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高等植物对环境胁迫的适应与其胁迫信号的转导

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摘要：高等植物适应环境胁迫有多种水平与尺度的生理与生化方式，但其本质却是分子水平的基因时空表达与调控，它又受到胁迫信号转导途径的多重调控与影响。环境胁迫的主要形式是冷害、干旱、盐碱胁迫与UV-B辐射等，而它们又是影响高等植物生长、发育、繁殖等重要过程的生态因子，同时 也是作物高效生产必需重视的因素，对其与植物相互作用的分子机理的认识有重要理论意义与实践意义。从细胞与组织和器官水平获得的分子生物学规律，只有应用到个体，群体，及生态系统中才会更有生命力。如何将这些数据资料成为宝贵的永续资源是21世纪植物系统生物学面临的主要挑战之一。主要从农业生态环境角度阐述环境胁迫信号转导的分子生物学作用方式，新进展资料的整合并建立起它们的可能联系及本领域中存在的相关问题和可能的解决途径，为高效的农业生态可持续发展提供分子生物学方面的理论基础。

关键词：高等植物；环境胁迫；适应；分子生物学机制；信号转导；信号途径网络；农林生态环境

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Adaptation of higher plants to environmental stressesland stress signal transduction

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Abstract: Higher plants play the most important role in keeping a stable environment on the earth, which regulate global circumstances in many ways in terms of different levels (molecular, individual, community, and so on), but the nature of the mechanism is gene expression and control temporally and spatially at the molecular level. In persistently changing environment, there are many adverse stress conditions such as cold, drought, salinity and UV-B (280-320mm), which influence plant growth and crop production greatly. Unlike animals, higher plants, which are sessile, can't escape from the surroundings, but adapt themselves to the changing environments by forming a series of molecular responses to copying with these problems. The physiological processing basis for these molecular responses is the integration of many transduced events

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into a comprehensive network of signaling pathways. Higher plant hormones occupy a central place in this transduction network, frequently acting in conjunction with other signals, to co-ordinately regulate cellular processes such as division, elongation and differentiation, which are the fundamental basis for higher plant development and related character expressions. In a word, it is at the molecular level-gene expression and control in time and space that we can bring out the mystery of living organisms and explore the nature of environmental changes. Ecological science is the fused and ramified field between natural sciences and social sciences where the frontier is molecular ecology and very important to conducting the practice of vegetation restoration and reconstruction and crop production on Loess Plateau. It is obvious that molecular biology is the purposeful basis for improving diverse types of eco-environment. The common stress factors mentioned above are those important ecological factors influencing environment, which are general environmental stimuli and cues to higher plants. Molecular responses to such common environmental stresses have been studied intensively over the last few years, in which there is an intricate network of signaling pathways controlling perception of these environmental stress signals, the generation of second messengers, signal transduction, and therefore, deeper understanding of these molecular processes is even vital to the agricultural production in the semiarid area of Loess Plateau. In this review, up-dated progresses were introduced in terms of functional analysis of signaling components and problems with respect to agricultural eco-environment, and a probable general network of stress-responsive gene expression -control model were summarized, with an emphasis on the integration between stress signal transduction pathways and agricultural eco-environment. The viewpoint is that the molecular information from higher plant cells, tissues, and organs should be efficiently popularized to levels of individuals, community, and ecosystem, which can play a greater role, and which is also one of the greatest challenges for plant systems biology during the 21st century.

Key words:higher plants; environmental stress;adaptation; molecular biological mechanisms; signaling transduction; network of signaling pathways; agricultural -forestry eco-environment

1 Introduction

Advances of sciences and technology are main driving force of social progression, through which human beings can have a better life, which is the eventual goal of human beings. The knowledge obtained by learning sciences and society is a means to utilize the nature optimally and serve human beings best. Eco-environment is the most important part of nature, on the basis of which human beings live for sustainable development[1~7]. The character expressions of higher plants are controlled by developmental cues and environmental stimuli, most of which are the important factors affecting eco-environment such as low temperature, drought, salinity and UV-B radiation, which often occur in the region of Loess Plateau. Understanding the mechanisms by which higher plants perceive environmental stimuli and transmit the signals (stimuli)to cellular machinery to activate adaptive responses is of vital importance to biology. Deep 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 (especially, wheat and maize), decomposing poisonous substances of circumstance, and vegetation succession[8,16]. In this paper, the authors focused on an integration of the up- dated information in this field and put forward a general stress signal transduction pathway model from the angle of agricultural eco-environment, the purpose of which is to establish a connecting bridge between molecular biology and ecology and to instruct agricultural eco-environmental construction in theory.

