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Salinity stress in plants: Growth, photosynthesis and adaptation review

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Abstract

Salinity is a significant abiotic stress that decreases plant growth and productivity in many parts of the world due to increased use of poor-quality water for irrigation and soil salinization. Salinity stress negatively impacts agricultural yields globally, affecting production for both subsistence and financial gain. Salt stress affects every aspect of crop growth, inhibiting plant growth and reducing the fresh and dry weight of roots, stems, and leaves. It also decreases leaf expansion and alters leaf morphology. Additionally, salt stress represses photosynthesis and disrupts plant ion homeostasis, leading to metabolic imbalances and oxidative stress. The adaptation or resistance of plants to salinity stress involves complex physiological features, metabolic pathways, and networks of molecules or genes. To develop salt-tolerant plant varieties for salt-affected areas, a comprehensive understanding of plant responses to salinity stress at various levels and an integrated approach combining molecular, physiological, and biochemical techniques are necessary. Recent research has identified many adaptive responses to salinity stress at genetic, cellular, metabolic, and physiological levels. However, the mechanisms underlying salinity tolerance are still not fully understood. In this review, we investigate the damage caused to plants by environmental salt stress and explore how plants tolerate this stress at the molecular level.

Keywords: Salinity Stress; Plant Growth; Photosynthesis; Physiological Adaptation; Salt Tolerance

1. Introduction

Salinity is one of the most significant factors limiting agricultural crop productivity, with negative impacts on germination, crop yield, and plant vigor [1]. Soil salinity is a major constraint on food production as it reduces crop yields and limits the use of previously uncultivated land. The United Nations Environment Programme estimates that salt stress affects approximately 20 percent of the world's agricultural land and 50 percent of the world's cropland [2].

Environmental abiotic stress factors, particularly drought and soil salinity, are major causes of declining agricultural yields worldwide [3, 4]. A significant challenge for global agriculture is to increase food crop production by 70% to feed about 2.3 billion people by 2050 [5].

Globally, salt has affected over 45 million hectares of irrigated land, and high salinity levels in the soil result in the loss of 1.5 million hectares of land each year [1]. High salinity impacts plants in various ways, including water stress, ion exposure, nutritional disorders, membrane disorganization, oxidative stress, metabolic cycle alterations, reduced cell division and expansion, and genotoxicity [6-8]. These effects collectively impair plant growth, production, and survival. Major processes such as photosynthesis, protein synthesis, and energy and lipid metabolism are disrupted during the onset and progression of salt stress [9]. Initial exposure to salinity causes water stress, reducing leaf expansion. The osmotic effects of salinity are evident immediately after salt application and can persist, leading to impaired cell expansion, cell division, and stomatal closure [7,10].

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Long-term exposure to salinity induces ionic stress, which can lead to premature senescence of adult leaves, thereby increasing the photosynthetic area available for continued growth [11]. Excess sodium and chloride can adversely affect plant enzymes, cause cell swelling, and result in reduced energy production and other physiological changes [12]. Ionic stress leads to premature apoptosis of older leaves and toxicity symptoms, such as chlorosis and necrosis, in mature leaves due to high Na⁺ levels affecting protein synthesis and enzyme activity [6,7,13,14]. Most plants have developed mechanisms to either remove excess salt from their cells or tolerate its presence. As salt accumulates in the root zone, it negatively impacts plant growth through water deficiency (osmotic stress), ion toxicity, and ion imbalance (ionic stress), or a combination of these factors [15]. This review primarily discusses salinity stress and its effects on plants. A fundamental understanding of salt stress and its impact on plants is essential for analyzing plant responses to salinity and for developing strategies to mitigate its effects, thereby improving the performance of species crucial to human health and sustainable agriculture.

2. Salinity causes

Salinity can be classified into primary and secondary categories, depending on the origin of the cause. Primary salinity originates from natural sources such as salt marshes, salt lakes, tidal swamps, or naturally occurring salt deposits. Secondary salinity, on the other hand, results from human activities such as urbanization and agriculture (both irrigated and dryland farming).

2.1. The factors responsible for salinity are as follows:

2.1.1. Primary salinity

- Weathering of rocks
- Capillary rise of shallow brackish groundwater
- Windblown sand containing salt from the sea
- Seawater intrusion along the coast
- Impeded drainage

2.1.2. 2- Secondary Salinity (due to human activity)

- Implementation of irrigation without an adequate drainage system
- Overuse of fertilizers
- Industrial effluents
- Removal of natural plant cover
- High water table and use of poor-quality water for irrigation
- Inundation with salt-rich waters

3. Types of salinity

- Sodic
- Saline

The main differences between these two types of salinity are the origin of the anions and the soil's pH. Studies show that sodic soils, which have a pH above 8.5, are characterized by carbonate or bicarbonate ions. In contrast, saline soils are dominated by chloride or sulfate ions and have a pH below 8.5. Some plants thrive in coastal areas affected by salt, such as the shores of backwater lakes and marshy lands. Halophytes are crops that thrive well in high salt concentrations. Many plants, however, which cannot tolerate even 10% seawater, are classified as glycophytes or non-halophytes [16-20].

4. The effect of salinity on plants

There are several aspects to the toxic effects of salt stress. Excessive uptake of Na⁺ and Cl⁻ interferes with many intracellular metabolic processes. High concentrations of salt in the soil induce osmotic pressure, reducing soil water absorption [1]. Elevated Na⁺ concentrations inhibit nutrient absorption, and the combined effects of ion toxicity and osmotic stress also cause metabolic and oxidative stress imbalances [2]. The toxic effects of salt stress can lead to plant death or reduced production capacity. Nearly all plants exhibit growth inhibition under salt stress, with the degree of growth repression and the critical concentration leading to death varying among species. Salt stress affects nearly every

aspect of biological processes, including plant growth, photosynthesis, protein synthesis, and protein and phospholipid metabolism.

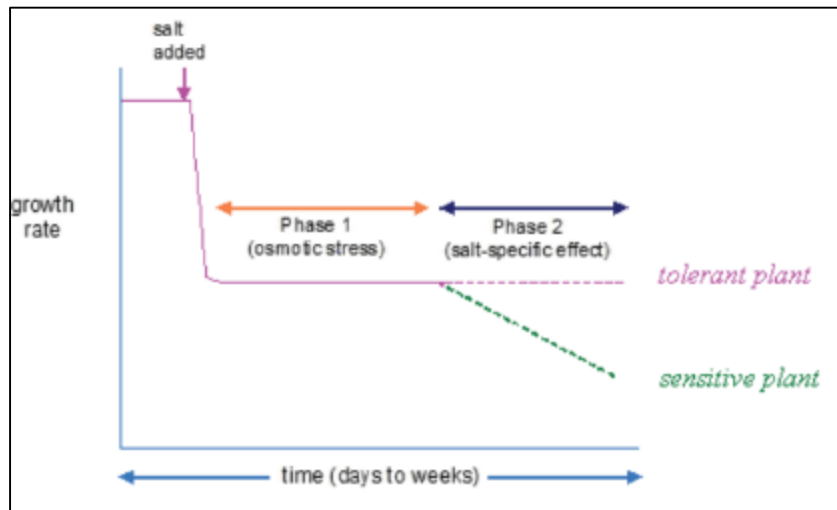


Figure 1 Scheme of the two-phase growth response to salinity.[22]

