Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Transcriptional Regulatory Networks in Cellular Responses and Tolerance to Dehydration and Cold Stresses

Kazuko Yamaguchi-Shinozaki[1,2,4]
and Kazuo Shinozaki[3,4]

[1]Laboratory of Plant Molecular Physiology, Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo 113-8657, Japan; email: akys@mail.ecc.u-tokyo.ac.jp

[2]Biological Resources Division, Japan International Research Center for Agricultural Sciences (JIRCAS), Ibaraki 305-8686, Japan

[3]RIKEN Plant Science Center, Yokohama 203-0045, Japan

[4]CREST, Japan Science and Technology Corporation (JST), Japan

Annu. Rev. Plant Biol.
2006. 57:781–803

The *Annual Review of Plant Biology* is online at plant.annualreviews.org

doi: 10.1146/annurev.arplant.57.032905.105444

Copyright © 2006 by Annual Reviews. All rights reserved

First published online as a Review in Advance on March 3, 2006

1543-5008/06/0602-0781$20.00

Key Words

gene expression, *cis*-element, transcription factor, stress tolerance

Abstract

Plant growth and productivity are greatly affected by environmental stresses such as drought, high salinity, and low temperature. Expression of a variety of genes is induced by these stresses in various plants. The products of these genes function not only in stress tolerance but also in stress response. In the signal transduction network from perception of stress signals to stress-responsive gene expression, various transcription factors and *cis*-acting elements in the stress-responsive promoters function for plant adaptation to environmental stresses. Recent progress has been made in analyzing the complex cascades of gene expression in drought and cold stress responses, especially in identifying specificity and cross talk in stress signaling. In this review article, we highlight transcriptional regulation of gene expression in response to drought and cold stresses, with particular emphasis on the role of transcription factors and *cis*-acting elements in stress-inducible promoters.

Contents

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

INTRODUCTION

Drought, high salinity, and low temperature are all environmental conditions that have an adverse effect on the growth of plants and the productivity of crops. Plants have adapted to respond to these stresses at the molecular and cellular levels as well as at the physiological and biochemical levels, thus enabling them to survive. Expression of a variety of genes is induced by these stresses in various plants (39, 103, 114). The products of these genes function not only in stress tolerance but also in the regulation of gene expression and signal transduction in stress responses (5, 104, 125).

Abscisic acid (ABA) is produced under water-deficit conditions and plays an important role in the tolerance response of plants to drought and high salinity. Exogenous application of ABA also induces a number of genes that respond to dehydration and cold stress (104, 136). Nevertheless, the role of ABA in cold stress-responsive gene expression is not clear. Several reports have described genes that are induced by dehydration and cold stresses but that do not respond to exogenous ABA treatment (104, 132, 136). This suggests the existence of ABA-independent, as well as ABA-dependent, signal transduction cascades between the initial stress signal and the expression of specific genes. The molecular mechanisms regulating gene expression in response to dehydration and cold stresses

have been studied by analyzing the *cis*- and *trans*-acting elements that function in ABA-independent and ABA-responsive gene expression during the stresses in *Arabidopsis* (104, 132).

In this review article, we focus on transcriptional regulation of gene expression in response to dehydration and cold stresses, with particular emphasis on the role of transcription factors and *cis*-acting elements in stress-inducible promoters. The signal transduction pathways controlling abiotic stress responses are very complex, and many excellent review articles in this area were recently published (5, 9, 15, 126).

FUNCTION OF OSMOTIC- AND COLD-INDUCIBLE GENES

Transcriptome analysis using microarray technology is a powerful technique, which has proven very useful for discovering many stress-inducible genes involved in stress response and tolerance (96, 104). Numerous genes that are induced by various abiotic stresses have been identified using various microarray systems (12, 22, 52, 62, 72, 87, 93, 94, 121). Recently, more stress-inducible genes were identified using the Affimetrix 22K Gene Chip ATH1, and the data obtained are now avilable from TAIR URL (**http://www.arabidopsis.org/**).

Genes induced during stress conditions function not only in protecting cells from stress by producing important metabolic proteins, but also in regulating genes for signal transduction in the stress response. Thus, these gene products are classified into two groups (22, 62, 94). The first group includes proteins that probably function in stress tolerance, such as chaperones, LEA (late embryogenesis abundant) proteins, osmotin, antifreeze proteins, mRNA-binding proteins, key enzymes for osmolyte biosynthesis such as proline, water channel proteins, sugar and proline transporters, detoxification enzymes, enzymes for fatty acid metabolism, proteinase inhibitors, ferritin, and lipid-transfer proteins. Some of these stress-inducible genes that encode proteins, such as key enzymes for osmolyte biosynthesis, LEA proteins, and detoxification enzymes have been overexpressed in transgenic plants and produce stress-tolerant phenotypes in the transgenic plants (19, 36). These results indicate that the gene products of the stress-inducible genes really function in stress tolerance.

The second group contained protein factors involved in further regulation of signal transduction and gene expression that probably function in stress response. They included various transcription factors, suggesting that various transcriptional regulatory mechanisms function in the drought-, cold-, or high-salinity-stress signal transduction pathways (95). These transcription factors could regulate various stress-inducible genes cooperatively or separately, and may constitute gene networks. Functional analysis of these stress-inducible transcription factors should provide more information on the complex regulatory gene networks that are involved in responses to drought, cold, and high-salinity stresses. The others were proteins kinases, protein phosphatases, enzymes involved in phospholipids metabolism, and other signaling molecules such as calmodulin-binding protein and 14-3-3 proteins. At present, the functions of most of these genes are not fully understood. Some of these stress-inducible regulatory genes that encode proteins such as transcription factors have been overexpressed in transgenic plants and generate stress-tolerant phenotypes in the transgenic plants (113, 120, 135).

REGULATION OF GENE EXPRESSION BY OSMOTIC AND COLD STRESSES

The expression patterns of genes induced by drought, high-salinity, and cold stresses in *Arabidopsis* were analyzed by northern blot analyses and recently by microarray and quantitative Polymerase Chain Reaction (PCR)

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

(22, 62, 94, 121). Through this work more than 300 genes have been identified as being stress-inducible. Among these genes, more than half of the drought-inducible genes are also induced by high salinity, indicating the existence of significant cross talk between the drought and high-salinity responses. By contrast, only 10% of the drought-inducible genes were also induced by cold stress (94).

Results also indicate broad variations in the timing of induction of theses genes and that there are at least two groups showing different expression profiles. In one group gene expression was rapid and transient in response to drought, high-salinity, and cold stresses, reached a maximum at several hours, and then decreased. Most of these genes encode regulatory protein factors such as zinc-finger protein, SOS2-like protein kinase PKS5, bHLH transcription factor, DREB1A, DREB2A, AP2/ERF domain-containing protein RAP2, and growth factor-like protein. In the other group, gene expression slowly and gradually increased after stress treatment within 10 h. Most of these genes encode functional proteins such as LEA proteins, detoxification enzymes, and enzymes for osmoprotectant synthesis. On the other hand, some these stress-inducible genes respond to ABA, whereas others do not. ABA-deficient mutants were used to analyze cold-inducible and drought-inducible genes that respond to ABA (102, 104). Several genes were induced by exogenous ABA treatment, but they were also induced by cold or drought in ABA-deficient (aba) or ABA-insensitive (abi) *Arabidopsis* mutants. These results indicate that there are not only ABA-dependent pathways but also ABA-independent pathways involved in the abiotic stress response (**Figure 1**).

A MAJOR ABA-INDEPENDENT GENE EXPRESSION UNDER OSMOTIC AND COLD STRESSES

The *Arabidipsis RD29A/COR78/LTI78* gene is induced by drought, cold, and ABA. However, this gene is induced in *aba* or *abi* mutants by both drought and cold stresses, which indicates that it is governed by both ABA-dependent and ABA-independent regulation under drought and cold conditions (130). Analyses of this promoter have shown that a 9-bp conserved sequence, TACCGACAT, named the DRE, is an essential *cis*-element for regulating *RD29A* induction in the ABA-independent response to dehydration and cold (131). DRE is also found in the promoter regions of many drought- and cold-inducible genes (103, 114). Similar *cis*-acting elements, named C-repeat (CRT) and low-temperature-responsive element (LTRE), both containing an A/GCCGAC motif that forms the core of the DRE sequence, regulate cold-inducible promoters (4, 46, 109, 114). The cDNAs encoding DRE-/CRT-binding proteins, *CBF/DREB1* (C-repeat Binding Factor/DRE Binding protein 1), and *DREB2*, were isolated using yeast one-hybrid screening (68, 109). These proteins contained the conserved DNA-binding domain found in the ERF (etheylene-responsive element-binding factor) and AP2 proteins. These proteins specifically bind to the DRE/CRT sequence and activate the transcription of genes driven by the DRE/CRT sequence (**Figure 2**).

In *Arabidopsis*, three genes encoding DREB1/CBF lie in tandem on chromosome 4 in the following order: DREB1B/CBF1, DREB1A/CBF3, and DREB1C/CBF2. There are two DREB2 proteins, DREB2A and DREB2B (25). Expression of the *DREB1/CBF* genes is induced by cold, but not by dehydration and high-salinity stresses (68, 105). By contrast, expression of the *DREB2* genes is induced by dehydration and high-salinity stresses but not by cold stress (68, 79). Later, Sakuma et al. (90) reported three novel *DREB1/CBF*-related genes and six novel *DREB2*-related genes that were not expressed at high levels under various stress conditions. The three DREB1 proteins are probably major transcription factors involved in cold-induced gene expression and the DREB2A and DREB2B proteins are involved

