



Role of *Dof* Transcription Factors under Abiotic Stresses

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Abstract: For the survival of the rapidly growing global population, plant species must exhibit tolerance towards climate change. Plants possess mechanisms to respond to stress by changing their biological processes and stimulating stress-responsive genes. The *Dof* (TFs) family, which binds to DNA with a single finger, reflects a plant-specific group of TFs that play an important part in regulating plants that are facing different types of abiotic stresses which may influence their growth and development. Discovery of this family has made a significant impact on the field of plant sciences. However, the characterization of *Dof* transcription factors in crop plants is currently limited reported. Several *Dof* transcription factors (TFs) of plants have been shown in nature. The transcription factors *TaDofs*, *StDof*, *MnDofs*, *JrDof3TF*, *Va/VvDofs*, *GhDof1*, *OsDof1*, *SmeDof*, *ZmDof*, *CsDof*, *DcDof*, *CaDofs*, *ThDof*, *BraDof*, and *AcDof* are important for abiotic stressors such as heat, cold, salt, drought, and heavy metals. In addition, *Dof* transcription factors play a role in the regulation of factors related to yield and quality. Nevertheless, some outstanding issues remain. The review article provides a summary of the role of various stress-responsive *Dof* transcription factors in response to abiotic stresses. Additionally, this study investigates the limitations and possible opportunities associated with *Dof* transcription factors in the development of crops that are capable of withstanding climate change. Therefore, it is recommended to conduct comprehensive research on *Dof* transcription factors (TFs) across many different transcription factors fields to find their potential novel functionality, which will be beneficial to our retention of the delicate biological processes in plants.

Keywords: Abiotic stress, *Dof*, Transcription factor, Salinity stress, Crop improvement

1. INTRODUCTION

Transcription factors (TFs) are essential to plant regulation and signaling networks [1, 2]. TFs control gene expression by binding to promoter DNA sequences [3-5]. In adaptation to abiotic stress, such as osmotic stress, cold, heat, and drought [1, 6-10] plants need more TFs than animals [5]. Drought, salinity, cold, etc. significantly reduce plant productivity. Stresses can reduce major crop yields by 50 %. Genes or other transcription factors (TFs) linked to abiotic stress increase proline content, close stomata to decrease transpiration, enhance stress-protective enzyme synthesis, and enhance abiotic stress tolerance [11-13]. The

genetic factors TATA, CAAT Box, ARR1, GATA, AGAAA, CAAT, and DNA-binding are major contributors to genetics. A Zinc Finger (*Dof*) factor that's found in the promoter region of *OsRGLP2* is responsible for regulating several plant processes such as defense, light responses, development, and growth. [14]. Transcription factors (TFs) known as DNA-binding with one finger (*DoF*) are linked to the processes of plant growth and development. The *Dof* transcription factors exhibit a DNA-binding domain (C2/C2) that consists of 52 amino acids and a zinc finger that's capable of binding to the 5-(T/A) AAAG-3 target DNA sequence along with a resilient target DNA sequence [15]. The first *Dof* gene in maize was successfully identified [16]

and the interaction of multiple regulatory proteins responsible for the regulation of *Dof* transcription factors via their C-terminal region [17, 18]. Low/high temperatures, high salt treatment, and drought significantly influence plant development and productivity. Abiotic stresses reduce vegetable quality and production [19]. Pepper showed the expression of *CaDofs* as its response to abiotic stress [20], and researchers in the field of tea plant cultivation have carried out investigations into many different transcription factors (TFs). However, the regulatory mechanism of *Dof* transcription factors in tea plants remains difficult to identify [17, 21]. The *Dof* transcription factors (TFs) have significance in various biological processes throughout every stage of the life cycle of plants, and have importance for growth, seed storage protein synthesis, germination of seeds and development, regulatory metabolism, the photosynthesis process, flowering, and responses to stress [22-24]. *Dof* transcription factors regulate secondary metabolic processes like glucosinolate biosynthesis, cell cycle regulation, and flavonoids [25, 26]. They also regulate the cell cycle, phytochrome and cryptochrome signaling, plant hormonal signaling, abaxial-abaxial polarity, nitrogen use, and abiotic and biotic stress tolerance [27, 28]. The *DcDof* transcription factor, as compared to other plant *Dof* factors, has been given little focus in academic research. Furthermore, certain *Dof* genes can regulate both plant growth and stress responses. The enhanced expression of *Arabidopsis CDF3* has been observed to enhance the resistance to drought, cold, and osmotic stress, while also slowing down the start of flowering. This suggests that the gene in concern exerts a regulatory effect over both flowering time and tolerance to abiotic stress [29]. Overexpression of the *Dof* transcription factor *TDDF1* in tomatoes increased flowering-time control gene expression, causing early flowering and increased tolerance to drought, salt, and *Phytophthora infestans* late blight [30]. Under salt stress, the growth of the primary root in rice is decreased. This can be attributed to the suppression of *OsDOF15* expression in the roots, resulting in to decrease in the production of ethylene [31] and studies have shown the importance of *Dof* transcription factors in various biological processes, promoting plant growth and development [32]. Current investigation showed that *Dof* transcription factors play an important role in multiple signaling pathways regulation, in

