

Minireview

# A New Insight of Salt Stress Signaling in Plant

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Many studies have been conducted to understand plant stress responses to salinity because irrigation-dependent salt accumulation compromises crop productivity and also to understand the mechanism through which some plants thrive under saline conditions. As mechanistic understanding has increased during the last decades, discovery-oriented approaches have begun to identify genetic determinants of salt tolerance. In addition to osmolytes, osmoprotectants, radical detoxification, ion transport systems, and changes in hormone levels and hormone-guided communications, the Salt Overly Sensitive (SOS) pathway has emerged to be a major defense mechanism. However, the mechanism by which the components of the SOS pathway are integrated to ultimately orchestrate plant-wide tolerance to salinity stress remains unclear. A higher-level control mechanism has recently emerged as a result of recognizing the involvement of GIGANTEA (GI), a protein involved in maintaining the plant circadian clock and control switch in flowering. The loss of GI function confers high tolerance to salt stress via its interaction with the components of the SOS pathway. The mechanism underlying this observation indicates the association between GI and the SOS pathway and thus, given the key influence of the circadian clock and the pathway on photoperiodic flowering, the association between GI and SOS can regulate growth and stress tolerance. In this review, we will analyze the components of the SOS pathways, with emphasis on the integration of components recognized as hallmarks of a halophytic lifestyle.

## INTRODUCTION

For maintaining photosynthesis and growth in plants, water supply is essential in natural settings and cropping systems to produce high yields. In agriculture, water supply is increasingly dependent on irrigation systems that currently cover approxi-

mately 15% of agriculturally useful land, which produces more than a third of all food (Ghassemi et al., 1995; see also: USDA Salinity Laboratory, <http://www.ars.usda.gov/Aboutus/docs.htm?docid=10201>). The accumulation of sodium ions, although low in irrigation water, in soils is unavoidable unless leaching of salts into groundwater is economically possible.

Na<sup>+</sup> tolerance widely differs in plant species; for example, citrus, tomato, and avocado have a low tolerance, while cotton and barley have a high tolerance (Flowers et al., 2010). Most crops are glycophytes, indicating a requirement for fresh water, and their growth may be severely inhibited by often low (millimolar) Na<sup>+</sup> concentrations. Most crops are destroyed or will not produce fruits or set seeds in 100 mM NaCl, i.e., approximately one fourth of the NaCl concentration of seawater (Flowers, 2004; Maas and Hoffman, 1977; Zhu, 2001).

Some plants, termed halophytes, naturally grow in or even depend on elevated or high NaCl environments (200 mM NaCl) (Bohnert and Cushman, 2000; Bohnert et al., 1995; Flowers and Colmer, 2008; Flowers et al., 1977; 2010). Numerous plant orders include many halophytic species, such as *Atriplex*, *Salicornia*, *Mesembryanthemum*, *Rhizophora*, and *Suaeda*, that can grow in an environment having up to 1000 mM NaCl (Black, 1960; Ushakova et al., 2005; Yeo and Flowers, 1980). Halophytes are found in all flowering plant taxa, although in different abundances, but constitute only approximately 5-10% of all known angiosperms (Yensen, 2006).

Salt stress negatively affects most plant growth phases and alters development (Munns, 2002; Sairam and Tyagi, 2004). Ion imbalances are particularly detrimental during germination and seedling growth; less so during the vegetative growth, more so when flowering is initiated, and again less as seeds are set. Salt shock is often used in experiments, although in nature, the ion concentrations typically gradually change. Within minutes following salt shock, water deficit and wilting occur because of rapid change in the osmotic potential difference between the plant and exterior environment (Fricke et al., 2006; Munns, 2002). Accompanying this water deficit stress are ABA biosynthesis and transportation throughout the plant initiating stomatal closure, among many other responses. The consequences, which are also contributed by ABA-independent mechanisms, are reduced transpiration and photosynthesis and increased photoinhibition and oxidative stress. Such stresses may be countered by the scavenging defenses of reactive oxygen species (ROS) that are induced by hormonal changes. Ultimately, a decreased in leaf and root growth rates will occur that may accelerate over time. Water deficit, hyperosmotic stress, nutritional imbalance, and hyperionic toxicity are physiological hallmarks that may eventually lead to death (Cheong and Yun, 2007; Cramer and Jones, 1996; Sairam and Tyagi,

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2004).

All plants express proteins for the uptake of ions into cells, excretion from cells, distribution across organs and cells, and storage in vacuoles that may often be confined to dedicated cells or older tissues that then senesce. Responding to ion imbalance changes in gene expression and metabolism can adjust to some degree that is species- and condition-specific respond to ionic challenges and osmotically to a new equilibrium (Fig. 1). As NaCl is partitioned in the vacuoles of elongating cells (Munns, 2005; Nawaz et al., 2010), signs of injury may appear first in older leaves within days or weeks. Subsequently, younger leaves are damaged, reducing photosynthetic performance, followed by delayed flowering and eventually affecting seed maturation in sensitive plants (Munns, 2002). However, altered development and flowering cannot be simply understood as a result of damaging salt concentrations that accumulate in plants. The susceptibility of plants to salinity stress is because of changes in molecular programs that affect development (Krasensky and Jonak, 2012).

In *Arabidopsis*, as observed earlier in rice, NaCl stress delays flowering (Li et al., 2007; Lutts et al., 1995); however, this behavior is not exhibited by all species, strongly suggesting that delayed flowering is genetically controlled (Andres and Coupland, 2012). However, the *Arabidopsis* relatives *Thellungiella salsuginea* and *Schrenkiella parvula* (formerly *T. parvula*) do flower faster, better, and earlier (Oh et al., 2014). Among other plants, the euhalophyte *Mesembryanthemum crystallinum* also employs this strategy (Adams et al., 1998).

