Volume 50(1-2):1-9, 2006
Acta Biologica Szegediensis
http://www.sci.u-szeged.hu/ABS

REVIEW ARTICLE

Plant Gene Regulatory Network System Under Abiotic Stress

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ABSTRACT Plants differ from animals in many aspects, but the important may be that plants are more easily influenced by environment than animals. Plants have a series of fine mechanisms for responding to environmental changes, which has been established during their long-period evolution and artificial domestication. These mechanisms are involved in many aspects of anatomy, physiology, biochemistry, genetics, development, evolution and molecular biology, in which the adaptive machinery related to molecular biology is the most important. The elucidation of it will extremely and purposefully promote the sustainable utilization of plant resources and make the best use of its current potential under different scales. This molecular mechanism at least include environmental signal recognition (input), signal transduction (cascades of biochemical reactions are involved in this process), signal output, signal responses and phenotype realization, which is a multi-dimensional network system and contain many levels of gene expression and regulation. We will focus on the molecular adaptive machinery of plants under abiotic stresses and draw a possible blueprint for it. Meanwhile, the issues and perspectives are also discussed. **Acta Biol Szeged 50(1-2):1-9 (2006)**

KEY WORDS

abiotic stress
agricultural sustainable development
biointerfaces
ion homeotasis
plant gene regulatory network sytem
physiological mechanisms
signal

Human being has stepped into the 21th century, during which sustainable - healthy utilization for environment and resources and its own health concerns are the most important issues (Rosenberg et al. 1993). These issues are tightly linked with agriculture (food) and eco-environment, in which biology, in particular plant biology plays the greatest role, because plants offer the globe its only renewable resource of food, building material and energy and thus plant biology is the most powerful tool to reasonably use natural resources (Bazzaz 2001; Charlesworth et al. 2001; Agraval et al. 2003; Anand et al. 2003; Chaves et al. 2003; Munns 2003, 2005; Shao et al. 2003, 2005; Angela 2004; Arnholdt-Schmitt 2004; Brian et al. 2004). In the broad field of plant biology, its core is the study for life activities at molecular level (mainly DNA and protein macromolecules), whose interactions at various biointerfaces at different scales are quite important to keep a steady state between plants and changing environment, especially adverse surroundings (Doebley and Lukens 1998; Avramova 2002; Kreps et al. 2002; Ambros et al. 2003; Chaves et al. 2003, 2004; Shao et al. 2003, 2004, 2005a-d; Beer and Tavazoie 2004; Casati and Walbot 2004; Chinnusamy et al.2004; European Commission 2004; Jiang and Zhang 2004; Ashraf and Chu et al. 2005; Foolad 2006. So, adaptation in plants is an important and timely topic in basic and applied biology (Bonnie et al. 1998; Eckardt et al. 2001; Dufty et al. 2002; Brill and Watson 2004; Castle et al. 2004; David et al. 2004; Editor's choice 2004; Hiral et al.2004; Ma 2004; Shao et al. 2004; Andrew et al. 2006; Humphreys et al. 2006). On the one hand, it is very interesting to understand interaction between plants and their environment. On the other hand and in view of the needs for human life, we more want to create crop plants that are able to confront successfully unfavorable natural conditions (Fischer et al. 2000; Chen et al. 2002; Doelle 2002; Brill and Watson 2004; Capell et al. 2004; Casu et al. 2004; Costa et al. 2004; Delessert et al. 2004; De Ronde et al. 2004). The main aim in plant breeding is to obtain plants that combine higher yields, reliable yield stability, better quality and obvious characters resisting stresses (abiotic and biotic) over years and locations (Liu et al. 2000; Chen et al. 2002; Fiehn 2002; Gesch et al. 2002; Graves and Haystead 2002; Castle et al. 2004; Chen and Gal-

