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Cys2His2 Zinc Finger Proteins Boost Survival Ability of Plants against Stress Conditions

Kemal Yuce and Ahmet Ismail Ozkan

Abstract

Zinc finger (ZnF) proteins are the largest transcription factors family. They constitute of nine sub-groups including Cys2His2, Cys3His, Cys3HisCys4, Cys2HisCys5, Cys4HisCys3, Cys2HisCys, Cys4, Cys6 and Cys8. ZnFs perform tasks of recognizing DNA, packaging RNA, transcriptional activity, regulating apoptosis, folding and collecting proteins, and binding lipids. One of the largest sub-groups of these proteins is ZF-Cys2His2, containing SIZ1, ZAT, ZAT7, ZFP1, ZFP252, DST, ZFP1, SIZF3, ZFP179, ZjZFN1, SICZFP1, and ZF-Cys2His2 proteins are found in plants tissues and fulfill important tasks in their defense to struggle with biotic and abiotic stresses (i.e., salt, drought, cold, oxidative). The aim of this chapter is to reveal importance of ZF-Cys2His2 proteins against various stress conditions.

Keywords: Cys2His2 Zinc finger proteins, plant stress physiology, salinity stress, cold stress, oxidative stress

1. Introduction

Cys2His2 zinc finger (ZF-Cys2His2) proteins have been found in a number of plants including *Arabidopsis*, cotton, rice and wheat. The ZF-Cys2His2 is built by two Cys and two His residues. This structure provides a conservative motif together with Zn^{2+} . The core has an α -helix and an anti-parallel double-stranded β -sheet so that the ZF-Cys2His2 proteins have stable and relatively independent protein domains. ZF-Cys2His2 proteins form a relatively wide family of transcriptional factors in plants. Current studies have revealed that ZF-Cys2His2 proteins operate as important transcriptional regulators in plant responses to a large broad of stress conditions (like drought, excessive light, extreme temperatures, oxidative stress, salinity, and silique shattering) [1]. Over-expression of some ZF-Cys2His2 genes has led to an increased tolerance to various stresses and activation of some stress-related genes [2]. Absciscic acid (ABA) is an important phytohormone involved in regulating stress responses and plant growth and development. In addition, ABA is involved in many important processes of plants such as stomatal closure, leaf senescence, cuticle wax accumulation, bud dormancy, osmotic regulation, seed germination and growth inhibition. Since the ABA regulates downstream responses to biotic and abiotic environmental changes through both transcriptional and post-transcription mechanisms, the responses of ABA and ZF-Cys2His2 proteins to various stresses are also mentioned here [3].

The world population has exceeded 7.5 billion. To supply the nutritional needs of this population, it is important to know the proteins and genes related to the response of plants to stress conditions. In this context, to increase the durability and yield of plants, transgenic plant researches are carried out. And the most commonly focused proteins in these researches are ZF-Cys2His2 proteins. For this reason, in this chapter, the changes occurring in ZF-Cys2His2 proteins with transgenic methods and various stress conditions and what these changes bring to the plant have been discussed (**Table 1**).

The kind of C2H2 zinc finger proteins	The kind of stress	References
AtSIZ1	Salt stress	[4]
GmZAT4	Salt stress	[5]
ZAT7	Salt stress	[6]
AhZFP1	Salt stress	[7]
ZFP252	Salt stress	[8]
ZmZF1	Salt stress	[9]
DST	Salt stress	[10]
GhZFP1	Salt stress	[11]
SIZF3	Salt stress	[12, 13]
ZFP179	Salt stress	[14]
ZjZFN1	Salt and cold stress	[15]
TaZNF	Salt stress	[16]
SICZFP1	Salt and cold stress	[17]
TaDi19A	Salt osmotic and cold stress	[18]
AtDi19-3	Salt and drought stress	[19]
AZF2 STZ	Salt, cold and drought stress	[20]
GsZFP1	Cold and drought stress	[21]
ZFP245	Cold and drought stress	[22]
GbZF1	Cold stress	[23]
PeSTZ1	Cold and oxidative stress	[24]
SCOF-1	Cold stress	[25]
OsCTZFP8	Cold stress	[26]
ZAT12	Oxidative stress	[27]
ZAT7		[28]
ZFP36	Oxidative stress	[29]
GsZFP1	Cold stress	[21]
ZAT18	Oxidative and drought stress	[30]
OsMSR15	Drought stress	[31]
VTA2	Oxidative and fungal stress	[32]
MtSTOP	pH and aluminum stress	[33]
ART1	Aluminum stress	[34]

Table 1.
C2H2 zinc finger proteins related with plant stress.