Correlative evidence is also provided by other observations. For one, flowering time is an important trait in breeding crops (Jung and Müller, 2009). Second, flowering time loci have been associated with quantitative trait loci (QTLs) for tolerance to abiotic stress such as drought or cold (Ducrocq et al., 2008; Sehgal et al., 2012). Here we will examine recent findings regarding the manner in which defense mechanisms against salt stress and decisions regarding flowering in a saline environment are genetically regulated. A biochemical association exists between the SOS salt exclusion pathway and proteins that regulate the entry into flowering (Kim et al., 2013; Park et al., 2013). Furthermore, we will discuss the emerging understanding regarding how changes in the plant growth phases can fundamentally alter the manner in which plants engage mechanisms that lead to stress tolerance or avoidance. Available data are insufficient to assert that the transition from the glycophytic to halophytic lifestyle may be relatively easy. However, hypothetically, plant-phase changes coincide with the initiation of new developmental programs that can or could evolve to adjust to prevailing environmental conditions. Thus, we will discuss how the circadian clock, day length, and progression from vegetative to reproductive growth altogether influence plant stress responses and how the imposition of salt stress can modulate phase changes and alter further growth (Bendix et al., 2013).

## SALINITY STRESS RESPONSES

As outlined in Fig. 1, numerous concepts, mechanisms, and factors have emerged that have led to some understanding of the defenses available in plants to cope with and survive salt stress conditions. Further details have been outlined in several reviews (Bohnert and Jensen, 1996; Craig Plett and Møller, 2010; Howell, 2013; Kronzucker and Britto, 2011; Munns and Tester, 2008; Nuccio et al., 1999; Pardo, 2010). We provide a short synopsis of the salient concepts.

Salt stress is typically experimentally induced by elevated or

increasing NaCl levels in the soil or medium. When a high salt concentration is rapidly applied, NaCl shock leads to a rapid osmotic challenge and water loss, followed more slowly by increased uptake of Na<sup>+</sup> and Cl<sup>-</sup>. When salt is gradually applied, as may be the case in nature, the osmotic stress component is less pronounced and Na<sup>+</sup> concentration increases more slowly. However, the mechanisms that have been recognized, analyzed, and then verified in transgenic experiments have often employed (moderate) shock treatments (Shavrukov, 2013).

### Membrane integrity

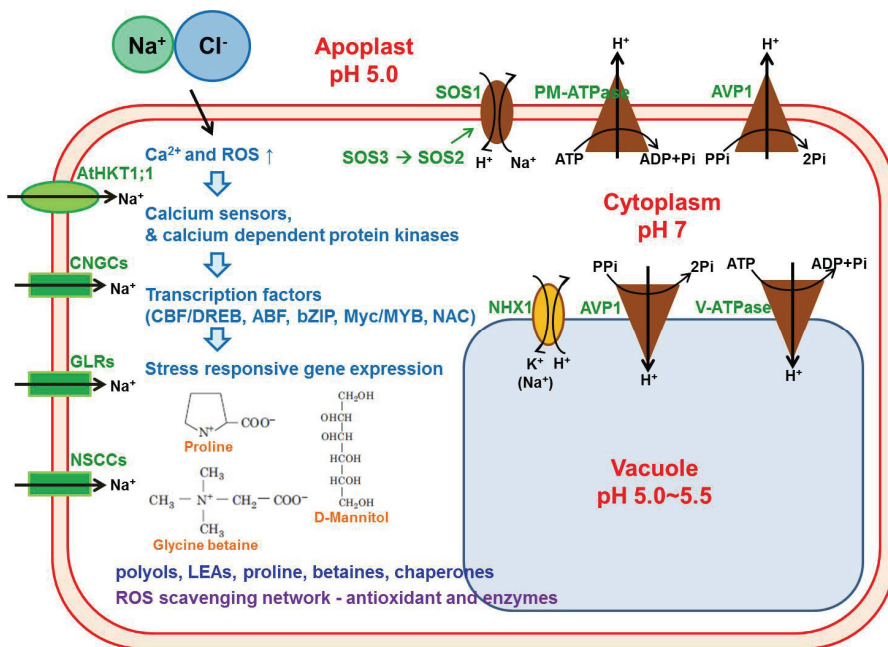
The most immediate event following salt-induced osmotic stress and water deficiency is the loss of turgor pressure, resulting from changes in cell structure and membrane leakage, and different compositions of cell membranes (Kinnunen, 2000; König et al., 2007). To maintain cell membrane integrity, membrane rearrangement processes occur in plant cells (Munnik and Vermeer, 2010). For example, the overexpression of phosphatidylinositol synthase genes in tobacco increases drought stress tolerance by modulating the membrane lipid composition (Liu et al., 2013a; Zhai et al., 2012).

### Ca<sup>2+</sup> and IP3

Osmotic stress imposed by NaCl, drought, or cold transiently increases Ca<sup>2+</sup> and inositol 1,4,5-trisphosphate (IP3) concentrations in the cytosol (DeWald et al., 2001). The biosynthesis of the IP3 precursor phosphoinositide phosphatidylinositol 4,5-bisphosphate [PtdIns(4,5)P<sub>2</sub>] is rapidly induced by NaCl treatment, and the increase in IP3 concentration appears to mediate cellular Ca<sup>2+</sup> mobilization. Cytosolic calcium is translocated through Ca<sup>2+</sup> pumps and channels that are present on the plasma membrane, tonoplast, and ER membrane. Ca<sup>2+</sup> and IP3 fluxes act as secondary messengers in stress signal transduction (Sanders et al., 2002; Sairam and Tyagi, 2004; Zhu, 2001). The downstream activation of mitogen-activated protein kinase (MAPK) cascades regulates the gene expression by phosphorylating many transcriptional activators (Cheong and Yun, 2007; Nakagami et al., 2005; Sairam and Tyagi, 2004; Zhu, 2001; 2002).

