Cell Signaling During Drought and Salt Stress

Faheema Khan and Khalid Rehman Hakeem

Abstract

Among abiotic factors, salinity and drought stress affect every aspect of plant from physiology to metabolic activities. Understanding of abiotic stress responses and signal transduction to control adaptive pathways is a crucial step in determining the plant resistance exposed to unfavorable environments. Molecular and genomic findings have shown several changes in gene expression profiling under drought and salt stresses in plants. Numbers of transcription factors which are accountable for inducing stress-responsive genes have been documented. To survive in adverse condition, plants have stress-specific and adaptive responses which provide them necessary protection. Although, there are several signaling pathways and stress-responsive perceptions, some of which are definite in function, while others may have cross talk. Expressions of a large number of transcripts and genes are induced by these abiotic stresses in plants which facilitate stress tolerance and stress response. Recently, progress has been made in investigating the complex cascades of gene expression in stress responses. Knowledge about plant stress signaling is essential for the development of transgenic and improving breeding strategies in crops under stress environment. This chapter provides an outline of the common features of stress signaling in plants with some current studies on the functional analysis of signaling machineries under salt and drought stresses.

Keywords

Drought • Salt • Signaling • SOS • ABA • Abiotic stress

F. Khan (✉)
Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11495, Kingdom of Saudi Arabia
e-mail: drfaheemakhan@gmail.com

K.R. Hakeem
Faculty of Forestry, Universiti Putra Malaysia, Serdang 43400, Selangor, Malaysia
e-mail: kur.hakeem@gmail.com

11.1   Introduction

In response to human population growth, agriculture faces a constant challenge to increase crop production annually. Throughout the world salinity and drought are responsible for much of the yield decline in agricultural lands. Moreover, constant salinization of arid and semiarid land is becoming more widespread because of poor local irrigation practices, thus decreasing the yield from formerly productive land (Kaya et al. 2010). As land and water resources become limiting, high-yielding crops even in environmentally stressful conditions will be essential. About 6 % of the world's land and 30 % of the world's productive areas are under salinity (UNESCO Water Portal 2007). Further, the rapid change in global climate, which is more than estimated (Intergovernmental Panel on Climate Change 2007), seems to increase dryness for the semiarid regions of the world (Bates et al. 2008; Lehner et al. 2005). Therefore, drought in concert with increasing population will lead to irrational utilization of water resources for crop production. It mostly affects every aspect of the growth and metabolic activity of plants and causes a significant reduction in crop yield (Passioura 2007) equally as salinity does. To avoid abiotic stresses, plant is dependent upon the stimulation of molecular cascades responsible for certain metabolites, stress perception, signal transduction, and controlling expression of stress-responsive genes (Huang et al. 2012). The physiological responses developed against salinity and drought stress were found analogous to each other as both of these stresses eventually lead to osmotic imbalance of the cell. A general response to salt and drought stress as a signaling pathway is shown in Fig. 11.1. High salt and drought stress show their impact on a plant cell by disturbing the osmotic and ionic equilibrium. Excess of Na^+ ions and osmotic imbalance cause changes in turgor pressure, these cellular activities consider as the major triggers of the stress signaling. These preliminary activities lead to a chain of events, which can be further divided as osmotic and ionic signaling pathways leading to stress tolerance. Abiotic stress responses can be noticed by stress in a form of injury such as necrosis and chlorosis. This stress injury causes its deleterious effect on cell division resulting in retarded growth and plant productivity. Shedding of the older leaves is also considered as one of the stress-tolerant response. The possible reasons for the injuries are high Na^+ toxicity, osmotic imbalance, ROS generation, or due to the degradation of plant cellular proteins and enzymes. To avoid stress-related damages, plants activate certain detoxifying processes, which consist of changes in enzymes, chaperones, molecular proteinases, gene synthesis of LEA/dehydrin for ROS scavenging, and other metabolites (Table 11.1). These processes control and restore stress-induced damages and enhance plant stress tolerance. Plant plasma membrane directly or indirectly perceives environmental stress and plays a vital role in the conduction of peripheral signals in plant protection responses to initiate stress signaling pathway. It is reported that physical properties of cell membranes such as lipid and fatty acid composition have the potential to sense external stress (López-Pérez et al. 2009). Rapid advancement of molecular, transgenic, and functional genomics, technologies collectively with the accessibility of cDNA sequencing and gene knockout mutants (Chinnusamy et al. 2004; Yamaguchi-Shinozaki and Shinozaki 2006) have facilitated significant progress in analyzing molecular aspects of the drought and high salinity responses in plants. Many proficient protection responses exist in plants that allow them to perceive and adapt appropriately to a range of stress signal. A number of stress-responsive genes and gene products have been acknowledged against drought and salinity stress. Recently, several hundred genes have been identified that are induced or subdued at the transcriptional as well as proteomic levels when plants or plant parts are subjected to drought and salinity (Mahajan and Tuteja 2005; Miller et al. 2010; Hakeem et al. 2012a, 2013). It has been reported that under multiple stresses, plants elicit distinctive and complex responses regarding respiration, photosynthesis (Mittler 2006; Rizhsky et al. 2002; Hakeem et al. 2012b), and signaling stress (Okamoto et al. 2009). Therefore, the need to
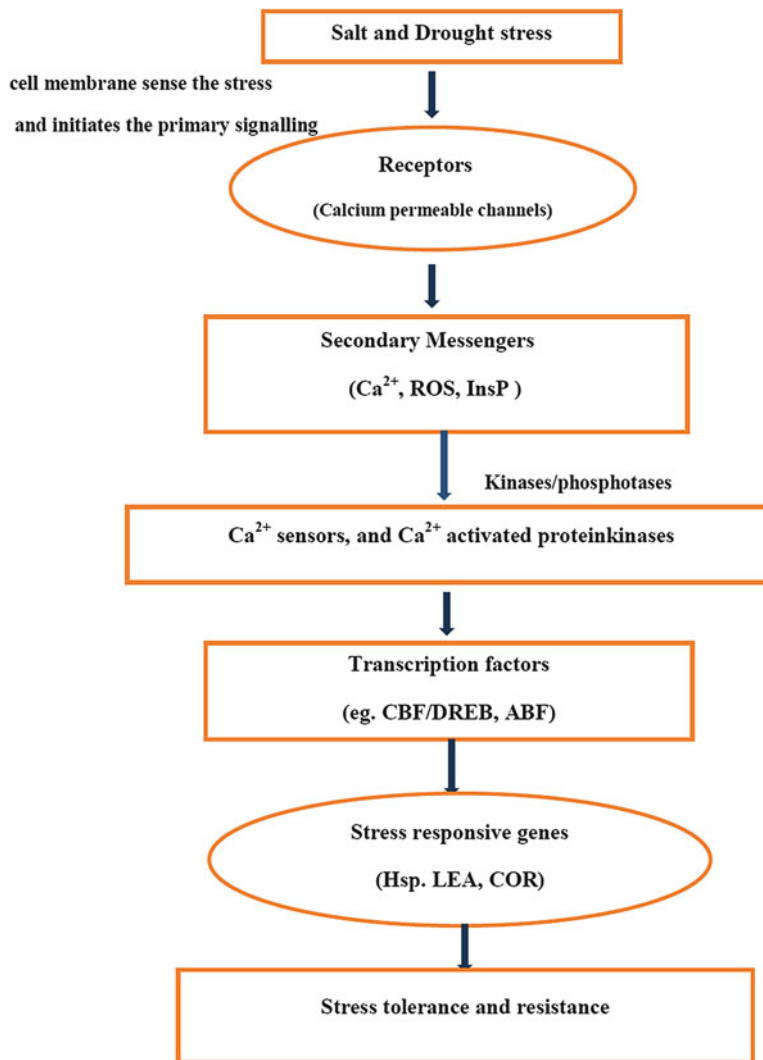
Fig. 11.1 Signaling pathway for plant response to salt and drought stress. The stress signal is sensed by the cell membrane triggering the complex signaling cascade in plants. The signaling transduction induces stress-responsive genes to provide stress resistance