Accepted May 5, 2006

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lie 2004; Glombitza et al. 2004; Hao et al. 2004; Lu and Chen 2004; Liu and Li 2005; Grennan 2006). However, in addition to biotic stress factors, disturbances of extreme or even mild abiotic stress are supposed to account for a high amount of unachieved potential in plant production all over the globe (Kasuga et al. 1999; Harmer et al. 2000; Johson et al. 2001; Halford and Paul 2003; Lokhandle et al. 2003; Shinozaki et al. 2003; Gregory et al. 2004; Harding et al. 2004; Kennedy and Wilson 2004; Liu et al. 2004; Mark and Antony 2005; Shao et al. 2006d). Diverse forms of abiotic stresses may occur, including drought, cold and freezing, heat, salinity, nutrient deficiency, toxic heavy metals, oxidative stress as well as oxygen shortage, and mechanical stress (Mlot 1998; Harmer et al. 2000; Kwon and Kim 2001; Meyerowitz 2002; Halford and Paul 2003; Miyao 2003; Hernandez et al. 2004; Higuchi et al. 2004; Kim et al. 2004; Liu and Baird 2004; Medict et al. 2004; Munne-Bosch and Alegre 2004; Bartha et al. 2005; Kolbert et al. 2005; Grennan 2006; Liu and Bush 2006). Although it is accepted that diverse environmental stress factors never act alone, experimental study of plant responses to abiotic stress is normally restricted to plant reactions on isolated stress factors (Neumann 1997; Riechmann et al. 2000; Somerville and Dangl 2000; Mette et al. 2002; Noctor et al. 2002; Pellegrineschi et al. 2002; Travis et al. 2002; Millar et al. 2003; Tang et al. 2003; Wang et al. 2003; Manival et al. 2004; Puhakainen et al. 2004; Rae et al. 2004; Soltani et al. 2004; Taylor et al. 2004; Philippe et al. 2005; Shao et al. 2005, 2005a-e, 2006d; Sun et al. 2005; Tan et al. 2006). However, it has to be considered that stress always occurs as a complex of various interacting environmental factors that contribute in varying degrees to the overall stressed phenotype (Zhou et al. 2000; Vranova et al. 2002; Yong et al. 2003; Salt 2004; Wang et al. 2004; Wei et al. 2004; Winichayakul et al. 2004; Yang et al. 2006; Yang and Zhang 2006). Consequently, plants usually respond to a unique complex of growth conditions (Zhu 2002; Zhu 2003; Zhu T 2003; Zhu et al. 2004; Shao et al. 2006). Stress inducers from the abiotic as well as biotic world have some common signal and responding pathways in plants (Samis et al. 2002; Schlighting 2002; Vranova et al. 2002; Shinozaki and Dennis 2003; Tang et al. 2003; Shao and Chu 2005; Shao et al. 2006b,f) and thereby have the potential to moderate the effect of each other through cross-talking (Riechmann et al. 2000; Samis et al. 2002; Shigeoka et al. 2002; Soltis and Soltis 2003). Further, plants, as sessile organisms, have to get alone with the dynamics of transiently changing environmental conditions and have the flexibility for responding to these complicated changes (Manival et al. 2001; Poethig 2001; Pellegrineschi et al. 2002; Munns 2003, 2005; Rae et al. 2004), and this has to be achieved at the various stages of plant development (Kreps et al. 2002; Meyerowitz 2002; Hiral et al. 2004; Kim et al. 2004; Mark and Antony 2005; Shao et al. 2005d; Liu and Bush 2006).

Considering the interacting complexity (at least including water movement, solute transport, information exchange, ion homeostasis regulation, and other related physico-chemical changes) between plants and their surroundings, it is necessary to generalize first the performance of physiological functions for plants under soil water stress in this article. We then focus on the aspects of plant gene regulatory network system, which is the core controlling the interrelationship between plants and environment at the molecular level in a complex and coordinated manner. Drought will be selected as an example of abiotic stresses to illustrate the above issue.

