Functional role of DRE-binding transcription factors in abiotic stress

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Abstract

The growth and development of plants is greatly affected by abiotic stress conditions such as drought, soil salinity and low temperature. Plants respond to these environmental challenges through a number of homeostatic mechanisms that maintain the water balance and the integrity of tissues. This includes several regulatory mechanisms that activate the expression of tolerance-effector genes. Here, we summarize recent studies highlighting the role of specific members of the DRE-binding family of transcription factors in the adaptive responses to abiotic stresses.

Introduction

Plants are exposed to many types of abiotic stress during their life cycle. Water deficit caused by drought, low temperature or high salt concentration in the soil, is one of the most common environmental stresses that affects growth and development of plants and leads to alterations in metabolism and gene expression. Water deficit causes various alterations in plants, such as stomatal closure, decrease of turgor and changes in the composition of the cell wall or plasma membranes, which can act as signals triggering adaptation responses. Although relatively little is known about the mechanisms for sensing these changes, it is well established that abscisic acid (ABA) is a major physiological signal that induces drought responses (Gomez et al. 1988; Mundy and Chua 1988). ABA-dependent signalling systems have been described that mediate adaptation to drought by activation of bZIP proteins, which then bind to ABA-responsive regulatory elements (ABREs) in target genes and induce their transcription (Busk and Pagés 1998; Shinozaki and Yamaguchi-Shinozaki 2000). Another ABA-dependent pathway
requires protein biosynthesis of the MYC and MYB transcription factors, which function cooperatively to regulate the expression of target genes (Abe et al. 1997).

However, in Arabidopsis not all drought responses appear to be mediated by ABA, since a number of genes are known to be induced by drought, salt and cold in aba (ABA-deficient) and abi (ABA-insensitive) mutants (Yamaguchi-Shinozaki and Shinozaki 1994). This suggests the existence of alternative regulatory systems of gene expression during the stress response. In addition, recent studies have identified ABA-dependent and ABA-independent pathways that lead to rapid responses to drought or cold and function through members of the AP2/ERF family of transcription factors (Yamaguchi-Shinozaki and Shinozaki 1994, Kizis and Pagés, 2002). Although these different pathways are usually considered to function independently from each other, it is certainly possible that some cross-talk exists between them (Figure 1).

![Diagram](image_url)

**Figure 1.** Regulation of Drought-Responsive gene expression via ABA-dependent and independent pathways.

194
Drought Responsive Elements (DREs)

Molecular analyses of genes induced under environmental stress conditions have led to the identification of specific *cis*-regulatory elements that mediate this activation. Drought Responsive Elements (DREs) have been reported to be involved in various types of abiotic stress responses via ABA-dependent and ABA-independent pathways as shown in Table 1 (Busk et al. 1997; Shinozaki and Yamaguchi-Shinozaki 1997; Busk and Pagès 1998; Haarke et al. 2002; Kizis and Pagès 2002). The DRE sequence (5′-TACCGACAT-3′) plays an important role in regulating gene expression in response to drought and other types of abiotic stress in plants. The DRE element was first identified in the promoter of the drought-responsive gene *rd29A* (also, known as *cor78* and *lti78*) (Yamaguchi-Shinozaki and Shinozaki 1994). *rd29A* encodes a protein similar to the so-called late embryogenesis abundant proteins (LEAs, Wise 2003), which is induced both during the maturation of embryos and by several types of stresses in vegetative tissues and probably functions as a tolerance effector. The DRE element is essential for the induction of *rd29A* gene expression by osmotic stress such as drought and high salinity as well as by low temperature, but not for the activation of this gene in response to ABA (Yamaguchi-Shinozaki and Shinozaki 1994).