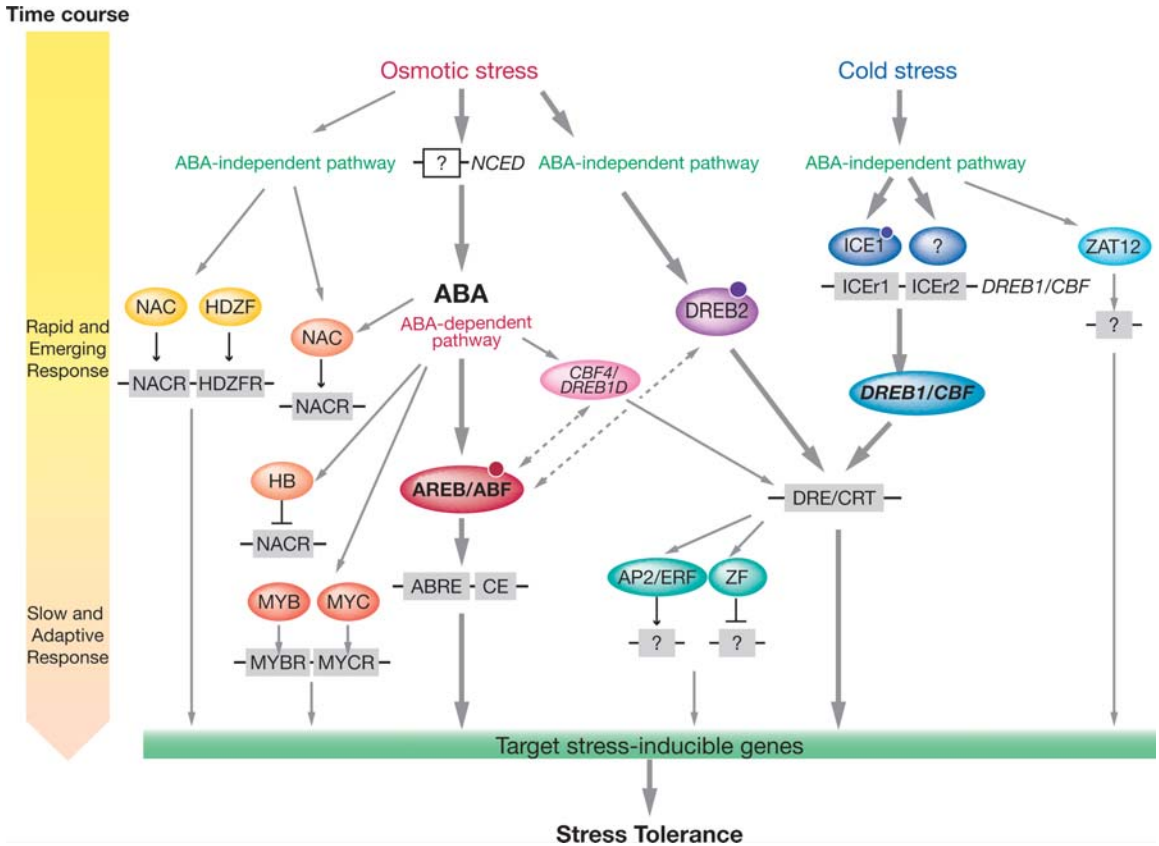

Figure 1

Transcriptional regulatory networks of *cis*-acting elements and transcription factors involved in osmotic- and cold-stress-responsive gene expression in *Arabidopsis*. Transcription factors controlling stress-inducible gene expression are shown in colored ellipses. *cis*-acting elements involved in stress-responsive transcription are shown in boxes. Small filled circles reveal modification of transcription factors in response to stress signals for their activation, such as phosphorylation. Regulatory cascade of stress-responsive gene expression is shown from top to bottom. Early and emergency responses of gene expression are shown in the upper part, and late and adaptive responses in the bottom. Thick gray arrows indicate the major signaling pathways and these pathways regulate many downstream genes. Broken arrows indicate protein-protein interactions.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

in high-salinity- and drought-induced gene expression. However, the expression of one of the *CBF/DREB1* genes, *CBF4/DREB1D*, is induced by osmotic stress (31) and the other two CBF/DREB1 genes, DDF1/DREB1F and DDF2/DREB1E, are induced by high-salinity stress (71), suggesting the existence of cross talk between the CBF/DREB1 and the DREB2 pathways.

DREB1/CBFs: Major Transcription Factors that Regulate Many Cold-Inducible Genes Involved in Stress Tolerance

Transgenic *Arabidopsis* plants overexpressing *CBF1/DREB1B* under control of the cauliflower mosaic virus (CaMV) 35S promoter showed a high tolerance to freezing stress (44). Overexpression of the

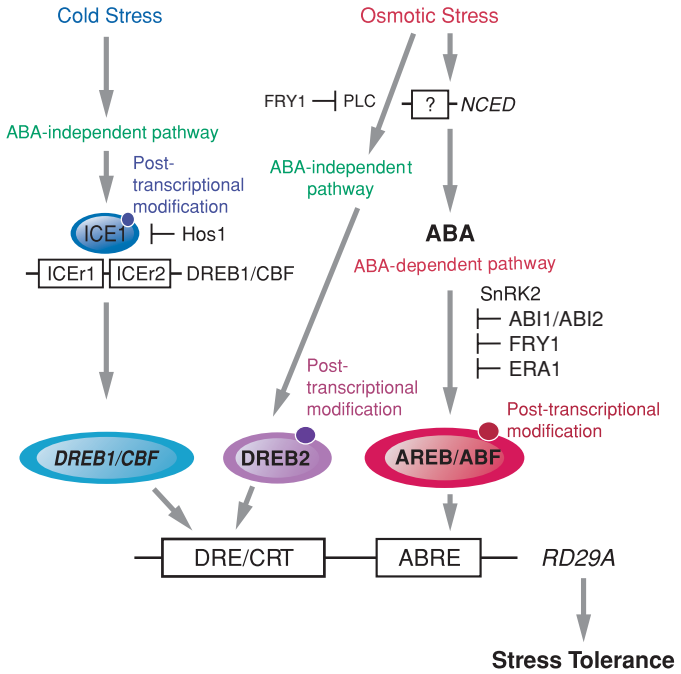

Figure 2

A model of the induction of the *RD29A/cor78/lti78* gene. The *RD29* gene contains both ABRE and DRE/DRT *cis* elements in its promoter. Two different DRE/CRT-binding proteins, DREB1/CBF and DREB2, distinguish two different signal transduction pathways in response to cold and drought stresses, respectively (68). A transcriptional activator, ICE1 (Inducer of CBF Expression 1), functions upstream of the DRE/DREB regulon (14). HOS1 functions as a negative regulator of ICE1 (64). FRY1 functions as a negative regulator of drought, cold, and ABA responses (124). SnRK2 is involved in ABA signaling. ABI1, ABI2, and ERA1 function as negative regulators for ABA signaling.

DREB1A/CBF3 under the control of the CaMV 35S promoter also increased the tolerance to drought, high-salinity, and freezing stresses (28, 50, 68). These transgenic plants also caused growth retardation under normal growth conditions. Use of the stress-inducible *RD29A* promoter instead of the constitutive CaMV 35S promoter for the overexpression of DREB1A/CBF3 minimizes the negative effects on plant growth (50).

More than 40 genes downstream of DREB1/CBF have been identified through the use of both cDNA and GeneChip microarrays (22, 72, 94, 121). Many of their protein products, such as RNA-binding proteins, sugar transport proteins, desaturase, carbohydrate metabolism-related proteins, LEA proteins, KIN (cold-inducible) proteins, osmoprotectant biosynthesis protein, and protease inhibitors, function against stresses and are probably responsible for the stress tolerance of the transgenic plants. The downstream genes also included genes for transcription factors such as C2H2 zinc-finger-type and AP2/ERF-type transcription factors, suggesting the existence of further regulation of gene expression downstream of the DRE/DREB regulon (72, 89). The product of one such downstream gene, *STZ*, functions as a transcriptional repressor, and its overexpression retards growth and induces tolerance to drought stress (89). The target downregulated genes of STZ might promote plant tolerance and inhibit plant growth under stress conditions. Conserved sequences in the promoter regions of the genes directly downstream of *DREB1A* were analyzed, and A/GCCGACNT was found in their promoter regions between –51 and –450 as a consensus DRE (72). The recombinant DREB1A/CBF3 protein bound to A/GCCGACNT more efficiently than to A/GCCGACNA/G/C. Thus, analysis of promoter regions of direct target genes of a transcription factor allows the accurate elucidation of a *cis*-acting element that functions in plants.

Recently, Vogel et al. (121) reported analysis of the upregulated and downregulated genes of CBF2/DREB1C using the Affymetrix GeneChip containing probe sets for approximately 24,000 *Arabidopsis* genes. This analysis revealed that the CBF2/DREB1A-regulated genes included a significant portion (28%) of these cold-induced genes. Additionally, the changes that occur in the *Arabidopsis* metabolome in response to cold were examined and the role of the CBF/DREB1 cold-response pathway were assessed (18). When the metabolite profiles for nonacclimated and cold-acclimated wild-type plants were compared with nonacclimated CBF3/DREB1C overexpression plants and the data were subjected to hierarchical clustering, the results indicated

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

that the metabolome of the nonacclimated CBF3/DREB1C overexpressor was more similar to that of cold-acclimated than to that of nonacclimated wild-type plants. Thus, DREB1/CBF regulates many stress-inducible genes and has a prominent role in the cold-responsive gene expression in *Arabidopsis*.

The DREB/DRE Regulons in Plants Other Than *Arabidopsis*

DRE/CRT functions in gene expression in response to stress in tobacco plants, which suggests the existence of similar regulatory systems in tobacco and other crop plants (131). The DRE/CRT-related motifs have been reported in the promoter region of cold-inducible *Brassica napus* and wheat genes (46, 84). However, the orthologous genes of DREB1/CBF have been isolated in many plant species such as wheat, *B. napus*, rice, barley, maize, and cherry (17, 20, 26, 43, 54, 86, 100, 101, 119, 128). Overexpression of the *Arabidopsis DREB1/CBF* genes in transgenic *B. Napus* or tobacco plants induced expression of orthologs of *Arabidopsis* CBF/DREB1-targeted genes and increased the freezing and drought tolerance of transgenic plants (43, 51). Constitutive overexpression of CBF1/DREB1B in transgenic tomato increased drought, chilling, and oxidative stress tolerance (37, 38, 135).

In rice, four DREB1/CBF homologous-genes and one DREB2 homologous gene, OsDREB1A, OsDREB1B, OsDREB1C and OsDREB1D, and OsDREB2A, respectively, have been isolated (20). Overexpression of OsDREB1A in transgenic *Arabidopsis* resulted in improved high-salinity and freezing stress tolerance. A DREB1/CBF-type transcription factor, ZmDREB1A, was also identified in maize (86). The ZmDREB1A protein was shown to be involved in cold-responsive gene expression, and the overexpression of this gene in *Arabidopsis* resulted in improved stress tolerance to drought and freezing. These transgenic plants also showed growth retardation. These results indicate that similar regulatory systems are conserved in monocots as well as dicots. Pellegrineschi et al. (85) showed that overexpression of DREB1A/CBF3 driven by the stress-inducible *RD29A* promoter in transgenic wheat improved drought stress tolerance. Oh et al. (82) reported that constitutive overexpression of DREB1A using the 35S promoter in transgenic rice resulted in increased stress tolerance to drought and high salinity. These observations suggest that the DRE/DREB regulon can be used to improve the tolerance of various kinds of agriculturally important crop plants to drought, high-salinity, and freezing stresses by gene transfer.