### Osmolytes

Osmotic imbalance and continued salt exposure inevitably leads to a water deficit, which is phenotypically shown by a partial loss of turgor. Plants activate mechanisms that lower the osmotic potential by generating osmotically active metabolites such as proline, sugars, and sugar alcohols (Bohnert et al., 1995). The type of accumulating osmolytes is to some degree species specific, and many of these compounds are also found in response to freezing, drought, and heat stresses. These include sugars (sucrose and fructose), polyols (sorbitol, mannitol, glycerol, arabinitol, and pinitol), complex sugars (fructans, trehalose, and raffinose), ions (predominantly K<sup>+</sup>), specific proteins, and charged metabolites (betaine, proline, glutamate, aspartate, glycine, choline, putrescine, oxalate, and malate) (Cheong and Yun, 2007; Sairam and Tyagi, 2004). All osmolytes share a common characteristic, i.e., lowering the osmotic potential in the cytosolic compartment while not inhibiting metabolic reactions at relatively high concentrations. Osmolytes may also function as osmoprotectants of proteins, macromolecular aggregates, and membranes; as antioxidants in redox balance; and as signaling molecules. Consequently, transgenic plants that overexpress osmolytes, such as glycine betaine, proline, sugar alcohols, and fructans, demonstrate tolerance to multiple abiotic stresses such as salinity, freezing and heat (for further



**Fig. 1.** A simplified model of plant cell sensing of stress, transduction of signals by transcriptional regulation, enzyme activity control, and translocational control. CYCLIC NUCLEOTIDE-GATED CHANNELS (CNGCs), GLUTAMATE RECEPTOR (GLR), NON-SELECTIVE CATION CHANNEL (NSCC), and HIGH AFFINITY  $K^+$  TRANSPORTER (HKT) mediate  $Na^+$  influx. SOS1 (plasma membrane  $Na^+/H^+$  antiporter) is involved in the extrusion of  $Na^+$  from the cytoplasm and AtNHX1 mediates  $K^+/H^+$  exchanges, involved in controlling the vacuolar osmotic potential and regulating cytosolic  $Na^+-K^+$  ratio through vacuolar compartmentalization of  $K^+$ .

details regarding the protective roles of osmolytes refer to Cheong and Yun, 2007; Nuccio et al., 1999; Rontein et al., 2002; Sairam and Tyagi, 2004; Sakamoto and Murata, 2002; Wahid et al., 2007; Zhu, 2001).

Water uptake and transportation also constitute important parameters for maintaining osmotic balance, which is associated with aquaporins. Aquaporins are present in the plasma and tonoplast membranes and transport water, small neutral solutes, and gases, such as carbon dioxide or ammonia, across other internal membranes (del Martínez-Ballesta et al., 2006; Shatil-Cohen et al., 2011; Tyerman et al., 1999; Zhou et al., 2012).

### Soluble sugars as signals

Soluble sugars are metabolic resources and structural components and may serve as signaling molecules under stress. Sucrose and glucose play roles as substrates for cellular respiration and as osmolytes, respectively. Fructose appears to be involved in secondary metabolite synthesis. Fluctuations in soluble sugar concentrations under stress affect  $CO_2$  assimilation, carbon partitioning, enzyme activities, and related gene expressions (for details, see Rosa et al., 2009).

### ROS

Another phenotypic indicator of stress is stomatal closure, which is initiated by water deficit. The stomatal closure generates over time a multifaceted feedback process by which leaf and plant temperature increases,  $CO_2$  deficit becomes acute, and photosynthesis decreases or ceases. Altogether these factors lead to increased ROS production that must be countered by mechanisms such as flavonoid generation,  $H_2O_2$  detoxification, and/or OH-radical scavenging (Blokhina et al., 2003; Shao et al., 2008). The biochemical inventory of plants for proteins in these defense mechanisms is large and multifaceted, indicating the fundamental importance of ROS scavenging (Dietz, 2003; Kar, 2011; Rodrigo-Moreno et al., 2013; Shen et al., 1997; Tripathy and Oelmüller, 2012).

Plants cope with reactive oxygen stress by increasing the enzymatic and non-enzymatic scavenging activity of ROS, with reactive oxygen itself acting as a signal for inducing defense responses (Gill and Tuteja, 2010; Miller et al., 2010). Non-enzymatic scavengers of reactive oxygen include ascorbic acid, glutathione, phenolic compounds, carotenoids, flavonoids, and tocopherol. Enzymatic scavengers include superoxide dismutase, catalase, glutathione S-transferase, glutathione peroxidase, and ascorbate peroxidase. Salt tolerance in some plants appears to correlate with their ability to scavenge reactive oxygen (de Azevedo Neto et al., 2006; Mittova et al., 2002; Vaidyanathan et al., 2003). Transgenic plants with a high scavenging ability improve salt tolerance (Nagamaya et al., 2007; Yoshimura et al., 2004).

### Ion balance

In plants,  $K^+$  is the major cellular cation and an essential nutrient.  $K^+$  is critical for maintaining cell turgor, membrane potential, and membrane integrity and function and for the activity of many enzymes in different pathways (Ashley et al., 2006; Zhu et al., 1998). Excess cytosolic  $Na^+$  displaces bound  $K^+$ , leading to a reduced activity of many proteins. Accordingly, supplementing soil or growth media with  $K^+$  alleviates NaCl toxicity in plants (Kopittke, 2012). Halophytes attempt to maintain low  $Na^+$  concentrations in the cytosol and in general, have evolved  $K^+$  uptake systems that lead to efficient  $Na^+/K^+$  discrimination (Ali et al., 2012). Thus, halophytes may maintain a higher  $K^+/Na^+$  ratio than glycophytes.

Potassium uptake is mediated by ion channels and transporters that are distinguished by the levels of selectivity and affinity (Ashley et al., 2006). Their expression is influenced by the severity of stress (Zhu, 2003). High extracellular  $Na^+$  concentration generally affects  $K^+$  uptake by low-selectivity systems. In contrast, high-affinity systems continue to operate under NaCl stress and are important for salt tolerance (Shabala and Cuin, 2007; Szczerba et al., 2009; Zhu, 2003; Zhu et al., 1998).

NaCl interferes with  $\text{Ca}^{2+}$  uptake and lowers cytosolic  $\text{Ca}^{2+}$ , which is essential for membrane stability, maintaining osmotic balance, and intracellular signaling (Rengel, 1992).  $\text{Ca}^{2+}$  supplementation that restores cytosolic  $\text{Ca}^{2+}$  and the growth rate and ameliorates stress symptoms enables the tolerance of higher NaCl concentrations.