Soil salinity is a major factor limiting agricultural crop yields, jeopardizing agriculture’s capacity to sustain the burgeoning human population [1, 10, 18]. At low salt concentrations, yields may be only slightly affected or not affected at all [21]. However, as concentrations increase, yields may fall to zero, as most crops, including glycophytes (which include most crop plants), do not thrive at high salt concentrations and are severely inhibited or even killed by 100-200 mM NaCl. This is because these plants evolved under low salinity conditions and lack salt tolerance [13]. In contrast, halophytes can tolerate salinity levels exceeding 300-400 mM NaCl. These plants have developed specific salt tolerance mechanisms during their phylogenetic adaptation, enabling them to grow in salinized soils in coastal and arid regions. Depending on their salt tolerance, these plants can be classified as either obligate or facultative halophytes. Obligate halophytes exhibit low morphological and taxonomic diversity and can grow in environments with up to 50% seawater. Facultative halophytes, on the other hand, are found in less saline environments along the boundary between saline and non-saline areas and have a broader physiological scope, allowing them to cope with both saline and non-saline conditions [9]. Measurements of ion content in salt-stressed plants show that halophytes accumulate salts, whereas glycophytes tend to exclude them [8].

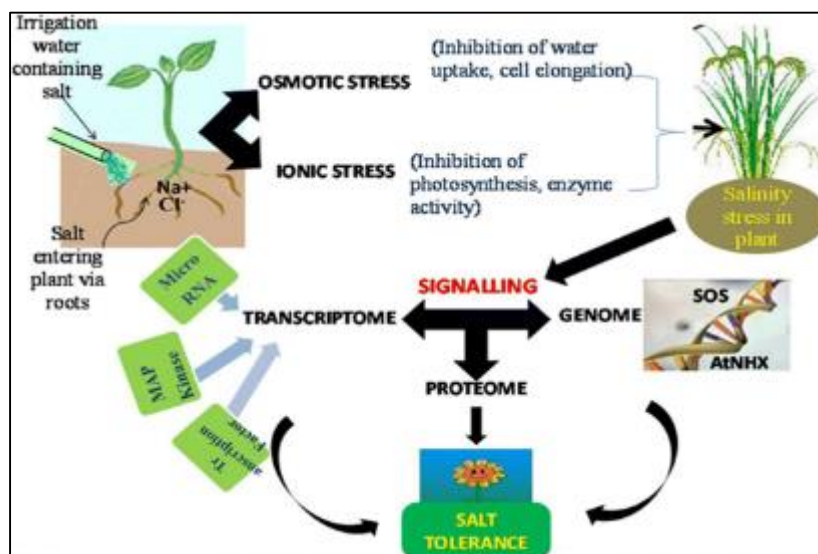


Figure 2 Effect of salinity stress on plants

High salinity affects plants in two main ways: it disrupts the roots' ability to extract water due to high salt levels in the soil, and it causes harmful effects within the plant itself, impairing various physiological and biochemical processes,

such as nutrient uptake and assimilation [1,6,7,22]. These effects collectively minimize plant growth, production, and survival. Munns (1995) proposed a two-phase model to explain the osmotic and ionic effects of salt stress [22] (Figure 2). The frequency at which salt reaches toxic levels in leaves varies between salt-sensitive and salt-resistant plants. Depending on the species and salinity levels, this time scale can range from days to weeks or even months.

During Phase 1, the osmotic effect of the saline solution reduces development outside the roots for both plant types. In Phase 2, old leaves in salt-sensitive plants die, which can increase the plant's photosynthetic capacity and further affect growth.

In the initial osmotic phase, which begins as soon as the salt concentration around the roots reaches a threshold level, it becomes more difficult for the roots to extract water, causing a significant drop in shoot growth. Stomatal closure is an immediate response to this osmotic effect, which also reduces ion flux to the shoots. However, this is not a practical long-term tolerance strategy for managing the water potential difference between the atmosphere and leaf cells and for maintaining carbon fixation [6]. Shoot growth is more susceptible to salt-induced osmotic pressure compared to root growth, possibly because a reduction in the leaf's production area relative to root growth helps minimize the plant's water use, allowing it to conserve soil moisture and avoid high soil salt concentrations [1]. This often results in reduced shoot growth, characterized by decreased leaf area and stunted shoots [23]. Growth inhibition in salt-sensitive leaves also involves the inhibition of Ca^{2+} symplasty and xylem function in the roots [15]. The final size of the leaf depends on both cell division and cell elongation. Leaf initiation, which is governed by cell division, has been shown to be unaffected by salt stress in sugar beet, but leaf extension is found to be salt-sensitive [24], depending on the Ca^{2+} status. Additionally, salt-induced inhibition of essential mineral nutrient absorption, such as K^+ and Ca^{2+} , further hinders root cell growth [12], particularly affecting the expansion of root tips.

The second phase, ion-specific, involves the accumulation of ions, particularly Na^+ , in the leaf blades. Na^+ accumulates in the leaves rather than in the roots after being transported via the transpiration stream [7]. This accumulation becomes toxic, especially in older leaves that are no longer expanding and therefore do not dilute the incoming salt as young leaves do. If the rate of leaf death exceeds the rate of new leaf formation, the plant's photosynthetic ability may no longer meet the carbohydrate needs of the young leaves, further reducing their growth rate [1]. Na^+ accumulation affects photosynthetic components, such as enzymes, chlorophylls, and carotenoids in photosynthetic tissues [25]. In salt-sensitive plants, reduced photosynthetic activity may also increase the production of reactive oxygen species (ROS). Normally, antioxidant mechanisms quickly remove ROS, but salt stress can impair this removal [27]. ROS signaling is integral to the salinity acclimation response, playing a dual role in plant response to abiotic stresses as both toxic by-products and essential signals for stress response pathways, including calcium, hormone, and protein phosphorylation-mediated networks [27]. ABA (abscisic acid) plays a crucial role in the plant response to salinity, and ABA-deficient mutants perform poorly under salt stress [28]. Salt stress signaling by Ca^{2+} and ABA mediates the expression of late embryogenesis abundant (LEA)-type genes, including stress-responsive components like DRE/C-repeat (CRT) class genes. Activating LEA-type genes may reflect pathways for repairing damage [29].

The modulation of LEA gene expression by salt and osmotic stress is mediated by both ABA-dependent and ABA-independent signaling pathways. Both pathways utilize Ca^{2+} signaling during salinity to trigger LEA gene expression. It has been shown that ABA-dependent and ABA-independent transcription factors can intersect synergistically to enhance the response and develop stress tolerance [30].