Plant physiological function performance under soil water stress

Plants live in soil-plant-atmosphere continuum (SPAC) environment, and they have to coordinate the mechanisms of diverse types to respond to the above changing environment at any time for sustainable survival (Dufty et al. 2002; Fiehn 2002; Glombitza et al. 2004; Gregory et al. 2004; Shao et al. 2005). Plant production realization is obtained eventually through physiological pathways at least at the level of individual and community (Charlesworth et al. 2001; Chaves et al. 2003; Angela 2004; Arnholdt-Schmitt 2004; Brill and Watson 2004; Capell et al. 2004; Chen and Gallie 2004; Shao et al. 2005, 2006a,c; Andrew et al. 2006). One molecule, one kind of tissue or an organ can not produce any economic yield in terms of the need for human being (Soltani et al. 2004; Munns 2005; Shao et al. 2005, 2006c).Under the condition of ensuring plant survival, plants can produce corresponding yield. Water is one of key factors influencing plant production and many reports have proved this clearly (Travis et al. 2002; Salt 2004; Yang and Zhang 2006). Loss of water in soil will lead to great reduction in plant production, which has been reflected from total grain yield of many countries in the world (Doelle 2002; Wang et al. 2003; Shao et al. 2006c,e). Water is the important material for photosynthetic reactions that plants depend on to finish accumulation of photosynthetic products, which are impacted greatly by physiological pathways and environmental factors (such as soil water supply; Angela 2004; David et al. 2004) Thus, different soil water supplying will result in quite different physiological pathways, which directly determine the ability for plants to make photosynthetic products. Water deficits in soil environment also influence solute transport (ion and nutrient uptake of plants) to larger extent, which effects on photosynthetic reactions in plant chloroplasts in many ways (Salama et al. 1994; Zhu 2002; Halford and Paul 2003; Lokhandle et al. 2003; Chaves and Oliveira 2004; Costa et al. 2004; Higuchi et al. 2004; Salt 2004; Andrew et al. 2006). This is the reason that ion homeostasis and redox state have been brought to attention (Noctor et al. 2002; Samis et al. 2002; Shigeoka et al. 2002; Vranova et al. 2002; Millar et al. 2003; Harding et al. 2004; Taylor and McAinsh 2004; Grennan 2006). The series of the above reactions and processes occurring at different biointerfaces is regulated and controlled by plant gene regulatory network system spatially and temporally on the basis of responding to plant developmental cue, through which plants can elegantly respond to the changing environment (Hernandez et al. 2004; Grennan 2006). This network system has been formed by the interaction between plants and environment for a long time of evolution, which will continue to evolve with environmental succession (Dufty et al. 2002; Gesch et al. 2002; Charlesworth et al. 2004; David et al 2004; De Ronde et al. 2004). From the angle of individual plant development, Plant Growth Periodicity curve can reflect and show the above trend (Doebley and Lukens 1998; Soltani et al. 2004; Shao et al. 2005c,e). Besides, plant responses to soil water deficits take a "slow-fast-slow" shaped curve in terms of main physio-biochemical indices change and this is in agreement with Plant Growth Periodicity, which also illustrates this fact and wide plasticity for plants (Neumann 1997; Poethig 2001; Schlighting 2002; Shao et al. 2005a, 2006a). Surely, concerted expression of corresponding genes in plant gene regulatory network system makes it possible that we can see the phenotype and phenotype change under given temporal-spatial condition (Shinozaki et al. 2003; Shinozaki and Dennis 2003; Zhu 2003; Taylor and McAinsh 2004; Shao et al. 2006d).

Aspects of plant gene regulatory network system

Recent progress in molecular biology (especially, DNA microarray), genomics, proteomics and metabolomics has provided insight into plant gene regulatory network system, which is mainly composed of inducible-genes (environmental factors and developmental cues), their 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; Zhu T 2003; Munns 2005). Under the condition of soil water deficits, related stress factors always result in overlapping responses, including anatomical, physiological, biochemical, molecular biological changes, which make plant gene regulatory network system more complicated and difficult to explore. Much information with respect to this topic is from the model plant, *Arabidopsis thaliana*. Main aspects will be illustrated below.