2. Salinity stress and Cys2His2 zinc finger

One of the stress factors is salt. Plants are affected with development and yield from salt stress. Transgenic plant studies in combating salt stress have become one of the most important issues of our century and ZnF proteins attract a lot of attention in this context. Salt application has induced expression of AtSIZ1. The germination energy, index and rate, cotyledon growth rate and root length were found to be importantly higher than wild-type in lines where AtSIZ1 was over-expressed under various stress applications at the germination stage. However, these indicators decreased significantly in AtSIZ1 mutants. Higher proline, potassium and soluble sugar, lower sodium, malondialdehyde, sodium/potassium ratios were observed in the lines where over-expression occurred in the mature seedling stage compared to the wild-type. Stress-related marker genes such as AtGSTU5, AtP5CS1, COR15A, RD29A, RD29B and SOS1 have been found to be over-expressed in lines with an excessive expression than those of wild-type and mutant under salt application. Due to the results AtSIZ1 functions in maintaining both ionic homeostasis and osmotic balance to improve salt tolerance in *Arabidopsis* [4]. It has also been shown that GmZAT4 plays a significant role in both polyethylene glycol and sodium chloride stresses tolerance and ABA responses in both *A. thaliana* and soybean. Over-expression of GmZAT4 increased the tolerance of *A. thaliana* to 20% polyethylene glycol and 150 mM sodium chloride and increased the germination rate after 1 or 2 μ M ABA administration [5]. The EAR motif for ZAT7 has a significant role of defense response to salt stress in *Arabidopsis*. Suppressing growth and being more tolerant to salt stress have observed in transgenic *Arabidopsis* plants expressing ZF-Cys2His2 protein ZAT7. Mutation or deletion of ZAT7's EAR motif did not affect growth suppression, but eliminated salt tolerance. These results showed that ZAT7's EAR motif is important in increasing salt stress tolerance of the transgenic plants. On the other hand, the EAR motif appears not to be involved in suppressing transgenic plants growth. Other analyzes of ZAT7 using RNAi lines suggested that ZAT7 functions as a suppressor of the defense response's suppressor [6]. Semi-quantitative RT-PCR studies have revealed that AhZFP1 expression is stimulated by salt stress in the peanut root, stem and leaves [7]. Excessive expression of ZFP252 in rice increased the amount of free proline, soluble sugar, stress defense genes expression and improved the plant's response to both salt and drought stress. This result showed that ZFP252 plays a significant role in both salt and drought stresses of rice plant. And it is also useful for genetically modified plants to increase both salt and drought stresses tolerance [8]. ZmZF1 transcripts are strongly stimulated by salt stress. It is also stimulated by drought stress and ABA. Over-expression of ZmZF1 under cauliflower mosaic virus 35S promoter control increased both salt and drought tolerance in young seedling phase of transgenic *Arabidopsis* [9]. Stomata control the absorption of carbon-dioxide and improve water use efficiency. Thus, it plays an important role in abiotic stress tolerance. H_2O_2 , stimulates stomatal closure, is an important signaling molecule. Another ZFP, DST is directly organizing genes related to H_2O_2 homeostasis. Therefore, the stomatal closure is regulated negatively. The loss of DST function decreases stomatal density and increases stomatal closure. As a result, increased salt and drought tolerance appears in the rice plant. These findings provide a different perspective on the abiotic stress tolerance mechanism associated with stomata and also a significant genetic engineering approach in developing abiotic stress tolerance [10]. GhZFP1 over-expression in transgenic tobacco plant increased salt stress tolerance and *Rhizoctonia solani* resistance. This indicates that the plant can act as a significant regulator in responding to biotic and abiotic stress [11]. Ascorbic acid supports stress tolerance by breaking down reactive oxygen species (ROS). ROS degradation capacity of ascorbic acid is increased

