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Insights into molecular mechanisms of mutual effect between plants and the environment. A review

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Abstract – Higher plants play a major role in keeping a stable environment on the globe. They regulate global climate and surroundings in many ways at different levels such as molecular, cellular, organ, individual, community, regional, ecosystem and global ecosystem levels. This article will focus on the abiotic aspect of the environment. Readers interested in the biotic aspect can read recent publications by Garcia-Brugger et al. [Early signalling events induced by elicitors of plant defenses, *Mol. Plant Microbe In.* 19 (2006) 711–724], Lecourieux et al. [Calcium in plant defence-signalling pathways, *New Phytol.* 171 (2006) 249–269], and Conrath et al. [Priming: Getting ready for battle, *Mol. Plant Microbe In.* 19 (2006) 1062–1071], for related progress. Plant behavior and character expression are controlled at the molecular level by gene expression and environmental cues. In a persistently changing environment there are many abiotic adverse stress conditions such as cold, drought, salinity and UV-B, which influence plant growth and crop production. Unlike animals, higher plants, which are sessile, cannot escape from their surroundings, but adapt themselves to changing environments by inducing a series of molecular responses to cope with these problems. The physiological processing basis for these molecular responses is the integration of many transduced events into a comprehensive network of signaling pathways. Here, higher plant hormones occupy a central place in this transduction network, frequently acting in conjunction with other signals, to regulate cellular processes such as division, elongation and differentiation, which are the fundamental basis for higher plant development and related character expression. Stress factors are also major ecological factors influencing the environment, which are general environmental stimuli and cues to higher plants. Molecular responses to environmental stresses have been studied intensively over the last few years. The findings show an intricate network of signaling pathways controlling perception of environmental signals, the generation of second messengers and signal transduction. In this review, up-to-date progresses are introduced in terms of functional analysis of signaling components and issues with respect to the agricultural environment and sustainable development. These advances mainly include identification of the abiotic stress-responsive genes, extensive realization of the mutual concerted relationship between plants and the environment on different scales, molecular mechanisms of stress signal transduction and pathways, and so on. Here, a general network of stress-responsive gene expression-control model is proposed, with an emphasis on the integration between stress signal transduction pathways and the agricultural environment.

higher plants / environmental stresses / global climate change / biological measures / plant biology / network of signaling transduction / eco-environment / agricultural sustainable development

1. INTRODUCTION

Human beings have stepped into the 21st century, during which sustainable and healthy utilization of the environment and resources and their own health concerns are the most important issues. Those issues are tightly linked with agriculture and the environment, in which biology, in particular plant biology, plays a major role because plants offer the globe a renewable resource of food, building material and energy (Abbott, 2003; Balare, 2003; Asada, 2006; Bergantion, 2002; Becker et al., 2002; Bao and Li, 2002; Breusegem and Dat, 2006; Brodribb et al., 2005; Cook et al., 2005; Darnell, 2002; Deng et al., 2002, 2003; Garcia-Mata and Lamattina 2002; Finkestein et al., 2002; Gao and Li, 2002; Dharmasiri and Estelle, 2002; DeLong et al., 2002;

Dodds and Schwegheimer, 2002; Eckardt, 2002; Flexas and Medrano, 2002; Friml and Palme, 2002). The biological environment is a crucial part of nature, on which human beings depend for sustainable development. The character expressions of higher plants are controlled by developmental cues and environmental stimuli, most of which are factors such as low temperature, drought, salinity and UV-B radiation (He et al., 2002; Helliwell et al., 2002; Hagen and Guilfoyle, 2002; Ha et al., 2005; Hui and Jackson, 2006; Liscum and Reed, 2002; Leon et al., 2001; Liu J. et al., 2000; Liu et al., 2003; Liu and Zhu, 1998; Jia et al., 2003; Jordan, 2003; Kolbe et al., 2006; Milborrow, 2001; Medina et al., 1999; Marfinez-Madrid et al., 2002; Moller et al., 2002; Chow and McCourt, 2003; Mouradov et al., 2002; Mlotshwa et al., 2002; Mao et al., 2002; Shao et al., 2004, 2005, 2006). Understanding the mechanisms by which higher plants perceive environmental stimuli and transmit the signals to cellular machinery to activate adaptive responses is of vital importance to biology