response to different abiotic stresses, plant growth and development, and other biological processes. The results indicate that *Dof* transcription factors have the potential for regulating both lipid metabolism and stress responses. Nevertheless, the members of the *Dof* TF family have currently to be reported. Current research provides an extensive overview of the resistance to abiotic stress, as well as the evolutionary links and the *Dof* transcription factor family.

2. STRUCTURE, FUNCTION, AND MECHANISM OF ACTION OF VARIOUS GROUPS OF *DOF* TRANSCRIPTION FACTORS

Suspendisse Sequence motifs that match DNA binding domains classify TFs. As shown by comparing the principal classes, *Dof* transcription factors have distinct functions in the hierarchy of response, although many interact as part of their response. Plants use several mechanisms to tolerate ecological problems such as drought, salinity, oxidative stress, cold, heat, and other infections that affect plant growth and development. Due to their sessile nature, environmental challenges can cause suboptimal growth conditions, requiring metabolic pathways to be changeable to allow plants to resist, tolerate, or recover from stress. The complex structure of the abiotic stress response in plants results from the polygenic nature and association between events involving signal transduction and stress response factor synthesis during a time of stress. As plants are sessile (immobile), environmental cues including drought, water logging, salt, mineral toxicity, and temperature change (frost, cold, heat) negatively affect their metabolism, growth, and development [33, 34].

In the same way, the upregulation of *ZmDOF36* resulted in a reduction in the levels of reduced sugars and soluble sugars within the endosperm of maize seeds. On the other hand, an increase in soluble sugar levels was found to promote the synthesis of starch. *ZmDOF36* was found to exert a positive regulatory effect on the expression of various genes associated with starch synthesis, including *ZmAGPS1a*, *ZmAGPL1*, *ZmISA1*, *ZmISA3*, *ZmGBSSI*, and *ZmSSIIa*. This regulation was achieved through the binding of *ZmDOF36* to specific motifs located in the promoters downstream

of these genes [35]. The previous study showed that *ThDOF14* enhances the ability of plants to tolerate salt and osmotic stress. This is achieved through an increase in proline levels and an improvement in the plant's ability to scavenge reactive oxygen species (ROS) [36]. Similarly, it has been observed that *ThDOF14* exhibits a specific affinity for the *DOF* motif present in the downstream promoter region of *TheIF1A*. This interaction suggests that *ThDOF14* may play a role in the plant's response to salt stress and osmotic stress by regulating the expression or engaging in molecular interactions with *TheIF1A* [37]. The study conducted by Cai et al. (2016) showed that the tomato *SIDOF22* gene had an impact on the accumulation of ascorbic acid (AsA) and also enhanced salt tolerance in plants [38]. Figure 1 shows how plants respond to various stresses via activating pathways, gene interaction, and molecular "crosstalk". Plants can defend themselves against different types of stress, which makes possible the identification of the most adaptable and resistant varieties for the benefit of producing a plant with desirable characteristics. Abiotic resistance genes usually stimulate a signal transduction pathway to identify pathogens and acquire resistance. The molecular understanding of

abiotic stress response primarily depends on genetic engineering techniques, such as over-expression or mutation studies, to provide insight into the sensor, signal transduction factors, and antimicrobial factor genes.

3. ROLE OF *DOF* TRANSCRIPTION FACTORS UNDER ABIOTIC STRESSES

Abiotic stressors like heat, cold, drought, flooding, heavy metals, and salt are affecting crop life due to global warming. Abiotic factors limit maize, cotton, rice, and wheat yields by 50 % [39]. Table 1 shows how *Dof* TFs/genes/proteins affect plant abiotic stress tolerance.

3.1. Drought Stress

Drought stress, which is caused by excessive groundwater, decreased precipitation, and high temperatures, depicts a primary contributor to agricultural problems, which exert an adverse effect on the worldwide economy and the food security of a significant number of people by limiting crop growth and production [39, 58].

