



What is known about phytohormones in halophytes? A review

Analia Llanes¹ · Mariana Reginato¹ · Genoveva Devinar¹ · Virginia Luna¹

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Abstract

Phytohormones participate in many aspects of the plant life cycle, including responses to biotic and abiotic stresses. They play a key role in plant responses to the environment with direct bearing on a plant's fitness for adaptation and reproduction. In recent years, there have been major advances in our understanding of the role of phytohormones in halophytic plants. The variability in maximal salinity level that halophytes can tolerate makes it difficult to characterize the specific traits responsible for salt tolerance. However, the most evident effect of salinity is growth disturbance, and growth is directly governed by phytohormones. Phytohormones such as abscisic acid, salicylic acid ethylene and jasmonates are traditionally related to stress responses, while the involvement of cytokinins, gibberellins and auxins has started to be analyzed. Polyamines, although they can't be considered phytohormones because of the high concentrations required for cell responses, have been proposed as a new category of plant growth regulators involved in several plant processes and stress responses. This review integrates the advances in the knowledge about phytohormones in halophytes and their participation in salt tolerance.

Keywords Halophytes · Phytohormones · Abscisic acid · Ethylene · Salicylic acid · Jasmonates · Gibberellins · Auxins · Cytokinins · Polyamines

Introduction

The devastating consequences of soil salinization can be seen all over the world and the need for more salt tolerant crops increases as substantial percentages of cultivated land are affected by salinity worldwide (FAO 2016). The prospect is that fresh water will become scarce as a result of an increasing demand of the growing world population (Black 2016). Moreover, as a result of global warming, arable land may suffer from increasing saline and dry conditions in the future, whereas sea level rise will particularly threaten coastal lowlands. Excessive salt accumulation in the soil can produce sodic (or alkaline) and saline soils. Sodic soils have a poor soil structure and are generally found in arid and semi-arid regions. They retain high concentrations of Na⁺ at the exchangeable site of clay particles in the soil, which shows high pH (greater than 8.5) with a high exchangeable sodium

percentage (ESP > 15). Saline soils can be generally found in arid regions, estuaries, and coastal fringes where Na⁺ ions predominate, with electrical conductivity (EC) greater than 4 dS/m corresponding to approximately 40 mM NaCl (Sosa et al. 2005; Hauser and Horie 2010).

An increase in plant salt tolerance would allow greater yields in salt-affected soils. The key to plant engineering for salt tolerance lies in a better understanding of the underlying physiological mechanisms of plant adaptive responses. Plants growing in saline soils face several challenges, and their success depends on their ability to cope with several major constraints such as water deficit, restriction of CO₂ uptake, ion toxicity and nutrient imbalance (Munns and Tester 2008). However, breeding of salt-tolerant crops is hampered by the complexity of plant salt tolerance mechanisms as it can be seen in halophytes (Flowers et al. 2010). One important aspect of this problem is solving the question of how salt tolerance is regulated in plants.

Plants are classified as glycophytes or halophytes according to their capacity to grow on high salinity (Sairam and Tyagi 2004). A promising approach under discussion is the use of xerophytic or halophytic crops instead of glycophytes (Koyro and Lieth 2008). In recent years, salt tolerant plants with high economic value have been recommended as ecoengineering tools for alternative agricultural production

✉ Analia Llanes
allanes@exa.unrc.edu.ar

¹ Laboratorio de Fisiología Vegetal, Departamento de Ciencias Naturales, Universidad Nacional de Río Cuarto, Route 36 Km. 601, CP X5804BYA, Río Cuarto, Córdoba, Argentina

and re-vegetation in salt-affected coastal zones or saline farmlands (Li et al. 2010; Wu et al. 2012). In fact, halophytes are especial plants that tolerate salt concentrations even above sea water salinity (Flowers and Colmer 2008; Atzori et al. 2017), and some of them can yield as much as conventional crops, even when irrigated with seawater (Ventura et al. 2011). Although the agricultural development of halophytic crops is still scarce, plant irrigation with saline water at small-scale production sites using seawater, diluted seawater, or brackish water is already being practiced (Lieth 2000). The diversity of halophytic plants translates into a wide range of potential applications (Koyro et al. 2011) being tested as fodder crops (El Shaer 2010), for phytoremediation (Manousaki and Kalogerakis 2011), as renewable energy sources (biofuel) (Eganathan et al. 2006), for saline aquaculture effluent treatment (Brown and Glenn 1999), as landscaping ornamentals (Zia et al. 2008) and as food for human consumption (Ventura et al. 2011).

Additionally, halophytes have the ability to survive under a salt shock as for example due to tidal or rainfall events, which allow these species to develop a metabolic steady state for growth in a saline environment as compared to glycophytes (Ali and Yun 2017). Halophytes respond to salt stress at three levels i.e. cellular, tissue and whole plant level. Studying the mechanisms operating at each level is important to develop complete understanding of their salt tolerance. Molecular mechanisms involved against different types of abiotic stresses have long been in progress in recent years (Rejeb et al. 2014; Ozfidan-Konakci et al. 2016). Most of halophytes utilize the basic mechanism of controlled ion accumulation and sequestration, which in turn is used to adjust their internal osmotic balance to external salinity (Flowers et al. 2010). However, halophytes differ into which extent they accumulate ions as well as in their overall degree of salt tolerance (Ali and Yun 2017). Some plants tolerate the presence of certain salt within the cells, and some exclude salt from their cells either at root level or as salt secretion and export by means of salt excreting glands in aerial organs. It is obvious that not only one of these control processes is active in different types of halophytes. Their salt tolerance responses depend also upon activation of cascades of molecular networks involved in stress sensing, signal transduction and specific stress-related gene expression. However, the variability in plant responses to different salt levels makes it difficult to characterize a specific trait responsible for salt tolerance.