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(Mark and Antony, 2005; Munns, 2005; Napier et al., 2002; O'Connell and Panstruge, 2006; Sudha and Ravishankar, 2002; Sa et al., 2003; Shen et al., 2003; Swarup et al., 2002; Shao et al., 2001, 2003, 2005). Knowledge about stress signal transduction is also the basis for continued development of crop breeding and transgenic strategies to improve stress tolerance in forest, grass, crops and, especially, decomposing poisonous substances of circumstance, and vegetation succession (Shao et al., 2006; Sessitsch et al., 2006; Somerville and Dangel, 2000; Sakuma et al., 2006; Rabbani et al., 2003; Rensink and Buell, 2004; Roberts, 2002; Tardieu, 2003; Tarcgnski et al., 1993; Torres et al., 2006; Rossel et al., 2002; Rizhsky et al., 2002; Trewavas, 2002; Xue et al., 2002; Xiong et al., 2002; Yu et al., 2002; Yang et al., 2006; Vasil, 2002, 2003; Voloudadis et al., 2002; Vardy et al., 2002; Wang and Peng, 2003; Wang et al., 2003; Nguyen, 2003; Sakuma et al., 2006; Schumpp et al., 2003; Chinnusamy et al., 2006; Malamy, 2005; Zhang et al., 2002, 2003; Bauer and Berczky, 2003; Conrath et al., 2006; Garcia-Brugger et al., 2006; Lecourieux et al., 2006). Here, we integrate up-dated information and put forward a general stress signal transduction pathway model from the angle of the agricultural environment, the purpose of which is to establish a connecting bridge between molecular biology and ecology and to instruct environmental construction.

2. A GENERAL MODEL FOR THE STRESS SIGNAL TRANSDUCTION PATHWAY IN HIGHER PLANTS

Animals perceive their local environments by complex signal transduction processes. Intelligent responses are computed, and fitness is increased by behavioral changes that commonly involve movement. Movement is a fundamental part of the animal lifestyle that arises in evolution from the requirements to find food and to mate. The same happens in higher plants and sessile higher plants must also change behavior to increase fitness as the local environment fluctuates (Bonioti and Griffith, 2002; Zhu T., 2003; Zhang et al., 2002, 2003; Liu and Zhu, 1998; Liu J. et al., 2000; Swarup et al., 2002; Wu and Tang, 2004; Wright et al., 2006; Zhou et al., 2004). The ubiquitous distribution of light has never provided evolutionary pressure to develop movement; instead, behavioral changes are exemplified by phenotypic plasticity (Jordan, 2003; Moller et al., 2002; Munns, 2005). However, the need for detailed environmental stimuli, accurate sensing, assessment and intelligent computation is just as strong (Trewavas, 2002). A stronger spatial dimension network underlies signal transduction, for instance, and higher plants must be able to detect gradients in signals such as light and resources such as nitrate and water (Shao et al., 2003, 2005, 2006; DeLong et al., 2002; Wright et al., 2006). Higher plant development itself is also polar (Zaninotto et al., 2006; Zhu J.K., 2000, 2001; Zhu J.K. et al., 1997, 1998). The spatial dimension is satisfied in many ways. Higher plant cells place receptors, channels, G proteins and kinases in specific membranes. Some signaling protein complexes are permanent, such as relatively sta-