4.1. The effect of salt stress on plant development

Salt stress affects all facets of plant growth, from germination to vegetative growth to reproductive development. Sodium is an important microelement for plant growth, but while low salt concentrations can promote plant growth and increase biomass, high salt concentrations inhibit growth and reduce the fresh and dry weight of roots, stems, and leaves [31, 32]. For example, the fresh weight of *Alhagi pseudoalhagi* increased under low salt stress (50 mM NaCl), but decreased with higher concentrations (100 and 200 mM NaCl). Excessive NaCl concentration also resulted in decreased biomass in cotton roots, shoots, and leaves [33].

Many crops are sensitive to soil salinity. Salt stress can inhibit the growth of plant tissues and organs, shorten the flowering period, accelerate aging, and cause the premature senescence and shedding of mature leaves [34]. The most immediate response to high salt concentration is a reduction in the leaf expansion rate [35]. For instance, 100 mM NaCl can shorten the leaf region in sorghum and decrease the cell growth rate in this area [36]. Salt stress can also delay the development of the main stem in wheat by 18 days and advance reproductive structure formation. The flowering time of salt-stressed wheat is significantly earlier compared to untreated wheat, indicating that salt stress can speed up plant growth. Additionally, salt stress can reduce the number of phyllopodia and leaves [37].

Salt stress can also lead to dry material deposition and slow down cell wall maturation [38]. It can alter leaf morphology by increasing the thickness of the leaf epidermal cells, mesophyll cells, and palisade cells [39]. Conversely, NaCl-induced salt stress can decrease the thickness of leaf epidermal cells and intercellular spaces [40]. In potatoes, salt stress results in rounded leaf cells, reduced cell spaces, and fewer chloroplasts [41]. Additionally, salt stress can reduce leaf surface area and cause stomata to open [42].

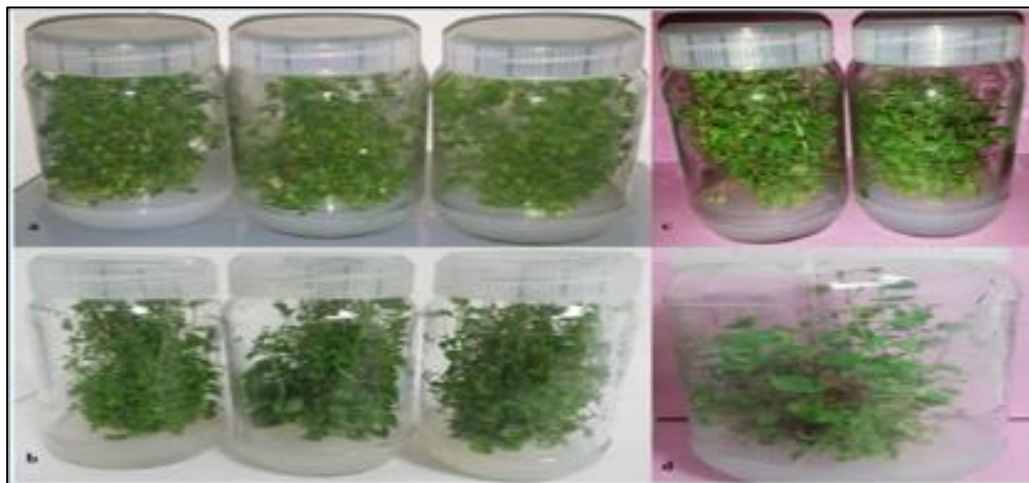


Figure 3 Effect of salinity stress on plant growth and development at different NaCl concentrations: 25 (a), 50 (b), 75 (c) and 100mM (d) after 30 days of culture

4.2. The effect of salt stress on plant photosynthesis

Salt stress impacts plant photosynthesis both in the short term and long term. The short-term effects occur within a few hours to one or two days of salt exposure, leading to a critical response where carbon assimilation is halted completely. In the long term, after a few days of exposure to salt stress, carbon assimilation naturally decreases due to salt accumulation in the leaves [34, 43]. Numerous studies have shown that salt stress suppresses photosynthesis [42, 44, 45]. However, some research indicates that under certain salt conditions, photosynthesis levels may not decrease and might even be slightly higher than in untreated plants [42, 46]. For example, in *Alhagi pseudoalhagi*, the rate of carbon dioxide assimilation was slightly higher under low salt stress. At 100 mM NaCl, the assimilation rate was unaffected, but at 200 mM NaCl, the rate dropped to 60% of that in untreated plants. Similarly, stomatal behavior mirrored the carbon dioxide assimilation rate. Additionally, the carbon dioxide concentration in the plant's intercellular space was lower compared to the control group [46]. In *Bidens parviflora*, the carbon dioxide assimilation rate increased under low salt stress but decreased under high salt stress [40].

Salt treatment also disrupts the thylakoid structure of chloroplasts. The number and size of plastids increase, while starch content decreases [47, 48]. In salt-treated potatoes, chloroplast expansion and thylakoid membrane changes were observed [49]. In salt-treated tomato leaves, chloroplasts aggregated, and no grana or thylakoid structures were present [50]. Similarly, salt treatment altered the ultra-microstructure of chloroplasts in *Eucalyptus microcorys*, leading to increased starch granule production [51].

4.3. The effect of salt stress on plant ion homeostasis

Excessive NaCl has inhibited the synthesis of other nutrient ions, contributing to K^+ deficiency. An increase in NaCl in the soil leads to elevated levels of cellular Na^+ and Cl^- , while decreasing Ca^{2+} , K^+ , and Mg^{2+} [52, 53]. In broad beans, salt stress increases the content of Na^+ , Ca^{2+} , and Cl^- while decreasing the K^+/Na^+ ratio [54]. In *U. fasciata*, increased Na^+ and Cl^- levels lead to proline accumulation, while proline dehydrogenase (PDH) activity and soluble Ca^{2+} content decrease [55].

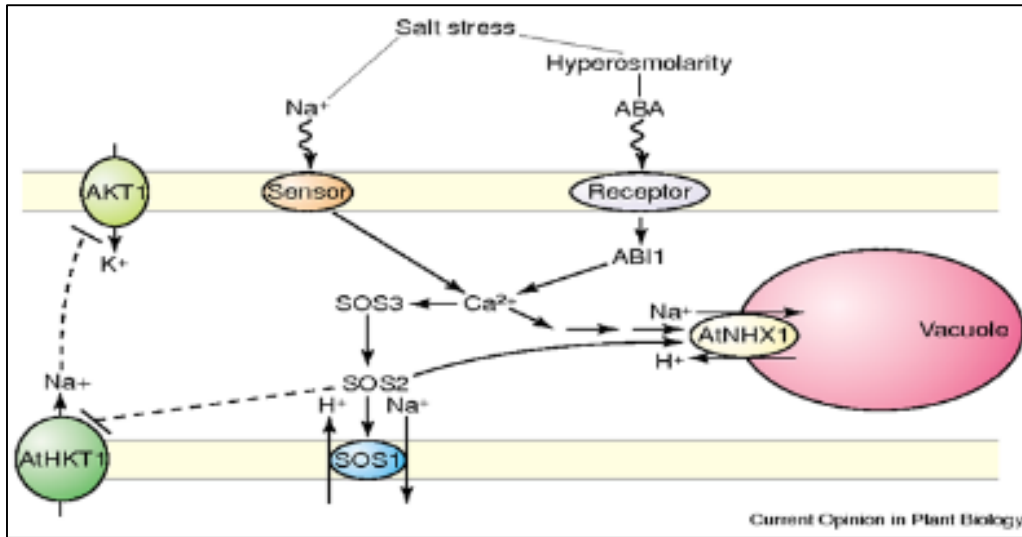


Figure 4 Regulation of ion homeostasis under salt stress

4.4. Molecular mechanisms of plant salt stress tolerance

Tolerance to salt stress in plants involves regulating multiple physical and biochemical responses. Several proteins and metabolites play a role in this process, which involves complex gene network communication. Different plants exhibit varying responses and mechanisms for adaptation.