Sequestering excess NaCl in the vacuole is an important mechanism for establishing ionic balance, thereby reducing the  $\text{K}^+$  concentration required for maintaining turgor. Cytosolic calcium regulates the activity of tonoplast and plasma membrane-localized ion channels (Hedrich and Neher, 1987; Shabala and Cuin, 2007; Zhu, 2007). Calcium also regulates intracellular signaling pathways that lead to the expression of potassium and sodium transporters (Cheong et al., 2003; Ketchum and Poole, 1991; Kim et al., 2007a; Lee et al., 2007). Vacuolar sequestration of  $\text{Na}^+$  is mediated by the action of tonoplast-localized  $\text{Na}^+/\text{H}^+$  antiporters that depend on proton gradients that are generated by tonoplast proton-ATPase and vacuolar pyrophosphatase (Barragán et al., 2012; Jiang et al., 2010; Zhu, 2007). This process is probably more important for halophytes than for glycophytes, given that the former accumulate higher ion concentration in their vacuoles than the latter (Zhu, 2007). In these species,  $\text{Na}^+$  acts as a cheap osmoticum (Adams et al., 1998). In our opinion, such a bulk transport pathway will be discovered in the next decade.

### Gene expression of genome structures

Transcriptome analyses revealed that approximately 30% of transcriptome is regulated by abiotic stresses (Kreps et al., 2002). Acute stress induces a shared stress response, where late responses are largely stress or stimulus specific (Kreps et al., 2002), suggesting that late responses favor adaptation (Sairam and Tyagi, 2004). Not surprisingly, large numbers of early response genes are involved in transcription, membrane transport, phosphoregulation, and immediate ROS defense. Late-response genes specific to NaCl include a large component involved in redox regulation. A substantial proportion of NaCl-regulated genes are involved in metabolic adjustment and ABA signaling, suggesting that metabolic readjustments are central to NaCl stress adaptation in *Arabidopsis* and rice (Kim et al., 2007b; Sahi et al., 2006). NaCl-regulated genes include those involved in the synthesis of osmolytes, defense proteins, and ABA; proteins that protect membranes; proteins that conic homeostasis such as ion transporters, amino acid transporters, and aquaporins; proteins and small RNAs that control translation; and proteins involved in protein degradation (Sahi et al., 2006; Sunkar et al., 2006). Salt stress tolerance (at least in shock experiments) appears to be decided during the initial phase; although photosynthesis in the salt-tolerant rice line Pokkali declined to one tenth of normal photosynthesis on addition of salt (150 mM NaCl), the line could recover, grow, and maintain water content in the shoot. However, plants of the salt-sensitive line IR19 did not recover and died within a few days after treatment. Moreover, 10% of tested transcripts in functions relevant to ionic response were up- or downregulated within 1 h of salt stress in Pokkali, whereas IR29 showed a slower, less pronounced, and incomplete transcriptional response (Kawasaki et al., 2001).

## THE SOS PATHWAY

The SOS signaling pathway regulating ionic homeostasis under salt stress has received much attention, and the functions of the three genes in this pathway have been studied by analyzing

*Arabidopsis* salt overly sensitive (*sos*) mutants. The SOS pathway plays an important role in regulating  $\text{Na}^+/\text{K}^+$  homeostasis and salt tolerance and includes SOS1, a plasma membrane-localized  $\text{Na}^+/\text{H}^+$  antiporter that mediates  $\text{Na}^+$  efflux from the roots and loading of  $\text{Na}^+$  ions in the xylem (Munns, 2002; Olías et al., 2009; Shi et al., 2000; 2002; Zhu, 2003). The second protein component is the Ser/Thr protein kinase SOS2 and the third is the calcium-binding protein SOS3, a myristoylated, EF-hand-containing protein. The SOS pathway invokes a salt stress-generated  $\text{Ca}^{2+}$  signal that is perceived by SOS3, enabling the formation of the SOS3-SOS2 complex, which phosphorylates and activates the transport activity of SOS1. The activated SOS3-SOS2 complex also stimulates, among other genes, the transcriptional activation of SOS1 and stabilizes cellular levels of SOS1 mRNA (Ji et al., 2013; Zhu, 2003).

The  $\text{Ca}^{2+}$ -activated SOS pathway directly or indirectly affects  $\text{K}^+$  homeostasis. *sos1*, *sos2*, and *sos3* mutants are hypersensitive to  $\text{K}^+$  deficiency. However, activated SOS1 does not transport  $\text{K}^+$  (Quintero et al., 2002).  $\text{K}^+$  uptake in *sos* mutants is inhibited by even mild NaCl stress. The activity of *ARABIDOPSIS K TRANSPORTER1* (*AKT1*), a major highly selective potassium channel mediating potassium uptake under low  $\text{K}^+$  conditions, is inhibited by high cytoplasmic NaCl concentration (Pyo et al., 2010; Qi and Spalding, 2004), suggesting that the SOS pathway is affected by the activity of *AKT1*. Some mutations and deletions of the  $\text{Na}^+$ -transporter *HKT1* suppress the salt-hypersensitive phenotype of *sos* mutants by inhibiting the accumulation of  $\text{Na}^+$ . Hypersensitivity to  $\text{K}^+$  deficiency of the *sos* mutants was suppressed by the expression of mutated *HKT1* (Rus et al., 2001; 2004). The SOS pathway is also suggested to mediate salt tolerance by modulating the activity of vacuolar  $\text{H}^+$ -ATPase (*V-ATPase*), which is both tonoplast and endosome localized. SOS2 binds to regulatory subunits of *V-ATPase* and stimulates its activity (Batelli et al., 2007). An endosomal *V-ATPase* mediates salt tolerance (Krebs et al., 2010). Finally, the SOS pathway controls endocytosis, vacuolar shape and function, and intracellular pH (Oh et al., 2010), although the mechanisms by which this is accomplished are unknown.

The SOS pathway genes are conserved in many plant species (Martínez-Atienza et al., 2007; Olías et al., 2009; Tang et al., 2010; Wu et al., 2007; Xu et al., 2008) and their overexpression increases salt tolerance in *Arabidopsis* and in heterologous species (Shi et al., 2003; Yang et al., 2009; Zhang and Blumwald, 2001; Zhang et al., 2009). *SOS1* mRNA is unstable under normal growth conditions but is stabilized by salt (ionic) and dehydration stresses (Chung et al., 2008; Shi et al., 2003). The stabilization of *SOS1* mRNA is also mediated by reactive oxygen species with SOS1, a component in oxidative stress signaling (Chung et al., 2008; Katiyar-Agarwal et al., 2006). SOS2 may also participate in reactive oxygen signaling (Verlues et al., 2007).