The most evident effect of salinity is growth disturbance, and the growth is controlled by phytohormones. Indeed, evidence shows that many environmental factors (i.e., changes in nutrient concentration) affect endogenous plant hormone levels thus the hormonal balance of the plant is disturbed. It therefore seems logical to assume a relationship between stress effects on hormonal balance and the effect of a disturbed hormonal balance on plant growth and development.

Therefore, phytohormones emerge as cellular signal molecules with key functions in the regulation of plant responses to abiotic stresses. Their signaling pathways are interconnected in a complex network, which provide plants with an enormous regulatory potential to rapidly adapt to environmental factors and to utilize their limited resources for growth and survival in a cost-efficient manner. Recently, a considerable amount of evidence has shown that phytohormones are signals connecting root and shoot, triggering responses to external stress (Llanes et al. 2014).

The phytohormones reported to play important roles in stress responses and adaptation are mainly abscisic acid (ABA), salicylic acid (SA), ethylene and jasmonic acid (JA) (Peleg and Blumwald 2011; Wasternack 2014). However, much less is known about the role of cytokinins (CKs), gibberellins (GAs) and auxins, traditionally not related to stress responses except for some few examples. Also, polyamines (PAs) have been proposed as a new category of plant growth regulators essential for eukaryotic cell growth, are involved in a wide variety of physiological processes and stress responses (Liu et al. 2007). Strigolactones and brassinosteroids constitute a new class of plant hormones which are of increasing importance in plant science; however information on involvement of these phytohormones in halophytes is unknown, so are not included in this review. The homeostasis of phytohormones is tightly controlled between the biosynthetic and metabolic pathways. Small variations in the phytohormone contents may change its physiological activity, although their specific roles in different biological processes still remain to be elucidated (Pieterse et al. 2009). In recent years, studies using plants bearing mutations in hormone-biosynthetic pathways have been essential in understanding the processes associated with plant responses to changing environments. However, these studies have been made in glycophytes and very little is known about phytohormones role and their cross-talk in halophytic plants. The present review intends to improve our understanding on the effects of salinity on endogenous phytohormones and their role in halophytes physiology, to elucidate the potential mechanisms of phytohormone-mediated salinity responses.

Abscisic acid

ABA was discovered during the early 1960s, when it was found to be involved in the control of seed dormancy and organ abscission (Cornforth et al. 1965). Since then, its role has been broadened to the regulation of plant development and adaptation to adverse environmental conditions. Thus, ABA is one of the most-studied hormones in applied and fundamental plant science research (Danquah et al. 2014; Guo et al. 2017). The fastest plant responses to abiotic stress are due to biosynthesis and redistribution of this hormone

causing stomatal closure, thereby reducing water loss via transpiration and eventually restricting cellular growth (Peleg and Blumwald 2011). ABA biosynthesis pathway is through production from carotenoids. The zeaxanthin epoxidase catalyzes the epoxidation of zeaxanthin to produce all-trans-violaxanthin. The next step is the conversion of violaxanthin to neoxanthin. The oxidative cleavage of cis-isomers of violaxanthin and neoxanthin to the C15 compound xanthoxin and several cleavage processes from cis-isomers of violaxanthin and neoxanthin to a C15 compound (xanthoxin). This compound is converted to abscisic aldehyde, which is oxidized to ABA (Nambara and Marion-Poll 2005). A rapid way to obtain free ABA by plants is the hydrolysis of the glucosyl conjugate ABA-GE by β -glucosidase homologs (Xu et al. 2012).

ABA can regulate numerous gene expressions under osmotic and salt stress conditions. The ABA-responsive element (ABRE) is the major cis-element for ABA-responsive gene expression. ABRE-binding protein (AREB)/ABRE-binding factor (ABF) transcription factors (TFs) regulate ABRE-dependent gene expression. Other TFs are also involved in ABA-responsive gene expression. SNF1-related protein kinases 2 are key regulators of ABA signaling including the AREB/ABF regulon (Nakashima and Yamaguchi-Shinozaki 2013). Recently, PYR/PYL/RCAR ABA receptors, protein phosphatases 2C (PP2Cs), and subclass III SnRK2 protein kinases were shown to govern the core ABA signaling constituents (Kim et al. 2012). Recent studies have suggested interactions between the major ABA signaling pathway and other signaling factors in stress-responses. However, most of these molecular studies on ABA signaling have been performed in glycophytes and their knowledge in halophytes is scarce. ABA endogenous concentrations were measured in shoots of the halophyte *Suaeda maritima* growing on medium with different salinity (100 and 400 mol m⁻³ NaCl) (Boucaud and Ungar 1976; Clipson et al. 1988). ABA levels were higher (41 ng g⁻¹ fr. wt) in plants grown on the medium without salts than in plants grown in 200 mol m⁻³ NaCl (24 ng g⁻¹ fr. wt). The increase of culture medium salinity resulted in a marked increase in ABA levels. The possible ABA role in the salt tolerance of this halophyte is not clear. However, some ABA roles have been proposed in some halophytic plants. In fact, ABA accumulation regulates salt stress tolerance in the facultative halophytic species *Lophopyrum elongatum* and the closely related but less salt-tolerant wheat *Triticum aestivum* L. The salt tolerance is enhanced when these plants are enabled to gradually acclimate to salt. This acclimation may be the result of enhanced osmotic adjustment by ABA. Indeed, there is evidence that ABA is involved in regulating Na⁺/K⁺ ratio and osmoprotectants levels in halophytic plants. For example, a relation between ABA production and Na⁺/K⁺ ratio and osmoprotectants accumulation was shown in halophytes of District Mardan, Pakistan. ABA content was found higher

in *Haloxylon salicornicum* and *Atriplex leuoclada*, while both *Salicornia virginica* and *Suaeda fruticosa* showed the lowest ABA levels. ABA production was significantly higher as compared to indole acetic acid (IAA) levels in these halophytes. *Atriplex leuoclada* had maximum ABA/IAA ratio as well as higher Na⁺/K⁺ ratio and higher proline and protein contents, while *H. salicornicum* and *S. virginica* had lower K⁺/Na⁺ ratio, lower ABA/IAA ratio as well as lower proline and protein content (Samiullah and Bano 2011). It is inferred that halophytes differ in their adaptability and use different compounds as phytohormones and osmoprotectants.