in plants that over-expressed SIZF3. This has increased the salt tolerance of plants. Findings in the studies showed that SIZF3 simultaneously supports both the collection of ascorbic acid and improves the plant salt tolerance response [12]. ZFP3 expression level was found to be highly suppressed by mannitol, sodium chloride and sucrose. The mutant *Arabidopsis* exhibited a reduced tolerance condition in terms of ZFP3. Excessive expression of ZFP3 reduced stress-related genes (such as AtP5CS1, KIN1, RD22 and RD29B) expression. These results showed that ZFP3 is important in osmotic and salt stress response [13]. Over-expression of ZFP179 increased salt tolerance in rice plant. And the transgenic seedlings showed hypersensitive activity to exogenic ABA. Increased amount of soluble sugars and free proline under salt stress have been observed in transgenic plants. In ZFP179 transgenic rice plant the oxidative stress tolerance, ability to break down ROS and expression level of stress-related genes such as OsDREB2A, OsLea3, OsP5CS and OsProT increased under salt stress. These findings showed that ZFP179 plays an important role in salt stress in plants and is useful for developing transgenic plants that are highly tolerant to salt stress [14]. Expression of ZjZFN1 was found to be increased by ABA, cold and salt. ZjZFN1 expression improved seed germination, plant adaptation to salt stress by growth under salt stress and increased green cotyledons in *Arabidopsis thaliana*. Physiological and transcriptional analyzes suggest that ZjZFN1 can affect the collection of ROS and regulate the transcription of genes associated with salt response. ZjZFN1 over-expressing plants RNA sequence analysis revealed that ZjZFN1 could function as a transcriptional activator in the regulation of stress response pathways such as alpha-linoleic acid metabolism, phenyl alanine metabolism and phenylpropanoid biosynthesis pathways. The results showed that ZjZFN1 plays an important role in the formation of salt stress response in plants [15]. In another study, it has been proven that TaZnF, a ZF-Cys2His2 protein, significantly improves salt tolerance of transgenic *Arabidopsis*. Various physiological indexes of transgenic plants showed improvement under salt stress compared to the control group. The noninvasive micro-test (NMT) technique showed the excretion of Na is significantly accomplished by the root end of the transgenic *Arabidopsis*. TaZnF is mainly found in the nucleus and has demonstrated transcriptional activity [16].

3. Cold stress and C2H2 zinc finger proteins

GsZFP1 was found to be stimulated by ABA (100 μ M), cold (4°C) and salt (200 mM sodium chloride) in leaves and by ABA (100 μ M), cold (4°C) and drought (30% PEG 6000) in root. It was found that over-expression of GsZFP1 in transgenic *Arabidopsis* resulted in higher tolerance in cold and drought stress and a reduced rate of water loss. Over-expression of GsZFP1 was found to increase the expression of CBF1, CBF2, CBF3, COR47, NCED3 and RD29A stress response genes in response to cold stress, and increased expression of NCED3, P5CS, RAB18, RD22 and RD29A in response to drought stress [17]. It was revealed by the semi-quantitative RT-PCR experiment that ZFP245 was strongly stimulated after 6 hours of cold and drought stress and then decreased to normal level. ZFP245 did not occur by the application of high salt or ABA [18]. High degree of aggregation of GmZF1 mRNAs stimulated by exogenic ABA suggested that GmZF1 was involved in the ABA-dependent signal transduction pathway. GmZF1 over-expression increased expression of the cold-induced cor6.6 gene by recognizing the likely protein DNA binding site. This suggests that GbZF1 of soybean can improve *Arabidopsis* cold stress tolerance by regulating cold regulatory genes expression in transgenic *Arabidopsis* [19]. PeSTZ1 increases freezing tolerance through organizing the breakdown of ROS by directly regulating PeAPX. PeSTZ1 is preferably expressed in young roots. This ZFP has