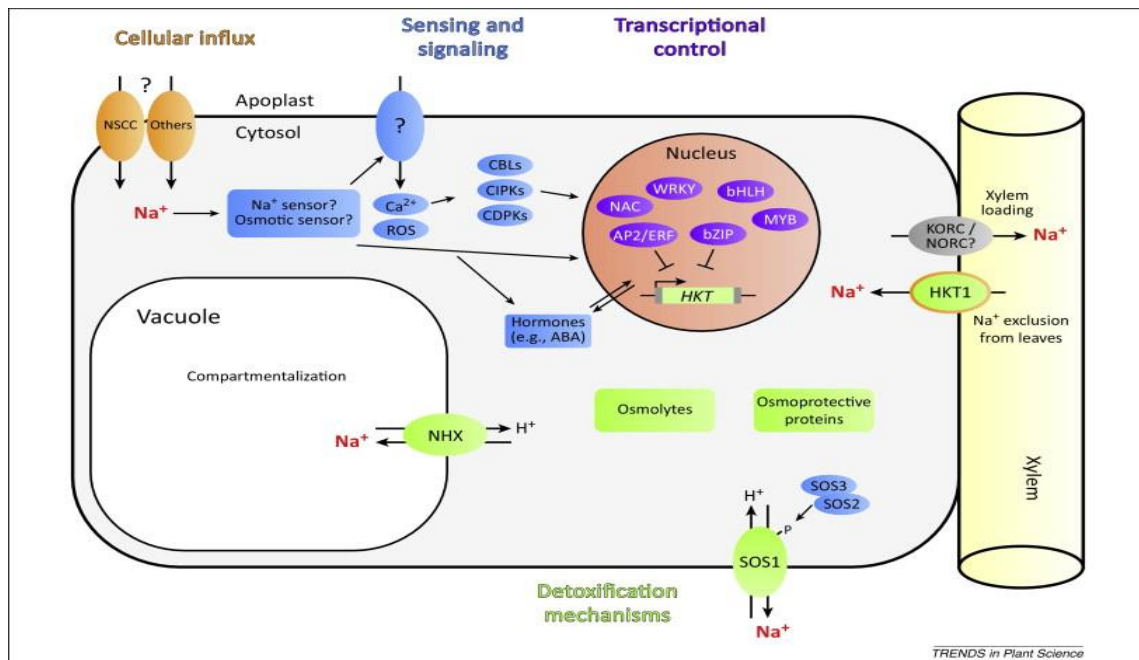


Figure 5 Mechanisms of plant salt tolerance

4.5. The salt-sensitive pathway

High salt stress levels can lead to Na⁺ toxicity, causing osmotic and oxidative stress that impairs plant growth and development. Under salt stress, plant cells can either export Na⁺ to reduce toxicity or sequester Na⁺ in the vacuole to maintain ion homeostasis. The genes Salt Overly Sensitive (SOS1, SOS2, and SOS3) are critical components of the SOS signal transduction pathway, which was identified through genetic research [56]. SOS1 encodes a Na⁺/H⁺ antiporter with 10-12 transmembrane domains [57]. It functions as a Na⁺ detector and helps to export Na⁺ out of the cell. SOS2 is a protein kinase with Ser/Thr residues, featuring a C-terminal regulatory domain and an N-terminal catalytic domain [58]. SOS3 is a calcium-binding protein located in the cytoplasm that detects transient increases in Ca²⁺ levels induced by salt stress [59, 60]. SOS3 then activates SOS2, which subsequently phosphorylates SOS1 to enhance Na⁺ extrusion

[61, 62]. Mutations in this pathway increase plant sensitivity to salt, while overexpression of SOS1 or activation of SOS2 can improve salt tolerance [63, 64].

Salt stress also increases ABA levels in the cell. ABA signaling can modulate the SOS pathway through SOS2. Yeast two-hybrid assays have shown that SOS2 binds to ABA Insensitive2 (ABI2), but not to the ABI2 mutant [65]. Plants with the *abi2* mutation are more susceptible to salt stress. Additionally, salt stress can induce oxidative stress. Research has demonstrated that SOS1 interacts with the RCD1 (radical-induced cell death 1) protein, an oxidative stress transcription regulator in Arabidopsis. Under salt or oxidative stress, RCD1 is present in both the nucleus and the cytoplasm, whereas it is absent from the nucleus under normal conditions. Mutants lacking SOS1 and RCD1 are more prone to oxidative and salt stress [66].

Excessive Na⁺ in the cytosol can also impede potassium absorption. Salt-sensitive mutants often lack K⁺. Screening for *sos3* suppressors led to the identification of AtHKT1, a Na⁺ transporter that helps to transport Na⁺ into cells. The AtHKT1 mutant fails to compensate for the salt-sensitive phenotype of other mutants. Another effective strategy for managing cytoplasmic Na⁺ is transporting it into the vacuole. AtNHX1, an Na⁺/H⁺ antiporter, facilitates Na⁺ uptake into the vacuole. Salt stress induces the expression of AtNHX1, as well as its homologues AtNHX2 and AtNHX5, which also contribute to Na⁺ sequestration in the vacuole [68-70].

4.6. Signal path of MAPK

There are three key components in the typical mitogen-activated protein kinase (MAPK) signaling pathway: MAPKKK, MAPKK, and MAPK. In plants, MAPK signaling plays a critical role in development, cell division, hormone regulation, and tolerance to both biotic and abiotic stresses [71]. Salt stress can activate the MAPK protein SIMK, while SIMKK can activate SIPK. Additionally, salt stress enhances MAPK activation [72], leading to increased expression and kinase activity of various MAPKs. Under salt stress, AtMPK6 and AtMPK4 are activated [73]. These two MAPKs are activated by the phosphorylated upstream kinase AtMKK2. The *mkk2* mutant is particularly susceptible to salt stress [74]. Studies have shown that MPK6 can bind to and phosphorylate SOS1. Furthermore, research indicates that phosphatidic acid binds to MPK6 following salt application [75]. MPK6 immunoprecipitated from Arabidopsis thaliana may increase the phosphorylation of SOS1 under salt stress, along with an increase in phosphatidic acid [76].

