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Plant Genes for Abiotic Stress

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1. Introduction

Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crop plants by more than 50%. Plants as sessile organisms are constantly exposed to changes in environmental conditions. When these changes are rapid and extreme, plants generally perceive them as stresses. However stresses are not necessarily a problem for plants because they have evolved effective mechanisms to avoid or reduce the possible damages.

The response to changes in environment can be rapid, depending on the type of stress and can involve either adaptation mechanisms, which allow them to survive the adverse conditions, or specific growth habitus to avoid stress conditions. In fact, plants can perceive abiotic stresses and elicit appropriate responses with altered metabolism, growth and development. The regulatory circuits include stress sensors, signalling pathways comprising a network of protein-protein interactions, transcription factors and promoters, and finally the output proteins or metabolites (table 1).

A number of abiotic stresses such as extreme temperatures, high light intensity, osmotic stresses, heavy metals and a number of herbicides and toxins lead to over production of reactive oxygen species (ROS) including H_2O_2 causing extensive cellular damage and inhibition of photosynthesis.

Normally, ROS are rapidly removed by antioxidative mechanisms, but this removal can be impaired by stresses themselves (Allan & Fluhr, 2007), causing a rise in their intracellular concentration and an increase of the damage. To prevent or repair these damages, plant cells use a complex defence system, involving a number of antioxidative stress-related defence genes that, in turn, induce changes in the biochemical plant machinery. Studies have shown that ROS probably require additional molecules to transduce and amplify defence signals. ROS production and anti-oxidant processes, all act in a synergistic, additive or antagonistic way, related to the control of oxidative stress.

Responses to stress are not linear pathways, but are complex integrated circuits involving multiple pathways and in specific cellular compartments, tissues, and the interaction of additional cofactors and/or signalling molecules to coordinate a specified response to a given stimulus (Dombrowski, 2009). Onset of a stress triggers some (mostly unknown) initial sensors, which then activate cytoplasmic Ca^{2+} and protein signalling pathways, leading to stress-responsive gene expression and physiological changes (Bressan et al., 1998;

Stress	Consequences	Plant Responses
Heat stress	High temperature lead to high evaporation and water deficit. The consequent increased turnover of enzymes leads to plant death.	Efficient protein repair systems and general protein stability support survival, temperature can lead to acclimation.
Chilling and cold stress	Biochemical reactions proceed at slower rate, photosyntesis proceeds, carbon dioxide fixation lags, leading to oxigen radical damage. Indeed, freezing lead to ice crystal formation that can distrupt cells membranes.	Cessation of growth in adaptable species may be overcome by changes in metabolism. Ice crystal formation can be prevent by osmolyte accumulation and synthesis of hydrophilic proteins.
Drought	Inability to water transport to leaves leads to photosyntesis declines.	Leaf rolling and other morphological adaptations. Stoma closure reduces evaporative transpiration induced by ABA. Accumulation of metabolities, consequently lower internal water potential and water attracting.
Flooding and submergence	Generates anoxic or microaerobic conditions interfering with mitochondrial respiration.	Development of cavities mostly in the roots that facilitate the exchange of oxigen and ethylene between shoot and root (aerenchyma).
Heavy metal accumulation and metal stress	In excess, detoxification reactions may be insufficient or storage capacity may exceeded.	Excess of metal ions may be countered by export or vacuolar deposition but metal ions may also generate oxygen radicals.
High light stress	Excess light can lead to increased production of highly reactive intermediates and by-products that can potentially cause photo-oxidative damage and inhibit photosynthesis.	Exposure of a plant to light exceeding what is utilized in photochemistry leads to inactivation of photosynthetic functions and the production of reactive oxygen species (ROS). The effects of these ROS can be the oxidation of lipids, proteins, and enzymes necessary for the proper functioning of the chloroplast and the cell as a whole.

Table 1. Consequences of abiotic stress and plant responses

Xiong et al., 2002). Also, accumulation of abscisic acid (ABA) plays an important role in abiotic stress signalling and transduction pathways, mediating many responses (Wasilewska et al., 2008).

It is well known that abiotic stresses in general, through regulation of both gene expression and protein turnover, alter the abundance of many transcripts and proteins (Wong et al., 2006; Yan et al., 2006; Jiang et al., 2007), indicating that transcriptional and post-transcriptional regulation play an essential role in the adaptation of cellular functions to the environmental changes.

Recent advances in molecular biology, genomics, proteomics and metabolomics have provided insight into plant gene regulatory network system, which is mainly composed of inducible-genes (environmental factors and developmental cues), expression programming and regulatory elements (*cis*-element and *trans*-element), corresponding biochemical pathways and diverse signal factors (Tang et al., 2003; Wang et al., 2003; Zhu, 2003; Munns, 2005). Genetic studies revealed that stress tolerance traits are mainly quantitative trait loci (QTLs), which make genetic selection of traits difficult.

Responses to abiotic stress require the production of important metabolic proteins such as those involved in synthesis of osmoprotectants and of regulatory proteins operating in the signal transduction pathways, such as kinases or transcriptional factors (TFs). In addition, new transcripts are made and within a few hours a steady level of stress adaptation has been reached. In general, the transcriptional regulation of genes is directly controlled by a network of TFs and transcription factor binding sites (TFBS) (Chaves & Oliveira, 2004). TFs are proteins with a DNA domain that binds to the *cis*-acting elements present in the promoter of a target gene. They induce (activators) or repress (repressors) the activity of the RNA polymerase, thus regulating gene expression. TFs can be grouped into families according to their DNA-binding domain (Riechmann et al., 2000). The presence or absence of transcription factors, activators and suppressors regulating transcription of target genes often involves a whole cascade of signalling events determined by tissue type, developmental stage or environmental condition (Wyrick & Young, 2002).

Environmental stress-inducible genes can be mainly divided into two groups in terms of their protein products: one type of genes, whose coding products directly confer to plant cells the resistence to environmental stress such as late embryogenesis abundant (LEA) protein, anti-freezing protein, osmotic regulatory protein, enzymes for synthesizing betaine, proline and other osmoregulators; the other groups of genes, whose coding products play an important role in regulating gene expression and signal transduction such as the transcriptional elements. At least four different regulons can be identified, two ABA independent (1 and 2) and two ABA dependent (3 and 4): (1) the CBF/DREB regulon; (2) the NAC (NAM, ATAF and CUC) and ZF-HD (zinc-finger homeodomain) regulon; (3) the AREB/ABF (ABA-responsive element-binding protein/ ABA-binding factor) regulon; and (4) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) regulon.

Our knowledge of the molecular mechanisms underlying the responses of plants to such environmental stresses is still rather limited, but an increasing number of genes have been identified in recent years that mediate these responses. Some of these genes are induced by stress stimuli and encode products that confer tolerance to adverse conditions, whereas others encode upstream regulators that function within signalling pathways controlling the stress response.

The aim of this book chapter is to describe the regulation of gene expression under abiotic stresses and report recent advances in the stress-response mechanisms.