Environmental stress-responsive transcriptional elements

Plants can sense, process, respond to environmental stress and activate related-gene expression to increase their resistance to stress. 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 to environmental stress such as LEA 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 MAP and CDP, bZIP, MYB and others (Liu et al. 2000; Szegletes et al. 2000; Liu et al. 2004; Lu and Chen 2004; Liu and Bush 2006). Transcriptional elements are defined as the protein combining with the specialized DNA sequence of eukaryotic promoters or the protein having structural characteristics of known DNA-combining region, whose main function is to activate or suppress transcriptional effect of corresponding genes (Kasuga et al. 1999; Liu et al. 2000; Manival et al. 2001; Mette et al. 2002; Gregory et al. 2004; Liu and Baird 2004; Shao et al. 2005). 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, pathogen and heat (Doebley and Lukens 1998; Tang et al. 2003; Delessert et al. 2004; Glombitza et al. 2004). 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 have been summarized in Table1 for reference.

Table 1. Typical transcriptional elements in higher plants.

Plant materials	Factors	Binding sites/Factor Types
Arabidopsis thaliana	ABI5/AtDPBF	ABA response elements(ABREs)/bZIP
A.thaliana	AtDPBF2	ABA response elements(ABREs)/bZIP
A.thaliana	AtDPBF3/AREB3	ABA response elements(ABREs)/bZIP
A.thaliana	AtDPBF4	ABA response elements(ABREs)/bZIP
A.thaliana	AtDPBF5/ABF3	ABA response elements(ABREs)/bZIP
A.thaliana	ABF1	ABA response elements(ABREs)/bZIP
A.thaliana	ABF2/AREB5	ABA response elements(ABREs)/bZIP
A.thaliana	ABF4/AREB2	ABA response elements(ABREs)/bZIP
A.thaliana	GBF3	ABA response elements(ABREs)/bZIP
A.thaliana	AB53	RY/sph elements/B3 domain proteins
A.thaliana	ATMTB2	MTC
A.thaliana	ATHB6	HD-Zip
A.thaliana	ATHB7	HD-Zip
A.thaliana	ATHB12	HD-Zip
A.thaliana	ABI4	AP2
Oryza	TRAB1	ABA response elements(ABREs)/bZIP
Oryza	OsVPI	RY/sph elements/B3 domain proteins
Zea mays	VP1	MYB
Triticum	EmBP-1	ABA response elements(ABREs)/bZIP
Avena	AtVPI	RY/sph elements/B3 domain proteins
Helianthus	DPBF5,-2,-3	ABA response elements(ABREs)/Bzip
Phaseolus	ROM2(repressor)	ABA response elements(ABREs)/Bzip
Phaseolus	PIARF	RY/sph elements/B3 domain proteins
Craterestinma	Cpvp1	RY/sph elements/B3 domain proteins
Daucus	C-ABI3	RY/sph elements/B3 domain proteins
Populus	PtABI3	RY/sph elements/B3 domain proteins

Complexity of plant gene regulatory network system specificity and crosstalk

Many transcriptional element families participate in plant stress responses, each of which has many members with highly-conservative DNA-binding domain, composing a complicated, temporal-spatial network system for plant gene expression and regulation (Zhu 2003; Zhu T 2003). Different members of TGA/OBF families have different DNA-binding specificities, protein-protein interaction and expressing profiles. Chromatin immunoprecipitation techniques indicated that tobacco TGA1a *in vivo* combined with xenobiotic-responsive promoters, but could not combine with PR promoter as cis-element (Beer and Tavazoie 2004; Chinnusamy et al. 2004). *Arabidopsis* TGA2 could be responsive to salicylic acid (SA) signal, but not be responsive to xenobiotic stress signals. Much analysis of genomic expression profiling by DNA microarray indicates that the mRNA coding transcriptional element genes in many plants are usually induced to express and accumulated (Avramova 2002; Arnholdt-Schmitt 2004; Casati and Walbot 2004). Most transcriptional element genes involved in plant stress responses have not only completely different expression profiles, but also some overlapping expression profiles, showing the complexity, specificity and crosstalk of plant gene regulatory network system (Bray 2004; Shao et al. 2005, 2006d). In other words, one kind of stress may simultaneously activate many transcriptional elements and one transcriptional element may be activated by many types of plant stress responses. For instance, CBF3/DREB1a can be responsive rapidly to cold, at the same time, regulated by circadian clock (Harmer et al. 2000; Chen et al. 2002; Brill and Watson 2004), which reflects the functional complement between plant cold-responsive pathway and circadian clock-regulated circle in terms of CBF3/DREB1a functions.

