G	I	V	V	T	T	Y	E	G	M	H	T	H						
JeWRKY19	DGYR	WRKYGQK	T	V	K	N	S	K	F	P	R	S	Y	Y	R	C	T	Q	N	---	GC	N	V	K	K	Q	I	Q	R	N	T	N	D	E	E	I	V	V	T	T	Y	E	G	I	H	T	H						
JeWRKY21	DGYR	WRKYGQK	A	V	K	N	S	T	H	P	R	S	Y	Y	R	C	T	H	H	---	T	C	N	V	K	K	Q	V	Q	R	L	S	K	D	T	S	I	V	V	T	T	Y	E	G	I	H	NH						
JeWRKY20	DGYR	WRKYGQK	V	V	K	N	S	I	H	Q	R	S	Y	Y	R	C	T	H	---	T	C	N	V	K	K	Q	I	Q	R	L	S	K	D	S	I	V	V	T	T	Y	E	G	I	H	NH								
JeWRKY16	DGYK	WRKYGQK	V	V	K	N	S	L	H	P	R	S	Y	Y	R	C	T	H	S	---	NC	R	V	K	K	R	V	E	R	L	S	E	D	C	R	M	V	I	T	T	Y	E	G	R	H	NH							
JeWRKY15	DGYK	WRKYGQK	V	V	K	N	T	L	H	P	R	S	Y	Y	R	C	T	Q	D	---	NC	R	V	K	K	R	V	E	R	L	A	E	D	P	R	M	V	I	T	T	Y	E	G	R	H	VH							
JeWRKY13	DGF	K	W	R	K	Y	G	K	K	A	I	K	N	N	T	N	P	R	N	Y	Y	R	C	S	N	E	---	GC	R	V	K	K	R	V	E	R	D	G	K	D	S	S	Y	V	I	T	T	Y	E	G	V	H	NH
JeWRKY12	DGF	K	W	R	K	Y	G	K	K	S	V	K	N	S	P	N	P	R	N	Y	Y	R	C	S	S	G	---	GC	N	V	K	K	R	V	E	R	D	R	E	D	S	R	Y	V	I	T	T	Y	D	G	I	H	NH
JeWRKY14	DGYK	WRKYGQK	I	V	K	S	S	P	N	P	R	N	Y	Y	R	C	S	I	E	---	GC	P	V	K	K	R	V	E	R	D	R	D	D	Q	K	Y	V	I	T	T	Y	E	G	V	H	NH							
JeWRKY58	DGYE	WRKYGQK	F	I	K	N	I	G	K	F	R	S	Y	F	K	C	H	K	O	---	NC	N	A	R	K	R	V	E	W	S	R	S	N	P	D	Y	L	R	V	V	Y	D	G	V	H	T	H						
JeWRKY44	DDYT	WRKYGQK	P	I	K	G	S	P	Y	P	R	S	Y	Y	K	C	S	S	M	R	---	GC	P	A	R	K	H	V	E	R	C	L	Q	D	P	S	M	L	L	V	T	Y	E	G	D	H	S	H					
JeWRKY42	DEYS	WRKYGQK	P	I	K	G	S	P	H	P	R	G	Y	Y	K	C	S	S	M	R	---	GC	P	A	R	K	H	V	E	R	A	L	D	D	S	M	L	I	V	T	Y	E	G	D	H	NH							
JeWRKY40	DEYS	WRKYGQK	P	I	K	G	S	P	H	P	R	G	Y	Y	K	C	S	S	L	R	---	GC	P	A	R	K	H	V	E	R	C	L	E	D	S	M	L	I	V	T	Y	E	G	E	H	NH							
JeWRKY41	DDYS	WRKYGQK	P	I	K	G	S	P	H	P	R	G	Y	Y	K	C	S	S	V	R	---	GC	P	A	R	K	H	V	E	R	A	L	D	D	P	T	M	L	V	T	Y	E	G	H	NH								
JeWRKY43	DEYS	WRKYGQK	P	I	K	G	S	P	Y	P	R	G	Y	Y	K	C	S	T	V	R	---	GC	P																														

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