4.7. Other kinase of protein

Protein kinases are essential molecules *in vivo* for signal transmission. In addition to mitogen-activated protein kinases, which play a significant role in salt stress signal transduction, many other protein kinases are critical in the signal transduction network under salt stress. Calcium-dependent protein kinase (CDPK) acts as an upstream signal that uses calcium concentration as a signal transduction factor. CDPK can sense calcium levels by binding downstream proteins to calcium ions and phosphorylating them to convert calcium signals into phosphorylated signals. In Arabidopsis, both high salinity and drought stress can induce AtCDPK1 and AtCDPK2 [77]. One salt-induced protein, McCDPK, found in the nucleus, may be involved in transcriptional regulation [78]. Additionally, a class of proteins on the cell membrane can sense external signals and participate in intracellular signaling. These proteins are classified as receptor-like protein kinases (RPKs). RPK1 is a receptor-like protein kinase on the Arabidopsis cell membrane, and its expression can be induced by high salinity or drought, indicating its involvement in the plant's response to salt stress [79]. AtGSK1 is another salt-induced protein kinase, a glycogen synthase kinase (GSK). Overexpression of AtGSK1 enhances Arabidopsis resistance to salt stress [80]. Studies have shown that AtGSK1 can induce the expression of certain salt-induced genes [81]. GRIK1, an upstream kinase of SnRK, can phosphorylate SOS2 *in vitro*. Mutants of GRIK1 are also more susceptible to high salt conditions [82].

4.8. Abscisic acid (ABA) signaling in moderate salt stress

Abscisic acid (ABA) is an essential plant hormone that plays a key role in plant growth and development. It is best known for its role in plant drought stress resistance, but ABA also plays a significant role in salt stress tolerance. Salt stress can cause the accumulation of ABA in certain tissues. For example, in maize, the concentration of ABA in salt-stressed roots may be ten times higher than in leaves [83]. Osmotic stress resulting from high salinity also leads to the synthesis and accumulation of ABA, which helps regulate the osmotic stress. By controlling stomatal closure, ABA maintains cellular water balance and regulates the expression of genes involved in osmotic stress responses [84,85]. Specifically, ABA modulates stomatal pore closure and downstream gene expression by regulating Ca²⁺ concentration [86,87].

ABA also regulates osmotic stress-related genes and ion transporters under salt stress. It activates the stress response genes RD29A and KIN2 [88] and may induce the expression of AtPLC1. Studies on transgenic plants expressing an antisense strand of AtPLC1 show that ABA induces the expression of RD22, RD29A, and KIN2 through AtPLC1 [89].

Genetic screening using the RD29A::LUC reporter gene has improved the identification of abiotic stress mutants and ABA signaling pathway mutants in *Arabidopsis* [90]. The expression of stress response genes under salt stress, such as RD29A, COR15A, COR47, RD22, and P5CS, was reduced in the *los5* and *los6* mutants. However, exogenous ABA application could restore RD29A::LUC expression induced by salt stress in these mutants. Cloning of the LOS5 and LOS6 genes revealed that they correspond to ABA3 and ABA1 alleles, respectively [91,92]. During germination, the ABA-deficient mutants *los5* and *los6* were more tolerant to salt stress, but during vegetative growth, *los5* was hypersensitive to salt stress [91,93]. These findings indicate that ABA mediates the expression of salt stress-responsive genes. The vacuolar Na⁺/H⁺ transporter AtNHX1 is upregulated by both salt stress and ABA. However, its expression is decreased in the ABA-deficient mutants *aba2-1* and *aba3-1*, but not in salt-deficient mutants. The mutant *abi1-1* showed reduced ABA content and salt-induced AtNHX1 expression, while *abi2-1* did not. AtNHX1 also contains ABRE elements, suggesting that the upregulation of AtNHX1 transcription under salt stress partly depends on ABA synthesis and signaling, which involves ABI1 [94]. The quantitative trait loci (QTL) for salt tolerance during germination differ from those at the seedling stage, indicating that the mechanisms of salt tolerance vary between these stages [95,96]. The inhibition of seed germination under salt stress is primarily due to the inhibitory effects of ABA [32].

4.9. Studies of other mutants related to salt stress

In addition to research on the previously mentioned kinases and their pathways, many other mutants linked to salt stress have been identified, although their precise roles in salt stress tolerance remain unclear. The *sos4* and *sos5* mutants were identified through screening for hypersensitive salt mutants, both of which exhibit significantly shorter root lengths than wild-type plants under salt stress. SOS4 encodes a pyridoxal kinase involved in the formation of pyridoxal 5-phosphate, a cofactor for many important enzymes. By producing pyridoxal 5-phosphate, SOS4 may contribute to plant salt tolerance [94]. SOS5 encodes a cell surface-adhering protein, and the *sos5* mutant is salt-sensitive due to the lack of the normal expansion of cells that SOS5 typically promotes [97].

To study salt tolerance, Ren et al. investigated the differences in salt stress sensitivity between *Landsberg erecta* (Ler), a salt- and ABA-sensitive ecotype of *Arabidopsis thaliana*, and *Shakdara* (Sha), an ecotype that is not sensitive to salt or ABA. Using quantitative trait locus (QTL) mapping, they cloned a salt stress- and ABA-induced gene, RAS1. Overexpression of this gene improved plant tolerance to both ABA and salt stress [98]. Salt stress leads to the accumulation of reactive oxygen species (ROS) in plant cells, which requires the plant to neutralize the excess ROS through various enzymes [99,100]. RSA3 is a bifunctional protein that can bind and stabilize cytoskeletons, thereby minimizing oxidative damage during salt stress [101].

5. Conclusion

Salt is essential to all forms of earthly life, including humans, plants, and bacteria. Modern biology shows that salt controls animal blood flow and stress responses, mediates plant osmosis, and acts as a vital messenger in cellular signal transduction. However, while these elements are crucial in moderate amounts, they become detrimental to life when they exceed appropriate levels. Salt stress is one of the major abiotic stresses that negatively impacts plant growth and reduces crop yield.

The issue of salinity is becoming increasingly severe worldwide. Over half a billion hectares of land are not being used effectively for crop production due to salinity. Thus, there is a pressing need to improve saline soils to transform them into highly productive and functional land-use systems, thereby addressing current global food security challenges.

In this study, we examined the damaging effects of environmental salt stress on plants and the molecular mechanisms that plants use to tolerate salt stress. Current research has significantly advanced our understanding of plant salt resistance mechanisms. We discussed various signaling pathways, including certain identified elements and several common determinants of salt tolerance, which are part of the complex signaling network that plants use to cope with salt stress. Other factors, such as proteins, signal molecules, non-coding RNAs, and epigenetic regulation, are also involved but were not covered in this study. Nevertheless, further research on these components of the signaling pathways is necessary to fully comprehend the mechanisms of plant stress tolerance.

References

- [1] Munns, R., & Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 59, 651-681.
- [2] Flowers, T.J. and Yeo, A.R. (1995) Breeding for salinity resistance in crop plants: where next? *Aust. J. Plant Physiol.* 22, 875-884.