Other ABA role proposed is that ABA accumulation promotes the switch from C3 to CAM metabolism under salt stress in some halophytic species. This role is available in ice common plant *Mesembryanthemum crystallinum*, which is a facultative halophyte (Adams et al. 1998). *M. crystallinum* has an ability to change the photosynthesis type from C3 to CAM under salinity conditions. An acceleration of transition to CAM metabolism was observed after pretreatments of plants with exogenous ABA (Chu 1990). Thus, the addition of 10⁻⁵ M ABA together with NaCl to culture medium induced CAM-type photosynthesis and enhanced stress tolerance. Furthermore, ABA treatment caused a 10% transpiration reduction in *M. crystallinum* and thus, decreased water loss and prevented negative influence of osmotic stress during salinity (Kuznetsov et al. 2003).

Studies in the halophyte *Prosopis strombulifera* demonstrated that ABA accumulation varied depending on type of salt in the medium of culture, salt concentration, organ analyzed and age of plant (Devinar et al. 2013; Llanes et al. 2014). ABA level in leaves was much higher than in roots showing the rapid biosynthesis and transport from roots. Leaves of Na₂SO₄-treated plants had the highest ABA levels, associated with sulfate toxicity symptoms. ABA metabolism occurred mainly through conjugation; ABA-glucose ester (ABA-GE) was accumulated in both roots and leaves, whereas phaseic acid (PA) and dihydrophaseic acid (DPA) were low. The highest levels of free ABA in leaves were correlated with high ABA-GE glucosidase activity in these organs, demonstrating ABA-GE transport from roots to leaves. Na₂SO₄-treated plants showed the highest levels of ABA-GE and free ABA. Therefore, both compounds work together to create and intensify the salt-specific stress signal. It is interesting to point out that in these plants stomata remained opened allowing high transpiration, suggesting that sulfate toxicity interfered at some point with ABA signaling (Llanes et al. 2014).

Recently, comparative genomics and experimental analyses identified genes related to abscisic acid production in *Thellungiella salsuginea*, a close relative of *Arabidopsis* and an extremophile model for abiotic stress tolerance studies. The *T. salsuginea* genome as compared to *Arabidopsis* showed an expansion of gene numbers of ZEP, AAO, and CYP707A families identified. This expansion may lead to a more

complex regulation of ABA biosynthesis and catabolism contributing to stress tolerance. In fact, the induction of gene expression by ABA in *Arabidopsis* was slower than in *T. salsuginea* under salinity conditions (Taji et al. 2004; Gong et al. 2005). This ABA response in *T. salsuginea* may confer a higher salinity-tolerance capacity by slowing down its growth rate. However, more experimental evidences are necessary to confirm this supposition. Taken together, these reports show that ABA is considered a global regulator of salinity responses in halophytic plants and its production may therefore be the crucial factor in determining how halophytes respond to both salinity and multiple stresses.

Ethylene

Ethylene is an essential gaseous plant hormone involved in many plant processes including: germination, flower development, fruit ripening and responses to many environmental stimuli. Ethylene is produced in almost all plant tissues, and during fruit ripening, flower wilting and plant stress response, ethylene production is quickly stimulated (Kendrick and Chang 2008). Biosynthesis of this hormone begins with the precursor S-adenosylmethionine (SAM) that is also required in many other pathways and is, therefore, abundant within plant tissues. The enzyme that catalyzes the first reaction is the ACC synthase, which converts SAM to 1-aminocyclopropane-1-carboxylic acid (ACC), and methylthioadenosine (MTA), which is recycled to L-methionine. This allows L-methionine levels to remain relatively unchanged even during high rates of ethylene production. It has been suggested that this is the committal step in the ethylene biosynthesis pathway, since the extremely labile ACC synthase enzyme has been shown to: (a) be rate limiting and (b) to rise proportionally to ethylene levels within the tissues of some plants (Abeles et al. 1992).

As mentioned above, ethylene is involved and regulates several stress-related processes in plant. It plays a distinct role in response to biotic and abiotic stress such as pathogen attack, heat stress, wounding, ozone stress and Fe deficiency (Abeles et al. 1992; Kendrick and Chang 2008). In many cases, ethylene accumulation is related to an increase in damage, implying that stress induced ethylene is deleterious to plants. Wi et al. (2010) reported the inhibition of biphasic ethylene production and consequent enhanced tolerance to abiotic stress by reducing the accumulation of reactive oxygen species in tobacco plants. In this study it is suggested that ethylene plays a potentially critical role as an amplifier for ROS accumulation, implying a synergistic effect between biosynthesis of ROS and ethylene. However, it was reported in tobacco that the

ERF protein (ethylene response factor) JERF3 transcriptionally activates the expression of genes related to both osmotic and oxidative stresses, and the expression of these genes subsequently results in the decreased accumulation of ROS, thereby enhancing adaptation to drought, freezing, and salt in seedlings (Wu et al. 2008). It may be that these discrepancies are due to differences in the amount of endogenous ethylene production, and in the period of stress treatment, in addition to the plant tissue studied.