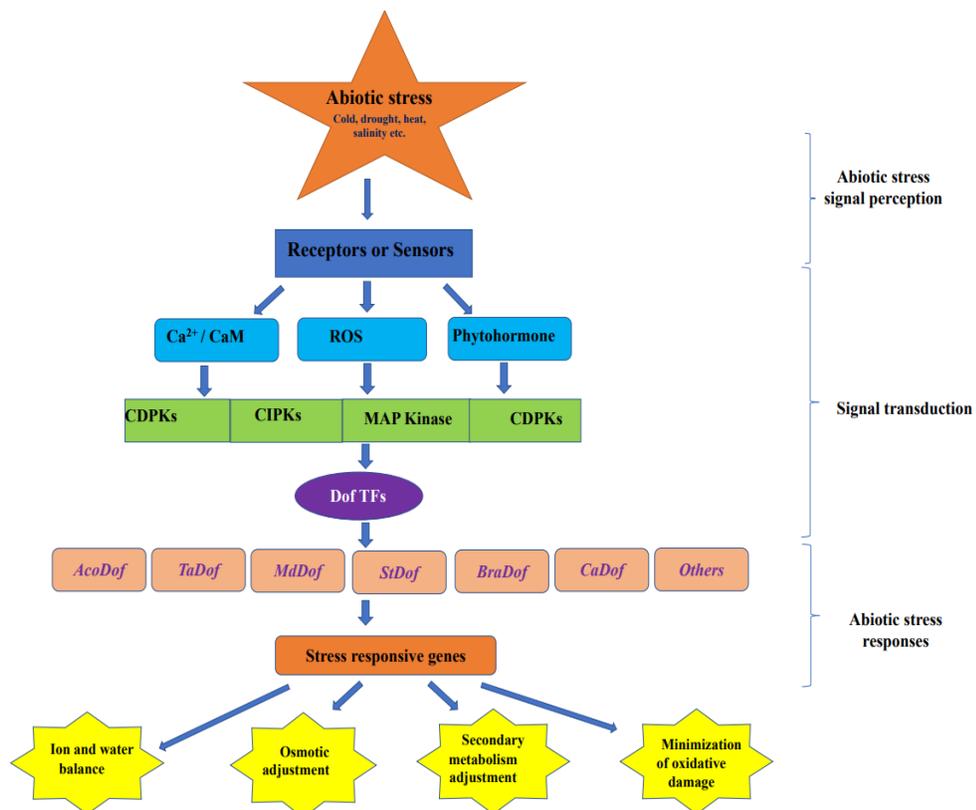


Fig. 1. Model for *Dof* TFs regulation abiotic stress signaling pathways.

Table 1. Role of different *Dof* transcriptional factor gene families in abiotic stress tolerance in plants

Stress	Crop	<i>Dof</i> TFs / Genes/ Proteins	References
Salinity, cold, heat, and drought stress	<i>Ananas comosus</i>	<i>AcoDof1</i> , <i>AcoDof12</i> , <i>AcoDof26</i> , <i>AcoDof22</i> , <i>AcoDof9</i> , <i>AcoDof19</i> , <i>AcoDof23</i> , <i>AcoDof11</i> , <i>AcoDof17</i> , <i>AcoDof20</i> , and <i>AcoDof1</i> .	[40]
Heat, drought, and heavy metals stress	<i>Triticum aestivum</i>	<i>TaDof</i> , <i>TaDof14</i> , <i>TaDof14</i>	[41, 42]
Salinity, drought, cold stress	<i>Malus domestica</i>	<i>MdDof</i>	[5]
Salinity, osmotic, heat and low temperature, and drought stresses	<i>Solanum lycopersicum</i>	<i>SICDFs</i> , <i>SICDF1-5</i>	[27]
Drought, salinity, low temperature, and high temperature	<i>Glycine max</i>	<i>GmDof4.2</i>	
Cold, heat, salinity, and drought stress	<i>Brassica pekinensis</i> Rupr	<i>BraDof</i>	[18]
Salt and osmotic stress	<i>Tamarix hispida</i>	<i>ThDof</i> , <i>ThelF1A</i>	[37]
Temperature, salinity, heat, and irritation	<i>Daucus carota</i>	<i>DcDof</i>	[44]
Heat stress	<i>Oryza sativa</i>	<i>OsDOF27</i>	[45]
Salinity and drought stress	<i>Camellia sinensis</i>	<i>CsDof</i>	[17]
Cold stress	<i>Brassica napus</i>	<i>BnCDF1</i>	[46]
Salt stress	<i>Nelumbo nucifera</i>	<i>NnDofs</i>	[47]
Heat and salinity stress	<i>Capsicum annuum</i>	<i>CaDofs</i>	[20]
Salinity and heat stress	<i>Chrysanthemum morifolium</i>	<i>CmDOFs</i>	[48]
Salinity stress	<i>Camelina sativa</i>	<i>CsDof</i>	[49]
Drought Salt and stress	<i>Tamarix hispida</i>	<i>WRKY (ThWRKY4)</i>	[50]
Salinity stress	<i>Zea mays</i>	<i>ZmDof</i> , <i>ZmDof16</i> , <i>ZmDof22</i> , <i>ZmDof36</i>	[51]
Osmotic, heat, and drought stress	<i>Populus trichocarpa</i>	<i>PtrDofs</i>	[52]
Cold stress	<i>Vitis vinifera</i> grapevine	<i>VaDof17d</i>	[8]
Salinity and salt stress	<i>Gossypium hirsutum</i>	<i>GhDof1</i>	[53]
Heat, cold, heat, and salt stress	<i>Saccharum spontaneum</i>	<i>SsDofs</i>	[15]
Drought and salinity stress	<i>Solanum melongena</i>	<i>SmeDof</i>	[54]
Salt and drought stress	<i>Vaccinium corymbosum</i>	<i>VcDof</i>	[55]
Drought and salinity stress	<i>Solanum tuberosum</i>	<i>StDof</i>	[24]
Drought and salt stress	<i>Rosa chinensis</i>	<i>RchDofs</i>	[56]
Salt stress	<i>Medicago truncatula</i>	<i>MtDof32</i>	[57]