2 A General Model for 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 case happens on higher plants and sessile higher plants must also change behavior to increase fitness as the local environment fluctuates. The ubiquitous distribution of light has never provided evolutionary pressure to develop movement; instead, behavioral changes are exemplified by phenotypic plasticity. But the need for detailed environmental stimuli, accurate sensing, assessment, and intelligent computation are just strong[17,18]. A stronger spatial dimension network underlies signal transduction; for instance, and higher plants must be able to detect gradients in signalsl (such as light) and resources (such as nitrate and water)[19,20]. Higher plant development itself also is decidedly polar[20,21]. 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 stable and perhaps hardwired COP9 signalosome. Other signaling protein complexes are likely to be ephemeral and formed immediately as a result of signaling[1,22,23]. There are at least 600 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[24,25]. Although there are some differences in different higher plants, a common signal model for stress transduction pathways exist in higher plants[26,27] (Figure 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 messnengers 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 like the plant hormones abscisic acid(ABA), ethylene, and salicylic acid (SA). 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 one during the 21st century, by which many issues may get an eventual resolution to. It is the time that we should take much care about 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 confronted in front of us, which are the key points for us to improve our environment and conduct sustainable development on purpose[1,21,23,25,28,29]. We are facing a fluctuating world, in which the surrounding is worse and worse and the resource is more and more limited, our final goal just being to adapt ourselves to such circumstance and utilize it best 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 USA,from October 2001 to 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 the global changes[30,31]. Rossel *et al.* [32]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 environment from the starting point of gene expression. Much research is needed in this frontier and overlapped field.

The past more than ten years have seen impressive 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[13~16,30,31,33]. 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. No doubt, 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 possible as researchers can.

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 have evolved in other higher plant species and endeavor to adopt a comparative and integrative research approach from the viewpoint of global scale. Signaling may follow the above model, although some different components are often involved[11,15,16,32,33].

It is very clear that signal transduction processes are very much 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[27,28,34,35]. 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[36~43].