Ethylene involvement in plant response to salinity has been extensively studied, but there are still some obscure points left to be clarified. Generally, in glycophytes, ethylene production and signaling is indispensable for plant rapid response and tolerance to salinity stress and self-modification for better survival. But excessive ethylene production under continuous stress tends to inhibit plant growth and development, even leads to death. Therefore, tight control of ethylene homeostasis is critical for plants to survive under salinity and recover growth later (Tao et al. 2015). Silva et al. (2014) demonstrated that differences in salt tolerance to NaCl during germination in *Stylosanthes* species (*S. humilis*, *S. capitata* and *S. guianensis*) is directly correlated with the abilities to synthesize ACC, associated with corresponding ethylene biosynthesis. In *Arabidopsis thaliana* plants, application of the ethylene precursor ACC alleviated NaCl induced injury by maintaining a lower Na^+/K^+ ratio and an increased PM H⁺-ATPase activity in wild type callus but not in the ethylene insensitive mutant *etr1-3* callus (Wang et al. 2009). The response of *ERFs* to salt is contradictory in glycophytes; while salt treatment leads to an increase in the expression of *ERFs* in rice (Panda et al. 2015), it downregulates their expression in *Arabidopsis* (Shen et al. 2014).

In halophytes, Chrominsky et al. (1986) studied the ability of *Allenrolfea occidentalis* to metabolize the ethylene precursor, ACC, demonstrating a NaCl salinity dependent conversion of ACC to ethylene. Khan et al. (2009) demonstrated the key role of ethylene in germination in 22 halophytic species having different life forms, including salt secreting dicots, salt secreting monocots, stem succulents and leaf succulents, since the application of ethephon (an ethylene releasing compound) to seeds can alleviate salinity effects on germination. Ethylene is naturally produced during the last step of germination helping the radicle to grow faster and complete germination. Seeds of halophytes while germinating under high salt conditions will suffer due to the loss of turgor, and the application of ethylene may restore turgor and counter the effects of ABA produced due to high salinity. More recently, Ellouzi et al. (2014) show that the halophytes *Cakile maritima* and *Thellungiella salsuginea* exposed to short-term salt stress (400 mM NaCl) experience an early oxidative burst, improved antioxidant defenses and hormonal response in leaves and roots, in comparison to the glycophyte *A. thaliana*. This

differential signaling response converging into increased ERF1 expression seems to underlay, at least in part, the enhanced tolerance of the two studied halophytes to salt stress. Similarly, in the halophyte *Suaeda maritima*, the significant increases in the expression of S-adenosylmethionine (SAM) synthase, ACS, ACO and ethylene responsive factor in response to NaCl application indicate the important role of ethylene in salt tolerance in addition to the roles of transcription factors and the genes involved in ion transportation (Gharat et al. 2016). Moreover, Krishnamurthy et al. (2017) demonstrated that ethylene response factor (AoERF114) plays an important role in salt tolerance in the halophyte mangrove *Avicennia officinalis*. These studies suggest the involvement of ethylene and ethylene responsive factors (ERFs) in salt tolerance in halophytes. However, there are still many unresolved aspects of the ethylene roles. Clues to the role of ethylene in stress symptoms are cryptic in many cases, due to the interactions between ethylene and other phytohormones.

Salicylic acid

Salicylic acid (SA) is an endogenous growth regulator of phenolic nature. This phytohormone participates in the regulation of different physiological processes in plants. SA has the ability to induce systemic acquired resistance to different pathogens and is also considered to be a signaling molecule that plays a key role in plant growth, development and defense responses under stress conditions (Misra and Saxena 2009).

In early 1960s, it was suggested that salicylic acid is synthesized in plants from cinnamic acid by two possible pathways. One pathway involves the decarboxylation of the side chain of cinnamic acid to form benzoic acid, which in turn undergoes a 2-hydroxylation to form salicylic acid. Such biosynthetic pathway has been reported in tobacco and rice (Yalpani et al. 1993; Silverman et al. 1995). Other pathway proposed for SA biosynthesis involves a 2-hydroxylation of cinnamic acid to o-coumaric acid which is then decarboxylated to salicylic acid and the reaction is catalyzed by an enzyme trans-cinnamate-4-hydroxylase, which was first detected in pea seedlings (Russell and Conn 1967). Recently, two distinctive pathways that are dependent on chorismate are involved in SA biosynthesis (Dempsey et al. 2011; Shah et al. 2014). In the isochorismate pathway, which is the major SA biosynthesis pathway in *Arabidopsis*, SA is synthesized from isochorismate produced by the action of plastid-localized isochorismate synthase (ICS). An isochorismate pyruvate lyase activity is predicted to further convert isochorismate to SA. However, the importance of each of these pathways is still unclear. Recent studies point out that SA participates in the signaling of abiotic stresses (Hao et al. 2012). However, SA role in stressed plants is not yet clear as it