Subsequently, new *cis*-elements related to the DRE motif have been identified. One such motif is the C-repeat responsive element (CRT), which contains the core (5′-CCGAC-3′) and was initially identified in the promoter of cold-inducible genes from *Arabidopsis*. This sequence is essential for induction of several genes by low-tem-

**Table 1. DRE cis-elements.**

<table>
<thead>
<tr>
<th>Cis-element</th>
<th>Plant specie</th>
<th>Protein</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Drought Responsive Element (DRE)</strong></td>
<td><em>Arabidopsis thaliana</em></td>
<td>DREBs</td>
<td>Liu et al. 1998</td>
</tr>
<tr>
<td>5′-TACCGACAT-3′</td>
<td><em>Oriza sativa</em></td>
<td>OsDREBs</td>
<td>Dubouzet et al. 2003</td>
</tr>
<tr>
<td></td>
<td><em>Triticum aestivum</em></td>
<td>TaDREB</td>
<td>Shen et al. 2003b</td>
</tr>
<tr>
<td></td>
<td><em>Atriplex hortensis</em></td>
<td>AhDREB1</td>
<td>Shen et al. 2003a</td>
</tr>
<tr>
<td><strong>C-repeat Responsive Element (CRT)</strong></td>
<td><em>Arabidopsis thaliana</em></td>
<td>CBFs</td>
<td>Stockinger et al. 1997</td>
</tr>
<tr>
<td>5′-TGCCGAC-3′</td>
<td><em>Brassica napus</em></td>
<td>BnCBFs</td>
<td>Gilmour et al. 1998</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Haake et al. 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Gao et al.2002</td>
</tr>
<tr>
<td><strong>Drought Responsive Element 1 (DRE1)</strong></td>
<td><em>Zea mays</em></td>
<td>Unidentified maize protein</td>
<td>Busk et al. 1997</td>
</tr>
<tr>
<td>5′-ACCGAG -3′</td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Drought Responsive Element 2 (DRE2)</strong></td>
<td><em>Zea mays</em></td>
<td>DBF1 and DBF2</td>
<td>Kizis and Pagès 2002</td>
</tr>
</tbody>
</table>
perature including the *Brassica napus* BN115 gene and the wheat gene WCS120 (Baker et al. 1994; Jiang et al. 1996; Ouellet et al. 1998). The CRT motif was also described in the promoters of *kin1*, *kin2* and *rab18*, three other cold-regulated genes, from *Arabidopsis* (Kurkela and Borg-Franck 1992; Lang and Palva 1992). Studies of these genes in ABA-deficient and ABA-insensitive mutants showed activation of the genes during drought and cold stress independently of ABA. However, recent evidence indicates that some DRE/C-repeat motifs behave differently and can respond to an ABA-dependent mechanism (Haake et al. 2002). For example, the dehydration responsive element 2 (DRE2) identified in the maize *rab17* promoter is involved in ABA-dependent responses to osmotic stress. This site includes the typical core motif (5’-ACCGAC-3’) and was identified by *in vivo* footprinting analysis of embryos and leaves (Busk et al. 1997). Increased DRE2 occupancy was observed after both drought treatment and ABA induction, and *in vivo* analyses showed that this element is important for activation of the *rab17* promoter in both situations. In addition, the *rab17* promoter contains the related DRE1 cis-element (5’-ACCGAG-3’), which mediates ABA-dependent regulation in the embryo but appears insensitive to stimulation by drought in vegetative tissues (Busk et al. 1997; Busk and Pagès 1998).

**DRE-binding factors: a complex family**

Several DRE-binding proteins have been identified from *Arabidopsis*, rice, maize and other plants that specifically interact with the DRE sequence. The first cDNA clone for a DRE-binding protein was isolated in a yeast one-hybrid screening; it was named CBF1 (CRT-binding factor1) (Stockinger et al. 1997). In parallel, other authors have cloned additional CBF-related genes such as DREBs from *Arabidopsis* (Gilmour et al. 1998; Haake et al. 2002), ZmDBFs from maize (Kizis and Pagès 2002), BnCBFs from *Brassica napus*, HvCBF1 from barley (Xue 2002), OsDREBs from rice (Chen et al. 2003; Dubouzet et al. 2003), AhDREB1 from *Atriplex hortensis* (Shen et al. 2003a) and TaDREB1 from wheat (Shen et al. 2003b).