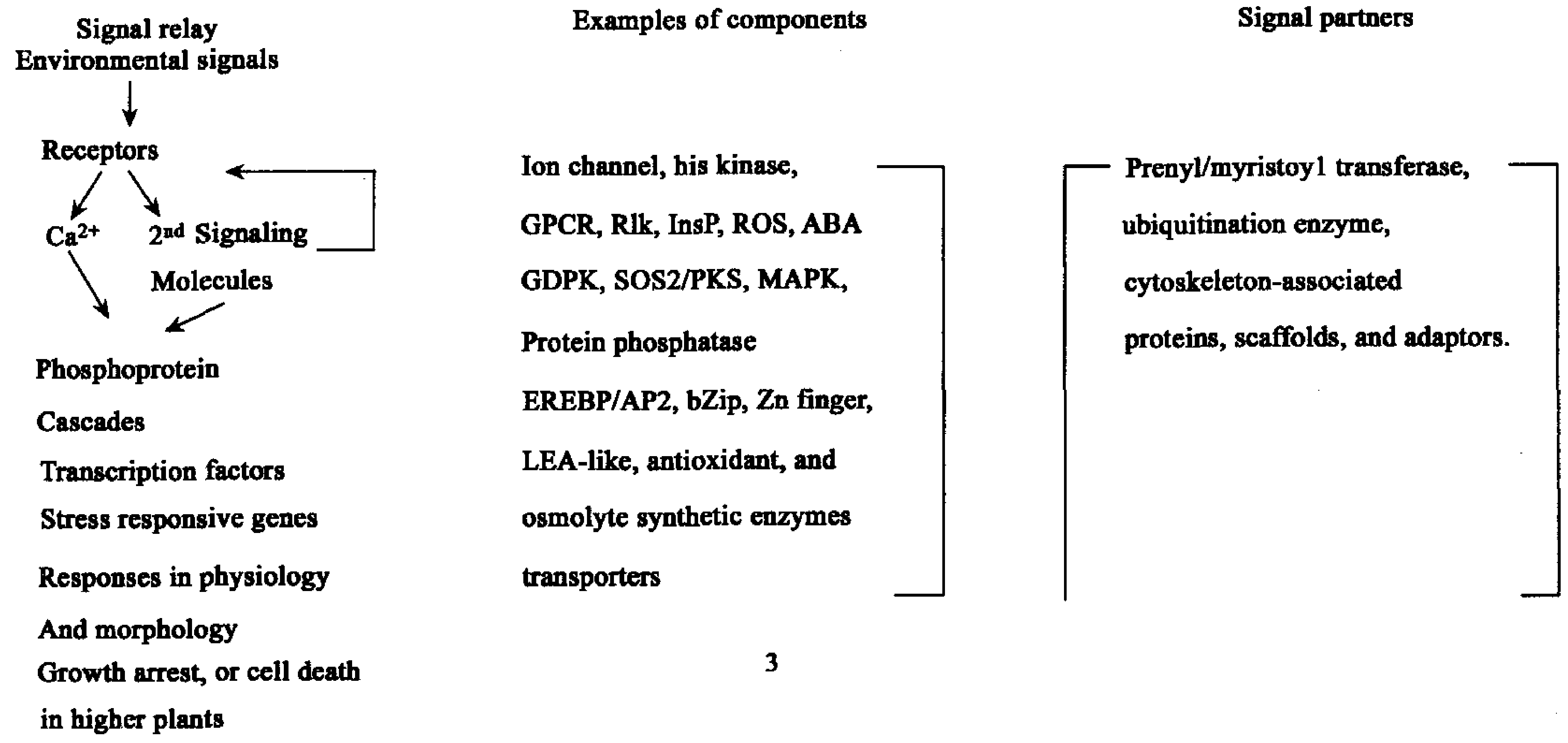

Fig. 1 A common framework model for the signal transduction of cold, drought, salinity, and UV-B stress in higher plants

3 Multiplicity of Higher Plant Stress Signals and Complexity in terms of Sensing to Environment

Low temperature, drought, high salinity, and UV-B radiation are common complex 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 environment for the sake of tuning well and succeeding highly, which involves cell-to-cell communication and coordination among different organelles-such as chloroplast and nucleus and mitochondrion, respectively and integratedly[44,45]. For instance, water stress may immediately brings about mechanical constraints, changes in activities of macromolecules, and decreased osmotic potential in the cellular milieu, and ion concentration change[46,47]. We indicated that different pre-treatments of barley mature embryos influenced heavily the hormone (ABA,GAs, IAA) and ion(Na,K, Ca, Mg, Fe) change in barley embryos and endosperms, further affecting morphological processes of subsequent callus due to abnormal signal transduction of environmental stress[48,49]. 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[18,34,49,50].

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 initiatedly one aspect of the stress condition. For example, cold is known to change membrane fludity[51~56]. 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[15,16,57~66].

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 with in or among cells, and their receptors may be in different sub-cellular locations from the primary sensors)[17,19,58,59,62,63,67]. 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 intertwined network[21,24,34,38,41~44,60,67,68].

4 Functional Analysis of Stress Signal Transduction and Related Stress-responsive Genes

Much functionally genetic analysis of stress signal transduction has been carried on by applying a wide range of *Arabidopsis thaliana* mutants. Many researches have implied that the process of signal transduction is quite complicated and includes a series of biochemical reactions, in which there are 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[46,47,59,60,65,69~72]. ABA is a main environmental-stress responsive plant hormone[47~53,59,60,70]. Many studies about the connection between ABA 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 ABA-CABA-responsive element [ABRE] and dehydration-responsive elements(DRF/CRT)[11~15]. 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 ABA treatments. The occurrence of mutations with different responses to stress or ABA or combinations of the stimuli revealed a complex signal transduction network in 3-dimensioned directions and suggested that these should be are extensive connections among cold, drought, salinity, UV-B and ABA signal transduction pathway[12,13,15,16,71]. The identification and cloning of some of the mutations have been to provide new insights into the mechanisms of stress and ABA signal transduction.