- [3] Boyer JS. Plant productivity and environment. *Science*. 1982; 218: 443±448. <https://doi.org/10.1126/science.218.4571.443> PMID: 17808529
- [4] Bartels D, Sunkar R. Drought and salt tolerance in plants. *Crit Rev Plant Sci*. 2005; 24: 23±58.
- [5] FAO, High Level Expert Forum—How to Feed the World in 2050, Economic and Social Development, Food and Agricultural Organization of the United Nations, Rome, Italy, 2009.
- [6] Hasegawa, P. M., Bressan, R. A., Zhu, J. K., & Bohnert, H. J. (2000). Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology*, 51, 463-499.
- [7] Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, Cell & Environment*, 25 (2), 239-250.
- [8] Zhu, J.-K. (2007). *Plant Salt Stress*: John Wiley & Sons, Ltd.
- [9] Parida, A. K., & Das, A. B. (2005). Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety*, 60 (3), 324-349.
- [10] Flowers, T. J. (2004). Improving crop salt tolerance. *Journal of Experimental Botany*, 55 (396), 307-319.
- [11] Cramer, G. R., & Nowak, R. S. (1992). Supplemental manganese improves the relative growth, net assimilation and photosynthetic rates of salt-stressed barley. *Physiologia Plantarum*, 84 (4), 600-605.
- [12] Larcher, W. (1980). *Physiological plant ecology*. In 2nd totally rev. edition ed., (pp. 303). Berlin and New York: Springer-Verlag.
- [13] Munns, R., & Termaat, A. (1986). Whole-Plant Responses to Salinity. *Functional Plant Biology*, 13(1), 143-160.
- [14] Bohnert, H. J. (2007). *Abiotic Stress*: John Wiley & Sons, Ltd.
- [15] Läuchli A, Grattan SR (2007) Plant Growth and Development Under Salinity Stress Advances. 1-32 p. In: Jenks MA et al. (Eds.). *Molecular Breeding Toward Drought and Salt Tolerant Crops*. pp. 285-315. (Eds.): M.A. Jenks, P.M. Hasegawa and S.M. Jain. Springer, Dordrecht, Netherlands.
- [16] Gorham J (1995) Mechanism of salt tolerance of halophytes. In: Choukr Allah CR, Malcolm CV, Handy A (eds) *Halophytes and biosaline agriculture*. Marcel Dekker, New York, pp 207-223.
- [17] Cherian S, Reddy MP, Pandya JB (1999) studies on salt tolerance in *Avicennia marina* (Forstk.) Vierh: effect of NaCl salinity on growth, ion accumulation and enzyme activity. *Indian J Plant Physiol* 4:266-270.
- [18] Pardia AK, Das AB (2005) Salt tolerance and salinity effect on plants: a review. *Ecotoxicol Environ Saf* 60:324-349.
- [19] Mane AV, Deshpande TV, Wagh VB, Karadge BA, Samant JS (2011) A critical review on physiological changes associated with reference to salinity. *Inter J Environ Sci* 1:1192-1216.
- [20] Yadav D, Irfan M, Ahmad A, Hayat S (2011) Cause of salinity and plant manifestation to salt stress: a review. *J Environ Biol* 32:667-685.
- [21] Maggio, A., Hasegawa, P. M., Bressan, R. A., Consiglio, M. F., & Joly, R. J. (2001). *Review*: Unravelling the functional relationship between root anatomy and stress tolerance. *Functional Plant Biology*, 28(10), 999-1004.
- [22] Munns, R., Schachtman, D., & Condon, A. (1995). The Significance of a Two-Phase Growth Response to Salinity in Wheat and Barley. *Functional Plant Biology*, 22(4), 561-569.
- [23] Läuchli, A., & Epstein, E. (1990). Plant responses to saline and sodic conditions. In K. K. Tanji (Ed.), *Agricultural salinity assessment and management*, (pp. 113-137). New York: American Society of Civil Engineers.
- [24] Papp, J. C., Ball, M. C., & Terry, N. (1983). A comparative study of the effects of NaCl salinity on respiration, photosynthesis, and leaf extension growth in *Beta vulgaris* L. (sugar beet). *Plant, Cell & Environment*, 6(8), 675-677.
- [25] Davenport, R., James, R., Zakrisson-Plogander, A., Tester, M., & Munns, R. (2005). Control of Sodium Transport in Durum Wheat. *Plant Physiology*, 137, 807-818.
- [26] Allan, A. C., & Fluhr, R. (1997). Two Distinct Sources of Elicited Reactive Oxygen Species in Tobacco Epidermal Cells. *Plant Cell*, 9, 1559-1572.
- [27] Miller, G. A. D., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. O. N. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, Cell & Environment*, 33(4), 453-467.

- [28] Xiong, L., Gong, Z., Rock, C. D., Subramanian, S., Guo, Y., Xu, W., Galbraith, D., & Zhu, J.-K. (2001). Modulation of Abscisic Acid Signal Transduction and Biosynthesis by an Sm-like Protein in Arabidopsis. *Developmental cell*, 1(6), 771-781.
- [29] Xiong, L., Schumaker, K. S., & Zhu, J.-K. (2002). Cell Signaling during Cold, Drought, and Salt Stress. *The Plant Cell Online*, 14(suppl 1), S165-S183.
- [30] Shinozaki, K., & Yamaguchi-Shinozaki, K. (2000). Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. *Current Opinion in Plant Biology*, 3(3), 217-223.
- [31] Munns R (2002) Comparative physiology of salt and water stress. *Plant Cell Environ* 25(2): 239-250.
- [32] Chinnusamy V, Zhu J, Zhu JK (2006) Salt stress signaling and mechanisms of plant salt tolerance. *Genet Eng* 27: 141-177.
- [33] AliDinar HM, Ebert G, Ludders P (1999) Growth, Chlorophyll Content, Photosynthesis and Water Relations in Guava (*Psidium guajava* L.) Under Salinity and Different Nitrogen Supply. *Garten bauwissens chaft* 64(2): 54-59.
- [34] Chartzoulakis K, Klapaki G (2000) Response of two greenhouse pepper hybrids to NaCl salinity during different growth stages. *Scientia Horticulturae* 86(3): 247-260.
- [35] Meloni DA, Oliva MA, Ruiz HA, Martinez CA (2001) Contribution of proline and inorganic solutes to osmotic adjustment in cotton under salt stress. *Journal of Plant Nutrition* 24(3) 599-612.
- [36] Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. *Eco toxicol Environ Saf* 60(3): 324-349.
- [37] Wang Y, Nii N (2000) Changes in chlorophyll, ribulose biphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in *Amaranthus tricolor* leaves during salt stress. *The Journal of Horticultural Science and Biotechnology* 75(6): 623-627.
- [38] Bernstein N, Lauchli A, Silk WK (1993) Kinematics and dynamics of sorghum (*Sorghum bicolor* L.) leaf development at various Na/Ca salinities (I. Elongation growth). *Plant Physiology* 103(4): 1107-1114.
- [39] Grieve C, Francois L, Maas E (1994) Salinity affects the timing of phasic development in spring wheat. *Crop science* 34(6): 1544-1549.
- [40] Taleisnik E, Rodríguez AA, Bustos D, Erdei L, Ortega L, et al (2009) Leaf expansion in grasses under salt stress. *J Plant Physiol* 166(11): 1123-1140.
- [41] Longstreth DJ, Nobel PS (1979) Salinity effects on leaf anatomy: consequences for photosynthesis. *Plant Physiol* 63(4): 700-703.
- [42] Parida AK, Das A, Mitra B (2004) Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove, *Bruguiera parviflora*. *Trees* 18(2): 167-174.
- [43] Bruns S, Hecht Buchholz C (1990) Light and electron microscope studies on the leaves of several potato cultivars after application of salt at various development stages. *Potato Research* 33(1): 33-41.
- [44] Romero Aranda R, Soria T, Cuartero J (2001) Tomato plant-water uptake and plant-water relationships under saline growth conditions. *Plant Sci* 160(2): 265-272.
- [45] Munns R, Termaat A (1986) Whole-plant responses to salinity. *Functional Plant Biology* 13(1): 143-160.
- [46] Chaudhuri K, Choudhuri M (1997) Effects of short-term NaCl stress on water relations and gas exchange of two jute species. *Biologia plantarum* 40(3): 373-380.
- [47] Kao WY, Tsai HC, Tsai TT (2001) Effect of NaCl and nitrogen availability on growth and photosynthesis of seedlings of a mangrove species, *Kandelia candel* Druce. *Journal of plant physiology* 158(7): 841-846.
- [48] Kurban H, Saneoka H, Nehira K, Adilla R, Premachandra GS, et al. (1999) Effect of salinity on growth, photosynthesis and mineral composition in leguminous plant *Alhagi pseudoalhagi* (Bieb.). *Soil science and plant nutrition* 45(4): 851-862.
- [49] Hernandez J, Olmos E, Corpas F, Sevilla F, Del Rio L (1995) Salt-induced oxidative stress in chloroplasts of pea plants. *Plant Science* 105(2): 151-167.
- [50] Hernandez J, Campillo A, Jimenez A, Alarcon J, Sevilla F (1999) Response of antioxidant systems and leaf water relations to NaCl stress in pea plants. *The New Phytologist* 141(2): 241-51.