2. Abiotic stress-inducible genes

The complex plant response to abiotic stress involves many genes and biochemical-molecular mechanisms. The analyze of the functions of stress-inducible genes is an important tool not only to understand the molecular mechanisms of stress tolerance and the responses of higher plants, but also to improve the stress tolerance of crops by gene

manipulation. Hundreds of genes are thought to be involved in abiotic stress responses (Seki, 2003; Avni Öktem et al., 2008).
Many drought-inducible genes are also induced by salt stress and cold, which suggests the existence of similar mechanisms of stress responses.
These genes are classified into three major groups: (1) those that encode products that directly protect plant cells against stresses such as heat stress proteins (HSPs) or chaperones, LEA proteins, osmoprotectants, antifreeze proteins, detoxification enzymes and free-radical scavengers (Bray et al., 2000; Wang et al., 2000); (2) those that are involved in signalling cascades and in transcriptional control, such as Mitogen-activated protein kinase (MAPK), Calcium-dependent protein kinase (CDPK) (Ludwig et al., 2004) and SOS kinase (Zhu et al., 2001), phospholipases (Frank et al., 2000) and transcriptional factors (Cho et al., 2000; Shinozaki et al., 2000); (3) those that are involved in water and ion uptake and transport such as aquaporins and ion transporters (Blumwald et al., 2000).

3. Transcriptional factor genes involved in abiotic stress

Plant growth and productivity are under constant threat from environmental changes in the form of various stress factors. The most common abiotic stresses are drought, flooding or submergence, salinity, extreme temperatures (heat and freezing) and high light. Furthermore, the continued modification of the atmosphere by human activities lead to increase in the concentration of ozone in the troposphere and this can generate oxidative stress, which leads to the destruction of proteins and cells, premature ageing and reduced crop yields.
Tolerance or susceptibility to these abiotic stresses is a very complex phenomenon, both because stress may occur at multiple stages of plant development and more than one stress simultaneously affects the plant. Therefore, the perception of abiotic stresses and signal transduction to switch on adaptive responses are critical steps in determining the survival and reproduction of plants exposed to adverse environments (Chinnusamy et al., 2004).
During the past few years, transcriptome analysis has indicated that distinct environmental stresses induce similar responses. Overlap between stress responses can explain the phenomenon known as cross-tolerance, a capability to limit collateral damage inflicted by other stresses accompanying the primary stress.
Responses to abiotic stresses require the production of important metabolic proteins such as those involved in synthesis of osmoprotectants and regulatory proteins operating in signal transduction pathways, that are kinases or transcription factors (TFs). The regulation of these responses requires proteins operating in the signal transduction pathways, such as transcriptional factors, which regulate gene expression by binding to specific DNA sequences in the promoters of respective target genes. This type of transcriptional regulatory system is called regulon. At least four different regulons that are active in response to abiotic stresses have been identified. Dehydration-responsive element binding protein 1 (DREB1)/C-repeat binding factor (CBF) and DREB2 regulons function in abscisic acid (ABA)-independent gene expression, whereas the ABA-responsive element (ABRE) binding protein (AREB)/ABRE binding factor (ABF) regulon functions in ABA-dependent gene expression (Saibo et al., 2009). In addition to these major pathways, other regulons, including the NAC (or NAM, No Apical Meristem) and Myeloblastosis-Myelocytomatosis (MYB/MYC) regulons, are involved in abiotic stress-responsive gene expression (Fig. 1). Particularly, NAC- type TF OsNAC6 is induced by abiotic stresses, including cold, drought

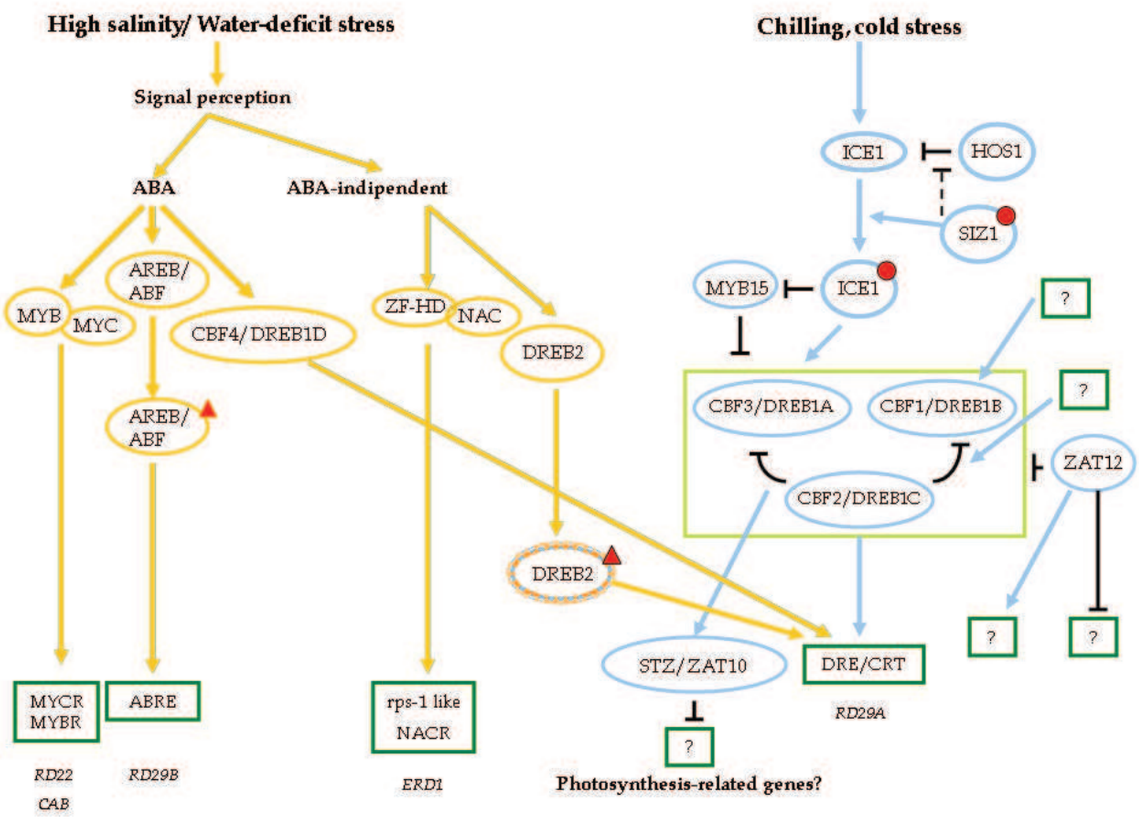


Fig. 1. Transcriptional network of abiotic stress responses.

and high salinity. Microarray analysis showed that many abiotic inducible genes were up regulated in rice plants over-expressing OsNAC6 (Nakashima et al., 2007).

TFs are powerful targets for genetic engineering in abiotic stress resistance in crop plants and many studies have been done in the last two decades on this topic.

Transcription factors are shown in ovals. Transcription factor-modifying enzymes are shown in circles. The small triangles correspond to post-translational modifications. Green squares with question marks represent putative MYC ICE1-like transcription factors that may activate CBF1/DREB1B and CBF2/DREB1C. The green boxes represent the *cis*-elements present in stress-responsive genes. The red dot corresponds to the sumoylation modification by SIZ1 of the ICE1 transcription factor. The dashed black line from SIZ1 to HOS1 represents competition for binding places on the ICE1 transcription factor. SIZ1 blocks the access of HOS1 to the ubiquitination sites on the ICE1. CBF4/DREB1D is a DRE cis-element binding factor that is ABA dependent.