## HORMONE-MEDIATED RESPONSES TO SALT STRESS

### ABA pathways in stress response pathways

The synthesis, sequestration, transportation, and turnover of numerous metabolites with hormone character generates a web of signals that correlate plant growth, flowering, and seed production in dependence on internal and external cues. Among these hormones, ABA is of particular importance for stress recognition and stress defense reactions. ABA signaling cascades, synchronized with the plant growth stage and other hormone levels, regulate important abiotic stress responses, in particular water balance and osmotic stress tolerance. Guard

cell movement that is regulated by ABA leads to stomatal closure as an immediate response to ion imbalance and water deficit. Furthermore, ABA induces the synthesis of dehydration tolerance proteins with general metabolic adjustments.

ABA biosynthesis genes and ABA accumulation are upregulated by NaCl, drought, or cold stress (Cheong and Yun, 2007; Umezawa et al., 2006; Zhang et al., 2006; Zhu, 2002). Although ABA, produced in roots in response to dehydration, is transported to the leaves via the xylem, it is believed that ABA produced *de novo* in various plant organs is more important for physiological responses (Seung et al., 2012).

### Other hormones and hormone balance

ABA-independent pathways for regulating gene expression in response to salinity, drought, and cold stress also exist (Cheong and Yun, 2007; Sairam and Tyagi, 2004). For example, brassinosteroids increase tolerance to stresses, including salinity, by mediating the synthesis of enzymatic or non-enzymatic antioxidant systems, proline, or lectins (Bajguz and Hayat, 2009). Although salicylic acid (SA), another growth mediator, generates ROS that may negatively affect the salt stress response (Barba-Espin et al., 2011; Hao et al., 2012), it can alleviate salt-induced oxidative stress through the MAPK pathway when externally applied at a sublethal level. The SA effect reduces salt-induced membrane depolarization (Gémes et al., 2011; Horváth et al., 2007; Jayakannan et al., 2013; Opendaker et al., 2012; Rivas-San Vicente and Plasencia, 2011; Yuan and Lin, 2008). Furthermore, salt alters the expression of auxin-responsive genes and auxin/IAA pathways in different plants (Jain and Khurana, 2009; Liu et al., 2013b; Wang et al., 2010). The model legume *Medicago truncatula* exhibits a higher tolerance to 300 mM NaCl treatment when indole-3-acetic acid-overproducing *Sinorhizobium meliloti* are present (Bianco and Defez, 2009). In addition, the polar distribution of auxin appears to be important for oxidative stress responses because auxin transporter mutants, such as *aux1*, *pin1*, and *pin2*, are hypersensitive to arsenite-induced oxidative stress compared with the auxin transporter wild-type (Krishnamurthy and Rathinasabapathi, 2013).

Ethylene and gibberellin (GA) signaling have been observed in salt stress responses. The bioactive GA amount is reduced on salt treatment in the wild-type. A *ga1-3* mutant lacking ent-copalyl diphosphate synthase, the first committed step enzyme in GA biosynthesis, is tolerant to salt. A quadruple DELLA mutant defective in genes associated with the GA pathway, lacking *GAI*, *RGA*, *RGL1*, and *RGL2*, is less tolerant to salt treatment compared with the wild-type at high salt concentrations (Achard et al., 2006). Delay in flowering by salt is reduced in the quadruple DELLA mutant and GA-induced DELLA degradation is inhibited by ABA (Achard et al., 2006). *spy*, a loss of function mutation in *SPINDLY* (*SPY*), encoding an O-linked N-acetylglucosamine transferase, exhibits higher expression of GA responsive genes, suggesting that *SPY* represses GA signaling (Olszewski et al., 2002; 2010; Qin et al., 2011). *spy* is tolerant to salt and drought stresses, wherein stress responsive genes, such as *RD20*, ABSCISIC ACID RESPONSIVE ELEMENTS-BINDING FACTOR 1-like transcription factor, and late embryogenesis-abundant proteins, are upregulated (Qin et al., 2011).

Ethylene is sensed by ENDOPLASMIC RETICULUM-membrane proteins and receptors, including ETHYLENE RESPONSE (ETR)1, ETR2, ETHYLENE RESPONSE SENSOR (ERS)1, ERS2, and ETHYLENE INSENSITIVE (EIN)4. Under normal conditions, the receptors of ethylene, which are characterized by low ethylene levels, bind to and activate the negative

regulator of ethylene signaling, CONSTITUTIVE TRIPLE RESPONSE1 (CTR1), a Raf-like MITOGEN-ACTIVATED PROTEIN KINASE KINASE. ER-integrated EIN2, which is downstream of CTR1, is a positive transducer of ethylene signaling whose stability is regulated by two F-box proteins EIN2-TARGETING PROTEIN and 26S proteasome-mediated degradation. Plants emanate ethylene gas on salt treatment (Achard et al., 2006). Treatment with ACC, a substrate of ethylene synthesis, increases tolerance to high salt. Similarly, the *ctr1-1* mutant, which displays constitutive ethylene responses on EIN3 accumulation, exhibits higher tolerance (Achard et al., 2006; Cao et al., 2007b). Mutations in *ACS7* (ACC synthase) reduce ethylene emission compared with the wild-type and enhance tolerance to salt, osmotic, and heat stresses because of the upregulated expression of stress responsive ABA-dependent genes (Dong et al., 2011).

### Developmental changes

Senescence, in particular leaf senescence, constitutes a regulated developmental process that coordinates metabolite redistribution, reproductive maturation, and programmed cell death. Senescence is affected by endogenous factors, responding to environmental signals. The endogenous factors include plant growth stage and phytohormonal levels, which are influenced by many adverse environmental conditions such as drought, nutrient limitation, heat, ozone, and UV irradiation (Jibran et al., 2013; Lim et al., 2007; Munné-Bosch and Alegre, 2004). For example, two ethylene-insensitive mutants *etr1* and *ein2* exhibit inhibited seed germination, enhanced leaf cell expansion, delayed flowering, and acceleration of senescence (Bleecker and Patterson, 1997; Kende and Zeevaert, 1997), thereby implicating ethylene during organ shedding. A group of senescence-associated genes (SAGs) is involved in nutrient recycling and transport and detoxification (Gepstein et al., 2003; Lim et al., 2007). Responses that affect stress tolerance include functions of the NAC transcription factor ANAC092/AtNAC2/ORE1 and the senescence-associated protein SAG29 that are related to salinity stress responses (Balazadeh et al., 2010; Seo et al., 2011). SAG29 gene expression is induced by abiotic stresses such as cold, NaCl, drought, and ABA treatment. A loss-of-function mutation in SAG29 is less sensitive to salt compared with the wild-type, whereas transgenic overexpression of SAG29 results in high sensitivity to salt and also early senescence (Seo et al., 2011).