The transcription factor *VyDOF8*, which comes from *Vitis yeshanensis*, a species of Chinese wild grapevine, exhibited a significant rise in expression levels under conditions of drought, cold, and salt-induced stress. *Dof* transcription factors play an important role in improving the responses of plants to drought stress. The overexpression of *VyDOF8*

in tobacco plants has the potential to enhance their ability to withstand drought conditions. This has led to the reported increase in abscisic acid (ABA) concentration, root growth, proline, and chlorophyll accumulation, stress response gene expression, and antioxidant activity [59]. *SICDF1* and *SICDF3* overexpression in *Arabidopsis* increased

drought tolerance [17, 60]. *TaDofs* are nucleus-based transcription factors that affect growth, development, and abiotic responses. Customized annotation revealed that drought stress produced *TaDofs*, which were associated with defense, phytohormone response, growth, development, and metabolism [61]. The increased expression of *Solanum tuberosum Dof (StDof)* genes which can improve growth, development, and abiotic stress tolerance, has been found in response to both drought stress and abscisic acid (ABA) treatments. [24].

3.2. Salinity Stress

The process of global climate change has resulted in several types of environmental stressors, including soil salinity. This abiotic factor is the second largest cause of global productivity in agriculture loss. The adverse impacts of salinity on the growth and productivity of plants are mediated through various physiological, biochemical, and molecular mechanisms. These responses include ion homeostasis regulation, biosynthesis of phytohormones, and antioxidant defense systems activation. Plants respond to salinity by inducing the expression of stress-related genes, proteins, and metabolites that help to alleviate some of the adverse effects of salinity. Increasing salt tolerance becomes essential for maintaining global agronomic productivity. Transcription factors play an important part in the mechanism that causes plants' salt tolerance [62, 63]. *MnDofs* improve lotus salt tolerance [47]. The salinity responses of transgenic tobacco plants have been improved through the application of *BZIP* transcription factors obtained from salt-tolerant lotus root tips [43, 64]. Overexpression of *SICDF1* or *SICDF3* in *Arabidopsis* plants improved salt tolerance, stress-responsive gene expression (*COR15*, *RD29A*, *RD10*), flowering time, and specific target genes and metabolites [65]. *GmWRKY54* overexpression reduced soybean salinity stress [66]. The overexpression of *GhWRKY34* in *Arabidopsis* plants results in a specific absorption of Na^+ or K^+ ions in both roots and leaves, which helps promote the development of salt tolerance [67].