Cis-Acting Regulatory Elements and Transcription Factors that Function Upstream of CBF3/DREB1A

A gene for a transcription factor, Inducer of CBF Expression 1 (ICE1), was identified through the map-based cloning of the *Arabidopsis ice1* mutation. The *ice1* mutation affects the expression of the *CBF3/DREB1A* promoter::*LUC* transgene (14). *ICE1* encodes a MYC-like bHLH protein that regulates the expression of *CBF3/DREB1A* but not that of other *CBF/DREB1* genes, indicting that there are different expression mechanisms among the three *CBF/DREB1* genes. Molecular analysis of the *DREB1C/CBF2* promoter identified multiple *cis*-acting elements involved in cold-responsive gene expression (105, 134; Y. Imura, unpublished information). Zarka et al. (134) reported two promoter sequences, designated *ICEr1* and *ICEr2*, that function cooperatively to induce gene expression under cold conditions. *ICEr1* contains the sequence CACATG, which includes a consensus recognition site for bHLH proteins, CANNTG (73). Therefore, *ICEr1* is a potential binding site for the ICE1 protein. However, ICE1 does not regulate the expression of *CBF2/DREB1C*. Thus, the transcription factors that bind to these *cis*-acting elements remain to be identified. A DNA-binding protein that interacts with

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

ICEr1 of the DREB1C/CBF promoter has been isolated using yeast one-hybrid screening and shown to be a MYC-like bHLH protein that is different from ICE1 (Y. Imura, unpublished information). These results suggest the redundant involvement of MYC-type bHLH transcription factors in the cold-responsive expression of DREB1/CBF genes.

Novillo et al. (81) reported that the *cbf2* mutant, in which the CBF2/DREB1C gene has been disrupted, has higher capacity to tolerate freezing, dehydration, and salt stresses. They found that CBF/DREB1-regulated genes showed stronger and more sustained expression in the *cbf2* plants, which results from increased expression of CBF1/DREB1B and CBF3/DREB1A in the mutant. Thus, CBF2/DREB1C functions as a negative regulator of *CBF1/DREB1B* and *CBF3/DREB1A* expression in *Arabidopsis*, indicating complex regulation of *DREB1/CBF* gene expression.

The DREB2 Proteins Function in Osmotic Stress-Responsive Gene Expression

The DREB2A protein has a conserved ERF/AP2 DNA-binding domain and recognizes the DRE sequence like DREB1A (68). Among the eight DREB2-type proteins, DREB2A and DREB2B are major transcription factors that function under dehydration and high-salinity stress conditions (79, 90). However, overexpression of DREB2A in transgenic plants neither caused growth retardation nor improved stress tolerance, suggesting that the DREB2A protein requires post-translational modification such as phosphorylation for its activation (68). Nevertheless, the activation mechanism of the DREB2A protein has not yet been elucidated. Domain analysis of DREB2A using *Arabidopsis* protoplasts revealed that a negative regulatory domain exists in the central region of DREB2A and deletion of this region transforms DREB2A to a constitutive active form. Overexpression of the constitutive active form of DREB2A resulted in growth retardation in transgenic *Arabidopsis* plants. These transgenic plants revealed significant tolerance to drought stress but only slight tolerance to freezing. Microarray analyses of the transgenic plants revealed that DREB2A regulates expression of many dehydration-inducible genes. However, some genes downstream of DREB2A are not downstream of DREB1A, which also recognizes DRE/CRT but functions in cold-stress-responsive gene expression (Y. Sakuma, unpublished information). The genes downstream of DREB2A play an important role in drought stress tolerance, but alone are not sufficient to withstand freezing stress.

OTHER ABA-INDEPENDENT GENE EXPRESSION UNDER OSMOTIC AND COLD STRESSES

There are several dehydration-inducible genes that do not respond to either cold or ABA treatment, suggesting the existence of another ABA-independent pathway in the dehydration stress response. These genes include early response to dehydration1 (*ERD1)*, which encodes a Clp protease regulatory subunit, ClpD (78). *ERD1* is not only induced by dehydration, but also upregulated during natural senescence and dark-induced senescence (106). Promoter analysis of *ERD1* in transgenic plants indicates that the *cis*-acting elements responsible for gene expression during dehydration and etiolation are separately located in two discrete portions of the *ERD1* promoter. Moreover, two different novel *cis*-acting elements, a MYC-like sequence (CATGTG) and a 14-bp *rps1* site 1-like sequence, are involved in induction by dehydration stress (106). Recently, three cDNAs encoding MYC-like sequence-binding proteins—*ANAC019*, *ANAC055*, and *ANAC072*—were isolated by the yeast one-hybrid screening method (115). Microarray analysis of transgenic plants overexpressing either *ANAC019*, *ANAC055*, or *ANAC072* revealed that several stress-inducible genes

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

were upregulated in the transgenic plants, and the plants showed significantly increased drought tolerance. However, *ERD1* was not upregulated in the transgenic plants. cDNAs for the transcription factor that binds to the 14-bp *rps1* site 1-like sequence was isolated by using one-hybrid screening. These cDNAs encoded zinc-finger homeodomain (ZFHD) proteins and one of these genes, ZFHD1, was shown to function as a transcriptional activator in response to dehydration stress (L.-S. P. Tran, unpublished information). Overproduction of both the NAC and ZFHD proteins increased expression of *ERD1*, indicating that both *cis*-acting elements are necessary for expression of *ERD1*. The NAC proteins function as transcription activators in cooperation with the ZFHD proteins or alone.

Several genes for transcription factors are also induced under cold conditions. One such gene, *ZAT12*, was overexpressed under the control of the CaMV 35S promoter in transgenic *Arabidopsis* plants, and upregulated genes in the plants were analyzed using microarray. More than 20 cold-inducible genes were upregulated in the transgenic plants and these transgenic plants showed a small, but reproducible, increase in freezing tolerance, indicating that ZAT12 functions in cold-responsive gene expression and plays an important role in cold acclimation (121).

A MAJOR ABA-RESPONSIVE GENE EXPRESSION UNDER OSMOTIC STRESSES

ABA plays an important role in the adaptation of vegetative tissues to abiotic stresses such as drought and high salinity, as well as in seed maturation and dormancy (11, 104). ABA promotes stomatal closure in guard cells, mediating by solute efflux, and regulates the expression of many genes that may function in dehydration tolerance in both vegetative tissues and seeds (33). Many ABA-inducible genes contain a conserved, ABA-responsive, *cis*-acting element named ABRE (ABA-responsive element; PyACGTGGC) in their promoter regions. The ABRE functions as a *cis*-acting DNA element involved in ABA-regulated gene expression. This sequence was first identified in the wheat *Em* gene, which functions mainly in seeds during late embryogenesis (30), and in the rice *RAB16* gene, which is expressed in both dehydrated vegetative tissues and maturating seeds (76). ABRE is a major *cis*-acting element in ABA-responsive gene expression.

However, a number of environmentally induced genes other than ABA contain a similar conserved *cis*-acting element called the G-box (CACGTGGC) (74). Deletion and mutational analyses of promoters responsive to light, UV radiation, and coumaric acid have also shown that disruption of the G-box compromises the ability of each promoter to respond to its respective stimulus. All of these promoters require at least one *cis*-acting element in addition to the G-box for appropriate transcriptional activation. For ABA-responsive transcription, a single copy of ABRE is not sufficient. ABRE and coupling elements such as CE1 and CE3 constitute an ABA-responsive complex in the regulation of wheat *HVA1* and *HVA22* genes (98, 99). Two ABRE sequences are necessary for the expression of *Arabidopsis RD29B* in seeds and for the ABA-responsive expression of *RD29B* in vegetative tissue (117). One of these ABRE sequences might function as a coupling element. Most of the known coupling elements have similarity with ABREs and contain an A/GCGT motif (35). Either additional copies of the ABRE or coupling elements are necessary for ABA-responsive gene expression.

Arabidopsis cDNAs encoding the bZIP transcription factors referred to as ABRE-binding (AREB) proteins or ABRE-binding factors (ABFs) were isolated using the yeast one-hybrid screening method (16, 117). Among these AREB/ABF proteins, expression of AREB1/ABF2, AREB2/ABF4, and ABF3 was upregulated by ABA, dehydration, and high-salinity stresses. They function as *trans*-acting activators through transient expression studies in protoplasts (117). Their

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

activities were reduced in the ABA-deficient *aba2* mutant and in the ABA-insensitive *abi1* mutant, but were enhanced in the ABA-hypersensitive *era1* mutant (60, 61, 117). In the *Arabidopsis* genome, 75 distinct bZIP transcription factors exist and 13 members are classified as a homologous subfamily of AREBs that contain three N-terminal (C1, C2, C3) and one C-terminal (C4) conserved domains (6, 45, 111). Most of the AREB subfamily proteins are involved in ABA-responsive signal transduction pathways in vegetative tissues or seeds (16, 21, 69, 117). *Arabidopsis AREB1/ABF2*, *AREB2/ABF4*, and *ABF3* were mainly expressed in vegetative tissues but not in seeds (16, 117), whereas *Arabidopsis ABI5* and *EEL* were expressed during seed maturation and/or germination (6, 21, 69). Rice homolog TRAB1 and barley homolog HvABI5 also activate ABA-responsive gene expression in seeds (13, 34). It is possible that redundancy and tissue-specific expression of these genes may be important for their function.

Kang et al. (49) reported that overexpression of ABF3 and ABF4/AREB2 resulted in ABA-hypersensitive phenotypes in germination and seedling growth stages in *Arabidopsis*. These transgenic plants also showed improvement of drought stress tolerance and the expression of some ABA-responsive genes, such as LEA class genes (*RD29B*, *rab18*), cell cycle regulator genes (*ICK1*), and protein phosphatase 2C genes (*ABI1* and *ABI2*), suggesting that AREB/ABF proteins are involved in ABA response and stress tolerance in plants. Moreover, ABF2/AREB1 was shown to be an essential component of glucose signaling, and its overexpression also improved stress tolerance to drought (53). However, AREB1/ABF2 and AREB2/ABF4 require ABA for their maximum activation, as shown by their low transactivation abilities in protoplasts prepared from the ABA-deficient *aba2* mutant (117). ABA-responsive 42-kDa kinase activities phosphorylate conserved regions of AREB/ABFs, which suggests that ABA-dependent phosphorylation may be involved in activation of the AREB subfamily proteins (117). In rice, TRAB1 was also shown to be phosphorylated rapidly in response to ABA (48).