ble and perhaps hardwired COP9 signalosome. Other signaling protein complexes are likely to be ephemeral and formed immediately as a result of signaling (Bonioti and Griffith, 2002; Bergantion, 2002; Becker et al., 2002; Bao and Li, 2002; Dodds and Schwechheimer, 2002; Liscum and Reed, 2002; Trewavas, 2002; Sudha and Ravishankar, 2002; Zhu T., 2003). There are at least 300 receptor kinases in *Arabidopsis*, and most of them are membrane-bound. Incompatibility and disease defense signal transduction use receptor kinases. After ligand binding and autophosphorylation, such kinases may act as nucleation sites for the construction of ephemeral signaling complexes that contain many proteins (Leon et al., 2001; Foyer and Noctor, 2005; Boudsocq and Lauriere, 2005; Takemoto and Hardham, 2004; Arholdt-Schmitt, 2004; Luan and Gupta, 2004; Desikan et al., 2003; Millar et al., 2003). Although there are some differences in different higher plants, a common signal model for stress transduction pathways exists in higher plants (Bonioti and Griffith, 2002; Darnell, 2002; He et al., 2002; Liu et al., 2003; Liu J. et al., 2000; Jia et al., 2003; Munns, 2005; Shao et al., 2003, 2006; Sessitsch et al., 2006; Rossel et al., 2002; Xiong et al., 2002; Yu et al., 2002) (Fig. 1). This model begins with the perception of signals from environments, followed by the generation of second messengers such as inositol phosphates and reactive oxygen species.

Second messengers can modulate intracellular Ca^{2+} levels, often initiating a protein phosphorylation cascade that finally targets proteins directly involved in cellular protection or transcription factors controlling specific sets of stress-regulated genes. The products of these genes may participate in the production of regulatory molecules such as the plant hormones abscisic acid, ethylene and salicylic acid (Marfinez-Madrid et al., 2002; Mouradov et al., 2002; Mark and Antony, 2005; Sakuma et al., 2006; Roberts et al., 2002; Chu et al., 2005; Bauer and Berczky, 2003). Some of these regulatory molecules can, in turn, initiate a second round of circulation. More and more facts from different disciplines of natural sciences and social sciences have clearly shown that molecular biology is the leading discipline during the 21st century, through which many issues may obtain an eventual resolution. It is time to take much more care with our environment, on the basis of considering a vast amount of data involved in biology, physiology, pedology, environmental stress and molecular biology. How to integrate this information available, how to analyze the data completely, how to establish a tied relationship among different data obtained at different levels and accuracy are the main challenges confronting us, which are the key points for us to improve our environment and conduct sustainable development (Hui and Jackson, 2006; Shao, 2001; Sessitsch et al., 2006; Bauer and Berczky, 2003; Malamy, 2005; Schumpp et al., 2003; Desikan et al., 2005).

We are facing a fluctuating world, in which the surroundings are worse and worse and the resources are more and more limited: our final goal is just to adapt ourselves to such circumstances and utilize them in the best way, and to have the optimum survival space through our knowledge. A recent Floral Genome Project, an ambitious undertaking linking phylogenetic, genomic and developmental perspectives on plant reproduction, funded by the National Science Foundation of

Figure 1. A common framework model for the signal transduction of abiotic stress in higher plants (Shao et al., 2005, 2006; Trewavas, 2002; Rizhsky et al., 2002; Wang et al., 2003; Takemoto and Hardham, 2004; Millar et al., 2003; Boudsocq and Lauriere, 2005).

the USA from October 2001 through 2006 will provide us with more comprehensive knowledge about the origin, conservation and diversification of the genetic architecture of flowers, which will also give us insights into global changes (Eckardt, 2002; Somerville and Dangel, 2000; Rossel et al., 2002; Chinnusamy et al., 2006; Nguyen, 2003). Rossel et al. (2002) used microarray techniques and *Arabidopsis* as experimental materials to explore the relationship between global changes and gene expression, enforcing and further bearing out the multiplicity and universality that higher plants are adapted to changing environments from the starting point of gene expression. Much research is needed on this frontier and overlapping field.