Shinozaki et al. (2003) thought that four signal pathways were involved in plant drought, cold and salinity responses, in which two were ABA-dependent (I and II), and two were non-ABA-dependent (III and IV). The process of stress signal sensing and transducing, transcriptional regulating, and functional expressing was existent in these pathways. It is obvious that transcriptional elements play a central role in the process (Liu et al. 2000; Shao et al. 2005, 2006d). Zhu T (2003) and Zhu JK (2003) concluded that molecular mechanism of plant stress responses to drought and salinity included three main steps, *i.e.* stress signal input, transducing process, and regulatory product output through the study of *Arabidopsis* drought and salinity for many years. Results of many genetic mutants and key intermediate molecules from his lab supported his view powerfully. Recent related anti-drought data (dynamic change of anti-oxidative enzymes and soil water stress threshold) from my lab also proved the point (Shao et al. 2005a-e, 2006b,e). From plant developmental context, plant responses to environmental stresses have a universal law, which has been reflected completely by Plant Growth Periodicity curve (Shao et al. 2005c). Our study on dynamic changing of wheat anti-oxidative enzymes under soil water deficit have indicated that wheat with different genotypes responded to soil water stress by taking a “slow-rapid-slow” characteristic curve during wheat life cycle (Shao et al. 2005, 2006b).This is the physiological basis for water-saving agriculture and dry land farming,which also provides substantial evidence for the above viewpoint (Chaves and Oliveira 2004; Munne-Bosch and Alegre 2004; Shao et al. 2006c).

Plant gene regulatory network system and plant drought resistance improvement

Previous gene engineering strategy for plant stress resistance was to express one (in most cases) or several stress-tolerant genes by constitutive or stress-induced promoters (Pellegrineschi et al. 2002). For instance by introducing betA gene derived from *E.coli* into tobacco and potato, betaine content in the transgenic plants increased to 5 μmol/g (dry mass) and tolerance to salt and cold for the transgenic plants was improved greatly. The goal of recently-established plant gene engineering strategy based on transcriptional elements is to improve plant comprehensive resistance characters (Puhakainen et al. 2004). Compared with the previous traditional method of introducing or improving individual functional genes, the new strategy will play more important role in plant molecular breeding because modifying regulatory activities of a transcriptional element can influence functions of many genes, easily reaching the aim of improving plant comprehensive resistance to drought, salinity, freezing, diseases, UV-B and others (Riechmann et al. 2000; Capell et al. 2004; Casati and Walbot 2004). Through constitutively overexpressing DERB1A, plant stress-responsive genes, Kin1, cor6.6/Kin2, cor15a, cor47/rd17, or d10 got higher

Table 2. Some examples of the osmotic regulating genes downstream in abiotic resistance.

Components	Metabolic Functions	Gene/Proteins
ROS scavenging	Increase in ROS scavenging enzymes	GP, PH, GPX
Chaperones	Heat-/cold-/salt-shock proteins; protein folding	Hsp,Csp,Ssp,*DnaJ*
Fructan	Osmoprotection	*SacB*
Trehalose	Osmoprotection	*Tps;Tpp,*trehalase
Glycine betaine	Protein protection and carbon sink	*codA*
Proline	Substrate for mitochondrial respiration; redox control	P5CS/P5CR
Ectoine	Osmoprotectant	*Ect*A,BC
K^+-transporters	High affinity K^+ uptake	Hkt1,Hak1
K^+-channels	Low affinity or dual affinity K^+ uptake	Akt1,Akt
H_2O channel proteins	Membrane cycling control	TIP