Phosphorylation-/dephosphorylation-regulated events play important roles in ABA signaling. Several type-2 SNF1-related protein kinases (SnRK2-type) such as AAPK (ABA activated protein kinase) in *Vicia faba* (67) and OST1/SRK2E in *Arabidopsis* (77, 133) were reported as ABA-activated protein kinases, and were shown to mediate the regulation of stomatal aperture and function upstream of ABA-responsive expression. In *Arabidopsis*, 9 of 10 SnRK2 are activated by hyperosmolarity and 5 of the 9 SnRK2 are activated by ABA (8). Recently, ABA-activated SnRK2 protein kinases were shown to phosphorylate the conserved regions of AREB/ABFs (25). These kinases might phosphorylate and activate the AREB/ABF-type proteins in *Arabidopsis*. In rice, 10 SnRK2 protein kinases were reported. All family members are activated by hyperosmotic stress and three of them are also activated by ABA (57). These rice ABA-activated SnRK2 can phosphorylate an ABRE-binding factor TRAB1 (58). Dominant negative mutations of both *ABI1* and *ABI2* encoding type 2C protein phosphatase cause the ABA-insensitive mutants *abi1* and *abi2* (65, 66, 75). Because null mutations of ABI1 and ABI2 resulted in ABA hypersensitivity, ABI1 and ABI2 are thought to negatively regulate ABA-dependent responses (29).

Overexpression of AREB1/ABF2 in transgenic plants is not sufficient to activate its downstream genes such as *RD29B*. Domain analysis of AREB1 using *Arabidopsis* protoplasts revealed that an activation domain exists in the N-terminal region of AREB1. To overcome the masked transactivation activity of AREB1, a constitutive active form of AREB1 was created using the N-terminal activation and bZIP DNA-binding domains. Transgenic *Arabidopsis* plants overexpressing the active form of AREB1 showed ABA hypersensitivity and enhanced drought tolerance, and eight

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

genes in two groups were upregulated: LEA-class genes and ABA- and dehydration-stress-inducible regulatory genes such as linker histone H1 and AAA ATPase. In the promoter region of each gene, two or more ABRE motifs were found. By contrast, an *areb1* null mutant and a dominant loss-of-function mutant of AREB1 with a repression domain exhibited ABA insensitivity and some of the upregulated genes were downregulated (24). Thus, AREBs/ABFs regulate ABA-mediated ABRE-dependent gene expression that enhances drought tolerance in vegetative tissues, and phosphorylation/dephosphorylation plays an important role in the activation of the AREB/ABF proteins.

OTHER TYPES OF ABA-DEPENDENT GENE EXPRESSION UNDER DEHYDRATION STRESS

ABRE-like motifs are not involved in the ABA regulation of some stress-inducible genes such as *RD22*. Induction of the dehydration-inducible *RD22* is mediated by ABA and requires protein biosynthesis for its ABA-dependent expression (1). MYC and MYB recognition sites in the *RD22* promoter function as *cis*-acting elements in the dehydration-inducible expression of *RD22* (2). A MYC transcription factor, AtMYC2 (rd22BP1), and a MYB transcription factor, AtMYB2, bind these *cis*-elements in the *RD22* promoter and cooperatively activate the expression of *RD22*. These two transcription factors are synthesized after the accumulation of endogenous ABA, indicating that they play roles in a late stage of the plant's response to different stresses. Transgenic plants overproducing MYC and MYB had higher sensitivity to ABA and revealed osmotic stress tolerance (2). Microarray analysis of the transgenic plants indicated the presence of several target genes such as ABA-inducible genes, including an *AtADH* gene, and jasmonic-acid (JA)-inducible genes (2). By contrast, an AtMYC2 mutant was less sensitive to ABA and showed significantly decreased ABA-induced gene expression of *RD22* and *AtADH1*. Recently, AtMYC2 was also reported as a transcription factor that functions in JA and JA-ethylene-regulated defense responses in *Arabidopsis* (3, 7, 70). Cross talk occurs on AtMYC2 between ABA- and JA-responsive gene expression at the MYC recognition sites in the promoters. In addition, genetic analysis of *AtMYC2* suggests that it acts as a negative regulator of blue-light-mediated photomorphogenic growth (129). AtMYC2 might be a common transcription factor of ABA, JA, and light-signaling pathways in *Arabidopsis*.

Arabidopsis RD26 encodes a NAC protein and is induced not only by dehydration but also by ABA. Transgenic plants overexpressing *RD26* were highly sensitive to ABA, whereas *RD26*-repressed plants were insensitive (23). Microarray analysis showed that ABA- and stress-inducible genes were upregulated in *RD26*-overexpressing plants and repressed in *RD26*-repressed plants, indicating that a *cis*-regulatory factor, the NAC recognition site, may function in ABA-dependent gene expression under stress conditions.

The homeodomain-containing transcription factor ATHB6 binds to an AT-rich *cis*-acting element CAATTATTG and interacts with ABI1. The interaction between ATHB6 and ABI1 is positively correlated with the PP2C activity of the ABI1 catalytic domain. Transgenic *Arabidopsis* plants that constitutively express *ATHB6* revealed ABA insensitivity in a subset of ABI1-dependent responses. Thus, ATHB6 functions as a negative regulator downstream of ABI1 in the ABA signal transduction pathway (32). AtERF7 binds to a *cis*-acting element, a GCC-box, and acts as a repressor of GCC-box-mediated transcription. AtERF7 interacts with the protein kinase PKS3, which is a global regulator of ABA responses and can be phsphorylated by PKS3. Overexpression of *AtERF7* in transgenic *Arabidopsis* plants reduced ABA responses in guard cells and decreased drought tolerance, whereas reductions in *AtERF7* expression caused ABA hypersensitivity in guard

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

cells, seed germination, and seedling growth. AtERF7 may bind to the GCC-box of ABA-induced genes and repress further gene expression. The DNA-binding and/or transcriptional repressor activity of AtERF7 may be regulated by PKS3 via phosphorylation (108).

Maize ERF/AP2-type transcription factors DBF1 and DBF2 can bind the DRE/CRT sequence of a maize *rab17* gene. However, these proteins were grouped into a different subfamily from those of DREB1A/CBF and DREB2A. DBF1 was shown to be an activator of the ABA-dependent expression of the *rab17* gene, whereas DBF2 overexpression reduced promoter activity in either control or ABA-induced conditions (55). Various kinds of transcription activators and repressors function in ABA-dependent transcription in plants.

REGULATION OF ABA BIOSYNTHESIS AND DEGRADATION DURING DEHYDRATION AND REHYDRATION

ABA is synthesized de novo during dehydration, and degraded during rehydration after dehydration. Recently, many genes involved in ABA biosynthesis during dehydration were identified based on genetic and molecular approaches, especially in *Arabidopdis* (80). Among them, AtNCED3 for 9-*cis*-epoxycarotenoid dioxygenase (42), AAO3 for abscisic aldehyde oxidase (97), AtABA3 for MoCo sulfurase (123), and AtZEP (121) for zeaxanthin epoxidase are upregulated by dehydration, but AtABA2 is not. NCED is a key enzyme of ABA biosynthesis, and *AtNCED3* is most strongly induced by dehydration and high salinity. Overexpression of *AtNCED3* improved dehydration stress tolerance in transgenic plants and its knockout mutant showed a dehydration-sensitive phenotype (42). This indicates that AtNCED3 must have an important role in ABA accumulation during dehydration. The regulation of *AtNCED3* gene expression is important in the dehydration-induced biosynthesis of ABA; however, this theory has yet to be fully demonstrated.

ABA is catabolized to inactive form by oxidation or conjugation (80). Recently, a major regulatory step in the oxidative pathway of ABA catabolism was shown to be ABA 8′-hydoxylase, a kind of cytochrome P450, and its gene was determined to be CYP707As (63, 88). CYP707As are strongly induced by exogenous ABA treatment, dehydration, and rehydration. Among the 4 CYP707As, CYP707A3 is the major ABA-catabolizing enzyme and is mainly expressed in vegetative tissues. Its expression is controlled by dehydration/rehydration (63, 116). The expression profile of *CYP707A3* in response to rehydration is very rapid compared with that of the rehydration-inducible gene, proline dehydrogenase ProDH (83, 116). Regulation of *CYP707A3* gene expression may be regulated by a novel regulatory system in response to rehydration.

REGULATION OF GENE EXPRESSION DURING REHYDRATION AFTER DEHYDRATION

Many genes that are regulated during rehydration after dehydration have been identified using microarray analysis (83). These rehydration-inducible genes function in recovery from stress conditions. Among them, gene expression for proline dehydrogenease ProDH has been extensively studied during dehydration and rehydration. ProDH functions in proline catabolism during rehydration. The ProDH promoter has been extensively analyzed to show that ACTCAT is an important *cis*-acting element in rehydration-responsive gene expression (91). Many rehydration-inducible gene promoters contain the ACTCAT motif that functions in rehydration-responsive gene expression (83). Recently, ACTCAT-binding proteins were identified as ATB2-type bZIP transcription factors (ATB2/AtbZIP11,

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

AtbZIP2, AtbZIP44, and AtbZIP53) based on the binding specificity (92). The ATB2 subgroup of bZIP proteins specifically bind to ACTCAT and transactivate the ACTCAT-containing promoter in transient expression using protoplasts. ATB2 subgroup bZIP transcription factors function in hypoosmolarity-inducible gene expression.

GENETIC ANALYSIS OF SIGNAL TRANSDUCTION IN RESPONSE TO DEHYDRATION AND COLD STRESSES

A unique mutant screening system in transgenic *Arabidopsis* plants using a firefly luciferase reporter gene (*LUC*) under the control of the *RD29A* promoter was developed to screen *Arabidopsis* mutants with altered induction of stress-responsive genes by dehydration, high salinity, cold, and ABA. Using this system, many *Arabidopsis* mutants have been isolated that exhibit altered expression of the *RD29A::LUC* gene at constitutive (*cos*), high (*hos*), or low (*los*) levels in response to various abiotic-stress or ABA treatments (40). The mutated genes function not only upstream of *RD29A* induction in signal transduction pathways but also in post-transcriptional regulation of the activation of the DREB1/CBF, DREB2, and/or AREB/ABF transcription factors.