The DRE-binding factors constitute a subgroup within a large family of plant transcription factors present in many plant species. These proteins, collectively known as AP2/ERF proteins, share a conserved DNA-binding domain of about 60-70 amino acids (Figure 2). This AP2/ERF domain was originally identified in APETAL2 of *Arabidopsis* (Jofuku et al. 1994) and EREBP1 of tobacco (Ohme-Takagi and Shinshi 1995). The AP2/ERF domain is a new type of DNA-binding sequence that includes two regions: the YRG region (YRG element) of about 20-amino acids-long and the N-terminal stretch rich in basic and hydrophilic residues. It was proposed to have a role in the DNA binding by making a direct contact with the DNA due to its basic character (Okamuro et al. 1997). The second region is the RAYD sequence of about 40 amino acids, which contains 18 amino acids capable of forming an amphipathic
α-helix in the C-terminal sequence and is thought to have an important role for the structure and function of the domain (Jofuku et al. 1994; Okamuro et al. 1997). The RAYD element was proposed to mediate protein-protein interactions through α-helix or to have an alternative role in DNA binding through interactions of the hydrophobic face of the α-helix with the major groove of DNA.

DRE-binding proteins contain specific residues within their AP2/ERF domain that may determine their capacity to bind the DRE/CRT element (Jofuku et al. 1994; Okamuro et al. 1997; Kizis et al. 2001; Sakuma et al. 2002). These factors do not present any apparent similarity outside this region. Together, these observations suggest the existence of a complex family of DRE-binding proteins with the potential to mediate different responses to abiotic stresses.

Gene regulation

Various stress conditions induce the expression of DRE-binding factor genes. Increased accumulation of these transcripts has been found in response to drought, high salinity, low temperature and ABA treatments. Also, the induction of these transcripts is organ-specific and proportional to the length of the stress treatment. Transcription fac-

![Multiple alignment of the AP2/ERF domain of DRE-binding proteins. The amino acid sequences of the AP2/ERF domain of DRE-binding proteins were aligned. The shaded boxes presented the amino acid identity (dark grey; the identical amino acids, medium grey: the similar amino acids, light grey: the rest of the amino acids). Protein names are indicated at the left. Accession numbers correspond to NCBI database of analysed proteins: ZmDBF1 (AAM80486), ZmDBF2 (AAM80485), OsDBF1 (AAP56252), OsDBF2 (AAP70033), OsCBF (AAG59619) OsDBF1 (AAP92125), OsDREB1A (AAP02486), OsDREB2A (AAP02487), TaDREB1 (AAL01124), DREB1A/CFB3 (BAA33791), DREB1B/CFB1 (BAA33792), DREB1C/CFB2 (BAA33793), CBF4/DREB1D (NP_200012), DREB2A (BAA33794), DREB2B (BAA33795), BnCBF5 (AAM18958), BnCBF7 (AAM18959), BnCBF16 (AAM18960), BnCBF17 (AAM18961) and LeDREB3 (AAO13360).]
tors CBF/DREBs control the expression of many stress-inducible genes in *Arabidopsis* (Stockinger et al. 1997; Gilmour et al. 1998; Seki et al. 2003; Shinozaki et al. 2003). Under normal conditions, neither CBF nor CBF-regulated target genes, such as COR genes are expressed. However, at 4 °C they are rapidly activated in response to cold treatments. The expression of the CBF genes is induced very early, followed by the expression of CBF-regulated target genes (Gilmour et al. 1998; Fowler and Thomashow 2002). Genes of the CBF family are mainly induced by cold stress (Zarka et al. 2003) However, a new member of the CBF family, CBF4, has recently been identified. This factor is up-regulated by drought, stress and ABA but not by low temperature (Haake et al. 2002). On the other hand, DREB2A and DREB2B subfamilies are induced by drought stress and are able to induce the expression of genes that contain the DRE/CRT cis-acting element in their promoters (Liu et al. 1998).

