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Review article

Arginine-rich motif-tandem CCCH zinc finger proteins in plant stress responses and post-transcriptional regulation of gene expression

Jyan-Chyun Jang*

Department of Horticulture and Crop Science, Molecular Genetics, and Center for Applied Plant Sciences, The Ohio State University, Columbus, OH 43210, USA

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ABSTRACT

Tandem CCCH zinc finger (TZF) proteins are evolutionarily conserved regulators of gene expression at the post-transcriptional level. TZFs target AU-rich RNA elements at 3′ un-translated region and recruit catabolic machineries to trigger mRNA degradation. The plant TZF families are over-represented by a class of proteins with a unique TZF domain preceded by an arginine-rich motif (RR-TZF). RR-TZF proteins are mainly involved in hormone- and environmental cues-mediated plant growth and stress responses. Numerous reports have suggested that RR-TZF proteins control seed germination, plant size, flowering time, and biotic and abiotic stress responses via regulation of gene expression. Despite growing genetic evidence, the underlying molecular mechanisms are elusive. This review outlines the highly conserved roles of plant RR-TZFs in various stress responses and the potential involvements of RR-TZF proteins in transcriptional and post-transcriptional regulation of gene expression. The dynamic subcellular localization of RR-TZF proteins, implication of predominant protein–protein interactions between RR-TZF proteins and stress response mediators and future directions of this research field are also discussed.

Contents

1. Tandem CCCH zinc finger proteins (TZFs)

Gene expression in eukaryotes is extensively regulated at the post-transcriptional level, in which RNA binding proteins have major roles in modulating mRNA processing, transport, localization, stability, and translation [1]. Zinc finger proteins are a large family of metalloproteins involved in both transcriptional (e.g., CCHH-type) and post-transcriptional (e.g., CCCH-type) modulation of gene expression [2]. This review discusses recent development in understanding the mechanisms by which a unique family of RNA binding zinc finger proteins affects plant growth, stress responses, and post-transcriptional regulation of gene expression.

Tandem CCCH Zinc Finger proteins (TZFs) are conserved from yeast to metazoans. The typical TZF proteins are characterized by a TZF domain consisting of two identical CCCH motifs separated by a spacer of 18 amino acids. Tristetraprolin (TTP), a prototype of mammalian TZFs, triggers mRNA degradation by targeting AU-Rich Elements (AREs) in the 3′ un-translated region of mRNAs encod-

Abbreviations: ABA, abscisic acid; ARE, AU-rich element; AtTZF, *Arabidopsis thaliana* tandem zinc finger protein; GA, gibberellic acid; MAPK, mitogen-activated protein kinase; MARD1, Mediator of ABA-Regulated Dormancy 1; PB, processing body; RD21A, Responsive to Dehydration 21A; RR-TZF, arginine-rich motif-tandem CCCH zinc finger proteins; SG, stress granule; TTP, tristetraprolin protein.

* Corresponding author.
E-mail address: jang.40@osu.edu

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Table 1
Arabidopsis thaliana arginine-rich motif-tandem CCCH zinc finger (RR-TZF) proteins.

Genes (accession number)	mRNA accumulation induced by	Subcellular localization	Positive regulators for	Negative regulators for	Key references	Paralogs in other plant species	Key references
AtTZF1 (At2g25900)	ABA, salt, sugar depletion	PB/SG, nucleus	ABA, sugar, and salt stress tolerance responses	GA responses	Han et al., 2014; Lin et al., 2011	Rice OsTZF1	Jan et al., 2013; Zhang et al., 2012
AtTZF2 (At2g19810)	ABA, cold, H_2O_2, osmotic stress, salt	cytoplasm, cytoplasmic foci	ABA, oxidative, and salt stress tolerance responses	MeJA responses	Huang et al., 2011; Huang et al., 2012; Lee et al., 2012;	Rice OsTZF2	Kong et al., 2006
AtTZF3 (At4g29190)	ABA, cold, H_2O_2, osmotic stress, salt	cytoplasm, cytoplasmic foci	ABA, oxidative, and salt stress tolerance responses	MeJA responses	D'Orso et al., 2015; Huang et al., 2011; Huang et al., 2012; Lee et al., 2012;		
AtTZF4 (At1g03790)	ABA	PB/SG, nucleus	ABA responses	GA- and phytochrome-mediated seed germination responses	Bogamuwa & Jang, 2013; Kim et al., 2008	cotton GhTZF1	Kong et al., 2006; Zhou et al., 2014
AtTZF5 (At5g44260)	ABA	PB/SG, nucleus	ABA responses	GA- and phytochrome-mediated seed germination responses	Bogamuwa & Jang, 2013	cotton GhTZF1	Kong et al., 2006; Zhou et al., 2014
AtTZF6 (At5g07500)	ABA	PB/SG, nucleus	ABA responses	GA- and phytochrome-mediated seed germination responses	Bogamuwa & Jang, 2013		
AtTZF7 (At2g41900)		cytoplasm, cytoplasmic foci, nucleus	vegetative growth and abiotic stress tolerance responses	stress-induced transition to flowering	Blanvillain et al., 2011	wheat TaZnFP	Min et al., 2013
AtTZF8 (At5g12850)		cytoplasmic foci				wheat TaZnFP	Min et al., 2013
AtTZF9 (At5g58620)		PB/SG, nucleus	vegetative growth and both abiotic and biotic stress tolerance responses	stress-induced transition to flowering	Blanvillain et al., 2011; Maldonado-Bonilla et al., 2014		
AtTZF10 (At2g40140)	salt	cytoplasmic foci	vegetative growth and abiotic stress tolerance responses	stress-induced transition to flowering	Blanvillain et al., 2011; Sun et al., 2007		
AtTZF11 (At3g55980)	salt	cytoplasmic foci, nucleus	vegetative growth and abiotic stress tolerance responses	stress-induced transition to flowering	Blanvillain et al., 2011; Sun et al., 2007		