- [51] Mitsuya S, Takeoka Y, Miyake H (2000) Effects of sodium chloride on foliar ultrastructure of sweet potato (*Ipomoea batatas* Lam.) plantlets grown under light and dark conditions in vitro. *Journal of plant physiology* 157(6): 661-667.
- [52] Khavari Nejad R, Mostofi Y (1998) Effects of NaCl on photosynthetic pigments, saccharides, and chloroplast ultrastructure in leaves of tomato cultivars. *Photosynthetica* 35(1): 151-154.
- [53] Keiper F, Chen D, De Filippis L (1998) Respiratory, photosynthetic and ultrastructural changes accompanying salt adaptation in culture of *Eucalyptus microcorys*. *Journal of Plant Physiology* 152(4-5): 564-573.
- [54] Khan MA, Ungar IA, Showalter AM (1999) Effects of salinity on growth, ion content, and osmotic relations in *Halopyrum mucronatum* (L.) Stapf. *Journal of Plant Nutrition* 22(1): 191-204.
- [55] Khan MA, Ungar IA, Showalter AM (2000) Effects of sodium chloride treatments on growth and ion accumulation of the halophyte *Haloxylon recurvum*. *Communications in Soil Science and Plant Analysis* 31(17-18): 2763-2774.
- [56] Gadallah M (1999) Effects of proline and glycinebetaine on *Vicia faba* responses to salt stress. *Biologia plantarum* 42(2): 249-257.
- [57] Lee TM, Liu CH (1999) Correlation of decreased calcium contents with proline accumulation in the marine green macroalga *Ulva fasciata* exposed to elevated NaCl contents in seawater. *Journal of experimental botany* 50(341): 1855-1862.
- [58] Chinnusamy V, Zhu JK (2003) Plant salt tolerance. *Plant responses to abiotic stress* 2(1): 241-270.
- [59] Shi H, Ishitani M, Kim C, Zhu JK (2000) The *Arabidopsis thaliana* salt tolerance gene *SOS1* encodes a putative Na⁺/H⁺ antiporter. *Proceedings of the National Academy of Sciences USA* 97(12): 6896-6901.
- [60] 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. *Proceedings of the National Academy of Sciences* 97(7): 3730-3734.
- [61] Liu J, Zhu JK (1998) A calcium sensor homolog required for plant salt tolerance. *Science* 280(5371): 1943-1945.
- [62] Ishitani M, Liu J, Halfter U, Kim CS, Shi W, et al. (2000) *SOS3* function in plant salt tolerance requires N-myristoylation and calcium binding. *The Plant Cell* 12(9): 1667-1678.
- [63] Halfter U, Ishitani M, Zhu JK (2000) The *Arabidopsis* *SOS2* protein kinase physically interacts with and is activated by the calcium-binding protein *SOS3*. *Proceedings of the National Academy of Sciences* 97(7): 3735-3740.
- [64] Zhu JK (2003) Regulation of ion homeostasis under salt stress. *Current opinion in plant biology* 6(5): 441-445.
- [65] Shi H, Lee BH, Wu SJ, Zhu JK (2003) Overexpression of a plasma membrane Na⁺/H⁺ antiporter gene improves salt tolerance in *Arabidopsis thaliana*. *Nature biotechnology* 21(1): 81-85.
- [66] Guo Y, Qiu QS, Quintero FJ, Pardo JM, Ohta M, et al (2004) Transgenic evaluation of activated mutant alleles of *SOS2* reveals a critical requirement for its kinase activity and C-terminal regulatory domain for salt tolerance in *Arabidopsis thaliana*. *The Plant Cell* 16(2): 435- 449.
- [67] Ohta M, Guo Y, Halfter U, Zhu JK (2003) A novel domain in the protein kinase *SOS2* mediates interaction with the protein phosphatase 2C *ABI2*. *Proceedings of the National Academy of Sciences* 100(20): 11771-11776.
- [68] Katiyar Agarwal S, Zhu J, Kim K, Agarwal M, Fu X, et al. (2006) The plasma membrane Na⁺/H⁺ antiporter *SOS1* interacts with *RCD1* and functions in oxidative stress tolerance in *Arabidopsis*. *Proceedings of the National Academy of Sciences* 103(49): 18816-18821.
- [69] Izhaki A, Swain SM, Tseng TS, Borochoy A, Olszewski NE, et al. (2001) The role of *SPY* and its TPR domain in the regulation of gibberellin action throughout the life cycle of *Petunia hybrida* plants. *The Plant Journal* 28(2): 181-190.
- [70] Yokoi S, Quintero FJ, Cubero B, Ruiz MT, Bressan RA, et al. (2002) Differential expression and function of *Arabidopsis thaliana* *NHX* Na⁺/H⁺ antiporters in the salt stress response. *The Plant Journal* 30(5): 529-539.
- [71] Gaxiola RA, Rao R, Sherman A, Grisafi P, Alper SL, et al. (1999) The *Arabidopsis thaliana* proton transporters, *AtNhx1* and *Avp1*, can function in cation detoxification in yeast. *Proceedings of the National Academy of Sciences* 96(4): 1480-1485.
- [72] Quintero FJ, Blatt MR, Pardo JM (2000) Functional conservation between yeast and plant endosomal Na⁺/H⁺ antiporters 1. *FEBS letters* 471(2-3): 224-228.