CBF homologues have also been found in other plants. BnCBFs factors from *Brassica napus* function in the same way, as trans-acting factors in low-temperature responses, controlling the expression of cold-induced genes through an ABA-independent pathway. In wheat, the TaDREB1 product is induced by low temperature, salinity and drought, and regulates the expression of the target gene, Wcs120, which contains DRE motifs in its promoter (Shen et al. 2003b). In rice, expression of OsDREB1A and OsDREB1B was induced by cold, whereas expression of OsDREB2A was induced by dehydration and salt stress.

In maize, we have identified a new DRE-binding factors subfamily (Figure 3). ZmDBF1 (Figure 3A), but not the related ZmDBF2 gene (Figure 3B), is induced during maize embryogenesis and in all tissues of seedlings exposed to desiccation, salt and ABA. Functional analyses using particle bombardment showed that ZmDBF1 acts as an activator of DRE2-dependent transcription of *nab17* by ABA. However, ZmDBF2 overexpression causes the opposite effects and represses *nab17* basal expression and its induction by ABA. These results suggest that ABA plays a role in the regulation of ZmDBFs activity, and indicates the existence of an ABA-dependent pathway for the regulation of genes through the DRE/CRT element (Kizis and Pagès 2002).

**Figure 3a and 3b.** Sequence comparison between ZmDBFs and close homologues.

3a. Comparison between ZmDBF1 and their homologues. The protein sequences of ZmDBF1, rice DBFs (OsDBF1 and 2), two putative DNA-binding proteins from *Arabidopsis* and tomato DREB3 were aligned. The shaded boxes presented the amino acid identity (dark grey: the identical amino acids; medium grey: the similar amino acids; light grey: the rest of the amino acids). Protein names are indicated at the left. Accession numbers correspond to NCBI database of analyzed proteins. ZmDBF1 (AAP80486), OsDBF1 (AAP56252), OsDBF2 (AAP70033), LeDREB3 (AAO13360), NP_195688 and NP_201318 from *Arabidopsis*.

3b. Comparison between ZmDBF2 and its homologue. The protein sequences of ZmDBF2 (AAP80485) and rice putative DNA binding protein (NP_922723) were aligned. The shaded boxes presented the amino acid identity (dark grey: the identical amino acids; medium grey: the similar amino acids; light grey: the rest of the amino acids). Protein names are indicated at the left. Accession numbers corresponding to NCBI database of analyzed proteins are also indicated.
Figure 3a.

Figure 3b.
An increasing number of DRE-binding factors have been identified in recent years that mediate stress responses. The challenge now is to understand the relative roles of these proteins in different pathways, their coordinated regulation and the interaction with other signalling elements. In the case of stress-regulatory factors, functional analyses in vivo are important not only to understand the molecular mechanisms of stress tolerance in plants but also to provide tools that might improve crop productivity. In this regard, transcription factors are promising tools for genetic engineering because their overexpression can lead to the up-regulation of a large array of downstream genes.

Indeed, overexpression of specific DRE-binding genes in transgenic plants resulted in plants more tolerant to drought, salt and freezing stresses, as shown in Table 2. Arabidopsis plants overexpressing CBF1 showed increased tolerance to cold stress without a cold acclimation period (Gilmour et al. 1998; Liu et al. 1998), while expression of cbf1 gene in tomato increased drought (Hsieh et al. 2002). The overexpression of CBF4 under non-stress conditions activated genes that are normally induced by cold and drought. These transgenic plants are also more tolerant to freezing and osmotic stress. These results indicate that CBF4 plays a role in the signal transduction of drought adaptation in Arabidopsis and suggest a cross-talk between DREB2 and CBF/DREB1 regulatory systems (Haake et al. 2002). Transgenic Arabidopsis plants expressing OsDREB1A up-regulate stress-inducible target genes regulated by DREB1A in Arabidopsis and present higher tolerance to drought, salinity and freezing (Dubouzet et al. 2003). In transgenic tobacco, AhDREB1 led to the accumulation of its putative downstream genes and these transgenic lines showed an increased stress tolerance (Shen et al. 2003a).