The occurrence of mutations with differential responses to dehydration, high salinity, cold, and/or ABA reveals complex cross talk among signaling pathways in dehydration, high-salinity, and cold-stress responses, and suggests that stress-signaling pathways are not completely independent. Recently, many genes were identified using map-based cloning such as *fiery1 (fly1)/hos2*, *fry2*, *hos1*, *hos9*, *hos10*, *los1*, *los2*, *los4*, *los5/aba3*, *los6/aba1*, and *sad1* (126). Some of the products of these genes function directly in the regulation of transcription. The *hos1* mutation causes enhanced induction of the CBF/DREB1 transcription factors by low temperature as well as of their downstream cold-responsive genes (41). HOS1 encodes a novel protein that contains a RING-finger motif, which may function in the degradation of the ICE protein (14, 64). *Hos1* is ubiquitously expressed in all plant tissues and the HOS1 protein resides in the cytoplasm at normal growth temperatures. However, in response to low-temperature treatments, it accumulates in the nucleus. FRY2/CBL1 functions as a transcriptional repressor and contains a region homologous to the catalytic domain of RNA polymerase II C-terminal domain phosphatases found in yeast and animals (59, 126). FLY2/CPL1 also contains two double-stranded RNA-binding domains that may function in mRNA processing.

The *hos9* mutation occurs in a homeodomain transcription factor gene that affects gene expression and freezing tolerance without changing the expression of *CBF/DREB1* genes. Mutation of *HOS9* also alters several developmental characteristics including growth rate, flowering time, and trichome density. *HOS*9 may control freezing tolerance mainly through constitutive pathways separate from the CBF/DREB1 regulon (137). The *hos10* mutants are extremely sensitive to freezing temperatures, completely unable to acclimate to the cold, and hypersensitive to salinity. Induction of *NCED3* (a gene encoding the rate-limiting enzyme in ABA biosynthesis) by dehydration and ABA accumulation are reduced by this mutation. *HOS10* encodes a putative R2R3-type MYB transcription factor that is localized to the nucleus. HOS10 is essential for cold acclimation and may affect dehydration stress tolerance in plants by controlling stress-induced ABA biosynthesis (138).

The *fly 1* mutation results in superinduction of ABA- and stress-responsive genes. FLY1 encodes an inositol polyphosphate 1-phosphatase, which functions in the catabolism of inositol 1, 4, 5-trisphosphate (IP3). *Fly1* mutant plants accumulate more IP3 than do the wild-type plants in both control and ABA-treated plants (124). FLY1 is a general negative regulator that controls cold, osmotic stress, and ABA signal

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Table 1 Transcription factors that function in osmotic- and cold-stress-responsive gene expression and their binding sites in the promoter regions of the stress-inducible *Arabidopsis* genes

Transcription factor name	Transcription factor type	*cis* element	Gene	Stress condition	References
DREB1A/CBF3	AP2/ERF	DRE/CRT	*RD29A*, *Cor15A*	Cold	(27, 68)
DREB1B/CBF1	AP2/ERF	DRE/CRT	*RD29A*, *Cor15A*	Cold	(68, 108)
DREB1C/CBF2	AP2/ERF	DRE/CRT	*RD29A*, *Cor15A*	Cold	(27, 68)
CBF4/DREB1D	AP2/ERF	DRE/CRT		Dehydration	(31)
DREB2A	AP2/ERF	DRE	*RD29A*	Dehydration	(68)
DREB2B	AP2/ERF	DRE	*RD29A*	Dehydration	(68)
DDF1/DREB1F	AP2/ERF			High salinity	(71)
DDF2/DREB1E	AP2/ERF			High salinity	(71)
ICE1	bHLH	ICEr1?	*CBF2/DREB1C*	Cold	(14)
ANAC019	NAC	NACR	*ERD1*	Dehydration	(115)
ANAC055	NAC	NACR	*ERD1*	Dehydration	(115)
ANAC072/RD26	NAC	NACR	*ERD1*	Dehydration	(23, 115)
ZFHD1	ZFHD	rps1 site	ERD1	Dehydration	(115)
ZAT12	Zinc finger			Cold	(121)
STZ	Zinc finger			Cold, dehydration	(89)
AREB1/ABF2	bZIP	ABRE	*RD29B*	ABA, dehydration	(16, 117)
AREB2/ABF4	bZIP	ABRE	*RD29B*	ABA, dehydration	(16, 117)
ABF3	bZIP	ABRE		ABA, dehydration	(16)
AtMYB2	MYB	MYBR	*RD22*	ABA, dehydration	(118)
AtMYC2	bHLH	MYCR	*RD22*	ABA, dehydration	(1)
ATHB6	Homeodomain	At rich		ABA	(32, 107)
AtERF7	ERF/AP2	GCC-box		ABA	(108)
ATB2/AtbZIP11	bZIP	ACTCAT	*ProDH*	Rehydration	(92)
AtbZIP2	bZIP	ACTCAT	*ProDH*	Rehydration	(92)
AtbZIP44	bZIP	ACTCAT	*ProDH*	Rehydration	(92)
AtbZIP53	bZIP	ACTCAT	*ProDH*	Rehydration	(92)
HOS9	Homeodomain			Cold	(137)
HOS10	MYB			ABA, dehydration	(138)

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

transduction, and provides genetic evidence that phosphoinositols play an important role in ABA and stress-related signal transduction in plants (127). Biochemical analysis has shown that phospholipase C functions upstream of *RD29A* expression in osmotic stress signaling (112), which may be negatively regulated by FLY1.

Five freezing-sensitive [sensitivity to freezing (*sfr*)] *Arabidopsis* mutants were isolated on the basis of their inability to survive freezing after cold acclimation and their chromosome positions were mapped on the *Arabidopsis* genome (122). Among these mutants, sfr6 plants were deficient in the expression of cold-inducible genes such as *KIN1*, *COR15A*, and *LTI78/RD29A* (56). Microarray analysis indicates that the *sfr6* mutation specifically affects the expression of genes containing the DRE/CRT motif under cold and osmotic stress conditions (10). As the expression level of *DREB1/CBF* or *DREB2* is not reduced in this mutant, the failure to express CRT/DRE-regulated genes correctly may involve the

interaction of DREB1/CBF and DREB2 transcription factors with the CRT/DRE promoter element (10).

CONCLUSIONS AND FUTURE PERSPECTIVES

Many plant genes are regulated in response to abitoic stresses, such as dehydration and cold, and their gene products function in stress response and tolerance. In the signal transduction network from perception of stress signals to stress-responsive gene expression, various transcription factors and *cis*-acting elements in the stress-responsive promoters function not only as molecular switches for gene expression but also as terminal points of stress signals in the signaling processes (**Figure 1**; **Table 1**). Timing of stress-responsive gene expression is regulated by a combination of transcription factors and *cis*-acting elements in stress-inducible promoters (**Figure 1**). DRE/CRT and ABRE are major *cis*-acting elements in abiotic stress-inducible gene expression. DRE/CRT functions in the early process of stress-responsive gene expression whereas ABRE functions after the accumulation of ABA during dehydration and high-salinity stress response. There are many ABA-inducible transcription factors that function downstream of ABA responses and stress responses. These transcription factors are involved mainly in late and adaptive processes during stress responses.

Different promoter *cis*-acting elements are involved in the cross talk between different stress signals that regulate gene expression. DRE/CRT is a major *cis*-acting element in cold-inducible gene expression. Thus, DRE/CRT functions in cross talk between dehydration/salinity stress response and cold stress response. Combinations of *cis*-acting elements and transcription factors are important to determine cross talk in stress signaling pathways. DRE is one of the coupling elements of ABRE, which results in cross talk at the promoter level between ABA-independent and ABA-dependent pathways.

Abiotic stresses affect plant growth and development, such as flowering time and cell growth. This indicates cross talk between environmental stress signals and plant growth. Plant hormones are involved in these cross talk events. Transcription is important in regulating plant development and environmental interactions, which may be affected by cross talk in transcriptional regulatory networks. Cross talk between signal transduction pathways will be an important subject in the near future.

Negative regulation as well as positive regulation are important for gene expression. The degradation of transcription factor proteins plays an important role in the negative regulation of gene expression. Specific F-box proteins are involved in stabilizing some transcription factors in stress response (64). Recently, RNA interference or mRNA degradation were suggested to function in stress-responsive gene expression (47, 110). Complex regulation of gene expression may cause complex and flexible responses of plants to abiotic stresses.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

ACKNOWLEDGMENTS

We thank Dr. Sean Simpson for critical review of the manuscript. Research in our laboratories is supported by the Program for Promotion of Basic Research Activities for Innovative Biosciences (BRAIN), project grants from the Ministry of Agriculture, Forestry and Fisheries, Japan, and Grants-in-Aid from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