study such interactions under conditions mimicking nature is emphasized (Cimato et al. 2010). Studies showed at molecular level, co-occurrence of different stresses can generate the coactivation of different response signaling pathways (abscisic acid, ethylene, jasmonic acid, etc.) (Mittler 2006). Nature has acquired different protective ways for avoiding and resisting unfavorable conditions, although some of the changes in plants are clearly adaptive, others may have cross talk with each other in response to the stress signals. These signaling pathways act in cooperation to alleviate environmental stress. Knowledge of these pathways is important because they may provide suitable candidate which can be genetically exploit through plant breeding to advance drought and salinity tolerance. In this chapter several abiotic stress signaling pathways are described with the latest research advances in drought and salt stress signaling.

Table 11.1 Response to the salt stress accumulating osmoprotectants and metabolites and there function(s) in conferring tolerance

Product group	Specific compound	Suggested functions	References
Ions	Sodium chloride	Osmotic adjustment	Blumwald et al. (2000)
		Potassium exclusion	Hasegawa et al. (2000)
Protein	Osmotin	Radical detoxification	Bohnert and Jensen (1996), Allen (1995), Hernandez et al. (2000)
	SOD, catalase		
Amino acid	Proline, ectoine	Osmotic adjustment	Khatkar and Kuhad (2000)
		osmoprotectant	
Sugars	Glucose, fructose, sucrose	Osmotic adjustment	Kerepesi and Galiba (2000)
		Carbon storage	Bohnert and Jensen (1996)
Polyols	Mannitol and pinitol	Carbon storage, osmotic adjustment, osmoprotectant	Bohnert et al. (1995)
		Radical scavenging	
Quaternary amines	Glycine betaine	Osmoprotectant	Khan et al. (2002)
Pigments	Carotenoids, anthocyanin, betaines	Protection against photoinhibition	Foyer and Noctor (2005)
			Adam et al. (1992)

11.2 Stress Signaling Pathways

To study stress adaptive responses, to study adaptive responses, drought and salt signaling transduction can be functionally grouped into three categories: first, ion homeostasis, which is generally significant to salinity and osmotic adjustment; second, controlling stress damage and toxic radical scavenging; and third, to manage cell division and development against stress conditions (Zhu 2001).

11.3 Ion Homeostasis

Homeostasis is defined as the tendency of a cell or an organism to maintain internal steady state in response to any environmental perturbation or stimulus tending to disturb normality. Hypersaline environment, mostly mediated by high level of NaCl, causing perturbation of steady ionic state for NaCl and Cl^- along with K^+ and Ca^{2+} (Niu et al. 1995). Plant cells regulate water relation imbalance through osmotic adjustment by synthesizing compatible organic solutes and ion accumulation. High NaCl concentration causes the disturbance in the steady transport of Na^+ and Cl^- ion and other ions, such as Ca^{2+} and K^+ (Hasegawa et al. 2000). High concentration of Na^+ and Cl^- disturbs ionic equilibrium and thermodynamics of plant tissue resulting in ionic imbalance hyperosmotic stress and toxicity. Excess of Na^+ negatively affects intracellular influx of K^+ ion and attenuates the acquisition of this vital element. Intracellular K^+ and Na^+ homeostasis is important for the actions of several cytosolic enzymes and for maintaining appropriate membrane potential across the cell wall. Ion homeostasis is regulated by transmembrane proteins that mediate ion fluxes. It includes H^+-translocating ATPase and pyrophosphatases, Ca^{2+} ATPases, and secondary transporters (Sze et al. 1999). Several transport proteins that mediate K^+, Na^+, and Cl^- transport have been reported on the basis of molecular studied. Dreyer et al. (1999) identified functional complementation of transport-deficient in yeast mutants. Excess NaCl enhances the cytosolic Ca^{2+} accumulation which consequently triggers stress responses. Thus, in salinity and drought it is important for the plant to maintain cellular ion homeostasis for normal growth and metabolic functioning.

11.3.1 Sodium Homeostasis and Ion Compartmentation

High Na^+ in the environment is of pronounced agricultural significance as saline solutions impose both ionic and osmotic stresses on plants. Na^+ ions disturb K^+ uptake by root cells (Hasegawa et al. 2000). Externally Na^+ is sensed by a cell membrane receptor, while intracellular Na^+ is perceived by membrane proteins or either by one, from the several known Na^+-sensitive cytoplasmic enzymes. It has been reported that a plasma membrane Na^+/H^+ antiport activity of *SOS1* (SALT OVERLY SENSITIVE1) stimulates efflux of excess Na^+ ions and maintains Na^+ ion homeostasis (Turkan and Demiral 2009). High Na^+ accumulation in the leaf cell becomes toxic to enzyme production (Hasegawa et al. 2000). Excess of Na^+ results leaf necrosis in older leaves, shortening the life time of individual leaves thus resulting low productivity (Munns 2002). To prevent tissue injuries, plant cell death and growth retardation of unwanted Na^+ has to be removed or follow ion compartmentation (Hasegawa et al. 2000). The pumping of the Na^+ ions in the vacuole involves energy-dependent transportation which alters vacuolar alkalization (Apse et al. 1999). Na^+ compartmentation in vacuole reduces cytosolic levels of Na^+ ions and further facilitates the energetically downhill influx across the plasma membrane. A wide range of membrane transporters assists plants with adaptable approaches to combat external stresses. Phylogenetic study of full genome sequence has shown a large number of putative cation/H^+ antiporters in *Arabidopsis* (Maser et al. 2002). The finest examples of the cation exchangers are the Ca^{2+}/H^+ and Na^+/H^+; they help in retaining the cytosolic concentration of the cell by extruding Ca^{2+} and Na^+, respectively (Hepler 2005). Analogous transport actions are found in plasma membrane and cell organelles (Hepler 2005). In plants the first cation exchanger for Na^+/H^+ was found in *Arabidopsis* (Gaxiola et al. 1999); these exchanger include NHXs, AtNHXl, and AtNHX2 protein. Yokoi et al. (2002) observed the upregulation of these protein exchangers under salt stress. AtNHXNa^+/H^+ antiporters also play a vital role in Na^+ compartmentation (Blumwald et al. 2000).