4. Drought stress transcriptional factors

The genome controls the regulation of the response to water deficit as well as the effectiveness of the response. Microarrays, largely performed using *Arabidopsis thaliana* as model plant, have been used to catalogue the many genes that are induced or repressed in

response to conditions that may lead to cellular water-deficit stress (Seki et al., 2002). These genes can be placed in at least four different functional groups: signal transduction, transcriptional regulation, cellular metabolism and transport and protection of cellular structures.

There are at least six different classes of TFs that participate in gene induction or repression in response to water deficit. Homeobox domain and NAC domain containing TFs are induced by multiple treatments that mimic water-deficit stress. Accumulation of proteins which have metabolic or structural functions promote adaptation to stress. One class of genes that could play a role in protection is called the late embryogenesis abundant (*Lea*) genes. The *Lea* genes are also developmentally programmed for expression in desiccating seeds. These genes encode small hydrophilic proteins that are predicted to protect proteins and membranes through chaperone-like functions. These proteins were thought to improve the performance of rice plants by protecting cell membranes from injury under abiotic stress (Chandra et al., 2004).

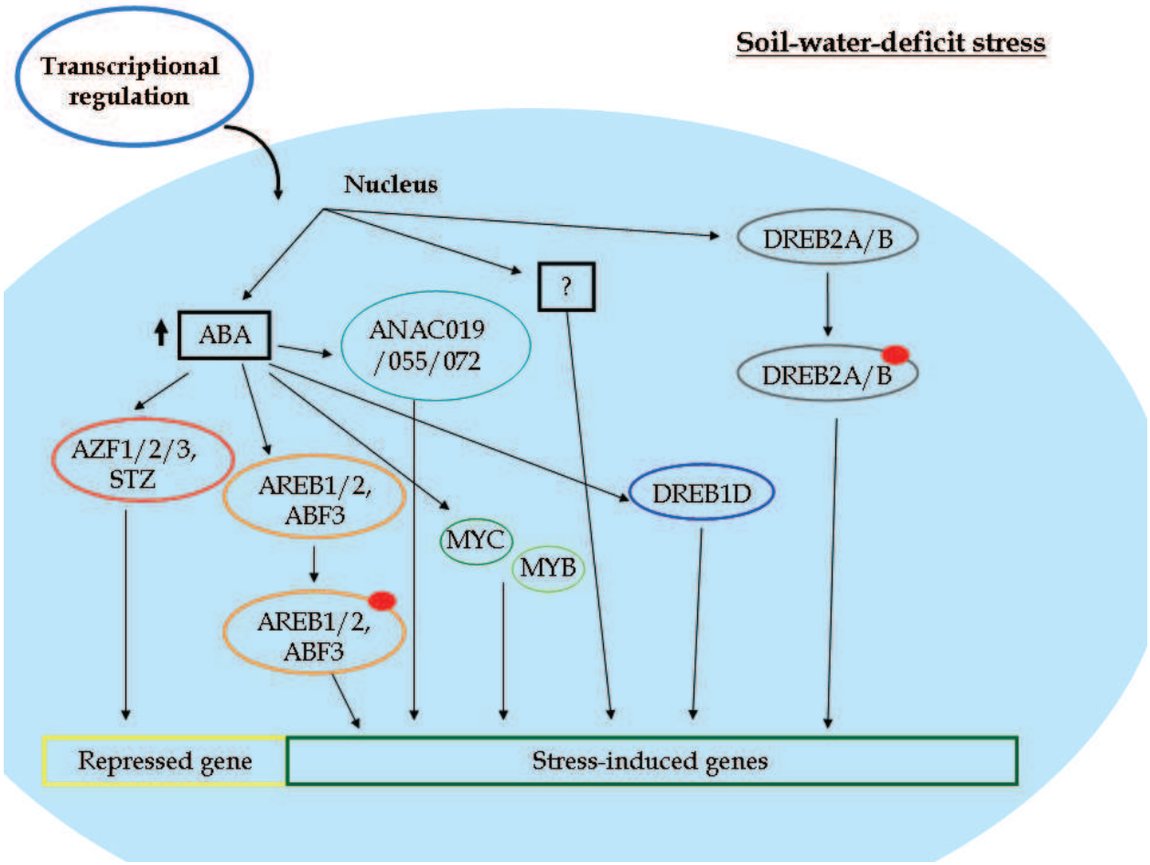
4.1 Gene regulation and transcriptional factors in water deficit

A recent review (Shinozaki & Yamaguchi-Shinozaki, 2007) on analysis of gene expression during drought stress response in plants show and summarize the functions of some genes in both stress response and tolerance. Microarray analysis performed on wheat genome, showed that among 300 unique single expressed sequences tag (ESTs), the 30% of genes were significantly up-regulated and the 18% were down-regulated under drought stress (Way et al., 2005).

Potential functions of approximatively 130 genes of *A. thaliana* up-regulated in water-deficit was reported by Bray (2002). These genes are involved in cellular response to drought stress by signalling events, detoxification and other functions. cDNA microarray analysis on 7000 Arabidopsis full-length cDNAs clarify relationship between rehydratation-, proline- and water-treatment inducible genes. Among the 152 rehydratation-inducible genes, 58 genes conteined in their promoter regions the ACTCAT sequence involved in proline- and hypoosmolarity- inducible gene expression, suggesting that this motif is a major cis-activing element involved in rehydratation-inducible gene expression (Oono et al., 2003).

Moreover, microarray analysis performed on two moderately drought-tolerant native Andeon potato clones revealed that there was 1713 differentially expressed genes with 186 up-regulated involved in drought tolerance by inducing of osmotic adjustment, changes in carbohydrate metabolism, membrane modifications and cell rescue mechanisms, such as detoxification of oxygen radicals and protein stabilization (Schafleitner et al., 2007).

These recent study underline how the expression of genes in response to water deficit is complex and can be regulated at the transcriptional, post-transcriptional and translational levels. Two major transcriptional regulatory pathways of gene expression play an important role in response to water-deficit stress: the ABA-independent pathway and ABA-dependent pathway. The first is controlled largely by a family of TFs called dehydration response element binding protein (DREB), which contains a DNA binding motif originally identified in a flower patterning protein called APETALA2 (AP2) (Fig. 2), while transcription factor families known to be as the most responsive to ABA signalling under drought are NAC, AREB/ABF, and MYB.



The inset shows the different types of transcription factors involved in induction/repression of regulons.

Fig. 2. Classes of genes that are induced by water-deficit stress.

4.1.1 ABA-independent pathway

DREB are important TFs which induce a set of abiotic stress-related genes and confer stress resistance to plants. The DREB TFs could be divided into two group: DREB1, involved signal transduction pathways under low temperature; DREB2, involved in signal transduction pathways under dehydration. They belong to the ethylene responsive element binding factors (ERF) family of TFs. ERF proteins are a sub-family of the AP2/ethylene responsive element binding protein (EREBP) TFs that is distinctive to plants. ERF proteins share a conserved 58–59 amino acid domain (the ERF domain) that binds to *cis*-elements, the GCC box, found in many pathogens related (PR) gene promoters conferring ethylene responsiveness (Gu et al., 2000), and to the C-repeat CRT/dehydration responsive element (DRE) motif involved in the expression of cold and dehydration responsive genes (Agarwal et al., 2006).