LITERATURE CITED

1. Abe H, Yamaguchi-Shinozaki K, Urao T, Iwasaki T, Hosokawa D, et al. 1997. Role of Arabidopsis MYC and MYB homologs in drought- and abscisic acid-regulated gene expression. *Plant Cell* 9:1859–68
2. Abe H, Urao T, Ito T, Seki M, Shinozaki K, et al. 2003. Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. *Plant Cell* 15:63–78
3. Anderson JP, Badruzsaufari E, Schenk PM, Manners JM, Desmond OJ, et al. 2004. Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in Arabidopsis. *Plant Cell* 16:3460–79
4. Baker SS, Wilhelm KS, Thomashow MF. 1994. The 5′-region of *Arabidopsis thaliana cor15a* has *cis*-acting elements that confer cold-, drought- and ABA-regulated gene expression. *Plant Mol. Biol.* 24:701–13
5. Bartels D, Sunkar R. 2005. Drought and salt tolerance in plants. *Crit. Rev. Plant Sci.* 24:23–58
6. Bensmihen S, Rippa S, Lambert G, Jublot D, Pautot V, et al. 2002. The homologous ABI5 and EEL transcription factors function antagonistically to fine-tune gene expression during late embryogenesis. *Plant Cell* 14:1391–403
7. Boter M, Ruiz-Rivero O, Abdeen A, Prat S. 2004. Conserved MYC transcription factors play a key role in jasmonate signaling both in tomato and Arabidopsis. *Genes Dev.* 18:1577–91
8. Boudsocq M, Barbier-Brygoo H, Lauriere C. 2004. Identification of nine sucrose nonfermenting 1-related protein kinases 2 activated by hyperosmotic and saline stresses in *Arabidopsis thaliana*. *J. Biol. Chem.* 279:41758–66
9. Boudsocq M, Lauriere C. 2005. Osmotic signaling in plants: multiple pathways mediated by emerging kinase families. *Plant Physiol.* 138:1185–94
10. Boyce JM, Knight H, Deyholos M, Openshaw MR, Galbraith DW, et al. 2003. The sfr6 mutant of Arabidopsis is defective in transcriptional activation via CBF/DREB1 and DREB2 and shows sensitivity to osmotic stress. *Plant J.* 34:395–406
11. Bray E, Bailey-Serres J, Weretilnyk E. 2000. Responses to abiotic stresses. In *Biochemistry and Molecular Biology of Plants*, ed. BB Buchanan, W Gruissem, RL Jones. pp. 1158–203. Rockville, MD: Amer. Soc. Plant Physiol.
12. Bray EA. 2004. Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. *J. Exp. Bot.* 55:2331–41
13. Casaretto J, Ho TH. 2003. The transcription factors HvABI5 and HvVP1 are required for the abscisic acid induction of gene expression in barley aleurone cells. *Plant Cell* 15:271–84
14. Chinnusamy V, Ohta M, Kanrar S, Lee BH, Hong X, et al. 2003. ICE1: a regulator of cold-induced transcriptome and freezing tolerance in *Arabidopsis*. *Gene Dev.* 17:1043–54
15. Chinnusamy V, Schumaker K, Zhu JK. 2004. Molecular genetic perspectives on cross-talk and specificity in abiotic stress signalling in plants. *J. Exp. Bot.* 55:225–36
16. Choi H, Hong J, Ha J, Kang J, Kim SY. 2000. ABFs, a family of ABA-responsive element binding factors. *J. Biol. Chem.* 275:1723–30
17. Choi DW, Rodriguez EM, Close TJ. 2002. Barley *Cbf3* gene identification, expression pattern, and map location. *Plant Physiol.* 129:1781–87

18. Cook D, Fowler S, Fiehn O, Thomashow MF. 2004. A prominent role for the CBF cold response pathway in configuring the low-temperature metabolome of Arabidopsis. *Proc. Natl. Acad. Sci. USA* 101:15243–48
19. Cushman JC, Bohnert HJ. 2000. Genome approaches to plant stress tolerance. *Curr. Opin. Plant Biol.* 3:117–24
20. Dubouzet JG, Sakuma Y, Ito Y, Kasuga M, Dubouzet EG, et al. 2003. OsDREB genes in rice, *Oryza sativa* L., encode transcription activators that function in drought-, high-salt- and cold-responsive gene expression. *Plant J.* 33:751–63
21. Finkelstein RR, Lynch TJ. 2000. The Arabidopsis abscisic acid response gene ABI5 encodes a basic leucine zipper transcription factor. *Plant Cell* 12:599–609
22. Fowler S, Thomashow MF. 2002. Arabidopsis transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. *Plant Cell* 14:1675–90
23. Fujita M, Fujita Y, Maruyama K, Seki M, Hiratsu K, et al. 2004. A dehydration-induced NAC protein, RD26, is involved in a novel ABA-dependent stress-signaling pathway. *Plant J.* 39:863–76
24. Fujita Y, Fujita M, Satoh R, Maruyama K, Parvez MM, et al. 2005. AREB1 is a transcription activator of novel ABRE-dependent ABA-signaling that enhances drought stress tolerance in Arabidopsis. *Plant Cell* 17:3470–88
25. Furihata T, Maruyama K, Fujita Y, Umezawa T, Yoshida R, et al. 2006. ABA-dependent multisite phosphorylation regulates the activity of a transcription activator AREB1. *Proc. Natl. Acad. Sci. USA*. 103:1988–93
26. Gao MJ, Allard G, Byass L, Flanagan AM, Singh J. 2002. Regulation and characterization of four CBF transcription factors from *Brassica napus*. *Plant Mol. Biol*. 49:459–71
27. Gilmour SJ, Zarka DG, Stockinger EJ, Salazar MP, Houghton JM, et al. 1998. Low temperature regulation of *Arabidopsis* CBF family of AP2 transcriptional activators as an early step in cold-induced COR gene expression. *Plant J.* 16:433–42
28. Gilmour SJ, Sebolt AM, Salazar MP, Everard JD, Thomashow MF. 2000. Overexpression of the Arabidopsis CBF3 transcriptional activator mimics multiple biochemical changes associated with cold acclimation. *Plant Physiol.* 124:1854–65
29. Gosti F, Beaudoin N, Serizet C, Webb AA, Vartanian N, et al. 1999. ABI1 protein phosphatase 2C is a negative regulator of abscisic acid signaling. *Plant Cell* 11:1897–910
30. Guiltinan MJ, Marcotte WR, Quatrano RS. 1990. A plant leucine zipper protein that recognizes an abscisic acid response element. *Science* 250:267–71
31. Haake V, Cook D, Riechmann JL, Pineda O, Thomashow MF, et al. 2002. Transcription factor CBF4 is a regulator of drought adaptation in Arabidopsis. *Plant Physiol.* 130:639–48
32. Himmelbach A, Hoffmann T, Leube M, Hohener B, Grill E. 2002. Homeodomain protein ATHB6 is a target of the protein phosphatase ABI1 and regulates hormone responses in *Arabidopsis*. *EMBO J.* 21:3029–38
33. Himmelbach A, Yang Y, Grill E. 2003. Relay and control of abscisic acid signaling. *Curr. Opin. Plant Biol.* 6:470–79
34. Hobo T, Kowyama Y, Hattori T. 1999. A bZIP factor, TRAB1, interacts with VP1 and mediates abscisic acid-induced transcription. *Proc. Natl. Acad. Sci. USA* 96:15348–53
35. Hobo T, Asada M, Kowyama Y, Hattori T. 1999. ACGT-containing abscisic acid response element (ABRE) and coupling element 3 (CE3) are functionally equivalent. *Plant J.* 19:679–89
36. Holmberg N, Bulow L. 1998. Improving stress tolerance in plants by gene transfer. *Trends Plant Sci.* 3:61–66

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

37. Hsieh TH, Lee JT, Yang PT, Chiu LH, Charng YY, et al. 2002. Heterology expression of the Arabidopsis C-repeat/dehydration response element binding factor 1 gene confers elevated tolerance to chilling and oxidative stresses in transgenic tomato. *Plant Physiol.* 129:1086–94
38. Hsieh TH, Lee JT, Charng YY, Chan MT. 2002. Tomato plants ectopically expressing Arabidopsis CBF1 show enhanced resistance to water deficit stress. *Plant Physiol*. 130:618–26
39. Ingram J, Bartels D. 1996. The molecular basis of dehydration tolerance in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47:377–403
40. Ishitani M, Xiong L, Stevenson B, Zhu JK. 1997. Genetic analysis of osmotic and cold stress signal transduction in Arabidopsis: interactions and convergence of abscisic acid-dependent and abscisic acid-independent pathways. *Plant Cell* 9:1935–49
41. Ishitani M, Xiong L, Lee H, Stevenson B, Zhu JK. 1998. HOS1, a genetic locus involved in cold-responsive gene expression in Arabidopsis. *Plant Cell* 10:1151–61
42. Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, et al. 2001. Regulation of drought tolerance by gene manipulation of 9-*cis*-epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in *Arabidopsis*. *Plant J.* 27:325–33
43. Jaglo KR, Kleff S, Amundsen KL, Zhang X, Haake V, et al. 2001. Components of the Arabidopsis C-repeat/dehydration-responsive element binding factor cold-response pathway are conserved in *Brassica napus* and other plant species. *Plant Physiol*. 127:910–17
44. Jaglo-Ottosen KR, Gilmour SJ, Zarka DG, Schabenberger O, Thomashow MF. 1998. *Arabidopsis* CBF1 overexpression induces *cor* genes and enhances freezing tolerance. *Science* 280:104–06
45. Jakoby M, Weisshaar B, Droge-Laser W, Vicente-Carbajosa J, Tiedemann J, et al. 2002. bZIP transcription factors in Arabidopsis. *Trends Plant Sci*. 7:106–11
46. Jiang C, Iu B, Singh J. 1996. Requirement of a CCGAC *cis*-acting element for cold induction of the *BN115* gene from winter *Brassica napus*. *Plant Mol. Biol.* 30:679–84
47. Jones-Rhoades MW, Bartel DP. 2004. Computational identification of plant microRNAs and their targets, including a stress-induced miRNA. *Mol. Cell* 14:787–99
48. Kagaya Y, Hobo T, Murata M, Ban A, Hattori T. 2002. Abscisic acid-induced transcription is mediated by phosphorylation of an abscisic acid response element binding factor, TRAB1. *Plant Cell* 14:3177–89
49. Kang JY, Choi HI, Im MY, Kim SY. 2002. *Arabidopsis* basic leucine zipper proteins that mediate stress-responsive abscisic acid signaling. *Plant Cell* 14:343–57
50. Kasuga M, Liu Q, Miura S, Yamaguchi-Shinozaki K, Shinozaki K. 1999. Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. *Nat. Biotechnol.* 17:287–91
51. Kasuga M, Miura S, Shinozaki K, Yamaguchi-Shinozaki K. 2004. A combination of the Arabidopsis *DREB1A* gene and stress-inducible rd29A promoter improved drought- and low-temperature stress tolerance in tobacco by gene transfer. *Plant Cell Physiol*. 45:346–50
52. Kawasaki S, Borchert C, Deyholos M, Wang H, Brazille S, et al. 2001. Gene expression profiles during the initial phase of salt stress in rice. *Plant Cell* 13:889–905
53. Kim S, Kang JY, Cho DI, Park JH, Kim SY. 2004. ABF2, an ABRE-binding bZIP factor, is an essential component of glucose signaling and its overexpression affects multiple stress tolerance. *Plant J.* 40(1):75–87
54. Kitashiba H, Ishizaka T, Isuzugawa K, Nishimura K, Suzuki T. 2004. Expression of a sweet cherry DREB1/CBF ortholog in Arabidopsis confers salt and freezing tolerance. *J Plant Physiol*. 161:1171–76