AtNHX1 and AtNHX2 are localized in tonoplast, the expression of these transcripts was found upregulated under osmotic stress and ABA (Yokoi et al. 2002). High salt level increases the transcripts of vacuolar H^+-ATPase components in response to salt tolerance (Dietz et al. 2001). Moreover, AtNHXl also plays an important role in Na^+ storage in the vacuoles of root hair. Since NHX is identified, the number of similar transporters has massively increased. The large number of DNA sequence-encoding NHX-like proteins from more than 60 species including dicot and monocots has been acknowledged in the database of different gene banks.

11.3.2 Ca^{2+} Homeostasis and Secondary Messengers

During abiotic stress the mechanism of signal perception remains unknown and may involve a complex protein-protein interaction and molecule signaling that usually increase or decrease in a temporary, e.g., hormones, ROS, sugars, and Ca^+. Calcium functions as a secondary messenger under various stress conditions and initiates cross talk. Various studies have reported that drought and high salt rapidly raise calcium levels in cells (Pardo 2010). The resulting signaling pathway activates numerous genes that play critical role to sustain cellular homeostasis. Several Ca^{2+} sensors were implicated to be involved in drought signaling. Sequential dynamics of Ca^{2+} transients in response to drought were studied revealing increase in cytosolic Ca^{2+} due to release of Ca^{2+} from the vacuole and cell-type specificity of (Ca^{2+}) transients (Kiegle et al. 2000). Study showed increased intracellular Ca^{2+} levels under salinity stress. Zhu et al. (1998) have identified the determinants of salt tolerance in *Arabidopsis* mutants by applying molecular approach. This approach was helpful in determining the genetic locus which is essential for salt resistance. *Arabidopsis* overexpress the ionotropic glutamate receptor AtGluR2, which decreases the efficiency of Ca^{2+} utilization, those plants become hypersensitive to Na^+ and K^+ ionic stresses (Kim et al. 2001). One of the Ca^{2+} sensor is calcium-dependent protein

kinases (CDPKs) which was reported to be drought induced and the importance of CDPK isoforms in facilitating the stress was demonstrated (Ozturk et al. 2002). Another Ca^{2+} sensor is calmodulin which is Ca^{2+}-binding protein stimulated by increased calcium level. Calmodulin-binding transcription factors were first reported in drought-stressed *Brassica napus* (Bouche et al. 2002). In *Arabidopsis* and rice (*O. sativa*), ABA-activated calmodulins were observed and suggested as harmful regulator of osmotic stress (Perruc et al. 2004). One more Ca^{2+}-binding protein is calcineurin B-like protein (CBLs), and CBL1 was shown to be the only drought-induced CBL (Kudla et al. 1999). The studies have been conducted on annexins which are a family of Ca^{2+}-dependent membrane-binding proteins. It is evident that certain annexins induced cytoplasmic Ca^{2+} under abiotic stress and their upregulation to tolerate osmotic stress is also well recognized. Thus, abiotic stress excites the Ca^{2+} influx from the apoplast and cell vacuoles, thus enhancing the level of cytosolic Ca^{2+}. The Ca^{2+} ions then function as secondary messenger to control K^+/Na^{2+} selectivity and increases K^+ influx (Xiong and Zhu 2001).

11.4 ROS Signaling and Antioxidants

In plants reactive oxygen species (ROS) are constantly produced as a result of different metabolic pathways localized in different cell compartments (Foyer and Harbinson 1994). ROS is a collective term that describes the chemical species that are generated upon incomplete reduction of oxygen. Main ROS molecules are hydroxyl radicals, singlet oxygen, superoxide anion radicals, and hydrogen peroxide. ROS are commonly generated during aerobic period of photorespiration and photosynthesis (Kotchoni et al. 2006). Under abiotic stress increase in these molecules can also be noticed in peroxisomes (Mittler 2002). During physiologically balanced conditions, the ROS molecules are scavenged by various components of antioxidative defense system (Alscher et al. 1997). The balance among generation and scavenging of ROS may be disturbed by a number of environmental conditions which rapidly increases the intracellular levels of these molecules (Tsugane et al. 1999). ROS function as intracellular signaling molecules and control stress damage, as showed by a number of studies. It is investigated that transgenic plants with higher ROS generation or mutants with more ROS-scavenging capacity showed better stress tolerance (Hasegawa et al. 2000; Kocsy et al. 2001). The ROS molecules are extremely reactive and highly energetic compound, they can perform catalytic functions in the lack of cellular enzymes. This property makes ROS molecule appropriate to activate plant stress signaling (Foyer and Noctor 2005). The major electron carriers such as plastoquinone (PQ) or the electron acceptors such as ferredoxin/thioredoxin along with ROS are involved in the redox signaling. To eliminate ROS, plants intrinsically develop different types of antioxidants which can reduce oxidative damage and confer drought and salt tolerance. The ROS-scavenging mechanisms comprise of enzymatic and nonenzymatic molecules. Antioxidative enzymes such as SOD, CAT, POX, GR, and APX are produced in subcellular organelles with a highly oxidizing metabolic activity such as mitochondria, chloroplasts, and peroxisomes to overcome ROS toxicity (Mittler 2006; Foyer and Noctor 2003; Miller et al. 2008; Ahmad et al. 2012). ABA accumulation induced by drought stress activates the generation of ROS, which leads to the upregulation of the antioxidant defense mechanism in plants (Hu et al. 2005). Free radical-mediated lipid peroxidation (MDA) results in highly reactive and toxic aldehydes, which are scavenged by either aldehyde dehydrogenases or aldehyde reductases. There are several studies evident of the involvement of these enzymes in drought stress response (Sunkar et al. 2003). ROS are known as second messengers in redox signaling and also involved in hormonal-mediated actions (Foyer and Noctor 2003). It has been reported that ABA induces the gene expression of some antioxidant enzymes such as CAT, SOD, and APX (Park et al. 2004) and also enhances the activities of these enzymes in cell (Zhang 2003). Recently, it was demonstrated that changes in the auxin substrate of a