The effect of UV-B on gene expression have been extensively reviewed[18,19,60,,72,73]. 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[42,44,47,48,51,53,56,57,74] 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[15,16,75]. 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 researchers suggest that gene expression can be modified by changes in light, perception/signal transduction, metabolic feedback, changes in *photosynthetically active radiation(PAR), or changes in the balance between phtotosytems*[36,39,43,49,52,58,61~64,76]. *For instance*, changes in carbonhydrate metabolism affect gene expression and UV-B is known to modify carbohydrate levels in higher plants[21,24,77]. 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[21,22,26,55,70,71].

Salt, drought, and to some extent old stress cause an increased biosynthesis and accumulation of ABA, which can be rapidly catabolized following the relief of stress[61,67,72,73]. Many stress-responsive genes are up-regulated by ABA. The role of ABA in osmotic stress signal transduction was previously addressed by studying the stress induction of several of these genes in the Arabidopsis ABA-deficient mutant abal-abal-1 and dominant ABA-insensitive mutants abi 1-1 and abi2-1. A general conclusion from these studies was that whereas low-temperature regulated gene expression is relatively independent of ABA, osmotic stress-regulated genes can be activated through both ABA-dependent and ABA independent pathways[15,16,36,39,63,74,77]. Increased ABA levels under drought and salt stress are mainly achieved by the induction of genes coding for enzymes that catalyze ABA biosynthetic reaction. The ABA biosynthetic pathway in higher plants is understood to a great extent[26,28,66,67,77]. 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 Ca^{2+} dependent on[61,62,69].

Molecular studies have identified many genes that are induced or unregulated by osmotic stress[19,29,30,61]. Gene expression profiling using cDNA microarrays or gene chips has identified many more genes that are regulated by cold, drought, or salt stress[16,25,37,49,55,57,67,70]. 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 RD 29A(also known as COR 78 /L7178)[61,62]. The promoters of this group of genes contain both the ABRE and the DRE/CRT. Transcription factors belonging to the EREBP/AP2 family that bind to DRE/CRT were isolated and termed CBF1/DREB1B, CBF2/DREBC, and CBF3/DREB IA[27,29,30~33,40~43,55,71]. These transcription factor genes are induced early and transiently by cold stress, and they, in turn, activate the expression of target genes. Similar transcription factors DREB2A and DREB2B are activated by osmotic stress and may confer osmotic stress induction of target stress-responsive genes[31,32,39,48,49]. Several basic leucine zipper (bZIP) transcription factors (named ABF/AREB)that can bind to ABRE and activate the expression of ABRE-driven reporter genes also have been isolated. AREB1 and AREB2 genes need ABA for full activation, since the activities of these transcription factors were reduced in the ABA deficient mutant aba 2and ABA-insensitive mutant abi1-1, but were enhanced in the ABA hypersensitive era1 mutant, probably due to ABA dependent phosphorylation of the proteins.