The past years have seen great strides in dissecting the molecular basis of environmental stress signal transduction in higher plants. Advances in our understanding of the integration of higher plant signaling processes at the transcription level have relied, rely and will continue to rely heavily on the application of genetic approaches in the model plant *Arabidopsis thaliana*. Such studies have helped, in the first instance, to identify important components of hormone and other stress signaling pathways. An integrative signaling function has often been elucidated through the pleiotropic hormone response phenotype of the null mutation or by subsequent second-sited mutation screens (Zaninotto et al., 2006; Jia et al., 2003; Xiong et al., 2002). At the protein level, novel interactions between newly discovered components from nominally discrete signaling pathways will be detected through the application of two-hybrid proteomic-based approaches or the use of high-throughput protein chip-based technologies. Microarray-based expression analysis represents the genomic

technology most likely to have an immediate impact on this area of research. The ability to profile the entire *Arabidopsis* genome opens up unprecedented opportunities to study different environmental stress signals at the level of gene expression. However, great care must be taken in experimental design to ensure that meaningful results are obtained. For instance, the researcher must ensure that comparisons are made between materials at equivalent developmental stages when profiling a hormone mutant versus wild type. Equally importantly, validation of initial expression profiling results must be obtained with either independent alleles or related hormone mutants. Remember, these results should be compared with those obtained from other higher plants as much as possible (O'Connell and Panstruga, 2006; Hui and Jackson, 2006; Sessitsch et al., 2006; Shao et al., 2005, 2006; Tardieu, 2003; Arnholdt-Schmitt, 2004; Foyer and Noctor, 2005).

In summary, given the rich molecular biology and other branch information resources available, *Arabidopsis* will continue to represent the model experimental system to study environmental stress signal transduction and cross-talk in higher plants. Nevertheless, we must not overlook the rich diversity of signaling mechanisms that has evolved in other higher plant species and endeavor to adopt a comparative and integrative research approach on a global scale. Signaling may follow the above model, although some different components are often involved (Bergantion et al., 2002; Breusegem and Dat, 2006; Cook et al., 2005; Dharmasiri and Estelle, 2002; Eckardt, 2002; Mark and Antony, 2005; Moller et al., 2002; Rabbani et al., 2003; Mlotshwa et al., 2002).

Signal transduction processes are very complicated, requiring the suitable spatial and temporal coordination of all

signaling molecules involved in the transduction process. Therefore, there are some molecules that take part in the modification, delivery or assembly of signaling components, but do not directly relay the signal. They are very critical for the precise transmission of stress signals. These proteins include protein modifiers (e.g. enzymes for protein lipidation, methylation, glycosylation and ubiquitination), scaffolds and adaptors (Finkelstein et al., 2002; Friml and Palme, 2002; Hagen and Guifoyle, 2002; Miborw, 2001; Medina et al., 1999; Liu J. et al., 2000; Jordan, 2003; Mao et al., 2002; Pinto et al., 2002; Shao et al., 2005, 2006; Chinnusamy et al., 2006).

3. MULTIPLICITY OF HIGHER PLANT STRESS SIGNALS

Low temperature, drought, high salinity and UV-B radiation are common complex abiotic stresses that possess many different related attributes, each of which may provide the higher plant cell with quite different information. This results in the multiplicity and complexity of higher plant adaptation to fluctuating environments for the sake of tuning well and succeeding, which involves cell-to-cell communication and co-ordination among different organelles – such as chloroplast and nucleus and mitochondrion, respectively and integrately (Jordan, 2003; Mao et al., 2002; Chow and McCourt, 2003; Malamy, 2005). For instance, water stress may immediately bring about mechanical constraints, changes in activities of macromolecules, and decreased osmotic potential in the cellular milieu, and ion concentration change (Deng et al., 2002, 2003; Rizhsky et al., 2002; Shen et al., 2003; Sakuma et al., 2006; Zhu J.K. et al., 1997). We indicated that different pretreatments of barley mature embryos heavily influenced the hormone (abscisic acid, gibberellic acid and others) and ion (Na, K, Ca, Mg and Fe) changes in barley embryos and endosperms, further affecting the morphological processes of the subsequent callus due to abnormal signal transduction of environmental stress (Sudha and Ravishankar, 2002; Shao et al., 2006; Sessitsch et al., 2006). High salt stress includes both an ionic and an osmotic component, each of which is chemical and physical stress, respectively. The multiplicity of the corresponding information embedded in such stress signals underlies one aspect of the complexity of stress signaling.