depends of species and the intensity and duration of abiotic stress (Horvath et al. 2007). Several reports indicate that exogenous application of SA to the stressed plants can potentially alleviate the toxic effects of salinity. An enhanced tolerance against salt stress was observed in wheat seedlings, raised from the grains soaked in SA (Al-Hakimi and Hamada 2001). Similar observations were found in tomato plants raised from the seeds soaked in SA and was presumed to be due to the enhanced accumulation of osmolytes (proline) and activation of antioxidant enzymes (ascorbate peroxidase) (Tari et al. 2004; Szepesi et al. 2009). In addition, it was demonstrated that SA accumulation is a fundamental requirement for a successful acclimation to regulate the oxidative chain-reactions and/or maintain effective repair and detoxifying mechanisms (Tari et al. 2004). On the contrary, a negative SA effect in salt tolerance was observed by Hao et al. (2012). To address the effect of SA accumulation and signaling on plant responses to salinity, biochemical and physiological analyses were performed on SA-altering *Arabidopsis* mutants including *sncl* with high level of SA, transgenic line *nahG* with low SA, *npr1-1* with SA signaling blockage, *sncl/nahG* plants (expression of *nahG* in the *sncl* background) (Hao et al. 2012). The *nahG* and *npr1-1* plants always exhibited more tolerance to salinity than wild type plants. Therefore, SA deficit or signaling blockage in *Arabidopsis* plants was favorable to salt adaptation, while a high accumulation of SA potentiated salt-induced damage to plants. In the halophyte *Prosopis strombulifera*, endogenous SA level differed depending on the salt type in the culture medium. Therefore, the higher SA levels were observed in Na₂SO₄-treated plants than NaCl-treated plants. This accumulation was correlated with a failure on ion compartmentalization by Na₂SO₄-treated plants (Devinar et al. 2013). These results are in agreement with the report by Macri et al. (1986), that SA can greatly perturb the trans-membrane electrochemical potential of mitochondria and the ATP-dependent proton gradient of tonoplast. NaCl-treated plants showed the lowest levels of SA with an efficient ion compartmentalization and osmoregulation with direct consequences on their growth. In addition, low humidity conditions (30% RH) accentuated the stressing effect of the salts presented in the medium and SA levels were also increased that in plants grown at 70% RH. These responses indicate that SA accumulation is not related to a protective role in the halophyte *P. strombulifera* under adverse conditions (Devinar et al. 2013). Therefore, in view of the ambiguous results in glycophytic and halophytic plants about the effects of SA and salt stress tolerance, which depends of species and salt stress intensity and duration, it still remains to be determined whether SA manipulation could be a tool for improving crop performance under salinity conditions.

Jasmonic acid and related compounds

JA and its derivatives, collectively called Jasmonates (JAs), are lipid-derived compounds synthesized from α -linolenic acid (18:3) in the octadecanoid pathway in plant cells, including numerous compounds as jasmonic acid (JA), its methyl ester (JAME), amino acid conjugates (JA-isoleucine (JA-Ile)), and metabolites such as 12-OH-JA and 11-OH-JA. (Wasternack and Hause 2013). The biosynthetic precursor of JA, the 12-oxophytodienoic acid (OPDA) is also considered as an important signaling molecule in the jasmonate pathway. JAs are detected throughout the plant, with the highest concentrations in growing tissues such as shoot apex, root tips, immature fruits and young leaves. JAs plays many roles in plants, ranging from defense factors to cell death regulators and, finally, promoters of leaf senescence. The common link between these, at first glance, unrelated processes could be the chloroplast where the first steps of JA biosynthesis take place (Reinbothe et al. 2009).

During plant development the following processes are mediated by JA, such as male and female organ development, embryo development, sex determination in maize, seed germination, seedling development, root growth, fruit ripening, gravitropism, trichome formation, tuber formation, leaf movement, and leaf senescence (Wasternack and Hause 2013; Wasternack 2014). Also, JAs are key signaling molecules involved in plant defence mechanisms in response to insect-driven wounding and various pathogens. Many studies showed that JAs play an important role in abiotic stress tolerance, and considerable interests have focused on these compounds due to its ability to induce a protective effect on plants under stresses (Takeuchi et al. 2011). Different JAs-mediated processes are plant responses to desiccation stress, ozone stress (Sasaki-Sekimoto et al. 2005), UV-stress, osmotic stress, cold stress (Yoshikawa et al. 2007), or light stress, but also formation of secondary metabolites (Chen et al. 2006) and adaptation to seasonal and circadian rhythm. Moreover, JAs are involved in the regulation of beneficial plant–microbe interactions, such as interactions with arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria (PGPR) (Wasternack and Hause 2013).

Several studies have investigated biological relevancies of JA signalling in salt stress in glycophytes as barley, tomato and others species. In barley, Tsonev et al. (1998) reported that pre-treatment with JA reduced the inhibitory effect of NaCl (30 mM) on growth and photosynthesis. In tomato plants JA increased in salt tolerant cultivar HF (Hellfrucht Fruhstamm) from the beginning of salinization, while in salt sensitive cultivar Pera, JA level decreased after 24 h of salt treatment (Pedranzani et al. 2003). Kang et al. (2005) reported that application of exogenous JA can ameliorate salt-stressed rice seedlings. They found that many physiological properties were remarkably recovered in salt-stressed rice plants after

JA application, such as leaf water potential, leaf photosynthetic rate, maximum quantum yield of photosystem II, and Ca^{+2} and Mg^{+2} uptake, possibly by changing the balance of endogenous phytohormones. However, further studies are necessary to identify hormone interaction between JA application and changes in GA, and ABA levels associated with plant recovery in rice. Del Amor and Cuadra-Crespo (2011) obtained similar results in broccoli plants subjected to salt stress, where foliar application of MeJA increased the salt tolerance as the growth, photosynthesis and root respiration were not impaired under moderate salt stress. These results demonstrate that exogenous JA may be involved in the defence not only during wounding and pathogen stress, but also during salt stress. Recently, Valenzuela et al. (2016) showed that the inhibitory effect of salinity on root growth partially involves the JA signaling pathway in *Arabidopsis*, although there is no evidence supporting the idea that JA-dependent root growth inhibition triggered by salt is playing a role in plant tolerance to this abiotic stress.