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

55. Kizis D, Pages M. 2002. Maize DRE-binding proteins DBF1 and DBF2 are involved in rab17 regulation through the drought-responsive element in an ABA-dependent pathway. *Plant J.* 30:679–89
56. Knight H, Veale EL, Warren GJ, Knight MR. 1999. The sfr6 mutation in Arabidopsis suppresses low-temperature induction of genes dependent on the CRT/DRE sequence motif. *Plant Cell* 11:875–86
57. Kobayashi Y, Yamamoto S, Minami H, Kagaya Y, Hattori T. 2004. Differential activation of the rice sucrose nonfermenting1-related protein kinase2 family by hyperosmotic stress and abscisic acid. *Plant Cell* 16:1163–77
58. Kobayashi Y, Murata M, Minami H, Yamamoto S, Kagaya Y, et al. 2005. Abscisic acid-activated SNRK2 protein kinases function in the gene-regulation pathway of ABA signal transduction by phosphorylating ABA response element-binding factors *Plant J.* 44:939–49
59. Koiwa H, Barb AW, Xiong L, Li F, McCully MG, et al. 2002. C-terminal domain phosphatase-like family members (AtCPLs) differentially regulate *Arabidopsis thaliana* abiotic stress signaling, growth, and development. *Proc. Natl. Acad. Sci. USA* 99:10893–98
60. Koornneef M, Reuling G, Karssen CM. 1984. The isolation and characterization of abscisic acid-insensitive mutants of *Arabidopsis thaliana*. *Physiol. Plant.* 61:377–83
61. Koornneef M, Jorna ML, Brinkhorst-van der Swan DLC, Karssen CM. 1992. The isolation of abscisic acid (ABA)-deficient mutants by selection of induced revertants in non-germinating gibberellin sensitive lines of *Arabidopsis thaliana* (L.) Heynh. *Theor. Appl. Genet*. 61:385–93
62. Kreps JA, Wu Y, Chang HS, Zhu T, Wang X, et al. 2002. Transcriptome changes for Arabidopsis in response to salt, osmotic, and cold stress. *Plant Physiol*. 130:2129–41
63. Kushiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, et al. 2004. The Arabidopsis cytochrome P450 CYP707A encodes ABA 8′-hydroxylases:key enzymes in ABA catabolism. *EMBO J.* 23:1647–56
64. Lee H, Xiong L, Gong Z, Ishitani M, Stevenson B, et al. 2001. The Arabidopsis *HOS1* gene negatively regulates cold signal transduction and encodes a RING finger protein that displays cold-regulated nucleo–cytoplasmic partitioning. *Genes Dev.* 15:912–24
65. Leung J, Bouvier-Durand M, Morris PC, Guerrier D, Chefdor F, et al. 1994. Arabidopsis ABA response gene *ABI1*: features of a calcium-modulated protein phosphatase. *Science* 264:1448–52
66. Leung J, Merlot S, Giraudat J. 1997. The Arabidopsis *ABSCISIC ACID-INSENSITIVE2* (*ABI2*) and *ABI1* genes encode homologous protein phosphatases 2C involved in abscisic acid signal transduction. *Plant Cell* 9:759–71
67. Li J, Wang XQ, Watson MB, Assmann SM. 2000. Regulation of abscisic acid-induced stomatal closure and anion channels by guard cell AAPK kinase. *Science* 287:300–3
68. Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, et al. 1998. Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low-temperature-responsive gene expression, respectively, in *Arabidopsis*. *Plant Cell* 10:1391–406
69. Lopez-Molina L, Chua NH. 2000. A null mutation in a bZIP factor confers ABA-insensitivity in *Arabidopsis thaliana*. *Plant Cell Physiol*. 41:541–47
70. Lorenzo O, Chico JM, Sanchez-Serrano JJ, Solano R. 2004. JASMONATE-INSENSITIVE1 encodes a MYC transcription factor essential to discriminate between different jasmonate-regulated defense responses in Arabidopsis. *Plant Cell* 16:1938–50

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

71. Magome H, Yamaguchi S, Hanada A, Kamiya Y, Oda K. 2004. Dwarf and delayed-flowering 1, a novel Arabidopsis mutant deficient in gibberellin biosynthesis because of overexpression of a putative AP2 transcription factor. *Plant J.* 37:720–29
72. Maruyama K, Sakuma Y, Kasuga M, Ito Y, Seki M, et al. 2004. Identification of cold-inducible downstream genes of the *Arabidopsis* DREB1A/CBF3 transcriptional factor using two microarray systems. *Plant J.* 38:982–93
73. Massari ME, Murre C. 2000. Helix-loop-helix proteins: regulators of transcription in eucaryotic organisms. *Mol. Cell Biol.* 20:429–40
74. Menkens AE, Schindler U, Cashmore AR.1995. The G-box: a ubiquitous regulatory DNA element in plants bound by the GBF family of bZIP proteins. *Trends Biochem. Sci.* 20:506–10
75. Meyer K, Leube MP, Grill E. 1994. A protein phosphatase 2C involved in ABA signal transduction in *Arabidopsis thaliana*. *Science* 264:1452–55
76. Mundy J, Yamaguchi-Shinozaki K, Chua NH. 1990. Nuclear proteins bind conserved elements in the abscisic acid-responsive promoter of a rice rab gene. *Proc. Natl. Acad. Sci. USA* 87:1406–10
77. Mustilli AC, Merlot S, Vavasseur A, Fenzi F, Giraudat J. 2002. *Arabidopsis* OST1 protein kinase mediates the regulation of stomatal aperture by abscisic acid and acts upstream of reactive oxygen spieces production. *Plant Cell* 14:3089–99
78. Nakashima K, Kiyosue T, Yamaguchi-Shinozaki K, Shinozaki K. 1997. A nuclear gene, erd1, encoding a chloroplast-targeted Clp protease regulatory subunit homolog is not only induced by water stress but also developmentally upregulated during senescence in *Arabidopsis thaliana*. *Plant J.* 12:851–61
79. Nakashima K, Shinwari ZK, Sakuma Y, Seki M, Miura S, et al. 2000. Organization and expression of two Arabidopsis *DREB2* genes encoding DRE-binding proteins involved in dehydration and high-salinity-responsive gene expression. *Plant Mol. Biol.* 42:657–65
80. Nambara E, Marion-Poll A. 2005. Abscisic acid biosynthesis and catabolism. *Annu. Rev. Plant Biol.* 56:165–85
81. Novillo F, Alonso JM, Ecker JR, Salinas J. 2004. CBF2/DREB1C is a negative regulator of CBF1/DREB1B and CBF3/DREB1A expression and plays a central role in stress tolerance in Arabidopsis. *Proc. Natl. Acad. Sci. USA* 101:3985–90
82. Oh SJ, Song SI, Kim YS, Jang HJ, Kim SY, et al. 2005. Arabidopsis CBF3/DREB1A and ABF3 in transgenic rice increased tolerance to abiotic stress without stunting growth. *Plant Physiol.* 138:341–51
83. Oono Y, Seki M, Nanjo T, Narusaka M, Fujita M, et al. 2003. Monitoring expression profiles of *Arabidopsis* gene expression during rehydration process after dehydration using *ca*. 7000 full-length cDNA microarray. *Plant J.* 34:868–87
84. Ouellet F, Vazquez-Tello A, Sarhan F. 1998. The wheat wcs120 promoter is cold-inducible in both monocotyledonous and dicotyledonous species. *FEBS Lett.* 423:324–28
85. Pellegrineschi A, Reynolds M, Pacheco M, Brito RM, Almeraya R, et al. 2004. Stress-induced expression in wheat of the *Arabidopsis thaliana DREB1A* gene delays water stress symptoms under greenhouse conditions. *Genome* 47:493–500
86. Qin F, Sakuma Y, Li J, Liu Q, Li YQ, et al. 2004. Cloning and functional analysis of a novel DREB1/CBF transcription factor involved in cold-responsive gene expression in *Zea mays* L. *Plant Cell Physiol.* 45:1042–52
87. Rabbani MA, Maruyama K, Abe H, Khan MA, Katsura K, et al. 2003. Monitoring expression profiles of rice genes under cold, drought, and high-salinity stresses and abscisic acid application using cDNA microarray and RNA gel-blot analyses. *Plant Physiol.* 133:1755–67

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

88. Saito S, Hirai N, Matsumoto C, Ohigashi H, Ohta D, et al. 2004. Arabidopsis CYP707As encode (+)-abscisic acid 8′-hydroxylase, a key enzyme in the oxidative catabolism of abscisic acid. *Plant Physiol*. 134(4):1439–49
89. Sakamoto H, Maruyama K, Sakuma Y, Meshi T, Iwabuchi M, et al. 2004. *Arabidopsis* Cys2/His2-type zinc-finger proteins function as transcription repressors under drought-, cold-, and high-salinity-stress conditions. *Plant Physiol*. 136:2734–46
90. Sakuma Y, Liu Q, Dubouzet JG, Abe H, Shinozaki K, et al. 2002. DNA-binding specificity of the ERF/AP2 domain of Arabidopsis DREBs, transcription factors involved in dehydration- and cold-inducible gene expression. *Biochem. Biophys. Res. Commun.* 290:998–1009
91. Satoh R, Nakashima K, Seki M, Shinozaki K, Yamaguchi-Shinozaki K. 2002. ACTCAT, a novel cis-acting element for proline- and hypoosmolarity-responsive expression of the *ProDH* gene encoding proline dehydrogenase in Arabidopsis. *Plant Physiol*. 130:709–19
92. Satoh R, Fujita Y, Nakashima K, Shinozaki K, Yamaguchi-Shinozaki K. 2004. A novel subgroup of bZIP proteins function as transcriptional activators in hypoosmolarity-responsive expression of the *ProDH* gene in *Arabidopsis*. *Plant Cell Physiol*. 45:309–17
93. Seki M, Narusaka M, Abe H, Kasuga M, Yamaguchi-Shinozaki K, et al. 2001. Monitoring the expression pattern of 1300 Arabidopsis genes under drought and cold stresses by using a full-length cDNA microarray. *Plant Cell* 13:61–72
94. Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M, et al. 2002. Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. *Plant J*. 31:279–92
95. Seki M, Kamei A, Yamaguchi-Shinozaki K, Shinozaki K. 2003. Molecular responses to drought, salinity and frost: common and different paths for plant protection. *Curr. Opin. Biotechnol*. 14:194–99
96. Seki M, Satou M, Sakurai T, Akiyama K, Iida K. et al. 2004. RIKEN Arabidopsis full-length (RAFL) cDNA and its applications for expression profiling under abiotic stress conditions. *J. Exp. Bot.* 55:213–23
97. Seo M, Peeters AJ, Koiwai H, Oritani T, Marion-Poll A, et al. 2000. The Arabidopsis aldehyde oxidase 3 (AAO3) gene product catalyzes the final step in abscisic acid biosynthesis in leaves. *Proc. Natl. Acad. Sci. USA* 97:12908–13
98. Shen Q, Ho TH. 1995 Functional dissection of an abscisic acid (ABA)-inducible gene reveals two independent ABA-responsive complexes each containing a G-box and a novel *cis*-acting element. *Plant Cell* 7:295–307
99. Shen Q, Zhang P, Ho TH. 1996. Modular nature of abscisic acid (ABA) response complexes: composite promoter units that are necessary and sufficient for ABA induction of gene expression in barley. *Plant Cell* 8:1107–19
100. Shen YG, Zhang WK, He SJ, Zhang JS, Liu Q, et al. 2003a. An EREBP/AP2-type protein in *Triticum aestivum* was a DRE-binding transcription factor induced by cold, dehydration and ABA stress. *Theor. Appl. Genet*. 106:923–30
101. Shen YG, Zhang WK, Yan DQ, Du BX, Zhang JS, et al. 2003b. Characterization of a DRE-binding transcription factor from a halophyte *Atriplex hortensis*. *Theor. Appl. Genet*. 107:155–61
102. Shinozaki K, Yamaguchi-Shinozaki K. 1997. Gene expression and signal transduction in water-stress response. *Plant Physiol*. 115:327–34
103. Shinozaki K, Yamaguchi-Shinozaki K. 2000. Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. *Curr. Opin. Plant Biol.* 3:217–23