On the basis of this multiplicity and complexity, it is impossible that there is only one sensor that perceives the stress condition and controls a subsequent signaling. Rather, a single sensor might only regulate branches of the signaling cascades that are initially one aspect of the stress condition. For example, cold is known to change membrane fluidity (Mark and Antony, 2005; Munns, 2005; Shao and Chu, 2005; Xiong et al., 2002; Chu et al., 2005; Wu and Tang, 2004). A sensor measuring this change could initiate a signaling cascade responsive to membrane fluidity but would not necessarily control signaling initiated by an intracellular protein whose conformation/activity is directly altered by cold. Therefore, there may be multiple primary sensors that sense the initial stress signal.

Secondary messengers such as higher plant hormones and other signals can trigger another cascade of signaling events, which can differ from the primary signaling in time, i.e., lag behind, and in space, e.g., the signals may diffuse within or among cells, and their receptors may be in different subcellular locations from the primary sensors (Bao and Li, 2002; Liscum and Reed, 2002; Swarup et al., 2002; Shao et al., 2005). These secondary signals may also differ in specificity from primary stimuli, may be shared by different stress pathways, and may underlie the interaction among signaling pathways for different stresses and stress cross-protection. Therefore, one primary stress condition may activate multiple signaling pathways differing in time, space and outputs. These pathways may connect or interact with one another using shared components generating an intertwined network (Mark and Antony, 2005; Shao, 2001; Shao et al., 2003, 2005, 2006; Zhu J.K., 2000, 2001; Bauer and Berczky, 2003; Zhang et al., 2002).

4. FUNCTIONAL ANALYSIS OF STRESS SIGNAL TRANSDUCTION AND RELATED STRESS-RESPONSIVE GENES

Much functionally genetic analysis of stress signal transduction has been carried out by applying a wide range of *Arabidopsis thaliana* mutants. Much research has implied that the process of signal transduction is quite complicated and includes a series of biochemical reactions, in which there is the stage of perception of the primary signal sensor, the generation of secondary signal molecules through the connection of repetitive Ca^{2+} transients, resulting in different outputs with different biological significance (Eckardt, 2002; Mouradov et al., 2002). Absciscic acid is a main environmental stress-responsive plant hormone (Flexas and Medrano, 2002; Finkelstein et al., 2002; Marfinez-Madrid et al., 2002; Pinto et al., 2002; Shao et al., 2003, 2006; Trewavas, 2002; Sakuma et al., 2006; Yang et al., 2006; Chinnusamy et al., 2006). Many studies of the connection between abscisic acid and different stress-signaling pathways have been limited by the paucity of signaling mutants. To facilitate genetic screens for stress-signaling mutants, transgenic *Arabidopsis* were engineered that express the firefly luciferase reporter gene (LUC) under control of the RD29A promoter, which contains both the abscisic acid-responsive element and dehydration-responsive element (Eckardt, 2002). Seeds from the RD29A LUC transgenic plants were mutagenized with ethyl methane sulfonate or T-DNA, and seedlings from mutagenized populations were screened for altered RD29A-LUC responses in response to stress and abscisic acid treatments. The occurrence of mutations with different responses to stress or abscisic acid or combinations of the stimuli revealed a complex signal transduction network in 3-dimensioned directions and suggested that there should be extensive connections among cold, drought, salinity, UV-B and the abscisic acid signal transduction pathway (Eckardt, 2002). The identification and cloning of some of the mutations have been able to provide new insights into the mechanisms of stress and abscisic acid signal transduction.