Despite that increasing evidence points to JA as a putative signal in the responses to abiotic stress in glycophytes (Arbona et al. 2010, Brossa et al. 2011), the role of JAs in the response of halophytic plants to salinity stress is still poorly understood. Studies performed in the halophytic shrub *P. strombulifera* growing under different sodium salts (NaCl and Na_2SO_4) showed that the same JAs (JA, 12-OH-JA, 11-OH-JA) and the precursor OPDA found in glycophytes were present. Large differences in total amount of JAs and in proportion of the components in roots vs. leaves were observed (Reginato et al. 2012). Miersch et al. (2008) reported similar differences in JAs levels among different tissues of various plant species. The major JAs in *P. strombulifera* roots were JA and the precursor OPDA, whereas those in leaves were OPDA and 12-OH-JA. Prevailing of OPDA and JA together with organ-specific patterns of different JA compounds indicate that the concept of an “oxylipin signature” (Weber et al. 1997) or “jasmonate signature” (Miersch et al. 2008) can be applied to the halophyte *P. strombulifera*. OPDA was the major compound found and the most affected by salt stress. A high concentration was found principally in roots, which suggest an active biosynthesis of the JAs route in this organ. *P. strombulifera* respond to salinity reducing the total JAs levels, particularly when was cultivated with Na_2SO_4 . NaCl-treated plants showed the lowest OPDA content at -1.0 MPa (250 mM), concomitant with enhanced root growth. JA content in roots of this halophyte did not differ among salt treatments, whereas in leaves, it was significantly decreased only at high salinity. This differential response of roots vs. leaves to salinity may be attributable to the root’s function as a “stress-receptor organ”, which responds to stress with more dramatic hormonal changes. In relation to the hydroxylated forms found in *P. strombulifera*, 12-OH-JA concentration was higher in leaves than in roots in both control and treated

plants; hence, possibly as a result of an active hydroxylation pathway in leaves, or transport of root-generated 12-OH-JA. The hydroxylate 11-OH-JA is usually present in lower levels than those of 12-OH-JA, as occur in *P. strombulifera*. Both hydroxylates were not affected by salinity. Thus, JAs seems not to be directly involved in salt tolerance in this halophyte (Reginato et al. 2012).

More recently, Ellouzi et al. (2014) showed enhanced oxidative stress in *A. thaliana* compared to the halophytes *Cakile maritima* and *Thellungiella salsuginea* under a short-term salt stress (400 mM NaCl). Both halophytes displayed enhanced accumulation of ABA, JA and ACC (precursor of ethylene) in leaves and roots, as compared to *A. thaliana* under salt stress. Moreover, the halophytes showed enhanced expression of ethylene response factor1 (ERF1), the convergence node of the JA and ethylene signaling pathways. More studies should be done in other species to elucidate JAs involvement and their relationship with ethylene in the salt stress response.

Gibberellins

Gibberellins have been known to regulate various aspects of plant development, including seed germination, stem elongation, and fruit development (Pearce et al. 2015). Given the number of GAs (more than 150 but only 4 are biologically active) and their multiple roles in plant development, the regulation of the GA levels is likely to be complex. Accordingly, many steps in the GA metabolism pathway are controlled by enzymes belonging to small multigenic families, with each member having a specific pattern of expression. In particular, GA biosynthesis is tightly regulated through the modulation of the expression of members of two gene families encoding GA 20-oxidases (GA20ox) and GA 3-oxidases (GA3ox) that catalyze the final steps in the synthesis of bioactive GAs (Hedden and Thomas 2012).

Plants exposed to salinity show a reduction in the growth rate and changes in GA levels. These responses could be related with the acquisition of salt stress protection in some plant species (Navarro et al. 2008; Ryu and Cho 2015). Achard et al. (2007) reported that salt-treated *Arabidopsis* plants contain reduced levels of bioactive GAs, supporting the idea that salinity slows down the growth by modulating the GA metabolism pathway. However, exogenous GA treatment of salt-stressed wheat plants resulted in an increased photosynthetic capacity, which was discussed as a major factor for greater dry matter production (Iqbal and Ashraf 2010). Evidence has emerged that GA metabolism pathway is altered in response to salinity and modulation of GA levels and the regulation of GA-mediated signaling components are important for plant developmental patterns in *Arabidopsis* (Zanten et al. 2009). It is also known that GA signaling is involved in adjustment of plants under limiting environmental conditions and maintains

source–sink relation (Iqbal et al. 2011) since salinity causes a reduction in sink enzyme activities, leading to an increase in sucrose in source leaves, with a decrease in photosynthesis rate by feedback inhibition (Poljakoff-Mayber and Lerner 1994) responses. However, the mechanisms by which GA-priming could induce stress tolerance in plants are not yet clear. In addition, few studies have demonstrated the ability of this phytohormone in halophytes to overcome adverse effects of salt stress (Chakrabarti and Mukherji 2003). For example, in halophytes, such as *Suaeda maritima* var. *macrocarpa* and *S. depressa*, GA₃ applications were found to stimulate growth under salinity levels up to 360 mM NaCl (Boucaud and Ungar 1976). At high salinity (800 mM NaCl) shoot growth of *Suaeda fruticosa* was stimulated by GA₃ applications, but shoot growth of plants grown in culture medium without salt was not promoted by GA (Khan et al. 2000). These results demonstrated that GA₃ application significantly stimulated growth of halophytes treated with NaCl (Ungar 1978; Wochok and Sluis 1980; Ke-Fu et al. 1986; Khan et al. 2000). However, GAs role in halophytic plants has been analyzed solely in experiments with exogenous applications by using the most commercially available gibberellin, GA₃, which is not a common endogenous gibberellin in some halophytic species. Notwithstanding, a possible explanation for the shoot growth promotion observed in the studies cited above, is that the same GA3β-hydroxylase that catalyzes the conversion of GA₂₀ to GA₃ in some species also catalyzes exogenously applied GA₃ to GA₁, as proposed by Chen et al. (2008). In addition, studies in the halophyte *P. strombulifera* demonstrated that GA₄ is the predominant active GA (Llanes et al. 2014). GA₄ is present in several species and would be the most important shoot growth regulator in *Arabidopsis* and some members of genus *Cucurbita* (Lange et al. 2011). The concentration and type of salts present in the culture medium (NaCl and Na₂SO₄) modulated the GA synthesis and metabolism. In *P. strombulifera* roots, GA₄ accumulation in NaCl-treated plants was very high during the whole experiment. In leaves, a 5-fold increase of GA₄ levels respect to plants grown in the medium without salts (controls) was determined in plants grown at −1.9 MPa, which was correlated with optimum growth for this species. High GA₄ levels were maintained at −2.6 MPa. In these organs, also GA₁ levels were high (3.5 fold at −1.9 MPa respect to controls) indicating that both gibberellins play a role in controlling shoot growth in this species under NaCl treatment. In Na₂SO₄-treated plants at high salinity (−2.6 MPa) the lowest levels of GA₄ and GA₁ were detected in coincidence with the maximum growth inhibition related to sulfate toxic effect. Furthermore, bisaline-treated plants showed intermediate levels of GA₄ and GA₁ in concordance with an intermediate shoot length, showing a partial reversion of sulfate toxicity when both anions (chloride and sulfate) were present in the medium (Llanes et al. 2014). Therefore, these results suggest that differential growth