H_2O_2-responsive enzyme involved in anthocyanin production facilitate drought resistance (Tognetti et al. 2010). In another study, mutants with decrease anthocyanin levels were more drought tolerant (Huang et al. 2010). These data support a role of anthocyanins, which are antioxidants, in drought tolerance along with ROS and phytohormones. The implicated molecules include glutathione peroxidase and cellulase-synthase-like protein (Zhu et al. 2010). Moreover, squalene epoxidase implicated in sterol biosynthesis was also reported to have a role in the localization of NADPH oxidases essential for regulation of ROS (Pose et al. 2009). Under high salt environment, regulation of NaCl responses is controlled by ROS. In *Arabidopsis* cells NaCl stress comprising both ionic and osmotic stresses has recently exhibit to induce development of endosomes having high level of hydrogen peroxide (Leshem et al. 2007). ROS production has been triggered within endosomes of *Arabidopsis* root cells (Leshem et al. 2007). The recent studies also suggest new vital regulatory roles of ROS in intracellular trafficking through vesicles in addition to their role in retrograde stress signaling in plants under abiotic stress (Miller et al. 2010). ROS-scavenging enzymes have been involved in signaling as well as their more customary role in protection from oxidative stress in recent years (Miller et al. 2010). In transgenic plants overproduction of antioxidant enzymes has improved drought and salt tolerance (Eltayeb et al. 2007; Lu et al. 2007; Tseng et al. 2007). It seems that integrated signaling networks are accountable for the stimulation of transduction pathways. Moreover, it has been also reported that while some changes in ROS metabolism enhanced resistance to stress, other changes caused enhanced sensitivity (Miller et al. 2010).

11.5 SOS Regulatory Pathway

To combat abiotic stresses, numbers of signaling pathways have been suggested, although not any is recognized in terms of signaling proteins inputs and outputs. Recently SOS pathway emerged as an exception from the result of biochemical, genetic,

and molecular analysis (Zhu 2001). Gene analysis associated in salt resistance was commenced in 1998, by Liu and Zhu where numbers of mutants were checked and through cloning SOS (salt overly sensitive) genes were identified. SOS pathway helps in eliminating excess Na^+ ions via plasma membrane and Na^+/H^+ antiporter which assist in maintaining ion homeostasis in the cell. Identification of SOS genes has broadened the way for revelation of a unique pathway associated with Ca^{2+} signaling in response to salt fluctuations (Liu et al. 1998). SOS pathway consists of a calcium-binding protein known as SOS3 which senses cytosolic fluctuations in calcium, stimulated by high salt. SOS3 also activates the protein kinase, SOS2. SOS1, SOS3/SOS2 kinase complex activates together and phosphorylates the transport action of the plasma membrane. Besides the transport function, SOS1 may also play a vital role in regulating and sensing Na^+ ions. SOS2 gene was isolated from *Arabidopsis* by the genetic selection of hypersensitive salt mutants. High salt concentration showed elevated SOS2 transcripts in response to stress tolerance in *Arabidopsis* roots (Liu et al. 2000). Moreover, SOS2 interacts with vacuolar Na^+/H^+ antiporter and considerably controls the cationic (Na^+/H^+) exchange activity (Qiu et al. 2002).

11.6 Protein Kinase Pathways for Osmotic Stress Signaling

The role of protein phosphorylation in response to osmotic has been proved experimentally (Zhu 2001). Many protein kinases in plants have been found activated in response to osmotic stress. The illustrated osmosensing pathway found in yeast (Gustin et al. 1988) created much attention to investigate a similar pathway in plants. In yeast the osmoregulatory pathways initiate with SH3 domain having membrane proteins which further activate MAP kinase cascade and elevate the osmolyte accumulation in the cell (Gustin et al. 1988). Under osmotic stress the plant synthesizes and accumulates compatible solutes for cellular adjustment. For synthesizing osmolyte it is indistinct whether they utilize similar

membrane sensors and MAP kinase cascades. In plants several MAPKs (mitogen-activated protein kinase) are stimulated against osmotic stress. MAP kinase (46 kDa) named SIMK (salt stress-inducible MAPK) found increased in response to adequate osmotic stress in alfalfa (Munnik et al. 1999). Hyperosmotic stress activated a SIMK-like MAP kinase named SIPK (salicylic acid-induced protein kinase) in tobacco cells (Mikolajczyk et al. 2000). MAPK cascade includes three protein kinases (MAPK, MAPKK, and MAPKKK) which are activated by serial phosphorylation. They result in specific localization of the module in cell compartments, phosphorylation, and regulating transcription factors and other proteins. A number of MAP kinases were identified using sequence information in *Arabidopsis* (Ichimura et al. 2002). Interestingly, during hyperosmotic stress SIMK was not stimulated and as an alternative a smaller kinase got triggered which suggest that the two kinases activated at different salt concentrations. Taking into consideration the different studies showed that one MAP kinase can respond to different stress conditions and there are different numbers of proposed and identified MAP kinases. From each of the three categories, there should be a convergence in the signaling of MAPK cascade, and it is possible that different stress factors activate MAP kinases to different levels (Bartels and Sunkar 2005). SNF-1-like kinases, divided into three families, SnRK1, SnRK2, and SnRK3, are another family of protein kinases which are activated by the phosphorylation of their serine or threonines (Halford and Hardie 1998). In various plant species, several SNF-1-like kinases were predicted and shown to be expressed in response to dehydration or ABA, including *Arabidopsis* OPEN STOMATA1 (OST1) protein kinase (Bartels and Sunkar 2005).

11.7 Phospholipid Signaling

In plants phospholipid membrane plays an important structural role. Environmental stress creates a dynamic system that produces a number of signal molecules, e.g., PA, IP3, and DAG. The signaling of phospholipids is grouped on the basis of phospholipases that catalyzes lipid production.

Studies suggest that some novel signaling pathways are involved in the production of lipid messengers which are not the direct yields of phospholipases. Examples of such lipid messengers are phosphatidylinositol 3,5-bisphosphate [PI(3,5)P2] and diacylglycerol pyrophosphate (DGPP) (Munnik 2001). Acting as a secondary messenger, phospholipase C (PLC) catalyzes the hydrolysis of phosphatidylinositol 4, 5-bisphosphate (PIP2) into IP3 and DAG. Under hyperosmotic stress condition, the level of IP3 found increased (DeWald et al. 2001). It is observed that osmotic stress enhances the activity of phospholipase D (PLD) in tomato and alfalfa (Frank et al. 2000). Phospholipase D found activated under drought stress in *Craterostigma plantagineum* and *Arabidopsis* (Katagiri et al. 2001). Plant PLD activity was analyzed in drought-tolerant and drought-sensitive cowpea cultivars; higher PLD activity was found in the drought-sensitive cultivars (Maarouf et al. 1999). In response to hyperosmotic stress, various plant systems showed rapid increase of 1,4,5-trisphosphate (IP3) (Takahashi et al. 2001; DeWald et al. 2001). According to current hypothesis drought activation of PLC leads to higher IP3 levels. A subsequent pH release of Ca^{2+} to cytoplasm and triggering of K^+ ion channels result in stomatal closure (Takahashi et al. 2001). In *Arabidopsis* SAL1 belongs to the latter group, and recently studies have supported drought-tolerant SAL1 mutants as a negative regulator in drought signaling pathways (Wilson et al. 2009). In another recent study, an inositol phosphate-lacking transgenic plant was generated by the expression of inositol polyphosphate 5-phosphatase (Perera et al. 2008) which showed higher drought resistance. Several plant species showed increase PLDs in response to induced ABA and drought stress (El-Maarouf et al. 2001; Frank et al. 2000; Katagiri et al. 2001).