On the other hand, constitutive overexpression of CBF/DREB genes generally causes negative effects on plant growth and development. One solution to overcome this problem is the use of stress-inducible promoters to control the expression specifically. This approach has been successfully used for the DREB1A/CFB3 Arabidopsis gene. Plants expressing DREB1A/CFB3 under control of the constitutive cauliflower mosaic virus 35S promoter show a dwarf phenotype; however, plants expressing the same gene under the regulation of rd29A, a stress-inducible promoter, were phenotypically normal and more tolerant to drought, salinity and freezing (Kasuga et al. 1999; Yamaguchi-Shinozaki and Shinozaki 2001). Similarly, tomato plants overexpressing CBF1 under the control of cauliflower mosaic virus 35S promoter showed severely reduced growth and were more tolerant to drought stress, while transgenic plants expressing the factor directed by the barley ABRC1 or the Arabidopsis cor15a stress-inducible promoters showed normal growth, while retaining water deficit resistance (Hsieh et al. 2002).

Post-translational modification such as phosphorylation may be necessary for the activation of protein factors under drought stress conditions (Busk and Pagès 1998). This modification enhances the DNA-binding activity of several transcription factors. Among the DRE-binding proteins, the DREB2A subfamily is induced...
by drought and high-salinity stress, which indicates an important role of this group of proteins in dehydration-responsive gene expression. However, the overexpression in *Arabidopsis* of both AtDREB2A and OsDREB2A genes induced a weak expression of the target genes. The authors suggest that not only transcriptional regulation but also post-translational modification may be required for the activation of DREB2A proteins under drought stress conditions. Both AtDREB2A and OsDREB2A factors contain a conserved serine/threonine-rich region adjacent to the AP2/ERF domain, with putative sites of phosphorylation (Liu et al. 1998; Nakashima et al. 2000; Dubouzet et al. 2003).

### DBF1 defines a new family of DRE-binding factors

Sequence comparison of ZmDBF1 from maize, and CBF/DREBs from *Arabidopsis* and other plants (Liu et al. 1998; Kizis and Pagès 2002; Dubouzet et al. 2003), show that sequence similarities are restricted to the AP2/ERF DNA-binding

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**Table 2.** Functional analysis of DRE-binding proteins in transgenic plants.

<table>
<thead>
<tr>
<th>Overexpression result</th>
<th>Gene overexpressed</th>
<th>Plant</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drought tolerance</td>
<td>AtDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Kasuga et al. 1999, Yamaguchi-Shinozaki and Shinozaki 2001</td>
</tr>
<tr>
<td></td>
<td>AtCBF1</td>
<td>Tomato</td>
<td>Hsieh et al. 2002</td>
</tr>
<tr>
<td></td>
<td>AtCBF4</td>
<td><em>Arabidopsis</em></td>
<td>Haake et al. 2002</td>
</tr>
<tr>
<td></td>
<td>OsDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Dubouzet et al. 2003</td>
</tr>
<tr>
<td></td>
<td>AhDREB1</td>
<td>Tobacco</td>
<td>Shen et al. 2003a</td>
</tr>
<tr>
<td>High salinity tolerance</td>
<td>AtDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Kasuga et al. 1999, Yamaguchi-Shinozaki and Shinozaki 2001</td>
</tr>
<tr>
<td></td>
<td>AtCBF1</td>
<td><em>Arabidopsis</em></td>
<td>Jaglo-Ottosen et al. 1998</td>
</tr>
<tr>
<td></td>
<td>OsDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Dubouzet et al. 2003</td>
</tr>
<tr>
<td></td>
<td>AhDREB1</td>
<td>Tobacco</td>
<td>Shen et al. 2003a</td>
</tr>
<tr>
<td>Freezing tolerance</td>
<td>AtDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Kasuga et al. 1999, Yamaguchi-Shinozaki and Shinozaki 2001</td>
</tr>
<tr>
<td></td>
<td>AtCBF1</td>
<td><em>Arabidopsis</em></td>
<td>Jaglo-Ottosen et al. 1998</td>
</tr>
<tr>
<td></td>
<td>AtCBF3</td>
<td><em>Brassica napus</em></td>
<td>Jaglo-Ottosen et al. 2001</td>
</tr>
<tr>
<td></td>
<td>AtCBF4</td>
<td><em>Arabidopsis</em></td>
<td>Haake et al. 2002</td>
</tr>
<tr>
<td></td>
<td>OsDREB1A</td>
<td><em>Arabidopsis</em></td>
<td>Dubouzet et al. 2003</td>
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</table>
domain (Figure 2). In this domain, two amino acids, the 14th valine and the 19th glutamic acid conserved in all DREB/CBF proteins have important roles in the determination the DNA-binding specificity (Liu et al. 1998; Sakuma et al. 2002; Dubouzet et al. 2003). However, DBF1 proteins have a conserved valine in the 14th position but there is a highly-conserved leucine at the 19th position which is present in all DBF1 homologues identified to date. The conversion of the glutamic acid to leucine might be responsible for different DNA-binding specificities between DBF1s and CBF/DREB proteins.