5 Classification of Stress Signaling Pathways

Many signal transduction processes occur when higher plants are challenged with environmental stresses. Although there has been no consensus for how to categorize these signaling events, we can apply some standards on the basis of the above discussion on the major signaling processes, to divide the signal transduction networks for cold, drought, salt stress, and UV-B into these main signaling types (Figure 2): (Ⅰ) osmotic/ oxidative stress signaling that makes use of MAPK modules, (Ⅱ) Ca^{2+} dependent signaling that lead to the activation of LEA type genes(such as the DRE/CRT class of genes) and (Ⅲ) Ca^{2+}- dependent SOS signaling that regulates ion homeostasis[61~67,69,70~72,77]. Type 1 signaling may contribute to the production of compatible osmolytes and antioxidants, and may also relate to cell cycle regulation under osmotic stress[1,55,59,64,73]. Representative mutants that might be affected in this signaling branch include the freezing-tolerant mutant eskino 1(esk1) and the salt-tolerant mutant photoautotrophic salt tolerance 1 (pst1). Esk1 accumulates increased amounts of proline and soluble sugars, but the expression of the DRE/CRT class of genes is unaffected[11~16]. The pst1 mutant shows increased ROS (reactive oxygen species, ROS) scavenging capacity but appears unaltered in the accumulation of Na +[50~52,66,73]. Type Ⅱ signaling leads to the activation of the DRE/CRT class and other types of LEA- like genes, and is the most extensively studied. Mutants defective in this signaling type include some of the cos, has, and los mutants isolated in an R D 29A-LUC reporter-facilitated genetic screen. Some of these mutations (e. g. , fry 1, hos1, los5, los6, and sad1) have been cloned. Type Ⅲ signaling appears to be relatively specific for the ionic aspect of salt stress. Targets of this type of signaling are ion transporters that control ion homeostasis under salt stress. The sos mutants (SOS3, SOS2, and SOS1) fall, into this category. These mutants are hypersensitive to salt stress, but activation of the DRE/ CRT class of genes unchanged in them[65~67,74~76]. In addition, salt induced accumulation of the compatible osmolyte proline was not reduced but rather was enhanced in the SOS mutants[32~36,52,76,77]. The enhanced proline production represents a compensatory response likely triggered by reduced salt tolerance in the mutants. Besides these major signaling routes, some additional pathways also exist to adapt higher plants to changing surroundings.

One important issue regarding various stress signal transduction pathways is their specificity with respect to the input stimuli. The specificity and interaction between pathways have been addressed explicitly. As discussed before, each of the stress conditions (i. e. , cold, drought, high salinity, UV-B) has more than one attribute. If two stress conditions have a common attribute(for example, hyperosmotic stress for drought and salinity), then the signaling arising from this common attribute might not be specific for either of the stress condition[61~63,75], Additionally, it is important to distinguish the particular pathways when signaling specificity is considered. Interaction among these three siganlling types (Figure 2) is not extensive, as evidenced by the lack of mutants defective in more than one of the signaling types and by results from additional transgenic studies, discussed above. Although both drought and salt stress result in a transient increase in cytosolic Ca^{2+}, drought stress does not appear to activate the SOS pathway. It is possible that these different stresses have different Ca^{2+} signatures that could be decoded by their respective Ca^{2+} sensors. Specific Ca^{2+} oscillations in guard cells in the regulation of stomatal movements have been reported[31]. In contrast to the limited interaction among the major different signaling routes (Figure 2), interaction within a signaling type can be fairly extensive. This is best illustrated by the study of RD29A-LUC induction, revealed by mutational analysis of the pathways and further characterization of several mutants, as discussed above. Additional discussion on pathway interaction for the activation of LEA type genes can be found in recent reviews[63~67,69~74,76,77].