3.3. Heat Stress

Heat stress is a major environmental issue

because of its negative impact on plant growth and development. The negative effects of high temperatures on cellular integrity and viability are well-studied. However, it is significant that plants have developed a mechanism of heat shock response that mitigates the negative impacts of abrupt temperature changes. Thermotolerant plants can endure heat stress, which can alter vegetable crop development, yield, and quality [2, 68-70]. Heat stress affects plant growth, health, and physiological, phenotypic, and genetic expressions [71, 72]. The *JrGRAS2* gene was recently identified as a regulator of heat shock protein (HSP) expression, thereby enhancing the capability of plants to tolerate heat stress. Therefore, *JrGRAS2* is considered an important gene for plant genetic engineering that focuses on improving heat response. The *HsfA1* protein is considered to be an important activator of the key response to heat stress [73-75]. Transcription factors have been found to have an adverse effect on gene expression in response to abiotic stress and the quality of grains. Additionally, the number of *Dof* family members has been shown to regulate glycogen and starch production in grains in response to high temperatures (HS) [76]. The findings suggest that *Arabidopsis* plants with an insertional mutant of *Mterf18* exhibit greater resistance to heat stress and elevated levels of HSP transcripts compared to their wild-type plants [77, 78]. Previous study shows that *shot1* mutants and *ATAD3*-disrupted plants exhibit mitochondrial absorption and signaling problems, ultimately resulting in enhanced heat tolerance in plants. The moso bamboo that survived heat stress exhibits a stimulation of LTR retrotransposons, especially *PHRE1* and *PHRE2* [79].

3.4. Heavy Metal Stress

The effect of heavy metal stress (HM) on plants can be seen through different pathways such as growth inhibition, physiological process delays, and decreased crop productivity. These effects occur due to the change in cell membrane integrity, cellular ionic balance, metabolic balance, protein, and enzyme activity [69, 70]. Heavy metals can cause reactive oxygen species (ROS) and affect physiological functions such as photosynthesis, respiration, and vascular and enzymatic activity. Furthermore, a high level of heavy metals can cause difficulties in ion homeostasis [80]. A previous

study showed that *OsHMP09*, *OsHMP018*, and *OsHMP22* exhibited higher expression levels throughout all tissues. Alternatively, *AtHMP20*, *AtHMP23*, *AtHMP25*, *AtHMP31*, *AtHMP35*, and *AtHMP46* showed higher expression levels in the roots and leaves under various heavy metal stresses [81]. The *NtSOD* gene family enhances heavy metal toxicity tolerance in *Nicotiana tabacum* [82]. A previous study showed that *JrDof3TF* improves the heat stress response of *JrGRAS2* and is a heat response candidate gene in plant molecular breeding [75].

3.5. Cold Stress

The distribution, growth, and yield of crops are all significantly affected by cold stress. Sessile plants have many kinds of physiological and biochemical responses to cold stress, resulting in a 40 % decrease in temperate yields for agriculture. Cold stress adaptation is regulated by TFs and proteins [83, 84]. Cold stress causes 51-82 % of global crop output losses [85]. The study found that overexpression of *Va/VvDofs* resulted in improvements in root development, germination rate, and seed development, which led to improved cold resistance. However, the *Dof17d-Ed* mutant exhibited reduced cold tolerance, as evidenced by a decrease in raffinose family oligosaccharides [8] and moreover, in *Gossypium hirsutum GhDof1* overexpression can improve cold tolerance [53]. Previous study showed that *OsDof1* can enhance cold tolerance in rice act as a potential target for rice genetic breeding [86].

4. CONCLUSION AND FUTURE PERSPECTIVE

This review shows how *Dof* TFs can improve plant responses to various abiotic stresses. These studies show how DNA-binding with one finger (*Dof*) transcription factors can combat environmental challenges and increase yield and productivity under stress. Climate change threatens growth, development, and crop yield due to abiotic factors such as salt, heat, cold, waterlogging, drought, and heavy metals. By focusing on various genes and their regulators, it is urgently necessary to create crops that are tolerant to abiotic stress. The considerable number of *Dof* functional studies presented in this review highlights the existence

of many unanswered questions regarding *Dof* transcription factors. The functional diversity of *Dof* transcription factors has garnered significant interest in recent years. However, the investigation into the molecular mechanisms through which these transcription factors regulate specific biological processes, such as plant growth, dormancy, and germination, has been restricted to a few model plants. Therefore, additional research must be conducted to further current knowledge in this area. In the future, it is of great interest to understand how these factors contribute to the stimulation of plant defense mechanisms against environmental stresses, ultimately resulting in an increase in crop yield and some members of *Dof* may become potential factors to have quite wide application prospects for the development of the food processing and biofuel industries. Therefore, it is important to conduct comprehensive research on *Dof* transcription factors (TFs) across many different fields in order to find their potential novel functionality, which will be beneficial to our retention of the delicate biological processes in plants.

5. CONFLICT OF INTEREST

The authors declared no conflict of interest.

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