### CIRCADIAN CLOCK RESPONSES TO ENVIRONMENTAL STRESS

The circadian clock controls the 24-h biological rhythms or oscillations, resulting from the rotation of the earth (refer to Harmer, 2009; McClung, 2011 for detailed information about the circadian clock). In plants, the circadian clock entrains a plant's memory and anticipation of the progression of time or predictable and daily changes (McClung and Davis, 2010; Sanchez et al., 2011). The plant clock is involved in plant biological processes, such as stomatal dynamics, shade avoidance, and metabolic activity, and in defenses against pathogens and in abiotic stress responses (Covington et al., 2008; Dalchau et al., 2011; Dodd et al., 2005a; Graf et al., 2010; Harmer et al., 2000; Hong et al., 2013; Hotta et al., 2007; Kreps et al., 2002; Seung et al., 2012; Wang et al., 2011). Levels of the stress hormone ABA in leaves and ABA biosynthesis, conjugation, and turnover exhibit diurnal oscillations (Seung et al., 2012). Transcript levels of genes involved in ABA sensing, core signaling, and signal

transduction exhibit diurnal oscillations, indicating gating by the clock (Legnaioli et al., 2009). Similarly, cyclic oscillations in cytosolic  $\text{Ca}^{2+}$  levels are under the circadian clock control (Dodd et al., 2005b; 2007; Xu et al., 2007; 2009). In addition, a large number of salt-, dehydration-, and osmotic stress-regulated or -responsive genes are under the circadian clock control (Covington et al., 2008; Harmer et al., 2000; Kreps et al., 2002). Gene expression at the transcription level with respect to drought responses is gated by the circadian clock (Wilkins et al., 2010). Genes, such as *SOS1*, *RD29A*, and *DREB2A*, that are involved in salinity stress exhibit a 24-h period of expression (diurnal web; <http://diurnal.mocklerlab.org/>), suggesting that salt tolerance may also be affected by the circadian clock. Moreover, the circadian clock modulates the cold signaling pathway (Dodd et al., 2006). Cold-induced expression of the C-repeat binding factor/dehydration-responsive element binding factor (CBF/DREB) genes *CBF1/DREB1B*, *CBF2/DREB1C*, and *CBF3/DREB1A* is dependent on the time of day at which the plants are exposed to low temperature (Fowler et al., 2005).

### Molecular mechanisms of the plant circadian clock responsive to environmental stress

The manner in which temporal information is passed from the clock to various plant processes is only partially understood. At the molecular level, four mechanisms appear to be involved (Thines and Harmon, 2011).

First, core clock proteins, such as *CCA1*, *LHY* and *TOC1*, have been demonstrated to directly bind to regulatory regions of the output genes, and thus, confer rhythmicity on their transcription (Barajas-López et al., 2011; Legnaioli et al., 2009; Maxwell et al., 2003; Schaffer et al., 1998; Wang et al., 1997). Accumulating genetic evidence indicates altered transcription of genes after core components of the clock have been deleted or altered in their expression (Blázquez et al., 2002; Michael et al., 2008; Thain et al., 2004).

Second, clock-controlled rhythmic chromatin modifications that lead to the modifications of gene expression are widespread in mammalian systems (e.g., Etchegaray et al., 2003). The acetylation of *HISTONE3* in nucleosomes associated with the *TOC1* promoter has been observed, and the inhibition of this acetylation by *CCA1* affects the rhythmic *TOC1* expression (Perales and Más, 2007). It appears likely that the clock controls the rhythmic chromatin modification of other genes as well. Third, the clock imposes a rhythmic expression on a large number of transcription factors (Covington and Harmer, 2007; Covington et al., 2008; Harmer et al., 2000). For example, enzymes involved in auxin biosynthesis and auxin-inducible genes for auxin signal transduction or auxin sensitivity are under the clock control (Covington and Harmer, 2007). Cold-induced *COR15b* and *DREB1a/CBF3* are clock controlled (Harmer et al., 2000).

The fourth mechanism has been recently researched and defines the physical interaction of core clock proteins with proteins associated with other pathways. To a large degree, such an interaction controls the availability or/and stability of clock components. *TOC1* interacts with proteins that do not function in the clock core but affect the clock output. For example, *TOC1* interacts with the PHYTOCHROME INTERACTING FACTOR 7 (*PIF7*), thus controlling the time of *CBF2/DREB1C* expression (Kidokoro et al., 2009). *PIF7* binds to the promoter of *CBF2* and represses its expression. Interaction with *TOC1* and *phyB* increases the repressive activity of *PIF7*. As the *CBF* genes play protective roles at a low temperature, *TOC1-PIF7* and *PHYB-PIF7* interactions reduce *CBF* expression at higher daytime