The effect of UV-B on gene expression has been extensively reviewed (Jordan, 2003; Wright et al., 2006; Boudsocq and Lauriere, 2005). It is very important to repeat a number of key points. The potential of UV-B to directly damage DNA suggests this could be a means to influence gene expression. The overwhelming evidence, however, suggests that modification of gene expression is far more complex and specific. For example, gene expression is simultaneously up- and down-regulated by exposure to UV-B. The effect of UV-B on gene expression is strongly influenced by developmental stage and DNA damage levels do not correlate with changes in gene activity. UV-B also affects the gene expression at different levels from transcription, translation and post-translational modification (Eckardt, 2002; Wright et al., 2006). The general belief is that most nuclear-encoded genes seem to be influenced at the level of transcription by light, whereas chloroplast-coded genes seem to be largely affected at translation. Many authors suggest that gene expression can be modified by changes in light, perception/signal transduction, metabolic feedback, changes in photosynthetically active radiation, or changes in the balance between photosystems (Bergantion et al., 2002; Flexas and Medrano, 2002; Munns, 2005; Shao et al., 2005; Nguyen, 2003; Liang et al., 2006). For instance, changes in carbohydrate metabolism affect gene expression and UV-B is known to modify carbohydrate levels in higher plants. Therefore, UV-B-induced changes in gene expression could be modified through carbohydrate feedback. High light has been demonstrated on many occasions to ameliorate UV-B-induced responses, including gene expression.

Salt, drought, and to some extent, old stress cause an increased biosynthesis and accumulation of abscisic acid, which can be rapidly catabolized following the relief of stress. Many stress-responsive genes are up-regulated by abscisic acid. The role of abscisic acid in osmotic stress signal transduction was previously addressed by studying the stress induction of several of these genes in the *Arabidopsis* abscisic acid-deficient mutant, abscisic acid1-1 and dominant abscisic acid-insensitive mutants *abi 1-1* and *abi 2-1*. A general conclusion from these studies was that whereas low temperature-regulated gene expression is relatively independent of abscisic acid, osmotic stress-regulated genes can be activated through both abscisic acid-dependent and abscisic acid-independent pathways (Eckardt, 2002; Xiong et al., 2002; Chinnusamy et al., 2006). Increased abscisic acid levels under drought and salt stress are mainly achieved by the induction of genes coding for enzymes that catalyze abscisic acid biosynthetic reaction. The abscisic acid biosynthetic pathway in higher plants is understood to a great extent. Most recent studies imply that all of these genes (i.e. ZEP, NCED, AAO3 and MCSU) are likely regulated through a common cascade that is dependent on Ca^{2+} (Zhu J.K. et al., 1998; Sakuma et al., 2006; Zaninotto et al., 2006).

Molecular studies have identified many genes that are induced or unregulated by osmotic stress (Zhu J.K. et al., 1997; Zhu T., 2003). Gene expression profiling using cDNA microarrays or gene chips has identified many more genes that are regulated by cold, drought or salt stress. Although the signaling pathways responsible for the activation of these genes

are largely unknown, transcriptional activation of some of the stress-responsive genes is understood to a great extent, owing to studies on a group of such genes represented by COR 78 /L7178 (Chinnusamy et al., 2006; Zhu J.K. et al., 1997). The promoters of this group of genes contain both the abscisic acid-responsive element and the dehydration-responsive element. Transcription factors belonging to the EREBP/AP2 family that bind to the above transcription factors were isolated and termed as CBF1/DREB1B, CBF2/DREB3 and CBF3/DREB 1A (Liu and Zhu, 1998; Liu J. et al., 2000; Medina et al., 1999; Marfinez-Madrid et al., 2002; Chinnusamy et al., 2006). These transcription factor genes are induced early and transiently by cold stress, and they, in turn, activate the expression of target genes. The similar transcription factors DREB2A and DREB2B are activated by osmotic stress and may confer osmotic stress induction of target stress-responsive genes (Liu and Zhu, 1998). Several basic leucine zipper transcription factors (named ABF/AREB) that can bind to ABRE and activate the expression of ABRE-driven reporter genes have also been isolated. AREB1 and AREB2 genes need abscisic acid for full activation, since the activities of these transcription factors were reduced in the abscisic acid-deficient mutants, abscisic acid 2 and abscisic acid-insensitive mutant, *abi1-1*, but were enhanced in the abscisic acid-hypersensitive *era1* mutant, probably due to abscisic acid-dependent phosphorylation of the proteins.

