

## Review article

## Zinc finger protein (ZFP) in plants-A review

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## Abstract

Zinc finger protein (ZFP) possesses one or more 'zinc finger' that bond one or more zinc ions by its residues Histidine (His) and Cysteine (Cys). ZFP also belongs to a large family of transcription factor. It plays many important regulatory roles in plants. Here, we explained that the percentage of ZFP transcription factor in total transcription factors is similar among plant species. The ZFP functions were implicated in development, growth, stress response and phytohormone responses based on the conclusion of four ZFP families, C2H2, CCCH, C3HC4 and C4. Meanwhile, there was one main function in each ZFP family. On the basis of analyses of the ZFP gene expression in the CCCH family of rice, the regulation controlled by rice ZFP in various tissues was significantly related with each other, as well as in responses to different abiotic stresses. Expression of some rice tissues-specific ZFP genes was significantly related to abiotic or biotic stresses.

**Keywords:** Plant; Zinc finger protein; Transcription factor; Stress; Regulation.

## Introduction

Zinc finger protein (ZFP) was first identified as a repeated motif in transcription factor IIIA (TFIIIA) from *Xenopus oocytes* (Miller et al., 1985). It has conserved zinc finger motif, which is proposed to be an independently folded DNA-binding domain which can recognize specific DNA sequences (Klug and Rhodes, 1987; Hollenberg and Evans, 1988; Payre and Vincent, 1988). ZFP binds with zinc ion through its Cysteine (Cys) and Histidine (His) using 'Zinc Finger'. The zinc finger binds a zinc ion in order to stabilize its three-dimensional structure consisting of a two-stranded anti-parallel  $\beta$ -sheet and  $\alpha$ -helix, which is very important for playing various biological roles of ZFP (Takatsuji, 1998).

ZFPs are divided into many families on the basis of the conserved zinc finger motif and/or other notable structures (Berg and Shi, 1996; Dai and Liew, 1998). However, the ZFPs with same biological functions are not completely distributed into the same ZFP family.

ZFPs can play important biological functions by interacting with DNA or chromatin, RNA and other proteins (Elrod-Erickson et al., 1996; Iuchi 2001; Yang et al., 2006; Gamsjaeger et al., 2007). ZFPs possess various biological functions, such as plant growth and development (flower, shoot, seed, pistil and leaf) (Sakai et al., 1995; Chrispeels et al., 2000; Yun et al., 2002; Luo et al., 1999; Kubo et al., 2000), phytohormone response (Molnar et al., 2002) and abiotic and biotic stresses responses (van Der Krol et al., 1999; Huang et al., 2002; Lippuner et al., 1996; Mukoko Bopopi et al., 2010; Tian et al., 2010).

In this view, we simply reviewed the types of ZFP, the characteristics and percentages of them in plants, their biological functions in the different ZFP families and the relationship between the expression of the ZFP genes in tissues and their expression in responses to abiotic and biotic stresses.

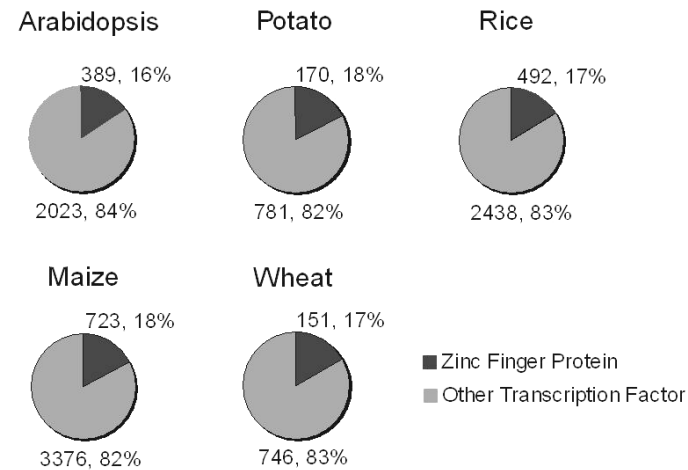
## The types and conserved motif of ZFP families