11.8 ABA and Osmotic Stress Signaling

In plants ABA is needed for various stress responses, comprising stomatal closure, metabolic changes, and stress-responsive gene regulation. During unfavorable conditions the endogenous

ABA plays a vital role in stress-induced ABA-dependent activities. ABA level varies widely in response to environmental stress, especially under drought and salinity. The level of ABA synthesis and catabolic activities measured the level of endogenous ABA. Lately, the molecular source of ABA biosynthesis was determined by genetic and biochemical approaches (Nambara and Marion-Poll 2005). Another precursor of ABA is xanthoxin which results from a direct cleavage of C40 carotenoids; this reaction is considered as a vital step in ABA biosynthesis. ABA is an important phytohormone and has wide range of action including plant growth and development. One of the main functions of ABA is to regulate osmotic stress plant maintain water balance. This role can be best justified by plant mutants that are unable to synthesize ABA. In *Arabidopsis* a number of ABA deficient mutants have been identified such as aba1, aba2, and aba3 (Koornneef et al. 1998). ABA produced in the roots is further carried to the shoots which cause the stomatal closure and ultimately restricts cellular growth of the plant (Wilkinson and Davies 2002). Drought and high salinity might cause higher pH in xylem sap (Jia and Davies 2007), resulting in modulation of stomata in response to abiotic stresses. Several genes which can synthesize ABA have now been reported, e.g., in tobacco zeathanxin epoxidase known as ABA2 and in *Arabidopsis* ABA1: they catalyzes the zeaxanthin and antheraxanthin to violaxanthin (Marin et al. 1996). It has been studied that induced ABA stomatal closure is moderately dependant on activity of NADPH oxidase (Kwak et al. 2003; Torres and Dangl 2005). It has been studied that osmotic stress caused by salinity or drought is conducted via two pathways. One is dependent on ABA and the other is ABA independent; genetic investigation found no clear difference between ABA-dependent and ABA-nondependent pathways, and therefore, the mechanisms of this signaling may often have cross talks (Xiong and Zhu 2001). Ca^{2+} which is one of the essential elements and conferred to act as a second messenger for several stress responses mediates such cross talk. Studies have proved that high salt, drought, and ABA increase intracellular calcium in plants (Sanders et al. 2002).

11.9 Transcriptional Signaling

Transcriptome profiling has acknowledged number of gene-encoding transcription factors that are either upregulated or downregulated by multiple stresses. The expression of these transcription factors provides us deeper insight in understanding the stress tolerance mechanism. Cheng et al. (2002) reported numbers of stress-induced transcription factors for biotic and abiotic stresses in *Arabidopsis*. Among this group approximately 20 genes were found upregulated in response to osmotic stress and salinity. Recently, gene expression profiling using gene chips and cDNA microarrays has identified number of potential genes that are either upregulated or downregulated under drought and salinity (Bohnert and Cushman 2001; Seki et al. 2001). Alterations in gene expression, in response to drought and salinity, varies to the type and degree of stress. *Arabidopsis* provided profound insights of functional genomics related to multiple stress response. Using 1,300 full-length clones (Seki et al. 2001) and 7,000 full-length clone inserts (Seki et al. 2002), multi-stress interactions in response to abiotic stress were studied. The study provided potential stress-induced genes in response to salinity and drought stress. To study abiotic stress treatments, multi-stress interactions were studied by Kreps et al. (2002) in *Arabidopsis*. The study provided the alterations in gene expression more than twofold over control for 2,409 out of 8,100 genes in response to drought and high salt. Under drought stress in chickpea roots, transcripts were found twofold (STCa-8875; arginine decarboxylase) and threefold (STCa-611; spermidine synthase) upregulated (Molina et al. 2008). The study showed a different influence of drought stress on mechanisms of osmolyte accumulation as an early stress response in chickpea roots. Numbers of transcription factors which belong to the EREBP/AP2 family bind to DRE/CRT were identified and group as CBF1/DREB1B, CBF2/DREBC, and CBF3/DREB1A (Liu et al. 1998). Analogous transcription factors DREB2A and DREB2B that are induced under hyperosmotic condition were also reported as stress-responsive genes (Liu et al. 1998).

11.10   Conclusion and Perspectives

Salinity and drought stress signal transduction has remained a major agriculture ambiguity until now and regarded as complex network. Recently, molecular biology has paved a way in identifying some stress-related signaling element which widens the knowledge of plant stress response. There are several views of convergence and divergence that facilitate stress signaling cascades. From this chapter, we know that to overcome drought and salinity, plants have stress-specific signaling pathways. Plant stress conditions enhance the production of ROS along with ABA accumulation, which has been suggested to be key constituents of cross tolerance to multiple types of stresses. The oxidative stress was used to be considered as a negative activity, but now observed as fundamental stress response which induces tolerance mechanism. Signaling pathway such as SOS found to play a critical function in regulating osmotic stress, whereas there are cross talks between MAPK cascade and ABA signaling pathway. Though latest progresses have acknowledged numerous transduction factors involved in stress tolerance, there is an urgent need to fill the gaps through wider application genetic engineering in model plants. With the emerging powerful tools such as genomics, transcriptomics, and proteomics, advancement in understanding plant stress signaling will positively increase and may provide better insight of stress tolerance mechanism.