5. ENVIRONMENTAL STRESS-RESPONSIVE TRANSCRIPTIONAL ELEMENTS

Plants can sense, process, respond to environmental stress and activate related gene expression to increase their resistance to abiotic stress (Shao and Chu, 2005; Chu et al., 2005; Shao et al., 2005, 2006; Rabbani et al., 2003; Vasil, 2002, 2003; Voloudadis et al., 2002; Xue et al., 2002; Vardy et al., 2002; Wang and Peng, 2003). Environmental stress-inducible genes can be mainly divided into two types in terms of their protein products: one type of genes, whose coding products directly confer the function of plant cells to resist environmental stress such as late-embryogenesis abundant protein, anti-freezing protein, osmotic regulatory protein, enzymes for synthesizing betaine, proline and other osmoregulators; the other type of genes, whose coding products play an important role in regulating gene expression and signal transduction, such as the transcriptional elements for sensing and transducing the protein kinases of mitogen-activated protein and basic leucine-zip factors and others (Eckardt, 2002; Miborrrw, 2001; Medina et al., 1999; Tardieu, 2003; Shao et al., 2006; Wu and Tang, 2004; Foyer and Noctor, 2005). Transcriptional elements are defined as the protein combining with the specialized DNA sequence of eukaryotic promoters or the protein with structural characteristics of a known DNA-combining region, whose main function is to activate or suppress the transcriptional effect of corresponding genes. Up to now, hundreds of transcriptional elements of environmental stress-responsive genes in higher plants have been isolated, which regulate and control the stress reaction related to drought, salinity, cold,

Table I. Typical transcriptional elements in higher plants.

Plant materials	Factors	Binding sites/Factor Types
<i>Arabidopsis thaliana</i>	ABI5/AtDPBF	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	AtDPBF2	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	AtDPBF3/AREB3	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	AtDPBF4	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	AtDPBF5/ABF3	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	ABF1	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	ABF2/AREB5	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	ABF4/AREB2	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	GBF3	ABA response elements(ABREs)/bZIP
<i>A. thaliana</i>	AB53	RY/sph elements/B3 domain proteins
<i>A. thaliana</i>	ATMTB2	MTC
<i>A. thaliana</i>	ATHB6	HD-Zip
<i>A. thaliana</i>	ATHB7	HD-Zip
<i>A. thaliana</i>	ATHB12	HD-Zip
<i>A. thaliana</i>	ABI4	AP2
<i>Oryza</i>	TRAB1	ABA response elements(ABREs)/bZIP
<i>Oryza</i>	OsVPI	RY/sph elements/B3 domain proteins
<i>Zea mays</i>	VPI	MYB
<i>Triticum</i>	EmBP-1	ABA response elements(ABREs)/bZIP
<i>Avena</i>	AtVPI	RY/sph elements/B3 domain proteins
<i>Helianthus</i>	DPBF5,-2,-3	ABA response elements(ABREs)/Bzip
<i>Phaseolus</i>	ROM2(repressor)	ABA response elements(ABREs)/Bzip
<i>Phaseolus</i>	PIARF	RY/sph elements/B3 domain proteins
<i>Craterestemma</i>	Cvpv1	RY/sph elements/B3 domain proteins
<i>Daucus</i>	C-ABI3	RY/sph elements/B3 domain proteins
<i>Populus</i>	PtABI3	RY/sph elements/B3 domain proteins

pathogens and heat. In the genome of *Arabidopsis* and rice, they have about 1300–1500 genes for coding transcriptional elements, most of which have not been identified functionally. Recent study has shown that the transcriptional elements involved in plant stress responses mainly include four kinds: APETALA2/EREBP, bZIP, WRKY and MYB. Typical transcriptional elements in relation to environmental stress have been summarized in Table I for reference.