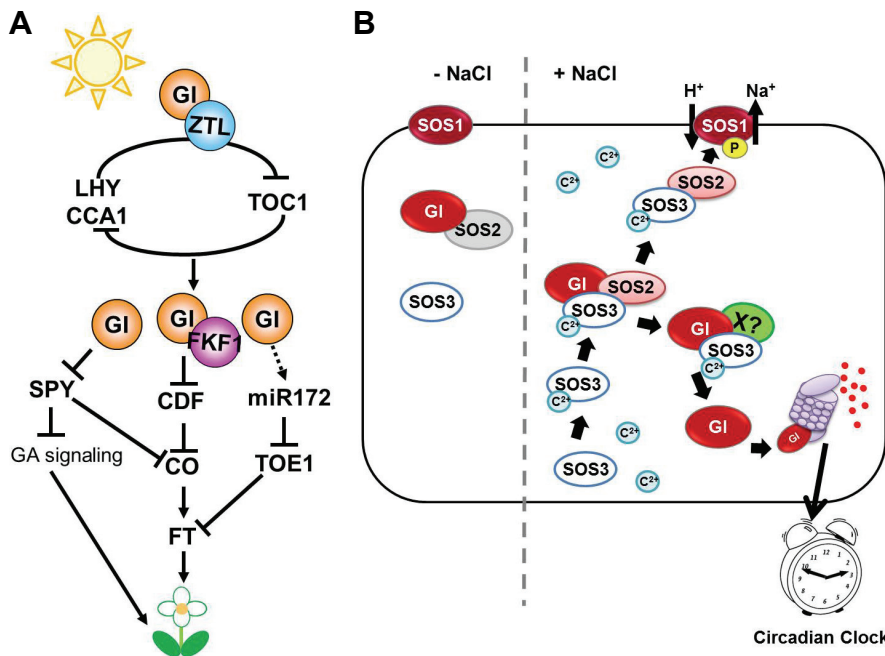
temperatures but enable the expression at lower temperatures during the night. *TOC1* also interacts with PHYTOCHROME INTERACTING FACTOR LIKE 1, and both proteins are necessary for rapid growth during shade avoidance (Salter et al., 2003). The ABA-associated gene *ABAR/CHLH/GUN5*, which is considered to be a plastid receptor for ABA that mediates ABA downstream signaling, interacts with *TOC1* (Legnaioli et al., 2009; Wang and Zhang, 2008). Although *GIGANTEA* (*GI*, see below) appears to mediate cold stress response by a *CBF*-independent pathway (Cao et al., 2005), the *TOC1* homologs *PRR5*, *7*, and *9* genes (Farré et al., 2005; Fujimori et al., 2005; Kim et al., 2010; Nakamichi et al., 2005a; 2005b; Salomé and McClung, 2005) have redundant functions in regulating the transcription of cold stress response genes through the *DREB1/CBF* pathway (Nakamichi et al., 2009).

### Integration of GI in diverse environmental stresses

The clock component *GI* is linked to several clock output components, such as photoperiod control of flowering, *PhyB* signaling, circadian clock, and carbohydrate metabolism. The *gi* mutant exhibits light-dependent resistance to paraquat-induced oxidative stress, possibly because of high superoxide dismutase and ascorbate peroxidase (Cao et al., 2006; Kurepa et al., 1998). The *gi* mutant with a longer hypocotyl than the wild-type under constant red light suggests a *GI* involvement in *PhyB* signaling (Huq et al., 2000). The *gi* mutant is sensitive to cold and freezing and shows reduced amounts of cold-induced sugars and high starch accumulation (Cao et al., 2005; 2007a; Eimert et al., 1995). *GI* appears to independently mediate a cold stress response of the *CBF*-mediated cold stress pathway (Cao et al., 2005). In addition, the *gi* mutants lose the drought escape response, which is the ability of plants to complete their life cycle before stress conditions result in death (Riboni et al., 2013).

*GI* is a large nucleoplasmatic protein that is encoded by a conserved single gene in most plant species (Fowler et al., 1999; Huq et al., 2000; Mizoguchi et al., 2005; Park et al., 1999). Circadian *GI* transcription appears to be positively regulated by temperature and light (Paltiel et al., 2006). In addition, *GI* is transcriptionally induced by cold stress but not by salt, mannitol, or ABA.

*GI* transcription is under the circadian control and peaks at 8-10 h after the start of the day. The *GI* protein amount or abundance, which is controlled by dark-induced proteolysis, closely follows this behavior (David et al., 2006). The amplitude, timing, and duration of this peak depend on the day length (Fowler et al., 1999). Mutational inactivation of *GI* alters the expression pattern with respect to amplitude and period length of two circadian oscillator genes *CCA1* and *LHY*. The loss of function in *GI* also incurs defectiveness in light signaling to the clock. The light-regulated association of *GI* with the light-sensing F-box protein *ZEITLUPE* is responsible for dark-dependent proteasomal degradation of *TOC1*, which reduces the transcription of *CCA1* and *LHY* (Kim et al., 2007c; Mas et al., 2003). Mutational inactivation of *GI* also affects clock outputs, leading to late flowering in long days but having little or no effect in short days (Fowler et al., 1999). The *GI* protein forms a protein complex with the blue-light sensing *FLAVIN-BINDING, KELCH REPEAT, F-BOX 1* (*FKF1*), which targets and degrades *CYCLING DOF FACTOR 1* (*CDF1*), a repressor of the transcription of *CONSTANS* (*CO*) (Sawa et al., 2007). The precise timing of the expression of *CO* is necessary for daylength discrimination and photoperiodic flowering (Fig. 2A). *GI* directly promotes FT as well (Sawa and Kay, 2011).



**Fig. 2.** GIGANTEA (GI) regulates flowering in a long day (A) and salt stress (B) response. (A) GI forms a complex with FKF1, which degrades CDF1, a repressor of CO, a central activator of photoperiodic flowering. Furthermore, GI independently promotes flowering of CO through *miR172*. *miR172* targets AP2-like genes, such as *TOE1*, which negatively regulates multiple floral organ identity. SPY is considered a negative regulator of GA and positively promotes flowering during long days. (B) Salt-dependent interaction between GI and SOS2 (Kim et al., 2013). SOS2 and GI form a complex in unstressed plants. This complex prevents the interaction of SOS2 with SOS1; thus, SOS1 is kept in an inactive state. On salinity stress, the elevation of cellular  $\text{Na}^+$  triggers a salt stress-specific calcium signature, which is recognized by a calcium-binding protein, SOS3. SOS2 binds to calcium-bound SOS3, releasing the

GI protein, which then is degraded. In turn, the free SOS2/SOS3 complex activates SOS1, a  $\text{Na}^+/\text{H}^+$  antiporter, and sodium ( $\text{Na}^+$ ) ions are exported from the cells.

Another mechanism through which GI influences photoperiodic flowering involves the induction of *FT* independently from CO. This induction is accomplished by regulating *miR172* processing, which affects *miR172* abundance (Jung et al., 2007). *miR172* targets and represses AP2-like genes such as *TARGET OF EAT1 (TOE1)*, *TOE2*, and *TOE3* (Fig. 2A) (Aukerman and Sakai, 2003). *GI* and *ELF4* regulate hypocotyl growth in response to daylength in a light-phase-specific manner (Kim et al., 2012). Furthermore, GI is involved in phyB and cryptochrome signaling (Crepny et al., 2007; Huq et al., 2000; Oliverio et al., 2007). Regulating *GI* expression depending on sucrose levels is also important, suggesting a link that measures and reports metabolic status to alter or reset the circadian clock (Dalchau et al., 2011).