References

Adams P, Thomas JC, Vernon DM, Bohnert HJ, Jensen RG (1992) Distinct cellular and organismic responses to salt stress. Plant Cell Physiol 33:1215–1223

Ahmad P, Hakeem KR, Kumar A, Ashraf M, Akram NA (2012) Salt-induced changes in photosynthetic activity and oxidative defense system of three cultivars of mustard (*Brassica juncea* L.). Afr J Biotechnol 11(11):2694–2703

Allen RD (1995) Dissection of oxidative stress tolerance using transgenic plants. Plant Physiol 107:1049–1054

Alscher RG, Donahue JH, Cramer CL (1997) Reactive oxygen species and antioxidants: relationships in green cells. Physiol Plant 100:224–233

Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na$^+$ antiport in *Arabidopsis*. Science 285:1256–1258

Bartels D, Sunkar R (2005) Drought and salt tolerance in plants. Crit Rev Plant Sci 24:23–58

Bates BC, Kundzewicz ZW, Wu S, Palutikof JP (eds) (2008) In: Climate change and water. Technical paper of the intergovernmental panel on climate change. IPCC Secretariat, Geneva, 210pp. ISBN 978-92-9169-123-4

Blumwald E, Aharon GS, Apse MP (2000) Sodium transport in plant cells. Biochim Biophys Acta 1465:140–151

Bohnert HJ, Jensen RG (1996) Strategies for engineering water stress tolerance in plants. Trends Biotechnol 14:89–97

Bohnert HJ, Cushman JC (2001) The ice plant cometh: lessons in abiotic stress tolerance. J Plant Growth Regul 19:334–346

Bohnert HJ, Nelson DE, Jensen RG (1995) Adaptations to environmental stresses. Plant Cell 7:1099–1111

Bouche N, Scharlat A, Snedden W, Bouchez D, Fromm H (2002) A novel family of calmodulin-binding transcription activators in multicellular organisms. J Biol Chem 277:21851–21861 by H$^+$ ATPases: regulation and biosynthesis. Plant Cell 11:677–689

Cheng WH, Endo A, Zhou L (2002) A unique short-chain dehydrogenase/reductase in *Arabidopsis* glucose signaling and abscisic acid biosynthesis and functions. Plant Cell 14:2723–2743

Chinnusamy V, Schumaker K, Zhu JK (2004) Molecular genetic perspectives on cross-talk and specificity in abiotic stress signaling in plants. J Exp Bot 55:225–236

Cimato A, Castelli S, Tattini M, Traversi ML (2010) An ecophysiological analysis of salinity tolerance in olive. Environ Exp Bot 68:214–221

DeWald DB, Torabinejad J, Jones CA, Shope JC, Cangelosi AR (2001) Rapid accumulation of phosphatidylinositol 4,5-bisphosphate and inositol 1,4,5-trisphosphate correlates with calcium mobilization in salt-stressed *Arabidopsis*. Plant Physiol 126:759–769

Dietz KJ, Tavakoli N, Kluge C, Miura T, Sharma SS, Harris GC, Hardonnens AN, Golldack D (2001) Significance of the V-type ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level. J Exp Bot 52:1969–1980

Dreyer I, Horeu C, Lemaillet G, Zimmermann S, Bush DR (1999) Identification and characterization of plant transporters using heterologous expression systems. J Exp Bot 50:1073–1087

El-Maarouf H, Arcy-Lameta A, Gareil M, Zuily-Fodil Y, Pham-Thi AT (2001) Cloning and expression under drought of cDNAs coding for two PIPLCs in cowpea leaves. Plant Physiol Biochem 39:167–172

Eltayeb AE, Kawano N, Badawi GH, Kaminaka H, Sanekata T, ShibaharaT IS, Tanaka K (2007) Overexpression of monodehydroascorbate reductase in transgenic tobacco confers enhanced tolerance to

ozone, salt and polyethylene glycol stresses. Planta 225:1255–1264

Foyer CH, Harbinson JC (1994) Oxygen metabolism and the regulation of photosynthetic electron transport. In: Foyer CH, Mullineaux PM (eds) Causes of photooxidative stress and amelioration of defense systems in plant. CRC, Boca Raton, pp 1–42

Foyer CH, Noctor G (2003) Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Physiol Plant 119:355–364

Foyer CH, Noctor G (2005) Oxidant and antioxidant signaling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 28:1056–1071

Frank W, Munnik T, Kerkmann SF, Bartels D (2000) Water deficit triggers phospholipase D activity in the resurrection plant *Craterostigma plantagineum*. Plant Cell 12:111–123

Gaxiola RA, Rao R, Sherman A, Grisa WP, Alper S, Fink GR (1999) The Arabidopsis thaliana proton transporters AtNhx1 and Avp1, can function in cation detoxification in yeast. Proc Natl Acad Sci U S A 96:1480–1485

Gustin MC, Zhou XL, Martinac B, Kung C (1988) A mechanosensitive ion channel in the yeast plasma membrane. Science 242:762–765

Hakeem KR, Chandna R, Ahmad A, Qureshi MI, Iqbal M (2012a) Genotypic variability among soybean genotypes under NaCl stress and proteome analysis of salt tolerant genotype. Appl Biochem Biotechnol 168:2309–2329

Hakeem KR, Chandna R, Ahmad P, Ozturk M, Iqbal M (2012b) Relevance of proteomic investigations in plant stress physiology. OMICS J Integr Biol 16(11):621–635

Hakeem KR, Chandna R, Rehman R, Tahir I, Iqbal M (2013) Unraveling salt stress in plants through proteomics. In: Ahmad P, Azooz MM, Prasad MNV (eds) Salt stress in plants: signalling, omics and adaptations. Springer science + Business Media LLC, New York, pp 47–61

Halford NG, Hardie DG (1998) SNF-1 related protein kinases: global regulators of carbon metabolism in plants? Plant Mol Biol 37:735–748

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Mol Plant Physiol 51:463–499

Hepler PK (2005) Calcium: a central regulator of plant growth and development. Plant Cell 17:2142–2155

Hernandez JA, FerrerMA JA, Barcelo AR, Sevilla F (2000) Antioxidant systems and O2_/H2O2 production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. Plant Physiol 127:817–831

Hu X, Jiang M, Zhang A, Lu J (2005) Abscisic acid-induced apoplastic H_2O_2 accumulation up-regulates the activities of chloroplastic and cytosolic antioxidant enzymes in maize leaves. Planta 223:57–68

Huang J, Gu M, Lai Z, Fan B, Shi K, Zhou YH, Yu JQ, Chen Z (2010) Functional analysis of the *Arabidopsis* PAL gene family in plant growth, development, and response to environmental stress. Plant Physiol 153:1526–1538

Huang G-T, Ma S-L, Bai L-P, Zhang L, Ma H, Jia P, Liu J, Zhong M, Guo Z-F (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39:969–987

Ichimura K, Shinozaki K, Tina G, Sheen J, Henry Y (2002) Mitogen activated protein kinase cascades in plants: a new nomenclature. Trends Plant Sci 7:301–308

Intergovernmental Panel on Climate Change (2007) In: Metz B, Davidson OR, Bosch PR, Dave R, Meyer LA (eds) Contribution of Working Group III to the fourth assessment report of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press, Cambridge/New York. http://ipcc.ch/publications_and_data/ar4/wg3/en/contents.html

Jia W, Davies WJ (2007) Modification of leaf apoplastic pH in relation to stomatal sensitivity to root-sourced abscisic. Plant Physiol 143(143):68–77