6. CONCLUSION

Globally, food production will have to be tripled to meet the demand for food of the 12 billion inhabitants of the world by the year 2050 (Vasil, 2002, 2003); meanwhile, including most of the people in our country, India, Northern Korea and Thailand, dietary requirements are changing as a result of their improving buying power. It is evident that food supply is the first challenge. The second challenge is eco-environmental degradation, mainly including deficits of water resources and pollution, soil erosion and desertification, decrease in biodiversity owing to widespread use of agro-chemicals, and increase in natural disasters resulting from different forms of bi-

otic/abiotic stress factors (Ballare, 2003; Liu and Zhu, 1998; Shao et al., 2005, 2006; Yang et al., 2006; Zhu J.K., 2000, 2001, Zhu T., 2003; Zhu J.K. et al., 1997, 1998). These factors lead to great losses in food production annually. Plants are evolving in a concerted manner (Abbott, 2003), and declining resources essentially enhance a rapid decrease in species, resulting in a vicious circle. Facing such severe global change and considering all of the technologies developed, it is firmly believed that biological measures (mainly plant methods) are the best solution not only for meeting the food needs of the ever-growing population, but also for protecting and improving our eco-environment (resources) in a sustainable development way (Vasil, 2002, 2003). Plant molecular biology is the basis of plant biotechnology, which is the best way to solve the problem above, at least to increase productivity on limited land under cultivation, with less water and under worsening eco-environmental conditions (Shao et al., 2003, 2005, 2006; Shao and Chu, 2005; Chu et al., 2005; Vasil, 2002, 2003).

The elaboration of higher plant form and function depends on the ability of a plant cell to divide and differentiate and the information-communicating status between higher plants and circumstances, e.g. soil compaction, water situation and

climate parameters. The decisions of individual cells to enter the cell cycle, maintain proliferation competence, become quiescent, expand, differentiate or die depend on the perception of various signals. These signals can include hormones, nutrients, light, temperature and internal positional and developmental cues, which also have an influence upon the function of stress signals displaying the condition of the plant. In fact, higher plant development is the basis for higher plants to be adapted to the environment; otherwise, the environment brings about diversity of higher plant development (Asada, 2006; Darnell, 2002; Dodds and Schwechheimer, 2002; Gao and Li, 2002; Mao et al., 2002; Liu et al., 2003; Mark and Antony, 2005; Munns, 2005; Shao et al., 2005, 2006; Boudsocq and Lauriere, 2005). From this point, there is a closed relationship among higher plants at different levels, the environment and their development, whose regulating mechanism is gene expression and control in time and space (Munns, 2005; Eckardt, 2002; Sa et al., 2003; O'Connell and Panstruga, 2006; Shao et al., 2005, 2006). Of course, it is possible to increase the water-use efficiency (WUE) of main crops through biotechnology after clear mastering of the mechanism (Deng et al., 2002, 2003; Marfinez-Madrid et al., 2002; Napier et al., 2002; Sudha and Ravishankar, 2002; Shao, 2001; Shao and Chu, 2005; Shao et al., 2005; Sakuma et al., 2006; Tarcgnski et al., 1993; Wang et al., 2003). Genetic approaches are important tools for analyzing complex processes such as stress signal transduction. Conventional genetic screens based on stress injury of tolerance phenotypes have been applied with success. However, such screens may not be able to identify all components in the signaling cascades due to functional redundancy of the pathways in the control of plant stress tolerance. The accessibility of the Arabidopsis genome and rice genome framework and various reverse genetics strategies for generating knockout mutants should lead to the identification of many more signaling components and a clear picture of abiotic stress signaling networks (Rensink and Buell, 2004; Xiong et al., 2002; Shao et al., 2005, 2006; Arnholdt-Schmitt, 2004; Chinnusamy et al., 2006). Molecular screens such as the one using the RD29A-LUC transgene as a reporter are beginning to reveal novel signaling determinants. Similar methods may prove useful for the study of their pathways, such as osmolarity sensing. Adoption of forward and reverse genetic approaches will improve our understanding of signaling mechanisms in higher plants.

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