There is no significant homology outside the AP2/ERF domain between DBF1 and CBF/DREB factors. It has been shown that AP2/ERF proteins contain a basic region in the N-terminal that might function as nuclear localization signal and an acidic C-terminal region that might function as a transcriptional activation domain. The highly conserved C-terminal region of the maize DBF1 in rice, tomato and Arabidopsis homologues suggests that the DBF1 C-terminal region might be involved in specific transcriptional roles of these proteins (Figure 3A).

Expression analyses of ZmDBF1, DREB2A, OsDREB2A and CBF4 show that these genes are induced by dehydration and high-salt stresses (Liu et al. 1998; Haake et al. 2002; Kizis and Pagès 2002; Dubouzet et al. 2003). The corresponding proteins specifically bound to the DRE sequence in vitro and activated the transcription of the β-glucuronidase (GUS) reporter gene driven by the DRE sequence in Arabidopsis leaf, rice protoplasts and maize callus cells (Liu et al. 1998; Kizis and Pagès 2002; Dubouzet et al. 2003). Comparative analyses under stress conditions of organ-specific gene expression revealed several differences. Thus, in roots and stems the ZmDBF1 gene expression is strongly induced by high salt, dehydration and ABA treatment, while DREB2A expression is induced only by high salt and dehydration in roots and specifically by high salt in stems. A weak induction of DREB2A was also observed in leaves by osmotic stress, while the ZmDBF1 expression was induced by dehydration, salt, and ABA treatment in this organ (Nakashima et al. 2000; Kizis and Pagès 2002).

The main difference between DBFs and CBF/DREB subfamilies consisted of the up-regulation by ABA. The CBF/DREB members with the CBF4 exception and the DBF2 factors are not induced by exposure to exogenous ABA, suggesting that these proteins probably participate in an ABA-independent signalling transduction pathway. By contrast, the CBF4 factor and the DBF1 subgroup are up-regulated by exogenous ABA and participate in ABA-dependent pathways (Liu et al. 1998; Haake et al. 2002; Kizis and Pagès 2002; Dubouzet et al. 2003). Like CBF4, DBFs factors may also be involved in the cross-talk between DREB/CBF regulatory networks in response to environmental stress.

In summary, based on sequence characteristics, specific expression in response to environmental stresses and regulation by ABA, the maize DBF1 defines a new family of DRE-binding factors that may play an important role in drought tolerance in plants.
Conclusions and perspectives

Understanding the molecular mechanisms of plant responses to environmental stresses such as drought, high salinity and low temperature is crucial for the manipulation of plants in order to improve their stress tolerance and crop productivity. DRE-binding factors are a subfamily of AP2/ERF transcription factors with important roles in directing changes in gene expression during stress. This family of transcription factors regulate various stress-inducible genes separately or co-operatively and constitute gene networks. Functional analysis of DRE-binding factors will provide more information on the complex regulatory networks that are involved in the responses to abiotic stresses and future work should help delineate the different signalling pathways and their cross-talk during adaptation of plants to drought and other stresses.

Acknowledgements

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Xue GP (2002) An AP2 domain transcription factor HvCBF1 activates expression of cold-responsive genes in barley through interaction with a (G/a)(C/t)CGAC motif. Biochim Biophys Acta 1577:63-72