responses to both salts would be mediated, at least in part, by GA₁ and GA₄ and the high levels of active GAs in *P. strobilifera* are correlated with their low ABA levels. These responses show the antagonistic roles of GA and ABA in plant developmental processes and environmental responses. Gómez-Cadenas et al. (2001) demonstrated in barley aleurone cell the molecular events involved in the interaction between ABA and GA signal transduction pathways. This study showed that an ABA-responsive serine/threonine protein kinase (PKABA1) acts as an intermediary of the ABA signal transduction pathway, repressing the GA induction of a GA-induced Myb-like protein (GAMyb) and therefore of hydrolytic enzymes. Recently, recent advances in aspects of GA and ABA antagonistic interactions have shown that proteins DELLAs form a central connection between GA and other signaling pathways, including ABA signaling. The ABA promoted accumulation of DELLA proteins in roots depends on ABI1, a core ABA-signaling repressor, and the phenotype of a quadruple-DELLA mutant resembles that of the gain-of-function mutant *abi1-1*, being resistant to the growth-inhibitory effects of ABA (Achard et al. 2006; Guo et al. 2014). By contrast, ABI1 does not mediate DELLAs' stability induced by salt stress (Duan et al. 2013), suggesting that the regulation of ABI on DELLA proteins occurs specifically upon exogenous ABA applications. Similarly, the tomato DELLA protein PROCERA promotes stomatal closure in guard cells in an ABA-dependent manner (Nir et al. 2017). However, molecular mechanisms behind the antagonistic actions of these two hormones are not fully understood and have not been investigated in halophytic plants.

Moreover, some studies suggest a GA role in the development of CAM in halophytic plants. Thus, Guralnick et al. (2001) showed that exogenously applied GA₃ increased the levels of phosphoenolpyruvate carboxylase (PEPcase) activity and the abundance of PEPcase protein in the facultative halophyte *Mesembryanthemum crystallinum* with a concomitant increase in acid metabolism. In addition, these authors showed a slower time course of increased expression of PEPcase of 3–6 weeks under the short day photoperiod. In this photoperiod, GA may accelerate development of CAM in *M. crystallinum* by inducing earlier branching and flowering. In addition, Chen and Edwards (1991) found that longer photoperiods accelerated branching and flowering of *M. crystallinum* and development of CAM. Therefore, exogenously applied GA may mimic the effect of long days in development. Future researches are needed to determine how GA exerts its effect and whether it can promote the induction of CAM by its actions on promoter of genes for the key enzymes of the CAM signaling pathway. Also, it would be of interest to evaluate endogenous GA levels under different photoperiods in induction of CAM in other facultative CAM plants and halophytes.

Cytokinins

Cytokinins (CKs) are often considered as ABA antagonists and auxin antagonists/synergists in various processes in plants (Pospíšilová 2003; Danilova et al. 2016). CKs could increase abiotic tolerance in some plants by interacting with other plant hormones, especially auxins and ABA (Iqbal et al. 2006). Plant endogenous CKs are adenine derivatives with either isoprenoid or aromatic side chains, being the aromatic CKs found in plants at a lower abundance (Sakakibara 2006). The isoprenoid CKs can be distinguished as isopentenyladenine (iP), trans-zeatin (tZ), cis-zeatin (cZ) or dihydrozeatin-type derivatives according the hydroxylation and reduction of the side chain. The rate-limiting step of isoprenoid CK biosynthesis is catalyzed by isopentenyltransferases (IPTs). Kudoyarova et al. 2007 reported that low cytokinin levels were associated with growth inhibition, a decline in stress-tolerance, and onset of senescence. Natural or stress-induced senescence is related to falling levels of cytokinin is well documented. Therefore, the discovery of IPT from *Agrobacterium tumefaciens* and its role in cytokinin biosynthesis were made to express this gene to up-regulate the production of cytokinin to delay senescence (Martineau et al. 1994; Rivero et al. 2010). Dexamethasone-inducible overexpression of the *Agrobacterium tumefaciens* IPT leads to higher de novo cytokinin biosynthesis in transgenic *Arabidopsis* plants (Sakakibara et al. 2005; Rivero et al. 2010). These transgenic plants were more tolerant of drought-induced leaf senescence. Though these efforts in using IPT in transgenic studies were successful in delaying senescence under drought and salinity conditions; there were detrimental effects on plant growth and morphology, likely due to altered expression without spatial and temporal regulation of the transgene.