Katagiri T, Takahashi S, Shinozaki K (2001) Involvement of a novel *Arabidopsis* phospholipase D, AtPLD delta, in dehydration-inducible accumulation of phosphatidic acid in stress signaling. Plant J 26:595–605

Kaya O, Cetin F, Aydoǧˇdu E, Ketenoǧˇlu MO, Atamov V (2010) Syntaxonomical analyses of the secondary vegetation of Harran Plain (Sanliurfa/Turkey) ensuing excessive irrigation by using GIS and remote sensing. Ekoloji 1975:1–14

Kerepesi I, Galiba G (2000) Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. Crop Sci 40:482–487

Khan MH, Singh LB, Panda SK (2002) Changes in anti-oxidant levels in *Oryza sativa* L. roots subjected to NaCl-salinity stress. Acta Physiol Plant 24:145–148

Khatkar D, Kuhad MS (2000) Short-term salinity induced changes in two wheat cultivars at different growth stages. Biol Plant 43:629–632

Kiegle E, Moore CA, Haseloff J, Tester MA, Knight MR (2000) Cell type-specific calcium responses to drought, salt and cold in the *Arabidopsis* root. Plant J 23:267–278

Kim SA, Kwak JM, Jae SK, Wang MH, Nam HG (2001) Overexpression of the AtGluR2 gene encoding an *Arabidopsis* homolog of mammalian glutamate receptors impairs calcium utilization and sensitivity to ionic stress in transgenic plants. Plant Cell Physiol 42:74–84

Kocsy G, Galiba G, Brunold C (2001) Role of glutathione in adaptation and signaling during chilling and cold acclimation in plants. Physiol Plant 113:158–164

Koornneef M, Léon-Kloosterziel KM, Schwartz SH, Zeevaart JAD (1998) The genetic and molecular dissection of abscisic acid biosynthesis and signal transduction in *Arabidopsis*. Plant Physiol Biochem 36:83–89

Kotchoni OS, Kuhns C, Ditzer A, Kirch H-H, Bartels D (2006) Over-expression of different aldehyde dehydrogenase genes in *Arabidopsis thaliana* confers tolerance to abiotic stress and protects plants. Plant Physiol 29:1033–1048

Kreps JA, Wu Y, Chang HS, Zhu T, Wang X, Harper JF (2002) Transcriptome changes for *Arabidopsis* in response to salt, osmotic, and cold stress. Plant Physiol 130:2129–2141

Kudla J, Xu Q, Harter K, Gruissem W, Luan S (1999) Genes for calcineurin B-like proteins in *Arabidopsis* are differentially regulated by stress signals. Proc Nat Acad Sci USA 96:4718–4723

Kwak JM, Mori IC, Pei ZM, Leonhardt N, Torres MA, Dangl JL, Bloom RE, Bodde S, Jones JD, Schroeder JI (2003) NADPH oxidase AtrbohD and AtrbohF genes function in ROS dependent ABA signaling in *Arabidopsis*. EMBO J 22:2623–2633

Lehner B, Doll P, Alcamo J, Henrichs H, Kaspar F (2005) Estimating the impact of global change on flood and drought risks in Europe: a continental, integrated assessment. Clim Change 75:273–299

Leshem Y, Seri L, Levine A (2007) Induction of phosphatidylinositol 3-kinase-mediated endocytosis by salt stress leads to intracellular production of reactive oxygen species and salt tolerance. Plant J 51:185–197

Liu J, Ishitani M, Halfter U, Kim CS, Zhu JK (2000) The Arabidopsis thaliana SOS2 gene encodes a protein kinase that is required for salt tolerance. Proc Natl Acad Sci U S A 97:3730–3734

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S et al (1998) Two transcription factors, DREBI and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought and low temperature responsive gene expression respectively, in Arabidopsis. Plant Cell 10:1391–1406

López-Pérez L, Martínez-Ballesta MC, Maurel C, Carvajal M (2009) Changes in plasma membrane lipids, aquaporins and proton pump of broccoli roots, as an adaptation mechanism to salinity. Phytochemistry 70:492–500

Lu Z, Liu D, Liu S (2007) Two rice cytosolic ascorbate peroxidases differentially improve salt tolerance in transgenic *Arabidopsis*. Plant Cell Rep 26: 1909–1917

Maarouf HE, Zuily-Fodil Y, Gareil M, d'Arcy-Lameta A, Pham-Thi AT (1999) Enzymatic activity and gene expression under water stress of phospholipase D in two cultivars of *Vigna unguiculata* L. Walp. differing in drought tolerance. Plant Mol Biol 39:1257–1265

Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: an overview. Arch Biochem Biophys 444: 139–158

Marin E, Nussaume L, Quesada A, Gonneau M, Sotta B (1996) Molecular identification of zeaxanthin epoxidase of *Nicotiana plumbaginifolia*, a gene involved in abscisic acid biosynthesis and corresponding to the ABA locus of *Arabidopsis thaliana*. EMBO J 15:2331–2342

Maser P, Eckelman B, Vaidyanathan R, Horie T, Fairbairn DJ, Kubo M, Yamagami M, Yamaguchi K, Nishimura M, Uozumi N (2002) Altered shoot/root NaR distribution and bifurcating salt sensitivity in *Arabidopsis* by genetic disruption of the NaR transporter AtHKT1. FEBS Lett 531:157–161

Mikolajczyk M, Olubunmi SA, Muszynska G, Klessig DF, Dobrowolska G (2000) Osmotic stress induces rapid activation of a salicylic acid-induced protein kinase and a homolog of protein kinase ASK1 in tobacco cells. Plant Cell 12:165–178

Miller G, Shulaev V, Mittler R (2008) Reactive oxygen signaling and abiotic stress. Physiol Plant 133:481–489

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R (2010) Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ 33:453–467

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19

Molina C, Rotter B, Horres R, Udupa SM, Besser B, Bellarmino L, Baum M, Matsumura H, Terauchi R, Kahl G (2008) SuperSAGE: the drought stress-responsive transcriptome of chickpea roots. BMC Genomics 9:553

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250

Munnik T, Ligterink W, Meskiene I, Calderini O, Beyerly J (1999) Distinct osmosensing protein kinase pathways are involved in signaling moderate and severe hyperosmotic stress. Plant J 20:381–388

Munnik T (2001) Phosphatidic acid: an emerging plant lipid second messenger. Trends Plant Sci 6:227–233

Nambara E, Marion-Poll A (2005) Abscisic acid biosynthesis and catabolism. Annu Rev Plant Biol 56:165–185

Niu X, Bressan RA, Hasegawa PM, Pardo JM (1995) Ion homeostasis in NaCI stress environments. Plant Physiol 109:735–742