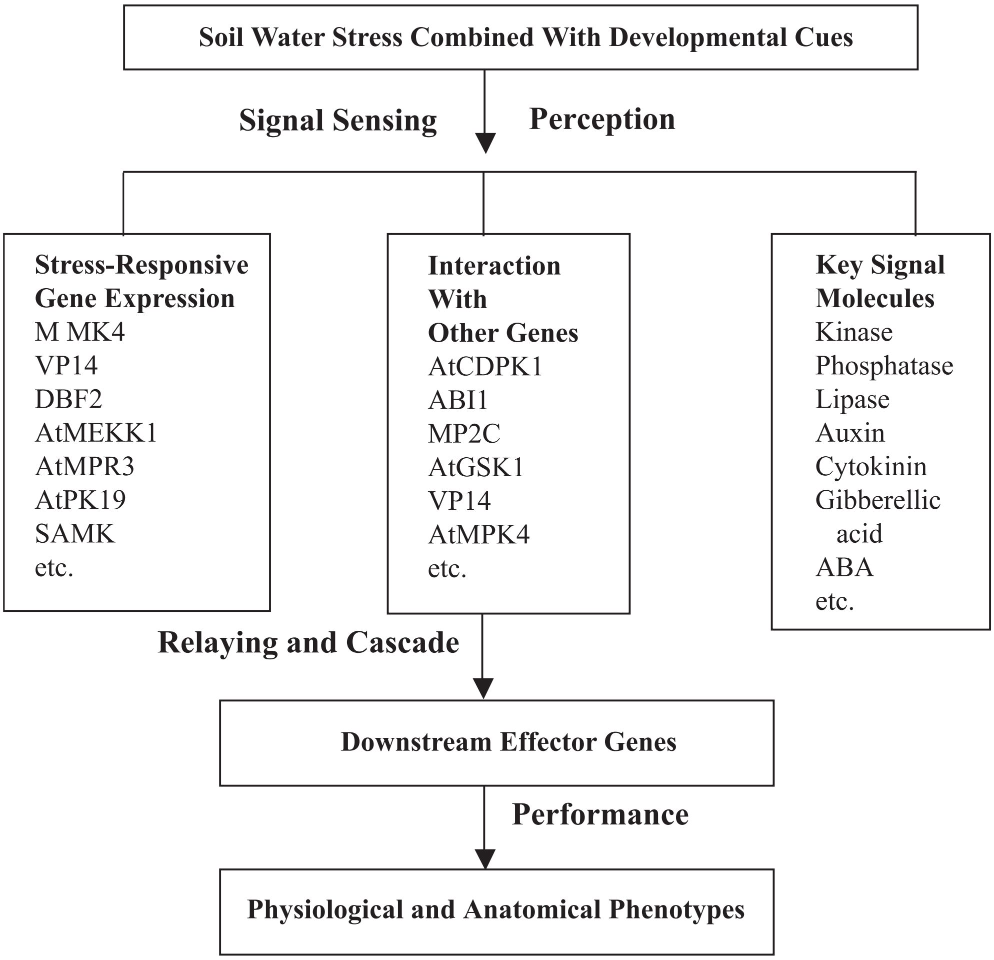

Figure 1. The basic draft for plant gene regulatory network system.

expression and the obtained transgenic *Arabidopsis* plants were resistant to drought, cold and salinity (Kasuga et al. 1999; Pellegrineschi et al. 2002, Puhakainen et al. 2004). Other related studies also provided a solid evidence for high efficiency of the above methodology.

Transferring a transcriptional element into *Arabidopsis*, which was thought previously not to be related to plant drought response many transgenic plants were obtained which were highly resistant to soil water deficits on the basis of selecting the *Arabidopsis* community with higher expression. By further introducing the members of this transcriptional element family into soybean, transgenic soybean lines were cultured and they were resistant to soil water deficits in greenhouse and field. This indicated that the function of this transcriptional element family was characteristic of conservativeness among diverse plant species. So, it is possible to obtain expected same stress-resistant phenotype by genetically modifying transcriptional elements and reach the aim of improving plants efficiently and purposefully (Tang et al. 2003; Wang et al. 2003; Zhu et al. 2004; Shao et al. 2006d). Besides, some transcriptional elements not only regulate metabolic pathways, but also influence transport and allocation of secondary metabolites. Plant secondary metabolism plays an important role in plant responding to environmental stresses. Long-step progress has taken place in terms of introducing transcriptional elements to regulate targeted pathways.