The DREB proteins contain an ERF/AP2DNA-binding domain quite conserved: amino acid alignment shows high sequence similarity in the nuclear localization signal at the N-terminal region and some similarity in the C-terminal acidic domain (Agarwal et al., 2006). Indeed, TFs containing ERF/AP2DNA-binding domain are widely found in many

plants such as Arabidopsis (Okamuro et al., 1997), tomato (Zhou et al., 1997), tobacco (Ohme-Takagi & Shinshi, 1995), rice (Sasaki et al., 1994; Weigel, 1995) and maize (Moose & Sisco, 1996).

Another ABA-independent pathway was identified after the observation that Early Responsive to Dehydration Stress 1 (ERD1) gene transcripts accumulated before any increase of ABA in response to dehydration and high salinity (Nakashima et al., 1997). Promoter analysis of ERD1 revealed TFs belonging to the NAC family and zinc finger homeodomain (ZF-HD) as essential to the activation of the ERD1 gene (Tran et al., 2007). The increased drought tolerance may be due both to the reduced transpiration rate (increased stomatal closure) and to an increased ABA sensitivity.

Many genes (e.g. Aquaporin, ERD10, ERD13 and ERF) already described as being involved in plant response to water stress are down-regulated in drought stress (Cominelli et al., 2005). A member of the *A. thaliana* family of R2R3-MYB TFs, AtMYB61, is also specifically expressed in guard cells in a consistent manner, being involved in the regulation of stomatal aperture (Liang et al., 2005).

The strong induction of Stress Responsive –NAC1 (SNAC1) gene expression by drought in guard cells suggests an effect in stomatal closure (Hu et al., 2006). It has been reported that modulation of transcription plays an important role in controlling guard cell activity. Recently two MYB-type TFs were identified as regulators of stomatal movements.

4.1.2 ABA-dependent pathway

ABA-dependent gene induction during water deficit is controlled by at least five different classes of TFs. The ABA response element (ABRE) with the consensus ACGTGG/TC is bound by basic Leucine Zipper Domain (bZIP-type) TFs (Fig. 2). Three Arabidopsis bZIP TFs (AREB1/ABF2, AREB2/ABF4, and ABF3) are expressed in response to water-deficit stress and ABA treatment. Activation of the TFs requires ABA accumulation and the induction of an ABA-responsive protein kinase which activates the TF through phosphorylation.

Other TFs are also involved in ABA regulation of gene expression during cellular water deficit. Three genes encoding a class of TFs that is unique to plants, the NAC domain proteins ANAC019, ANAC055, and ANAC072 are induced by water deficit and ABA treatment. The NAC domain is a 60 bp DNA binding domain that is predicted to form a helix-turn-helix motif.

MYB, MYC and homeodomain TFs, and a family of transcriptional repressors (Cys2/His2-type zinc-finger proteins) are also involved in the ABA response to water deficit. Expression of the drought-inducible gene Responsive to Dehydration 22 (RD22) from Arabidopsis was found to be induced by ABA. The promoter region of RD22 contains MYC (CANNTG) and MYB (C/TAACNA/G) *cis*-element recognition sites. MYC and MYB TFs only accumulate after an increase of ABA concentration. Over-expression of these TFs result in enhanced sensitivity to ABA and drought tolerance (Abe et al., 2003).

5. Transcriptional factor involved in response to flooding stress

Flooding and submergence are two conditions that cannot be tolerated by most plants for periods of time longer than a few days. These stresses lead to anoxic conditions in the root system. At a critical oxygen pressure, mitochondrial respiration that provides the energy for growth in the photosynthetically inactive roots will decrease, then cease and the cells will die (Bray, 2004).

Recent reviews on gene expression analysis performed by microarray tools reported as the expression of several transcription factors, such as heat shock factors, ethylene response-binding proteins, MADS-box proteins, AP2 domain, leucine zipper, zinc finger and WRKY factors, increases in response to various regimes of oxygen deprivation in Arabidopsis and rice (Loreti et al., 2005; Lasanthi-Kudahettige et al., 2007).
Recently Licausi et al. (2010), using a qRT-PCR platform (Czechowski et al., 2002; Scheible et al., 2004; Morcuende et al., 2007; Osuna et al., 2007; Barrero et al., 2009), have identified TFs that are differentially expressed by hypoxic conditions. Among the TFs that have been characterized, members of the AP2/ERF-type family are the most commonly represented in the set of up-regulated TFs, followed by Zinc-finger and basic helix-loop-helix (bHLH-type) TFs, while TFs belonging to the bHLH family are the most commonly represented in the set of down-regulated TFs, together with members from the bZIP and MYB families.
In silico experiments and *trans*-activation assays shown that some TFs active in flooding stress are able to regulate the expression of hypoxia responsive genes. Particularly, five hypoxia-induced TFs (At4g29190; LBD41, At3g02550;HRE1, At1g72360; At1g69570; At5g66980) from different TF families [Zinc Finger, Ligand Binding Domain (LBD) or Lateral Organ Boundary Domain, ERF, DNA binding with one finger (DOF), ARF] showed this ability (Licausi et al., 2010).
Accumulation of ROS is a common consequence of biotic and abiotic stresses, including oxygen deprivation. There is evidence of redox-sensitive TFs, at least one of which might be involved in the adaptive response to low oxygen. ZAT12, a putative zinc finger-containing TF, is recognized as a component in the oxidative stress response signalling network of Arabidopsis (Rizhsky et al., 2004), promotes expression of other TFs and the upregulation of cytosolic ascorbate peroxidase 1, a key enzyme in the removal of H_2O_2.
Advances have been made in molecular analyses of cDNAs and genes involved in the anaerobic response. Huq and Hodges (2000) reported early activation of a rice (*Oryza sativa* L.) gene by anoxia, the *aie* (anaerobically inducible early) gene. This gene encodes for a putative protein that shows short stretches of similarities to functionally interesting proteins (e. g. DNA binding proteins and nitric oxide synthase), indicating its putative involvement in signalling.

6. Salinity stress

High salinity is a critical environmental factor that inimically affects large areas of cultivated land. Plant growth, physiological and metabolic processes are affected, resulting in significant reductions in global crop productivity (Magomeet al., 2008; Zhang et al., 2009). Exposure to high levels of NaCl not only affects plant water relations but also creates ionic stress in the form of cellular accumulation of Cl^- and, in particular, Na^+ ions. Salt stress also changes the homeostasis of other ions such as Ca^{2+} , K^+, and NO^{3-} .
Salt accumulation can modify plant cell plasma membrane lipid and protein composition, cause ion imbalance and hyperosmotic stress and eventually disturb normal growth and development (Fujii & Zhu 2009; Lòpez-Pérez et al., 2009).
In general, high NaCl concentrations affect plant physiology and metabolism at different levels (water deficit, ion toxicity, nutrient imbalance, and oxidative stress; Vinocur & Altman, 2005), and at least two main responses can be expected: a rapid protective response together with a long term adaptation response. During initial exposure to salinity, plants experience water stress, which in turn reduces leaf expansion. During long-term exposure to

salinity, plants experience ionic stress, which can lead to premature senescence of adult leaves, and thus a reduction in the photosynthetic area available to support continued growth (Cramer & Nowak, 1992).