Okamoto M, Tanaka Y, Abrams SR, Kamiya Y, Seki M, Nambara E (2009) High humidity induces abscisic acid 8 '-hydroxylase in stomata and vasculature to regulate local and systemic abscisic acid responses in arabidopsis. Plant Physiol 149:825–834

Ozturk ZN, Talame V, Deyholos M, Michalowski CB, Galbraith DW, Gozukirmizi N, Tubrosa R, Bohnert HJ (2002) Monitoring large scale changes in transcript abundance in drought- and salt-stressed barley. Plant Mol Biol 48:551–573

Pardo JM (2010) Biotechnology of water and salinity stress tolerance. Curr Opin Biotechnol 21:185–196

Park SY, Ryu SH, Jang IC, Kwon SY, Kim JG, Kwak SS (2004) Molecular cloning of a cytosolic ascorbate peroxidase cDNA from cell cultures of sweet potato and its expression in response to stress. Mol Genet Genomics 271:339–346

Passioura J (2007) The drought environment: physical, biological and agricultural perspectives. J Exp Bot 58:113–117

Perera IY, Hung CY, Moore CD, Stevenson-Paulik J, Boss WF (2008) Transgenic *Arabidopsis* plants expressing the type 1 inositol 5-phosphataseexhibit increased drought tolerance and altered abscisic acid signaling. Plant Cell 20:2876–2893

Perruc E, Charpenteau M, Ramirez BC, Jauneau A, Galaug JP, Ranjeva R, Ranty B (2004) A novel

calmodulin-binding protein functions as a negative regulator of osmotic stress tolerance in *Arabidopsis thaliana* seedlings. Plant J 38:410–420

Pose D, Castanedo I, Borsani O, Nieto B, Rosado A, Taconnat L, Ferrer A, Dolan L, Valpuesta V, Botella MA (2009) Identification of the *Arabidopsis* dry2/sque1–5 mutant reveals a central role for sterols in drought tolerance and regulation of reactive oxygen species. The plant protects plants against lipid peroxidation and oxidative stress. Plant Cell Environ 29:1033–1048

Qiu QS, Guo Y, Dietrich M, Schumaker KS, Zhu JK (2002) Regulation of SOS1, a plasma membrane Na/H exchanger in *Arabidopsis thaliana*, by SOS2 and SOS3. Proc Natl Acad Sci USA 99:8436–8441

Rizhsky L, Hallak-Herr E, Van Breusegem F, Rachmilevitch S, Barr JE, Rodermel S, Inze D, Mittler R (2002) Double antisense plant slacking ascorbate peroxidase and catalase are less sensitive to oxidative stress than single antisense plants lacking ascorbate peroxidase or catalase. Plant J 32:329–342

Sanders D, Pelloux J, Brownlee C, Harper JF (2002) Calcium at the crossroads of signaling. Plant Cell 14:401–417

Seki M, Narusaka M, Abe H, Kasuga M, Yamaguchi-Shinozaki K, Carninic P, Hayashizaki Y, Shinozaki K (2001) Monitoring the expression pattern of 1300 *Arabidopsis* genes under drought and cold stresses by using a full-length cDNA microarray. Plant Cell 13:61–72

Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, Satou M, Akiyama K (2002) Monitoring the expression profiles of ca. 7000 *Arabidopsis* genes under drought, cold, and high-salinity stresses using a full-length cDNA microarray. Plant J 31:279–292

Sunkar R, Bartels D, Kirch HH (2003) Overexpression of a stress inducible aldehyde dehydrogenase gene from *Arabidopsis thaliana* in transgenic plants improves stress tolerance. Plant J 35:452–464

Sze H, Li X, Palmgren MG (1999) Energization of plant cell membranes by H^+ – pumping ATPases: regulation and biosynthesis. Plant Cell 11:677–689

Takahashi S, Katagiri T, Hirayama T, Yamaguchi Shinozaki K, Shinozaki K (2001) Hyperosmotic stress induced a rapid and transient increase in inositol 1,4,5-triphosphate independent of abscisic acid in Arabidopsis cell culture. Plant Cell Physiol 42:214–222

Tognetti VB, Van Aken O, Morreel K, Vandenbroucke K, van de Cotte B, DeClercq I, Chiwocha S, Fenske R, Prinsen E, Boerjan W, Genty B, Stubbs KA (2010) Perturbation of indole-3-butyric acid homeostasis by the UDP-glucosyltransferase UGT74E2 modulates *Arabidopsis* architecture and water stress tolerance. Plant Cell 22:2660–2679

Torres MA, Dangl JL (2005) Functions of the respiratory burst oxidase in biotic interactions, abiotic stress and development. Curr Opin Plant Biol 8:397–403

Tseng MJ, Liu CW, Yiu JC (2007) Enhanced tolerance to sulfur dioxide and salt stress of transgenic Chinese cabbage plants expressing both superoxide dismutase and catalase in chloroplasts. Plant Physiol Biochem 45:822–833

Tsugane K, Kobayashi K, Niwa Y, Ohba Y, Wada K, Kobayashi H (1999) A recessive *Arabidopsis* mutant that grows enhanced active oxygen detoxification. Plant Cell 11:1195–1206

Turkan I, Demiral T (2009) Recent developments in understanding salinity tolerance. Environ Exp Bot 67:2–9

UNESCO Water Portal (2007) Water e-newsletter no. 174: wetlands, in commemoration of world wetlands day. http://www.unesco.org/water. Accessed 25 Oct 2007

Wilkinson S, Davies WJ (2002) ABA-based chemical signalling: the coordination of responses to stress in plants. Plant Cell Environ 25:195–210

Wilson PB, Estavillo GM, Field KJ, Pornsiriwong W, Carroll AJ, Howell KA, Woo NS, Lake JA, Smith SM, von Harvey Millar A, Caemmerer S, Pogson BJ (2009) The nucleotidase/phosphatase SAL1 is a negative regulator of drought tolerance in *Arabidopsis*. Plant J 58:299–317

Xiong L, Zhu JK (2001) Abiotic stress signal transduction in plants: molecular and genetic perspectives. Physiol Plant 112:152–166

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803

Yokoi S, Quintero FJ, Cubero B, Ruiz MT, Bressan RA, Hasegawa PM (2002) Differential expression and function of Arabidopsis thaliana NHX Na+/H+ antiporters in the salt stress response. Plant J 30(5):529–539

Zhang JZ (2003) Overexpression analysis of plant transcription factors. Curr Opin Plant Biol 6:430–440

Zhu JK (2001) Plant salt tolerance. Trends Plant Sci 6:66–71

Zhu JK, Liu J, Xiong L (1998) Genetic analysis of salt tolerance in *Arabidopsis*. Evidence for a critical role of potassium nutrition. Plant Cell 10:1181–1191

Zhu J, Lee BH, Dellinger M, Cui X, Zhang C, Wu S, Nothnagel EA, Zhu JK (2010) A cellulose synthase-