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

104. Shinozaki K, Yamaguchi-Shinozaki K, Seki M. 2003. Regulatory network of gene expression in the drought and cold stress responses. *Curr. Opin. Plant Biol.* 6:410–17
105. Shinwari ZK, Nakashima K, Miura S, Kasuga M, Seki M, et al. 1998. An *Arabidopsis* gene family encoding DRE/CRT binding proteins involved in low-temperature-responsive gene expression. *Biochem. Biophys. Res. Commun.* 250:161–70
106. Simpson SD, Nakashima K, Narusaka Y, Seki M, Shinozaki K, et al. 2003. Two different novel *cis*-acting elements of *erd1*, a *clpA* homologous *Arabidopsis* gene function in induction by dehydration stress and dark-induced senescence. *Plant J.* 33:259–70
107. Soderman E, Hjellstrom M, Fahleson J, Engstrom P. 1999. The HD-Zip gene *ATHB6* in Arabidopsis is expressed in developing leaves, roots and carpels and up-regulated by water deficit conditions. *Plant Mol. Biol.* 40:1073–83
108. Song CP, Agarwal M, Ohta M, Guo Y, Halfter U, et al. 2005. Role of an Arabidopsis AP2/EREBP-type transcriptional repressor in abscisic acid and drought stress responses. *Plant Cell* 17:2384–96
109. Stockinger EJ, Gilmour SJ, Thomashow MF. 1997. *Arabidopsis thaliana CBF1* encodes an AP2 domain-containing transcription activator that binds to the C-repeat/DRE, a *cis*-acting DNA regulatory element that stimulates transcription in response to low temperature and water deficit. *Proc. Natl. Acad. Sci. USA* 94:1035–40
110. Sunkar R, Zhu JK. 2004. Novel and stress-regulated microRNAs and other small RNAs from Arabidopsis. *Plant Cell* 16:2001–19
111. Suzuki M, Ketterling MG, Li QB, McCarty DR. 2003. Viviparous1 alters global gene expression patterns through regulation of abscisic acid signaling. *Plant Physiol.* 132:1664–77
112. Takahashi S, Katagiri T, Hirayama T, Yamaguchi-Shinozaki K, Shinozaki K. 2001. Hyperosmotic stress induces a rapid and transient increase in inositol 1,4,5-trisphosphate independent of abscisic acid in Arabidopsis cell culture. *Plant Cell Physiol.* 42:214–22
113. Tester M, Bacic A. 2005. Abiotic stress tolerance in grasses. From model plants to crop plants. *Plant Physiol.* 137:791–93
114. Thomashow MF. 1999. Plant cold acclimation: freezing tolerance genes and regulatory mechanisms *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 50:571–99
115. Tran LSP, Nakashima K, Sakuma Y, Simpson SD, Fujita Y, et al. 2004. Functional analysis of *Arabidopsis* NAC transcription factors controlling expression of *erd1* gene under drought stress. *Plant Cell* 16:2482–98
116. Umezawa T, Okamoto M, Kushiro T, Nambara E, Oono Y, et al. 2006. CYP707A3, a major ABA 8′-hydroxylase involved in dehydration and rehydration response in *Arabidopsis thaliana*. *Plant J.* In press
117. Uno Y, Furihata T, Abe H, Yoshida R, Shinozaki K, et al. 2000. *Arabidopsis* basic leucine zipper transcription factors involved in an abscisic acid-dependent signal transduction pathway under drought and high-salinity conditions. *Proc. Natl. Acad. Sci. USA* 97:11632–37
118. Urao T, Yamaguchi-Shinozaki K, Urao S, Shinozaki K. 1993. An Arabidopsis myb homolog is induced by dehydration stress and its gene product binds to the conserved MYB recognition sequence. *Plant Cell* 5:1529–39
119. Vagujfalvi A, Galiba G, Cattivelli L, Dubcovsky J. 2003. The cold-regulated transcriptional activator Cbf3 is linked to the frost-tolerance locus Fr-A2 on wheat chromosome 5A. *Mol. Genet. Genomics* 269:60–67
120. Vinocur B, Altman A. 2005. Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Curr. Opin. Biotechnol.* 16:123–32

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

121. Vogel JT, Zarka DG, Van Buskirk HA, Fowler SG, Thomashow MF. 2005. Roles of the CBF2 and ZAT12 transcription factors in configuring the low temperature transcriptome of Arabidopsis. *Plant J*. 41:195–211
122. Warren G, McKown R, Marin AL, Teutonico R.1996. Isolation of mutations affecting the development of freezing tolerance in *Arabidopsis thaliana* (L.) Heynh. *Plant Physiol*. 111:1011–19
123. Xiong L, Ishitani M, Lee H, Zhu JK. 2001. The Arabidopsis LOS5/ABA3 locus encodes a molybdenum cofactor sulfurase and modulates cold stress- and osmotic stress-responsive gene expression. *Plant Cell* 13:2063–83
124. Xiong L, Lee Bh, Ishitani M, Lee H, Zhang C, et al. 2001. FIERY1 encoding an inositol polyphosphate 1-phosphatase is a negative regulator of abscisic acid and stress signaling in Arabidopsis. *Genes Dev*. 15:1971–84
125. Xiong L, Lee H, Ishitani M, Zhu JK. 2002. Regulation of osmotic stress-responsive gene expression by the LOS6/ABA1 locus in Arabidopsis. *J. Biol. Chem*. 277:8588–96
126. Xiong L, Schumaker KS, Zhu JK. 2002. Cell signaling during cold, drought, and salt stress. *Plant Cell* 14(Suppl.):S165–83
127. Xiong L, Lee H, Huang R, Zhu JK. 2004. A single amino acid substitution in the Arabidopsis FIERY1/HOS2 protein confers cold signaling specificity and lithium tolerance. *Plant J*. 40:536–45
128. Xue GP. 2003. The DNA-binding activity of an AP2 transcriptional activator HvCBF2 involved in regulation of low-temperature responsive genes in barley is modulated by temperature. *Plant J*. 33: 373–83
129. Yadav V, Mallappa C, Gangappa SN, Bhatia S, Chattopadhyay S. 2005. A basic helix-loop-helix transcription factor in Arabidopsis, MYC2, acts as a repressor of blue light-mediated photomorphogenic growth. *Plant Cell* 17:1953–66
130. Yamaguchi-Shinozaki K, Shinozaki K. 1992. A novel Arabidopsis DNA binding protein contains the conserved motif of HMG-box proteins. *Nucleic Acids Res*. 20:6737
131. Yamaguchi-Shinozaki K, Shinozaki K. 1994. A novel *cis*-acting element in an *Arabidopsis* gene is involved in responsiveness to drought, low temperature, or high-salt stress. *Plant Cell* 6:251–64
132. Yamaguchi-Shinozaki K, Shinozaki K. 2005. Organization of cis-acting regulatory elements in osmotic- and cold-stress-responsive promoters. *Trends Plant Sci*. 10:88–94
133. Yoshida R, Hobo T, Ichimura K, Mizoguchi T, Takahashi F, et al. 2002. ABA-activated SnRK2 protein kinase is required for dehydration stress signaling in *Arabidopsis*. *Plant Cell Physiol.* 43:1473–83
134. Zarka DG, Vogel JT, Cook D, Thomashow MF. 2003. Cold induction of *Arabidopsis* CBF genes involves multiple ICE (inducer of CBF expression) promoter elements and a cold-regulatory circuit that is desensitized by low temperature. *Plant Physiol.* 133:910–18
135. Zhang JZ, Creelman RA, Zhu JK. 2004. From laboratory to field. Using information from Arabidopsis to engineer salt, cold, and drought tolerance in crops. *Plant Physiol.* 135:615–21
136. Zhu J. 2002. Salt and drought stress signal transduction in plants. *Annu. Rev. Plant Biol.* 53:247–73
137. Zhu J, Shi H, Lee BH, Damsz B, Cheng S, et al. 2004. An *Arabidopsis* homeodomain transcription factor gene, *HOS9*, mediates cold tolerance through a CBF-independent pathway. *Proc. Natl. Acad. Sci. USA* 101:9873–78
138. Zhu J, Verslues PE, Zheng X, Lee BH, Zhan X, et al. 2005. HOS10 encodes an R2R3-type MYB transcription factor essential for cold acclimation in plants. *Proc. Natl. Acad. Sci. USA* 102:9966–71

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Annual Review
of Plant Biology

Volume 57, 2006

Contents

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.

Annu. Rev. Plant Biol. 2006.57:781-803. Downloaded from arjournals.annualreviews.org
by University of Oklahoma, Health Sciences Center on 12/04/08. For personal use only.