Salt tolerance determinants are categorized either as effectors that directly modulate stress etiology or attenuate stress effects, or as regulatory molecules that are involved in stress perception, signal transduction, or modulation of effector function. Genomics studies are focused on gene expression analysis following exposure of plants to high salinity, using salt shock experiments to mimic stresses that affect hydration and ion homeostasis.

The stress-responsive genes can be classified into two classes, i.e. early and delayed response genes (Sairam & Tyagi, 2004). The former are induced quickly and transiently, while the latter are activated more slowly and their expression is sustained. The early response genes encode transcription factors that activate downstream delayed response genes (Zhu, 2002).

When microarray expression profiles of wild type plants, a T-DNA insertion knockout mutant of AtNHX1 (nhx1), and a rescued line (NHX1::nhx1) exposed to both short (12 h and 48 h) and long (one and two weeks) durations of a non-lethal salt stress were investigated, 147 transcripts showed both salt responsiveness and a significant influence of AtNHX1. Fifty-seven of these genes showed differential regulation across all salt treatments, while the rest were regulated as a result of a particular duration.

A large number of genes from a variety of biochemical pathways participate in responses conferring salt tolerance. These pathways include notably those involved in: signal transduction; carbon metabolism and energy production; oxidative stress protection; uptake, exclusion, transport and compartmentalization of sodium ions; modifications of structural components of cell walls and membranes.

Several genes have been identified as functional components in the plant response to salt stress, including those encoding detoxifying enzymes like glutathione peroxidase (Roxas et al., 1997), Na^+/H^+ antiporter AtNHX1 (Apse et al., 1999), osmolytes such as glycine-betaine and LEA (late embryogenesis abundant protein) (Xu et al., 1996), flavoprotein AtHAL3 (Espinosa-Ruiz et al., 1999), signal mediator Ca2+/calmodulin-dependent protein phosphatase (Pardo et al., 1998) and transcription factor Alfin1 (Bastola et al., 1998). Analyses of complete transcriptomes suggest that systems like synthesis of osmolytes and ion transporters and regulation of transcriptional and translational machineries have distinct roles in salt-stress response. In particular, induction of transcripts of specific TFs, RNA-binding proteins, ribosomal genes and translation initiation and elongation factors has been reported to be important during salt stress (Sahi et al., 2006).

Since not many stress-specific consensus sequences were identified in promoters of stress specific genes to activate or repress transcription, transcription factors must be located in the nucleus, bind DNA and interact with the basal transcription apparatus. Transcription factors involved in stress responses include DRE-related binding factors, leucine zipper DNA-binding proteins, putative zinc finger proteins, myb proteins, bZIP/HD-ZIPs, and AP2/EREBP (Chen et al., 2002; Seki et al., 2002), interact with promoters of osmotic-regulated genes (Abe et al., 1997; Liu et al., 1998; Hasegawa et al., 2000 a-b). Particularly, AP2/ERF domain proteins include the DREB or CBF proteins binding to dehydration response elements (DRE) or C-repeats. A major transcriptional regulatory system is represented by DRE/C-repeat promoter sequences in stress-activated genes and DREBs/CBF factors that control stress gene expression (Stockinger et al., 1997; Liu et al.,

1998). Several stress-inducible genes such as rd29A, Cor6.6, Cor15a and Kin1 are target genes of DREBs/CBFs in Arabidopsis and contain DRE/C-repeat sequences in their promoters.

Moreover, basic region leucine zipper (bZIP) proteins contain a DNA binding domain rich in basic residues that bind to an ACGT core sequence. One bZIP subfamily has been linked genetically to an ABA response: ABI5 and its homologs, theABREbinding factors (ABFs/AREBs). ABRE binding factors (ABFs)/ABA-responsive element binding (AREBs) proteins respond at the transcriptional and post-transcriptional level to dehydration and salt stress (Choi et al., 2000; Uno et al., 2000).

Other regulatory intermediates that modulate plant salt stress responses include SOS3 (Ca^{2+} -binding protein), SOS2 (Suc nonfermenting- like) kinase, Ca^{2+} -dependent protein kinases, and mitogen-activated protein kinases (Halfter et al., 2000). Genetic and physiological data indicate that SOS3, SOS2, and SOS1 are components of a signal pathway that regulates ion homeostasis and salt tolerance and their functions are Ca^{2+} dependent. In particular, SOS1, encoding a plasma membrane Na^+/H^+ antiporter, plays a critical role in sodium extrusion and in controlling long-distance Na^+ transport from the root to shoot (Liu & Zhu, 1998). This antiporter forms one component in a mechanism based on sensing of the salt stress that involves an increase of cytosolic [Ca^{2+}] and reversible phosphorylation with SOS1 acting in concert with SOS2 and SOS3 (Shi et al., 2000). SOS2 encodes a Suc non-fermenting-like (SNF) kinase, and SOS3 encodes a Ca^{2+} -binding protein with sequence similarity to the regulatory subunit of calcineurin and neuronal Ca^{2+} sensors (Liu & Zhu, 1998; Liu et al., 2000). In yeast, co-expression of SOS1, SOS2, and SOS3 increases the salt tolerance of transformed yeast cells much more than expression of one or two SOS proteins (Shi et al., 2000), suggesting that the full activity of SOS1 depends on the SOS2/SOS3 complex.

Several studies have shown that reactive oxygen species (ROS) and oxidative stress may be mediating at least some of the toxic effects of NaCl on legumes (Jungklang et al., 2004) and other vascular plants (Attia et al., 2008). ROS are predominantly generated in the chloroplast by direct transfer of excitation energy from chlorophyll to produce singlet oxygen, or by univalent oxygen reduction at photosystem I, in the Mehler reaction (Allen, 1995) and to some extent in mitochondria. ROS have the potential to interact non-specifically with many cellular components, triggering peroxidative reactions and causing significant damage to proteins, lipids, and nucleic acids. To cope with ROS and to maintain redox homeostasis, living organisms evolved antioxidant defense systems, comprised of enzymatic and non-enzymatic components, which normally maintain ROS balance within the cell. Major nonenzymatic antioxidants include ascorbate (vitamin C) and glutathione in plants, although tocopherol (vitamin E), flavonoids, alkaloids, and carotenoids can also act as antioxidants.

Intracellular ROS can also influence the ROS induced MAPK signal pathway through inhibition of phosphatases or downstream transcription factors (Mittler et al., 2004) (Fig. 3).