ZFP families have been structurally postulated based on the combinations of Cys and His for coordination divalent zinc ions (Berg and Shi, 1996; Dai and Liew, 1998), such as C2H2 represented by TFIIIA (Miller et al., 1985), C3HC4, termed RING finger (Barlow et al., 1994), C4 (Omichinski et al., 1993), CCCH (DuBois et al., 1990), C4HC3 (Gabig et al., 1994) and C2HC5 (Freyd et al., 1990). The C2H2 family possesses two types, C-type and Q-type. The Q-type with conserved motif (QALGGH) is plant specific, whereas the C type is present in other organisms as well (Agarwal et al., 2007). The finger conformed to the proposed pattern of TFIIIA type finger  $\$-X-X-X_{2,4,5}-C-X_3-\$-X_5-\$-X_2-H-X_{3,4}-H$  where, X is any amino acid and \$ is a hydrophobic residue (Klug and Schwabe, 1995). The CCCH family is divided into 18 groups based on the different amino acid spacing numbers between C and H in zinc finger motif (Wang et al., 2008a). There is a conserved motif (C-X<sub>6-14</sub>-C-X<sub>4-6</sub>-C-X<sub>3</sub>-H) for ZFP in the CCCH family (Berg and Shi, 1996; Wang et al., 2008a). RING motifs can form a binding site for two zinc atoms, which included a consensus sequence (C-X<sub>2</sub>-C-X<sub>9,39</sub>-C-X<sub>1,3</sub>-H-X<sub>2,3</sub>-C/H-X<sub>2</sub>-C-X<sub>4,48</sub>-C-X<sub>2</sub>-C). On the basis of the fifth coordination site (C/H), the RING family can be categorized into seven types with different conserved motifs, RING-H2, RING-HC, RING-v, RING-D, RING-S/T, RING-G and RING-C2 (Kosarev et al., 2002; Stone et al., 2005; Lim et al., 2010). Most proteins with RING domain belong to E3 ubiquitin ligases (Deshaies and Joazeiro, 2009). Additionally, as for the ZFP in the C4 family, the structure of binding a zinc atom is complex. This family includes seven ZFP types, GATA, FYVE, Tim10/DDP,

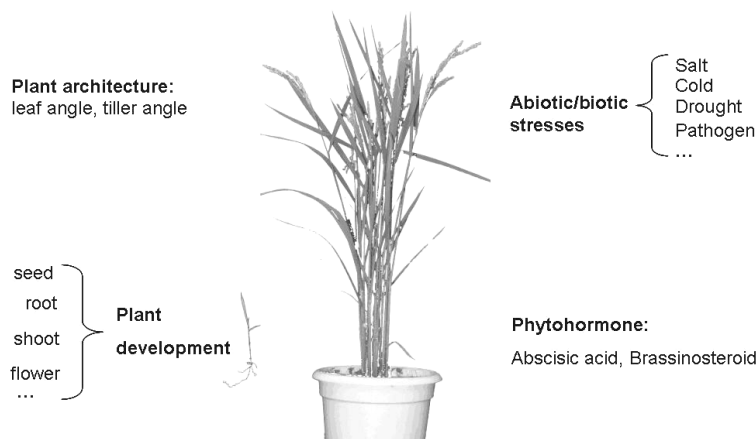
**Table 1.** Pearson correlation among tissues, biotic and abiotic stresses.

	Ovary	Suspension cell	Shoot	Root	Anther	Embryo	Endosperm	5day seed	Drought	Salt	Cold	FR13 3dpi <sup>#</sup>	FR13 4dpi <sup>#</sup>
Stigma	0.90**	0.67**	0.89**	0.91**	0.85**	0.63**	0.66**	0.67**	0.14	0.06	0.12	0.39**	0.16
Ovary		0.77**	0.84**	0.88**	0.84**	0.72**	0.64**	0.70**	0.16	0.12	0.12	0.36**	-0.01
Suspension cell			0.62**	0.72**	0.67**	0.84**	0.65**	0.81**	0.02	-0.05	-0.15	0.15	0.10
Shoot				0.91**	0.89**	0.67**	0.68**	0.65**	0.28*	0.17	0.19	0.41**	0.16
Root					0.87**	0.71**	0.69**	0.72**	0.22*	0.13	0.20	0.40**	0.16
Anther						0.68**	0.76**	0.74**	0.20	0.14	0.12	0.39**	0.14
Embryo							0.80**	0.85**	0.27*	0.17	-0.14	0.09	0.20
Endosperm								0.91**	0.21	0.18	-0.02	0.19	0.29**
5d seed									0.10	0.06	-0.06	0.24*	0.24*
Drought										0.89**	0.46**	0.10	0.31**
Salt											0.49**	0.01	0.07
Cold												0.28*	-0.06
FR13 3dpi <sup>#</sup>													0.01

<sup>#</sup> dpi: days past inoculation by FR13 (*Magnaporthe grisea*). \*\* Correlation is significant at the 0.01 level (2-tailed). \*Correlation is significant at the 0.05 level (2-tailed).



**Fig 1.** The percentage of ZFP transcription factor in all transcription factors of Arabidopsis, potato, rice, maize and wheat on the basis of plant transcription factor database (<http://planttfdb.cbi.edu.cn/>) (Zhang et al., 2011). The percentage of ZFP transcription factor was 16%-18% in these plant species.



**Fig 2.** The biological function of ZFP in Plant. The biological function mainly includes plant architecture, development, stresses and phytohormone responses. Rice is one of the most important crops in the world, which was taken as the reference of plants.

LSD1, A20, TFIIB and Zn-finger in Ran binding protein. Most ZFPs only contain one type of zinc finger, which can be classified into different types based on these notable structural features. Meanwhile, other evolutionarily conserved structural features were identified outside the finger domain for clustering, such as the finger-associated box (Knochel et al., 1989), Ser/Thr protein kinase domain (Stone et al., 2005), lysine-rich repeats and TIR (Toll/interleukin-1 receptor) domain (Drøbak and Heras, 2002).