been upregulated in cold applications. PeSTZ1 functions as a transcriptional activator to increase cold tolerance. PeSTZ1 upregulation decreases malondialdehyde and ROS aggregation by activating antioxidant systems. This is thought to be achieved through direct regulation of PeAPX2 expression [20]. SCOF-1 transcription is particularly stimulated by ABA and low temperature, but not neither with dehydration nor high salt. SCOF-1 over-expression stimulated the expression of genes regulated by cold and improved the cold tolerance of tobacco plants and non-acclimated transgenic *Arabidopsis*. SCOF-1 can function as a positive regulator of COR gene expression regulated by ABRE through protein-protein interaction and thus can improve the cold tolerance of plants [21]. SICZFP1 is strongly stimulated by cold stress, dehydration and salt stress, but not by ABA. SICZFP1 over-expression in transgenic rice and *Arabidopsis* plants increased expression of cold-response-related genes. This suggests that SICZFP1 plays an important role in the response of plants to cold stress [22]. TaDi19A has been found to be expressed in both leaves and roots of wheat seedlings grown under stress-free conditions, but is significantly upregulated in salt, osmotic and cold stress conditions, or in hormone applications such as stress-related ethylene and ABA. Heterologous over-expression of TaDi19A in *Arabidopsis thaliana* increased salinity, mannitol and ABA stress sensitivity during the germination of plants. Root elongation in these transgenic lines showed less salinity stress tolerance and less ethephon sensitivity. The expression of ABA signal path genes such as ABA1, ABF3, ERD15, RAB18 and SOS2 (SOS pathway) have changed in transgenic plants [23]. Transgenic rice expressing excessive OsCTZFP8 exhibited cold-tolerant phenotypes with significantly higher pollen fertility and seed placement rates than non-transgenic control plants. Yield of lines expressing OsCTZFP8 per plant was significantly higher ($p < 0.01$) than non-transgenic control plants under cold application. This result shows that OsCTZFP8 is a C2H2 zinc finger transcription factor that plays an important role in cold tolerance in rice [24].

4. Oxidative stress and C2H2 zinc finger proteins

Cytosolic Apx1, ascorbate peroxidase 1, is an important H_2O_2 -removing enzyme in plants. Both WRKY transcription factor (WRKY25) and two ZnF proteins (ZAT12 and ZAT7) expressions have increased in Apx1 gene suppressed plants that grown under the controlled conditions. When cells were exposed to oxidative stress, heat shock, and injury, the WRKY25, ZAT7 and ZAT12 expressions increased together. However, light and osmotic stresses did not increase them. Transgenic plants expressing ZAT7 and ZAT12 were able to tolerate oxidative stress. WRKY25, ZAT7 or ZAT12 expression in transgenic plants did not increase Apx1 expression under controlled conditions. Plants without ZAT12 could not increase Apx1, WRKY25 and ZAT7 expressions in response to H_2O_2 , so that plants without ZAT12 have become more sensitive to H_2O_2 applications than normal plants. It has been revealed that ZAT12 is an important component of oxidative stress signal transmission in *Arabidopsis* and needs Apx1, WRKY25 and ZAT7 during oxidative stress [25]. Transcription profiles of plants that are exposed to H_2O_2 stress, expressing excessive ZAT12 and normal have revealed that the basic expression of ZAT12 in *Arabidopsis* results in increased expression in oxidative and mild stress transcripts. Thus, ZAT12 has been shown to play a key role in reactive oxygen and abiotic stress signal in *Arabidopsis* [26]. ABA application stimulated the increase of both ascorbate peroxidase and superoxide dismutase activities and OsMPK1, OsMPK5 and ZFP182 expressions in rice plant leaves. It has been noted that ABA-induced antioxidant defense needs ZFP182. And the ZFP182 expression is regulated by rice MAPKs in ABA signaling [27]. ABA-activated mitogen active protein kinases

(MAPKs) and ABA-induced H_2O_2 production have been shown to regulate ZFP36 expression in ABA signaling, on the other hand, NADPH oxidase genes expression regulated by ZFP36, H_2O_2 production and the expression of OsMPK genes in ABA signaling. It has been noted that rice plants requires to ZFP36 for tolerance of both water stress and oxidative stresses, for ABA-induced antioxidant defense and for cross-interaction between NADPH oxidase, H_2O_2 and MAPK in the ABA signal [28].

5. Drought stress and C2H2 zinc finger proteins

Over-expression of ZAT18 has increased drought tolerance in *Arabidopsis* while ZAT18 mutation reduced plant tolerance to drought stress. It was found that ZAT18 is expressed in stems and herbal rosette leaves. Sub-cellularly, it has been noted that ZAT18 protein is mainly localized in the nucleus. Overexpressed ZAT18 plants exhibited higher leaf water content, lower ROS content, higher antioxidant enzyme activity compared to wild-type after drought application. RNA sequencing analysis showed that the 423 and 561 genes were transcriptionally regulated by the ZAT18 transgene before and after drought application, respectively. Path enrichment analysis showed that hormone metabolism, stress and signal were over represented in ZAT18 overexpression lines. Various stress-sensitive genes (including COR47, ERD7, LEA6 and RAS1) and hormone signal transduction-related genes (including JAZ7 and PYL5) have been identified as target genes of ZAT18. Taken together, ZAT18 acts as a positive regulator and plays an important role in the plant's response to drought stress [29].