7. Chilling and cold stress: Gene regulation and transcriptional factor

Cold stress prevents the expression of full genetic potential of plants owing to its direct inhibition of metabolic reactions and, indirectly, through cold-induced osmotic (chilling-induced inhibition of water uptake and freezing-induced cellular dehydration), oxidative and other stresses. Cold stress, which includes chilling (<20°C) and/or freezing (<0°C) temperatures, adversely affects the growth and development of plants. Chilling and freezing

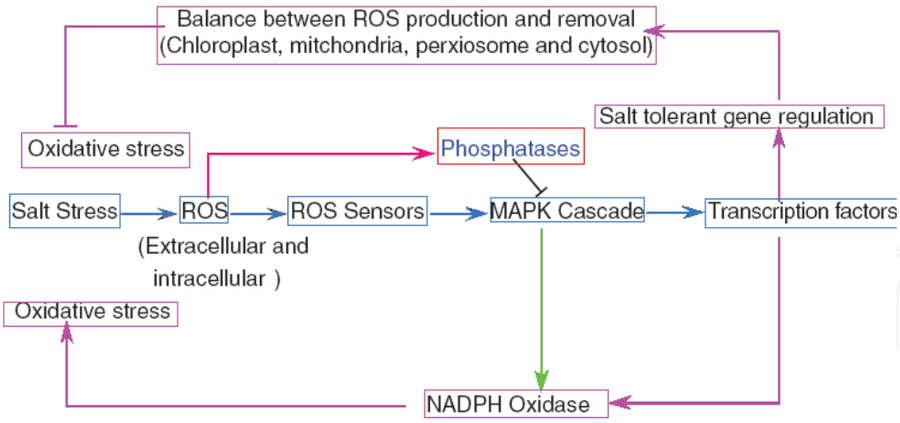


Fig. 3. ROS signal transduction pathway under salt stress.

are stresses that show different effects on plants: the first leads to slow biochemical reactions, such as enzyme and membrane transport activities; the second leads to ice crystal formation that can cause the disruption of cell membrane system (Chinnusamy et al., 2007).
A large number of studies have used a transcriptional profiling approach to identify genes in Arabidopsis that respond to cold (4°C) and chilling (13°C) temperatures. Results have shown that plants respond to low temperatures by altering mRNA levels of a large number of genes belonging to different and independent pathways. The quantitative and qualitative difference in transcriptional response to low temperature suggests the presence in higher plants of different molecular mechanisms to cold-stress response (Zhu & Provart, 2003).
The cold induction of genes involved in calcium signalling, lipid signalling or encoding receptor-like protein kinases are also affected by the ice1 mutation (Lee et al., 2005).
Controlled proteolysis of transcriptional regulators also plays an important role in shaping the cold-responsive transcriptome in plants.
TFs that bind to the DRE/CRT are named DREB1/CTR-binding factor (CBF) and DREB2. Cold stress induces the expression of AP_2/ERF family TFs, that is, CBFs, which can bind to *cis*-elements in the promoters of COR genes and activate their expression (Fig. 4). CBFs regulate the expression of genes involved in phosphoinositide metabolism, transcription, osmolyte biosynthesis, ROS detoxification, membrane transport, hormone metabolism and signalling and many others with known or presumed cellular protective functions (Fowler et al., 2002; Maruyama et al., 2004; Lee et al., 2005).
The first isolated cDNAs encoding DRE binding proteins were DREB1A and DREB2A (Liu et al., 1998) from Arabidopsis and then, DREB genes have been isolated from a wide variety of plants. In wheat and barley, a number of *CBF* homologs have been mapped to low temperature QTLs, *Fr-2* chromosomal region (Skinner et al., 2005; Vágújfalvi et al., 2005; Miller et al., 2006). Thus, it is clear that the DREB1/CBF regulon is ubiquitous within higher plants.
Expression of *DREB1* genes was extensively investigated in various crops with regard to different abiotic stresses. It was found that the expression of *AtDREB1* gene is induced by cold, but not by dehydration, or high salt stress (Liu et al., 1998; Shinwari et al., 1998). Similarly, *CBF* genes also showed high expression in response to low temperature treatment and its transcript was detectable after 30 min of exposure to 4°C, and showed maximum expression at 1 h (Medina et al., 1999). Indeed, CBF regulon could be sub-regulated by cold-responsive transcription factor genes RAP2.1 and RAP2.7 as shown by microarray analysis of transgenic Arabidopsis plants ectopically expressing CBFs (Fowler et al., 2002).

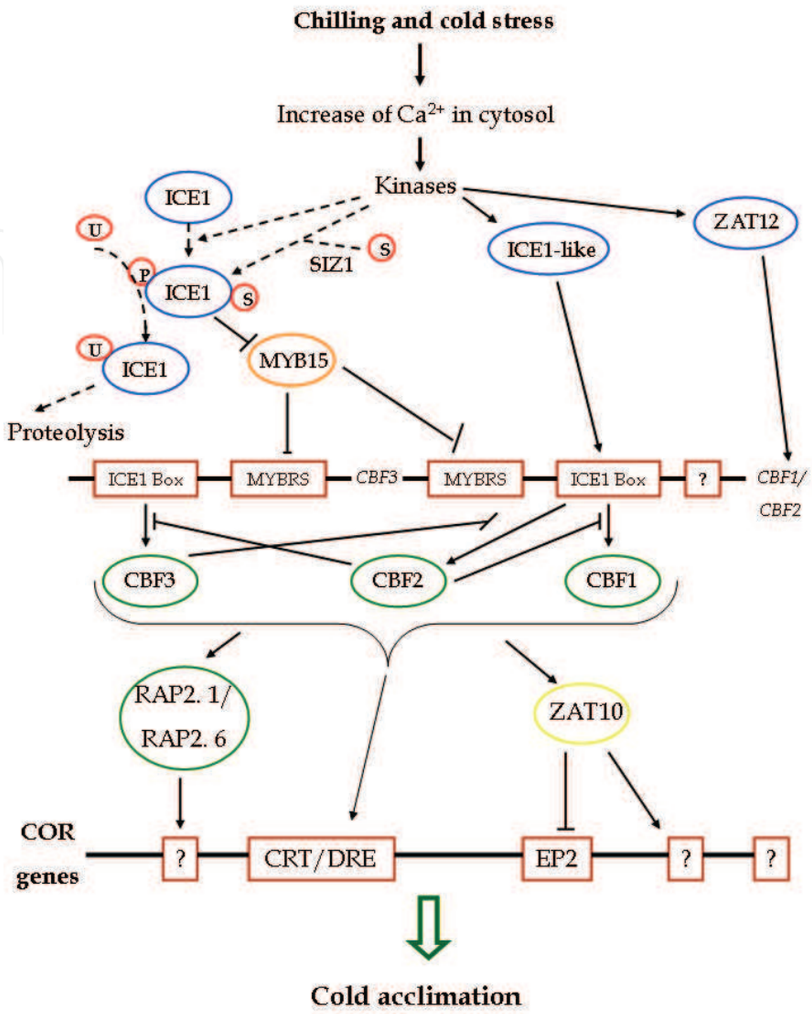


Fig. 4. Cold-responsive transcriptional network in Arabidopsis. CBFs regulate the expression of COR genes that confer cold tolerance. CBFs might cross-regulate the each other's transcription. CBFs induce the expression of ZAT10 which might downregulate the expression of COR genes. Costitutive expressed ICE1 is actived throught sumoylation and phosphorylation induced by cold stress. ICE1 actived induce the transcription of *CBFs* and reprime *MYB15*. The expression of *CBFs* is negatively regulated by MYB15 and ZAT12. HOS1 mediates the ubiquitination and proteolysis of ICE1, thus negatively regulates CBF regulons. Lines ending with bar indicate negative regulation; question mark (?) indicate unknown *cis*-elements; broken arrows indicate post-translational regulation; solid arrows indicate activation; lines ending with bar indicate negative regulation.

