

# Plant Transcription Factors and Drought

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Transcription factors (TFs) play a significant role in signal transduction networks spanning the perception of a stress signal and the expression of corresponding stress-responsive genes. TFs are multi-functional proteins that may simultaneously control numerous pathways during stresses in plants—this makes them powerful tools for the manipulation of regulatory and stress-responsive pathways.

3D structure

cis-elements

crops

plant biotechnology

stress-responsive mechanisms

transcriptional complexes

transcriptional regulation

## 1. Introduction

Drought is a major abiotic stress that severely affects crop productivity and distribution. Currently, up to 45% of the world's agricultural land, where 38% of the world human population resides, is subjected to continuous or frequent drought <sup>[1][2]</sup>. Water is essential at every stage of plant growth from seed germination to plant maturation, and the shortage of water is the single most important factor that reduces global crop yields, with far-reaching socio-economic consequences <sup>[2]</sup>. Although under these circumstances, it is challenging to describe drought, in the agricultural context, drought is defined as a prolonged, abnormally dry period when the soil and atmospheric moisture are low, and the ambient air temperature is high, and available water resources are insufficient for agricultural needs <sup>[3]</sup>. Similarly, Lipiec et al. <sup>[4]</sup> noted that drought stress occurs when there is an imbalance between evapotranspiration flux and water intake from the soil. Drought with its associated complexity impacts agriculture and contributes heavily to the development of drought-prone areas leading to poor plant growth and reduces crop yields <sup>[5][6]</sup>. Hence, managing drought is about managing risks that associate with dry-land agriculture, aiming to reduce the impact of drought.

Considering that drought and related stresses and how they affect plants attract significant research, the understanding of plant protective mechanisms and how they are acquired, is of paramount importance. A large body of data related to drought was published specifically on transcription factors (TFs) and in this review we examine this contested topic in seven inter-related sections.

## 2. Natural Variations in Transcription Factors during Drought and Associated Stresses

There is evidence that abiotic stresses could simultaneously affect plant growth and development [7][8][9][10][11][12][13][14], and that plants evolved sophisticated mechanisms to withstand multiple abiotic stresses due to strong selection to adapt to prevailing conditions [2][15][16][17][18]. Addressing multiple stresses by planned experimentation is a major challenge due to the complexity of exposure to these multiple stresses. To gain an insight into the plant adaptation to various stress-inducing conditions, both natural variation and complex mechanisms underlying stress tolerance/resistance should be considered [19][10][14]. Exploring natural variations contributed significantly towards elucidating the gene function without the confounding effects of expression outside of the natural genomic context [18]. Studies in natural variation provided novel insights into adaptive mechanisms shaping plant stress responses and helped uncover novel loci involved in stress responses [12]. For example, drought-responsive genes showed natural variation and allelic variation on previously described loci and novel loci [20][21]. Rao et al. [20] uncovered two alleles for DREBA1 in *Solanum pimpinellifolium*, using a screen of 94 genotypes. These alleles together accounted for 25% of trait-associated phenotypic variation [22]. Additional studies of allelic variation in TFs and downstream drought-responsive genes significantly contributed to plant selection and adaptation [23]. Here, GsZFP1, a new C2H2-type zinc-finger TF, was identified in the soybean wild relative *Glycine soja* [24] and the overexpression of GsZFP1 in alfalfa led to the high expression of various drought-responsive genes [25]. Similarly, Arms et al. [22] mapped a QTL in *Solanum habrochaites*, a drought-tolerant wild tomato that co-localized to C2H2-type zinc-finger TFs on chromosome 9 of the cultivated tomato. Natural variations were explored in the CBF gene family of complex evolutionary patterns. The CBF regulon consists of three regulatory proteins CBF1, CBF 2, and CBF 3, which play key roles under freezing stress. This was supported by population-level investigations in wild tomato *S. peruvianum* and *S. chilense*. Mboup et al. [24] found that CBF3 showed a reduced nucleotide diversity across all populations/species consistent with the strong purifying selection at that locus. Mboup et al. [24] using population-level data also highlighted the complex evolutionary history of CBF genes and showed the advantage of using natural variation to uncover the gene function within a genomic context.

Currently, phenotyping platforms can be used for screening thousands as opposed to hundreds of individual plants for tolerance traits [26][27][28][29][30]. Natural variation can also be used for understanding the genetic architecture of complex traits such as plant tolerance to stresses. For example, association studies in combination with the genetic disequilibrium linkage, are contributing towards dissecting complex trait loci in plants [31]. This technique highlights more precisely the resolution of genome-wide association studies (GWAS) at the gene level, subject to the availability of high-density and genome-wide DNA markers [32]. Additionally, after genome-scale sequencings of large numbers of varieties with different genetic backgrounds are available, GWAS accelerates the genetic dissection of complex traits in crops using natural variations [33][32]. Similarly, Yan et al. [30] suggested the candidate gene association analysis as one of the methods of choice for the discovery and detection of single nucleotide polymorphism. This technique ensures that markers are within or closely linked to genes that contribute to complex traits [30].

### 3. Conclusions and Outlook

In this review, we examined the aspects of plant tolerance to extreme abiotic stresses such as drought and how stress-inducible TFs participate in drought, which in turn regulate the expression of a large array of downstream genes. We advocate that TFs are powerful tools for genetic engineering as their controlled expression can lead to the up- or downregulation of genes under their control. The discovery and descriptions of structure-function relationships of several classes of plant TFs aided in the identification of pathways that control the plasticity of plant growth and control the modulation of plant development in response to abiotic stress. However, the work on plant defense mechanisms controlled by TFs is ongoing. While we need to acknowledge that the progress on molecular mechanisms of TFs progresses, in the future, we need to provide precise molecular descriptions of the function of TFs to understand their precise biological roles. It will be critical to describe: (i) Molecular basis of formation of transcriptional activation and repression complexes, and the influence of post-translational modifications on the formation of these complexes; (ii) mechanisms of activation and repression of target genes, of how TFs form oligomeric assemblies; (iii) 3D structures and folding pathways of TFs, and how structural determinants play roles in DNA recognition and in the activation of complexes; (iv) mechanisms on how these complexes are regulated. Answers to these questions will allow us to develop modified versions of TFs with improved DNA-binding properties and create TFs that will be independent of other upstream regulatory pathways. This information will be useful to define the mechanisms of formation of functional complexes of TFs, and most importantly, the new knowledge could hold promises for informed decisions on suitable TF applications to bioengineer plants with enhanced tolerance to drought and other abiotic stresses.

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