Di19 family, protein 19 induced by drought, is a ZF-Cys2His2 protein. AtDi19-3 is a transcription activator. In plants, AtDi19-3 is significantly stimulated by ABA, mannitol and sodium chloride. Mutation of AtDi19-3 increased tolerance of plants against ABA, drought and high salinity. Excessive expression of AtDi19-3 caused drought, salt and ABA sensitivity. Seed germination and cotyledon greening rates were higher in the AtDi19-3 mutant under the condition of applying sodium chloride, mannitol or ABA. But this data in transgenic plants, in which AtDi19-3 was over-expressed, was lower than in normal plants. Although the roots of AtDi19-3 mutant seedlings were longer, the roots of AtDi19-3 over-expressing transgenic seedlings were shorter than in normal plants. Although the chlorophyll and proline contents in the AtDi19-3 mutant were higher, these data of AtDi19-3 over-expressed seedlings were lower than that of normal plants. While the AtDi19-3 mutant tolerates more droughts, transgenic plants that over-express AtDi19-3 showed more susceptibility to drought than normal plants. In addition, ABA related genes expression signaling pathway varied in the AtDi19-3 mutant and in over-expressing plants of AtDi19-3 [30].

AZF2 and STZ expression has been shown to be strongly stimulated by ABA, cold and high salt stresses, and dehydration. Transgenic *Arabidopsis*, which over-expresses STZ, has become tolerant to growth delay and drought stress. In that study, it was suggested that STZ and AZF2 act as transcriptional suppressors on increased stress tolerance during the growth delay [31]. The expression of OsMSR15 in *Arabidopsis* provides it with drought resistance. Hypersensitive activity to exogenic ABA in this transgenic plant growth during sprouting and seed germination. Transgenic plants also showed less electrolyte leakage, high levels of free proline and increased expressions of a number of stress sensitive genes (such as LEA3, DREB1A, P5CS1 and RD29A) under drought stress. The results showed that OsMSR15 is a significant regulator that plays a role against plant drought stress [32]. In another study, over-expression of TaZFP34 has been shown to have a negative effect on yield performance and mimic the negative effect of drought stress on wheat productivity [33]. STF-2 is also a ZF-Cys2His2 protein.

And its transgenically over-expression increased significantly drought tolerance in transgenic tobacco. The results showed that STF-2 plays a significant role in the response of soybean's to drought stress [34].

6. Other stress and C2H2 zinc finger proteins

VTA2 contains the ZF-Cys2His2 proteins. It controls H_2O_2 detoxification and host plant root infection. And it is an important regulator of fungal pathogenesis [35]. StZFP2 is a Q-type C2H2 zinc finger transcription factor induced by injury and invasion. Previous studies show that Q-type C2H2 TFs are involved in responding to stress and may be protective against drought, salinity, or pathogenic infections when overexpressed. The increase in StPIN2, a classic marker for insect defense in potatoes, was consistent with decreases in larval weight gain [36]. MtSTOP is also a C2H2 zinc finger protein and regulates Medicago's response to H^+ and Al^{3+} toxicity. MtSTOP is expressed in root, stem, nodule and other tissues. MtSTOP is upregulated with acidic pH and Al^{3+} stress or a combination of both. Growth or morphology in mtSTOP mutants did not change under normal conditions; however, mutant seedlings are characterized by significantly reduced root elongation and are sensitive to low pH (pH 4.3) and Al^{3+} stress. Compared to its control, more Al accumulated in the mutant roots and citric acid secreted from the mutant roots was significantly lower in both normal and Al stress conditions. This indicates that MtSTOP hair roots synthesize more citric and malic acids [37]. Regarding aluminum, Rice (*Oryza sativa*) is one of the aluminum tolerant species among small grain cereals. This type of aluminum tolerance occurs with many genes involved in the detoxification of Al at the cellular level. These findings emerged with ART1. ART1 is a C2H2 type zinc finger transcription factor and regulates the expression of 31 genes as down-stream [38].

Conflict of interest

The authors declare no conflict of interest.

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