- [73] Morris PC (2010) Integrating lipid signalling, mitogen-activated protein kinase cascades and salt tolerance. *New Phytologist* 188(3): 640-643.
- [74] Kiegerl S, Cardinale F, Siligan C, Gross A, Baudouin E, et al. (2000) SIMKK, a mitogen-activated protein kinase (MAPK) kinase, is a specific activator of the salt stress-induced MAPK, SIMK. *The Plant Cell* 12(11): 2247-2258.
- [75] Ichimura K, Mizoguchi T, Yoshida R, Yuasa T, Shinozaki K (2000) Various abiotic stresses rapidly activate Arabidopsis MAP kinases ATMPK4 and ATMPK6. *The Plant Journal* 24(5): 655-665.
- [76] Teige M, Scheikl E, Eulgem T, Dóczi R, Ichimura K, et al. (2004) The MKK2 pathway mediates cold and salt stress signaling in Arabidopsis. *Molecular cell* 15(1): 141-152.
- [77] Testerink C, Dekker HL, Lim ZY, Johns MK, Holmes AB, et al. (2004) Isolation and identification of phosphatidic acid targets from plants. *The Plant Journal* 39(4): 527-536.
- [78] Yu L, Nie J, Cao C, Jin Y, Yan M, et al. (2010) Phosphatidic acid mediates salt stress response by regulation of MPK6 in Arabidopsis thaliana. *New Phytologist* 188(3): 762-773.
- [79] Urao T, Yakubov B, Satoh R, Yamaguchi Shinozaki K, Seki M, et al. (1999) A trans membrane hybrid-type histidine kinase in Arabidopsis functions as an osmo sensor. *The Plant Cell* 11(9): 1743-1754.
- [80] Patharkar OR, Cushman JC (2000) A stress-induced calcium-dependent protein kinase from *Mesembryanthemum crystallinum* phosphorylates a two-component pseudo-response regulator. *The Plant Journal* 24(5): 679-691.
- [81] Hong SW, Jon JH, Kwak JM, Nam HG (1997) Identification of a receptor-like protein kinase gene rapidly induced by abscisic acid, dehydration, high salt, and cold treatments in Arabidopsis thaliana. *Plant physiology* 113(4): 1203-1212.
- [82] Piao HL, Pih KT, Lim JH, Kang SG, Jin JB, et al. (1999) An Arabidopsis GSK3/shaggy-like gene that complements yeast salt stress-sensitive mutants is induced by NaCl and abscisic acid. *Plant Physiology* 119(4): 1527-1534.
- [83] Piao HL, Lim JH, Kim SJ, Cheong GW, Hwang I (2001) Constitutive over-expression of AtGSK1 induces NaCl stress responses in the absence of NaCl stress and results in enhanced NaCl tolerance in Arabidopsis. *The Plant Journal* 27(4): 305-314.
- [84] De Dios Barajas Lopez J, Moreno JR, Gamez Arjona FM, Pardo JM, Punkkinen M, et al. (2017) Upstream kinases of plant SnRKs are involved in salt stress tolerance. *The Plant Journal*.
- [85] Jia W, Wang Y, Zhang S, Zhang J (2002) Salt-stress-induced ABA accumulation is more sensitively triggered in roots than in shoots. *Journal of Experimental Botany* 53(378): 2201-2206.
- [86] Zhu JK (2002) Salt and drought stress signal transduction in plants. *Annual review of plant biology* 53(1): 247-273.
- [87] Wang ZY, Xiong L, Li W, Zhu JK, Zhu J (2011) The Plant Cuticle Is Required for Osmotic Stress Regulation of Abscisic Acid Biosynthesis and Osmotic Stress Tolerance in Arabidopsis. *Plant Cell* 23(5): 1971-1984.
- [88] Leung J, Giraudat J (1998) Abscisic acid signal transduction. *Annual review of plant biology* 49(1): 199-222.
- [89] Schroeder JI, Allen GJ, Hugouvieux V, Kwak JM, Waner D (2001) Guard cell signal transduction. *Annual review of plant biology* 52(1): 627-658.
- [90] Wu Y, Kuzma J, Maréchal E, Graeff R, Lee HC, et al. (1997) Abscisic acid signaling through cyclic ADP-ribose in plants. *Science* 278(5346): 2126-2130.
- [91] Sanchez JP, Chua NH (2001) Arabidopsis PLC1 is required for secondary responses to abscisic acid signals. *The Plant Cell* 13(5): 1143-1154.
- [92] Ishitani M, Xiong L, Stevenson B, Zhu JK (1997) Genetic analysis of osmotic and cold stress signal transduction in Arabidopsis: interactions and convergence of abscisic acid-dependent and abscisic acid-independent pathways. *The Plant Cell* 9(11): 1935-1949.
- [93] Xiong L, Ishitani M, Lee H, Zhu JK (2001) The Arabidopsis LOS5/ABA3 locus encodes a molybdenum cofactor sulfurase and modulates cold stress- and osmotic stress-responsive gene expression. *The Plant Cell* 13(9): 2063-2083.
- [94] Xiong L, Lee H, Ishitani M, Zhu JK (2002) Regulation of Osmotic Stress-responsive Gene Expression by the LOS6/ABA1 Locus in Arabidopsis. *Journal of Biological Chemistry* 277(10): 8588-8596.

- [95] Xiong L, Schumaker KS, Zhu JK (2002) Cell signaling during cold, drought, and salt stress. *The plant cell* 14(1): 165-183.
- [96] Shi H, Zhu JK (2002) Regulation of expression of the vacuolar Na⁺/ H⁺ antiporter gene AtNHX1 by salt stress and abscisic acid. *Plant molecular biology* 50(3): 543-550.
- [97] Quesada V, Garcia Martinez S, Piqueras P, Ponce MR, Micol JL (2002) Genetic architecture of NaCl tolerance in Arabidopsis. *Plant physiology* 130(2): 951-963.
- [98] Mano Y, Takeda K (1997) Mapping quantitative trait loci for salt tolerance at germination and the seedling stage in barley (*Hordeum vulgare* L.). *Euphytica* 94(3): 263-272.
- [99] Shi H, Kim Y, Guo Y, Stevenson B, Zhu JK (2003) The Arabidopsis SOS5 locus encodes a putative cell surface adhesion protein and is required for normal cell expansion. *The Plant Cell* 15(1): 19-32.
- [100] Ren Z, Zheng Z, Chinnusamy V, Zhu J, Cui X, et al. (2010) RAS1, a quantitative trait locus for salt tolerance and ABA sensitivity in Arabidopsis. *Proceedings of the National Academy of Sciences* 107(12): 5669-5674.
- [101] Nxele X, Klein A, Ndimba B (2017) Drought and salinity stress alters ROS accumulation, water retention, and osmolyte content in sorghum plants. *South African Journal of Botany* 108: 261-266.