#### How do the ZFP transcription factors work?

Regulation of gene expression is controlled by the sequence-specific binding of transcription factors to their DNA recognition sites, which is a key step in the regulation of networks. For instance, CCCH-type zinc finger is capable of binding to the 5'-UAUU-3' half site of the class II ARE 5'-UAUUUAUU-3' (Carrick et al., 2004; Hudson et al., 2004; Barreau et al., 2005). ZPT2-2 is a transcription factor of petunia that contains two canonical TFIIIA-type zinc finger motifs. Its optimal binding sequence for the N-terminal zinc finger is AGC(T), and that of the C-terminal one is CAGT (Yoshioka et al., 2001). As for the proteins in WRKY family, they can bind specifically to the DNA sequence motif (T)(T)TGAC(C/T), which is known as the W-box (Rushton et al., 1995; Rushton et al., 1996). However, DNA-binding is probably independent, when three or more Zinc fingers are present in one ZFP.

Regulation of gene expression is not completely controlled by binding DNA directly. ZFP can regulate downstream genes by interaction with other proteins (Elrod-Erickson et al., 1996; Iuchi, 2001; Yang et al., 2006; Gamsjaeger et al., 2007). For instance, SCOF-1 has to interact with SGBF-1, when regulating cool induced genes (Kim et al., 2001). Additionally, there are some genes with two or more binding sites. Their spaces between the two binding-core sites affect the binding affinity, when two or more ZFP domains are present (Yoshioka et al., 2001). Meanwhile, ZFPs can bind to RNA (Elrod-Erickson et al., 1996; Lu et al., 2003). For example, some ZFPs in the CCCH family can bind RNA in RNA processing, such as HUA1, AtCPSF30 (Li et al., 2001; Delaney et al., 2006).

#### The distribution of the ZFP transcription factor in plants

On the basis of plant transcription factor database (<http://plantfdb.cbi.edu.cn/>) (Zhang et al., 2011), it is shown that the percentage of ZFP transcription factors is similar (16%-18%), although the number of the total transcription factors is obviously different in Arabidopsis, potato, rice, maize and wheat (Fig. 1). The results showed that the percentage of ZFP transcription factor is almost similar among plant species. It is suggested that ZFP is probably conserved in plant evolution, and the important biological functions of ZFP transcription factor are probably similar among plant species.

#### The biological function of ZFPs in plants

In this review, we only integrated biological functions of four ZFP families, C2H2, CCCH, C3HC4 and C4. Lots of plant's ZFPs have been functionally validated. Their biological functions are implicated in plant architecture, development, stress response and phytohormone response (Supplementary Table 1, Fig. 2). Plant architecture just included the leaf angle and tiller angle, whereas phytohormone response only included abscisic acid and brassinosteroid. It showed that most of ZFPs have only one main biological function. However, some ZFPs, such as AZF2, OsDSG1, OsBIRF1 and PtarHE1 have two or three important biological functions, suggesting that the roles of these ZFPs are crossed.

As shown in Supplementary Table 1, most genes in C2H2 and CCCH types have the function of plant development, whereas the genes in C3HC4 type are mainly linked with abiotic and biotic stresses. As for the relationship between ZFP and phytohormone, the ZFP genes were mainly related with abscisic acid. These above mentioned results suggest that the main role of each ZFP type is different in plants.

#### The function analysis of the ZFP in the CCCH family

The ZFPs in the CCCH family have been known to play important roles in RNA processing as RNA-binding proteins



play very important role on the plant genetic improvement. ZFN is one of the most potential tools of site-specific mutagenesis and base substitution.

## Conclusions

The ZFP plays important biological functions in plant. It can be classified into lots of families based on the conserved 'Zinc Finger' motif and/or other notable structures. Meanwhile, ZFP belongs to a large family of transcription factor. The percentage of ZFP transcription factor in total transcription factors are obviously similar among plant species, suggested that ZFP is probably conserved in plant evolution. ZFP plays important role in plant, such as development, growth, stress response and phytohormone response. Meanwhile, there was a main biological function in each family, suggesting that family-specific of function was present in plants. However, the ZFP genes with the similar expression pattern are not clustered together based on the amino acid sequence similarity, and the expressions of some genes had tissue-specific biological function. The analysis of the expression of the ZFP genes showed that regulation controlled by ZFP in various tissues is significantly related with each other, as well as that in the responses to different abiotic stresses. Meanwhile, regulation controlled by ZFP in some specific tissue was specifically related with that in the response to stress-specific.

On the basis of this review, future studies should focus on (i) deeply biological analysis of different ZFP families on the basis of their characteristics, (ii) the relationship of the function among development, growth, stress response and phytohormone response, (iii) the biological contribution of ZFP expressed in specific tissues, (iv) developing application of ZFP in biotechnology based on the DNA/RNA recognition sites and biological function.

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