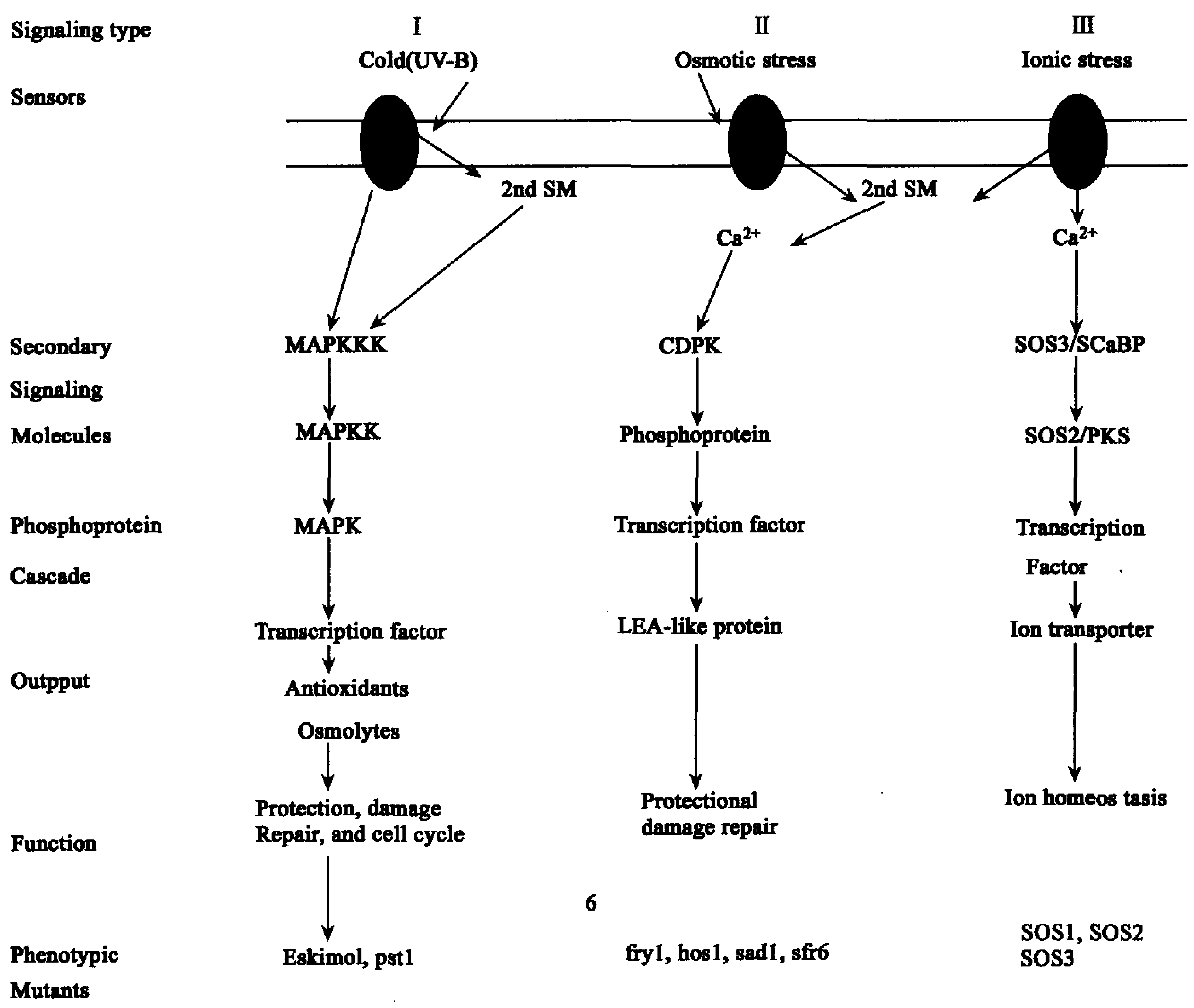

Fig. 2 Major types of signaling for higher plants during cold, drought, salt, and UV-B stress

6 Concluding Remarks

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, 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, ions (ion homeostasis change), light, temperature, and internal positional and developmental cues, which also have influence upon the function displaying of condition stress signals. In fact, higher plant development is the basis for higher plants to be adapted to environment, otherwise, environment brings about diversity of higher plant development[47~53,73~76]. From this viewpoint, there is a closed relationship among higher plants (at different levels), environment and their development, whose regulating mechanism is gene expression and control in time and space[47~53,61~67,73~76]. Of course, it is quite possible to increase water use efficiency (WUE) of main crops through biotechnology after clear mastering of the mechanism[18,19,73~76]. 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[62]. 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 mutant should lead to the identification of many more signaling components and a clear picture of abiotic stress signaling networks[66,67,77]. Molecular screens such as the one using the RD29A-LUC transegene as a reporter are beginning to reveal novel signaling determinants. The recent results from our laboratory have indicated that anti-oxidative enzymes played a central role in different wheat genotypes protecting themselves from damage from soil water deficits[71~76], exhibiting that modern plant physiology can not be substituted by molecular biology and that the combination of both is the key strategy. Similar methods may prove useful for the study of their pathways, such as osmolarity sensing (typeI signaling: Figure 2). Adoption of forward and reverse genetic (post-genomic) approaches by more researchers in this field will certainly expedite our understanding of signaling mechanisms in higher plants, meanwhile making healthy sustainable development of agricultural practice on the globe(in particular, in developing countries) come true.

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