In Arabidopsis, ICE1 (Inducer of CBF Expression1), a MYC-type bHLH TF, can bind to MYC recognition elements in the CBF3 promoter and is important for the expression of CBF3 during cold acclimation. ICE1 is constitutively expressed and localized in the nucleus, but it induces expression of CBFs only under cold stress (Fig. 4). This suggests that cold stress-

induced post-translational modification is necessary for ICE1 to activate downstream genes in plants (Chinnusamy et al., 2003).
Two important post-translational protein modifications are the ubiquitination and the sumoylation. Ubiquitination is mediated by High Expression of Osmotically Responsive1 (HOS1). For *HOS1* encodes for a RING finger ubiquitin E3 ligase that physically interacts with ICE1 and mediates the ubiquitination of ICE1 to regulate negatively the expression of ICE1 target genes (Fig. 4) and is thus critical for the de-sensitization of plant cells to cold stress (Dong et al. 2006). Sumoylation is induced by SUMO (Small Ubiquitin-related Modifier) proteins that are conjugated to proteins substrates in a process dependent on SUMO E3 ligases. Sumoylation might protect target proteins from proteasomal degradation preventing the ubiqiutination (Ulrich, 2005).

8. Heavy metal accumulation and metal stress

Uptake of excess metal ions is toxic to most plants. Phytotoxicity of heavy metals can be attributed to symplastic accumulation of heavy metals, particularly in the plasmatic compartments of the cells, such as the cytosol and chloroplast stroma (Brune et al., 1995). Metal-induced changes in development are the result of either a direct and immediate impairment of metabolism (Van Assche & Clijsters, 1990) or signalling processes that initiate adaptive or toxicity responses that need to be considered as active processes of the organism (Jonak et al., 2004). The detoxification of heavy metals by plants is achieved by uptake and translocation, sequestration into the vacuole and metabolization, including oxidation, reduction or hydrolysis and conjugation with glucose, glytanyl cysteine syntase (GSH) or amino acids (Salt et al., 1998; Meagher, 2000; Dietz & Schnoor, 2001).
So, in order to determine genes involved in response to heavy metal, recently, several studies, based on use of *A. thaliana* as model plant, performed the analysis of global gene expression after exposure to salts of lead (Pb) and cadmium (Cd). The analysis revealed 65 and 338 up- and down-regulated genes by Cd and 19 and 76 by Pb (Kovalchuk et al., 2005). Particularly, it was found that ABC transporters were differentially regulated after Cd treatments, suggesting for some plant ABC transponders a key role in glutathione-Cd or phytochelatins-Cd complex transport both into cellular compartments and outside of the cell (Bovet et al., 2005).
Subsequently studies performed on Arabidopsis, using microarray tools, demonstrated that exist a complex regulatory network which differentially modulates gene expression in a tissute-specific manner. Responses observed in roots included the induction of genes involved in sulphur assimilation-reduction and glutathione metabolism. Therefore, it was suggested that plants activate the sulphur assimilation pathway by increasing transcription of related genes to provide an enhanced supply of glutathione for phytochelatin biosynthesis (Fig. 5).
Non specific defense mechanisms include accumulation of osmolytes, antioxidants, aminoacids and changes in hormonal balances.
The significance of glutathione and the metal-induced phytochelatins (PCs) in heavy metal tolerance has been summarized intensely in excellent reviews (Rauser, 1995, 1999; Hall, 2002). Depletion of glutathione appears to be a major mechanism in short-term heavy metal toxicity and in accordance with this hypothesis, a good correlation between glutathione contents and tolerance index was observed with 10 pea genotypes differing in Cd sensitivity (Metwally et al., 2005).

In roots, after Cd exposure, three categories of genes were identified from transcriptome analysis: (1) common responses conserved across species; (2) metallophyte-specific responses representing candidate genes for Cd hypertolerance; (3) specific responses to Cd (Weber et al., 2006).

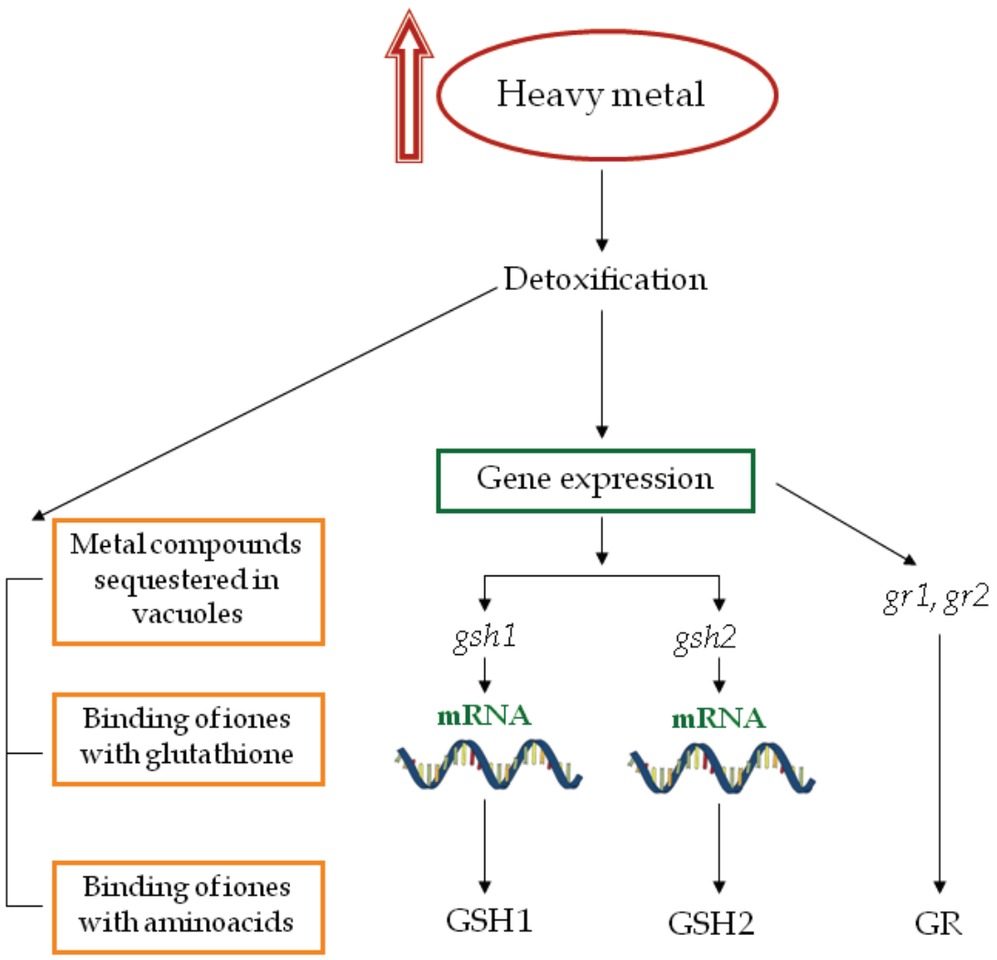


Fig. 5. Response of plant cell to toxic levels of heavy metals. The synthesis of phytochelatins (PCs) accompanies with decrease in cell glutathione pool and increase in the activities of glytanyl cysteine syntase (GSH1), glutathione synthetase (GSH2) and glutathione reductase (GR). The elevated activities of GSH1, GSH2 and GR is correlated with enhanced expression of corresponding genes gsh1, gsh2, gr1 and gr2.

In leaves, instead, was reported an early induction of several genes encoding enzymes involved in the biosynthesis of phenylpropanoids (Herbette et al., 2006).