SPINDLY, an O-linked  $\beta$ -N-acetylglucosamine transferase that acts as a negative regulator of GA signaling, participates in protein-protein interactions with GI, thereby acting as a negative regulator of salt stress response (Kim et al., 2013; Tseng et al., 2004). This specific two-protein interaction regulates the flowering time and circadian stomatal dynamics (Fig. 2A) (Sothern et al., 2002; Tseng et al., 2004).

### Function of GI in response to salt stress

Recently, an association between GI and NaCl and/or osmotic stresses has emerged (Kim et al., 2013; Park et al., 2013) that helps in identifying the direct regulation of ionic homeostasis through GI. GI is a partner in a protein-protein interaction with the SNF1-related protein kinase SOS2, a known key element of the SOS pathway. This interaction strongly reduces or prevents the main function of SOS2, i.e., the activation of the SOS1 antiporter under normal, nonstressed growth conditions. Salt stress induces or increases proteasomal degradation of GI, thus releasing the SOS2 protein, which then interacts with the SOS3 protein (Fig. 2B). This process of SOS2 caging and release is

reflected in the corresponding phenotypes. *GI*-overexpressing plants are more salt sensitive than wild-type plants, whereas the *gi* mutants are markedly salt tolerant. Incidentally, this observation strongly supports the notion that salt-induced activation of the SOS2 kinase promotes the phosphorylation and activation of the  $\text{Na}^+/\text{H}^+$  antiporter SOS1. Thus GI introduces another player underlying the dynamic behavior of SOS2 via its stress-induced release from interaction with GI. The presence or amount of GI and its degradation associate salt stress to the clock functions, thus associating pathways previously considered unrelated.

Yet another remarkable aspect of the salt-tolerant phenotype exhibited by *gi* plants is continued growth under high salinity. This behavior appears to indicate arrest in the vegetative growth phase during stress. The plants produce many more leaves than the wild-type *Arabidopsis* and exhibit extremely late flowering. This behavior may be the result of hierarchically structured responses governing salt exclusion, salt export, and salt compartmentalization in a mode that is growth-phase specific, while at the same time influencing growth phase transitions associated to the working of the clock. An appropriate and effective stress response appears to require an evolutionary history that entrains a series of interactive signaling and response measures based on changes in the environment. Such changes may not have been essential for most plant species.

### CONCLUSION

Salinity in natural settings, such as in estuaries; intrusion of brackish water from the sea; or salinization after the depletion of fresh water in aquifers is a common terrestrial feature. In lands under cultivation, the inevitable accumulation of salts during long-term irrigation remains to be studied. Humanity's influence will, again inevitably, require that at least some food

and feed be produced on degraded soils, including saline lands. All plants likely carry the genes that must be engaged to deal with salinity, but salinity tolerance acquisition requires modifications and alterations in their genomes. Similarly, the development of control structures, which engage these genes in a meaningful way and lead to protection, appears to be lacking in many plant species that are evolved in areas in which  $\text{Na}^+$  was low.

Previous studies have led to the recognition of likely most of the important stress defense components. Most appear to be the same or are very similar components in most species. Furthermore, we have very little knowledge regarding how the many different constituent proteins are generated by only partially outlined transcriptional programs and where they are located in plant organs and cells and how they are expressed in a developmental context. Equally, we do not know the dynamics of subcellular trafficking that accompanies adaptations to a stressful environment.

However, the appearance of next-generation DNA and RNA sequencing tools has generated genome sequences from species that were adapted to stressful environments (Dassanayake et al., 2011; Ma et al., 2013; Wu et al., 2012) and sequences for species in the genus *Arabidopsis* and *A. thaliana* ecotypes adapted to different ecological niches and lifestyles (Hanikenne et al., 2013; Hollister et al., 2012; Kellermeier et al., 2013; Weigel, 2012). We can now compare entire genomes at a chromosomal resolution, and we can add in unprecedented completeness, the transcriptomes of entire plants, plant organs, and cells under every conceivable external stimulus/stress.

Several initial analyses are currently available. Dassanayake et al. (2011) and Wu et al. (2012) compared the salt tolerant extremophiles *S. parvula* and *T. salsuginea*, respectively, to the genome of *A. thaliana*, a close relative in the Brassicaceae. The results may be summarized by three statements. First, at a genome sequence level, the distinguishing character of halophytes is the presence of gene duplications in functions that support salt tolerance. In addition, translocations of genes are found in halophytes that appear to have changed their expression. It is important to state that *Arabidopsis* shows approximately as many gene duplications in total as halophytes; however, those that are retained functions in biotic and not abiotic functions of stress protection. A recent study comparing two differently salt-tolerant poplar species reported very similar gene duplication events (Ma et al., 2013). The second statement is regarding gene transcription. Halophytes generally demonstrate higher expression levels of (known) stress-relevant genes even in the absence of a stress; however, stress may lead to an extremely high additional expression that is not observed in *Arabidopsis*. Moreover, comparisons of these genomes reveal extensive sequence changes in the presumptive promoter regions of differentially expressed transcripts, although no detailed analyses have been reported to date. The final statement is regarding the changes in the protein coding regions. Although differences are documented, it is largely unknown whether such changes impart qualities that support stress tolerance; for example, one of the duplicated *HKT1* genes in *T. salsuginea* (Ali et al., 2012). A single amino acid exchange converts this cation transporter from mainly transporting  $\text{Na}^+$  in highly saline media, as observed in *A. thaliana*, to a mainly  $\text{K}^+$ -importing protein in *T. salsuginea*. In addition, belonging in this category are observations indicating coding regions with altered domain structure and differently spliced transcripts in comparison with related salt-sensitive species.

Understanding plant salinity stress defense or avoidance mechanisms is a key challenge for improving crop breeding.

Even with the progress that is currently possible, the pathways for salt exclusion, compartmentation, and efflux are exceedingly complex. Screening crops, wide crosses of crops, and their wild relatives for gene duplication and stress-relevant expression characteristics should be one way forward. Much emphasis should be placed on obtaining more detailed information regarding plant hormone synthesis, transport, and perception and regarding its associated signaling systems that orchestrate growth under stress.

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