It is important to remember the fact that some transcriptional elements may regulate several metabolic pathways and one metabolic pathway may need orchestrated regulation from some transcriptional elements, which is the nature of plant gene regulatory network system (Shinozaki et al. 2003; Zhu 2003; Zhu T 2003; Shao et al. 2006d). So, in some cases, only introducing a transcriptional element can not obtain targeted phenotype and may lead to metabolic unbalance in plants. In addition, because of coordinated evolution of transcriptional elements and their regulating metabolic pathways the genetically-modifying strategy for the same transcriptional element could produce different phenotypes in different plant species. These issues need deeper exploration to establish an efficient genetically-modifying system by transcriptional elements and their network system for improving plant stress resistance and global eco-environment and feeding the world (Shao et al. 2006c).

Concluding remarks

Between plants and animals the most important difference is that plants are more easily influenced by environmental factors than animals. Consequently, plants have more refine mechanisms to regulate themselves from molecular level to ecosystem to respond to environmental changing. For instance, there are many coding-protein genes downstream only for osmotic regulation in abiotic stress resistance (Table 2). By contrast, animals are more active and have the ability to escape from environmental stresses in most cases (Meyerowitz 2002; Wei et al. 2004).Under the above background, plants are quite different compared to animals in their gene regulatory network system (Wei et al. 2004). Nerve system-based or nerve system-like-based structure and hormones are composed of the body for gene expression in animal network system, leading to animal activeness (Meyerowitz 2002; Shao et al. 2006d). In addition, developmental programming can not be easily effected by environmental cues (Munns 2005; Shao et al. 2005). Plants are always in the state of passiveness for confronting environmental succession and the related issue is more complicated, which is the main cause that plants are behind animals in the study of most fields (Shao et al. 2006d).

Charting plant gene regulatory network system under soil water deficits is a great challenge. Nowadays, there are indeed many favorable conditions for charting this blueprint, including much available data from *Arabidopsis*, rice, grass, yeast and fruit fly, but the range of tested plants is very much limited, many stress-responsive genes have not been unified in terms of their refine functions, and many genes participating in environmental stresses are interacted and overlapped, which have led to incorrect placing of key genes (gene effectors) and signal molecules in the whole plant gene regulatory network system. Besides, much data are from under condition of one type of stresses. It is a fact that plants always confront more than two kinds of individual environmental stresses or their combination simultaneously in field (Soltani et al. 2004; Liu and Li 2005; Shao et al. 2005; Andrew et al. 2006; Yang et al. 2006; Yang and Zhang 2006). Although drawing this dimensional plant gene regulatory network system with great details and complete pathways is impossible currently, the basic draft for this blueprint could be summarized in Figure 1. This draft was established in combination with recent advance in this hot topic and from the context of development, which will provide instructions for further investigation and insights into understanding of plant refine plasticity for abiotic environmental stresses.

In a word, precise elucidation of plant gene regulatory network system under abiotic stresses is of importance to molecularly engineering plant resistance, because of which many excellent scientists world-wide have been engaged in this frontier field, resulting in a long-step progress (Shao et al. 2005, 2005b; Shao and Chu 2005).There are also many issues remained to be solved and needed to make efforts. Scope of tested plants needs to be extended; comprehensive study on a combination of environmental stress factors in laboratories and in field should be given much attention; system development viewpoint and computer simulation analysis method should be also applied. With accumulation of data from being extended plant range, plant gene regulatory network system under environmental stresses will be clearer and clearer.

Acknowledgements

Shao HB is grateful for the support from Initiation Foundation of Chongqing University of Post&Telecom (2005A-92), Qingdao University of Science and Technology No-0022221, Natural Science Foundation of Shandong Province, to Shao HB and Taishan Scholar Construction Program (JS-200510036) to Guo QJ.

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