9. High light stress

Light plays a critical role in regulating plant growth and development through the modulation of expression levels of light-responsive genes that regulate developmental and metabolic processes. Light signals are perceived through at least four distinct families

of photoreceptors, which include phytochromes (Phy), cryptochromes, phototropins and unidentified ultraviolet B (UVB) photoreceptor(s). For each developmental response, more than one photoreceptor can contribute to the perception of light signals, indicating that signal integration points for different light signals must exist in transcriptional hierarchies. Light can modulate photoreceptor activity by inducing changes that alter their cellular localization. The best characterized light receptor is Phy, which exists in two photochemically interconvertible forms, Pr and Pfr, and is encoded by a small family of genes in angiosperms. Phytochromes are synthesized in the inactive Pr form, that absorbs red light, (660 nm), and are activated on light absorption by conversion to the biologically active Pfr form, that absorbs far-red light (730 nm). The photoconversion of phytochromes results in their translocation from the cytoplasm into the nucleus, which is crucial for allowing them to interact with transducers in initiating downstream transcriptional cascades (Quail, 2002).

The responses of plants to light are complex: seed germination, seedlings photomorphogenesis, chloroplast development and orientation, photodinesis, stem growth, pigment biosynthesis, flowering and senescence (Kendrick & Kronenberg, 1994). Collectively these processes are known as photomorphogenesis.

Besides excess light, a range of abiotic environmental conditions such as O_3, salt, toxic metals, and temperature can induce increased production of ROS by limiting the ability of a plant to utilize light energy through photosynthesis (Shinozaki & Yamaguchi-Shinozaki, 2000). Exposure of a plant to light exceeding what is utilized in photochemistry leads to inactivation of photosynthetic functions and the production of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide (O_2^-), hydroxyl radicals, and singlet oxygen ($^1O_2$; Niyogi, 1999). Indeed, high light drove change in the redox potential of plastoquinone (PQ) regulating the expression of two cytosolic peroxidases during HL stress (Karpinski et al., 1999). Furthermore, the redox state of PQ has been shown to be involved in the expression of chloroplast encoded genes (Pfannschmidt et al., 1999).

Classical genetic and molecular approaches have identified various regulators downstream of photoreceptors. Many of these encode TFs, as well as kinases, phosphatases and degradation-pathway proteins. Although some of these regulators are specific for light quality, others regulate signal transduction networks in response to various light signals, representing potential signal integration points. Several basic post-translational mechanisms are involved in regulating TF activities and the subcellular localization in response to light. The phosphorylation of TFs is a common modification that can influence their ability to bind to promoters. For example, the level of G-Box Binding Factor 1 (GBF1) is constant, but its affinity for the G-box is modulated by its phosphorylation status: its phosphorylation by nuclear Casein Kinase II (CKII) enables G-box binding (Klimczak et al., 1995).

In the dark, some TFs that positively regulate gene expression in response to light, such as Long After Farred Light 1 (LAF1), are ubiquitylated by Constitutive Photomorphogenic 1 (COP1), a ring-finger-type ubiquitin E3 ligase. In darkness, COP1 acts as E3 ligase in the nucleus, targeting TFs like Long Hypocotyl5 (HY5) and LAF1 to degradation via the 26S proteasome. Upon exposure to light, COP1 migrates from the nucleus to the citosol. The study by Ulm and coworkers (2004) established that HY5, a bZIP transcription factor that is one of the key regulators of cryptochrome and phytochrome controlled photomorphogenesis, is an important component of the UVB-induced signalling network. UVB promotes rapid transcriptional activation of HY5 (and its interacting partner Long

Hypocotyl5-Like [HYH]) independently of all known photoreceptors, and loss of HY5 results in the impairment of the transcriptional induction of a subset of UVB-responsive genes. Taken together, these observations demonstrate that UVB up-regulates HY5 transcription by yet-unknown signalling pathway (s), and that the signalling cascades that mediate responses to visible light and long-wavelength UVB (300–320 nm) use shared components. Additional studies suggested that HY5 also regulates the transcription of several photosynthesis-related genes, such as the ribulose bisphosphate carboxylase small subunit (RbcS1A) (Lee et al., 2007). Given that HY5 appears to regulate the expression of several Arabidopsis genes known to respond to abiotic stress conditions (e.g. CBF1, DREB2A, RD20 and MYB59) (Lee et al., 2007), it is inferred that HY5 could also be involved in the regulation of photosynthesis by adverse environmental conditions.

In vitro analysis showed that HY5 directly binds to the promoters of several light-inducible genes (Hiltbrunner et al., 2006) and a recent chromatin immuno-precipitation analysis in combination with a whole-genome tiling microarray revealed that HY5 binds directly to a large number of genomic sites, mainly at the promoter regions of annotated genes. HY5 interacts specifically with the G-box (CACGTG) and is required for normal control by light of promoters bearing this sequence (Lee et al., 2007).

Recently, some review showed as DNA *cis*-elements responsible for light regulated transcription are located within 5' upstream sequences.

The evolution of regulatory sequences, which determine where, when, and the level at which genes are transcribed, has been largely neglected. In the case of the photosynthesis-associated nuclear genes (PhANGs) from higher plants, interesting evolutionary aspects of the molecular mechanisms by which transcription is activated by light receptors (e.g. phytochrome) could be addressed through the comparative analysis of promoter sequences. For instance, why does light profoundly affect transcription of PhANGs in monocotyledonous and dicotyledonous plants, while PhANG promoters in conifers, ferns, and mosses are either light insensitive or, at most, weakly photoresponsive (Mukai et al., 1992).

Light-responsive Transcriptor Factors (TFs) have been identified through screens for light-responsive *cis*-element (LRE)-binding proteins and through genetic analyses of mutants that are deficient in their response to specific types of light. A combination of various methods has been used to identify these LREs. Such analyses have been successfully perdormed in identifying *cis*-acting elements involved in the light responsiveness of PhANGs, such as the G-box and I-box elements from rbcS genes (Giuliano et al., 1988) and the GATA motifs of Lhcb1 genes (Gidoni et al., 1989; Millar et., 1994).

Although many LREs and their binding proteins have been identified, no single element is found in all light-regulated promoters, suggesting a complex light-regulation network and a lack of a universal switch (Jiao et al., 2007). Sequence heterogeneity of regulatory elements may be functionally overcome if multiprotein regulatory complexes facilitate binding to imperfect target sites (Miner et. 1991). The individual elements found within a multipartite *cis*-regulatory region are termed phylogenetic footprints (PFs); they share high conservation over a segment of 6 contiguous base pairs in alignments of orthologous upstream sequences and represent potential binding sites for transcription factors (Gumucio et al., 1993).

The "phylogenetic-structural method" is based on the search of "homologous" (rather than "similar") DNA sequences of a functionally characterized promoter. Two sequences are homologous when they share common ancestry, regardless of the degree of similarity between them (Doolittle et al., 1987).

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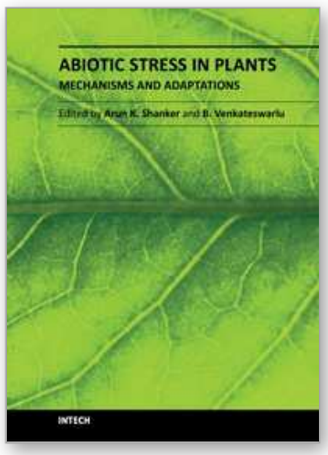

Abiotic Stress in Plants - Mechanisms and Adaptations

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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly dived into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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