In addition, some studies have shown that CK contents and transport are reduced by drought and/or salinity in several plant species (Nishiyama et al. 2011; Todaka et al. 2017). Cytokinin deprivation in *Arabidopsis* shoots under the stressed conditions may be due to IPT gene repression and/or cytokinin oxidase/dehydrogenase (CKX) activation and decreased transport of CKs (Nishiyama et al. 2011). Tobacco plants exhibiting a constitutive overexpression of CKX, which is associated with an enlarged root system and dwarf, stunted shoots, confers enhanced tolerance to both drought and heat stresses (Macková et al. 2013). Moreover, targeting of CKX overexpression to the roots using the WRKY6 promoter, which avoided the negative impacts on shoot growth, also resulted in enhanced stress tolerance. Therefore, the results obtained by Macková et al. 2013 demonstrate the importance of tissue and time dependent gene activation in responses to stresses. However, this assumption cannot fully explain the enhanced stress tolerance because some other dwarf mutants do not exhibit this feature; for instance, the *Arabidopsis* small ubiquitin-like

modifier (SUMO) E3 ligase *siz1* mutant, which is dwarf but sensitive to drought stress (Catala et al. 2007).

Studies about CK role in halophytic plants are very scarce. Nevertheless, CKs applications on halophytes could improve the stress tolerance. Treatment with applied CKs, as 6-Benzylaminopurine (BAP) to nutrient solution in hydroponic culture of *M. crystallinum* increased the expression of CAM metabolism key enzyme, PEPCase, which was correlated with the increase of NaCl added to culture medium; thus, exogenous cytokinin could mimic salt-induced responses, greatly increasing PEPCase, proline, ononitol, pinitol, and osmotin (Thomas and Bohnert 1993). Contrary, studies in *P. strombulifera* plants showed that CK accumulation, measure as kinetin, varies when different types of salts are present in the culture medium. In fact, leaves of Na₂SO₄-treated plants at high salinity (−2.6 MPa) showed the highest accumulation of this hormone, which may explain the high transpiration previously observed in these plants, in spite of the high ABA levels (Llanes et al. 2013). Moreover, the low transpiration observed in leaves of NaCl-treated halophyte *P. strombulifera* plants was correlated with their low zeatin (Llanes et al. 2014). Similarly, studies with the halophytes *Suaeda depressa* and *S. maritima* under water stress and CKs treated suggest that this hormone may increase the symptoms associated with water stress (Boucaud and Ungar 1976). This could be the result of the influence of CK on stimulating stomatal opening, thus facilitating transpiration, and therefore magnifying the effect of salt stress. (All together, these studies support the idea that CKs are negative regulators of stress tolerance in halophytic plants.

Auxins

Similarly to CKs, auxins act as endogenous regulators whose concentrations can be environmentally modulated to regulate the formation of roots and shoots and their relative growth (Sachs 2005). It has been demonstrated that auxins cooperate with CKs in the regulation of cell cycle progression and is also an essential regulator of cell expansion (Jurado et al. 2010). Plant growth responses under environmental stresses are also influenced by auxins, and subsequent perturbation in auxins homeostasis can lead to altered growth and development. These stress-induced morphogenic responses are considered to be part of a general acclimation strategy that prevents or attenuates the deleterious effects of environmental stresses (Potters et al. 2009; Tognetti et al. 2012).

Auxin biosynthetic pathways are based on identified intermediates, genetic studies, and in vitro assays. It has been proposed one tryptophan (Trp)-independent and four Trp-dependent pathways: the indole-3-acetamide (IAM) pathway, the indole-3-acetaldoxime (IAOx) pathway, the tryptamine

(TAM) pathway, and the indole-3-pyruvic acid (IPA) pathway (Woodward and Bartel 2005). However, the TAM and IPA pathways have been suggested as relevant to plant development. In addition, several auxin's actions are mediated by transcription factors of the auxin response factor (ARF) family, and several ARFs play critical roles in lateral root development (Wilmoth et al. 2005). Recently, Marin et al. (2010) have demonstrated that micro RNAs miR390 and *TAS3*, and their *ARFs* targets define a regulatory network quantitatively controlling lateral root growth. This complex network acts to fine-tune local auxin responses and thus provides robustness and flexibility to lateral root growth. However, the auxin-responsive genes involved in these environmental stress-dependent growth responses are still unidentified.

Auxin homeostasis, including auxin distribution and metabolism, is altered by a wide variety of abiotic stresses. Two possible molecular mechanisms have been suggested for altered distribution of auxin under stress: first, altered expression of PIN genes, which mediate polar auxin transport; and second, inhibition of polar auxin transport by phenolic compounds accumulated in response to stress exposure (Potters et al. 2009). On the other hand, auxin metabolism is modulated by oxidative degradation of IAA catalyzed by peroxidases, which in turn are induced by different stress conditions (Jain and Khurana 2009). Therefore, auxins could also act as stress hormones directly or indirectly, altering the expression of several stress-responsive genes, although validation of this assumption requires further experimentation. Among the most important functions of auxin in plants is the formation of lateral roots, which is of special significance to plant growth under different conditions including stress. The initiation of lateral roots plays a crucial role in plant development, since it determines the architecture of the root system and, thus, stability as well as nutrient and water uptake potential for the entire organism. Lateral root development is a typical example of a canalized developmental process (i.e., buffered against perturbation; Siegal and Bergman 2002), yet roots strongly adapt to the local environment to maximize acquisition of water and nutrients from the soil. In recent years, it has become clear that lateral roots initiate from a small number of pericycle cells (initiation) that differentiate into a primordia and grow out of the primary root (emergence) (De Smet et al. 2006). Auxin is a morphogenetic trigger for lateral root formation and its local maximum acts as an instructive signal for initiation of these organs (Wilmoth et al. 2005). This involvement of IAA (indole acetic acid) on the physiological responses of roots to stress was also observed in two halophytic species, *Suaeda fruticosa* and *Atriplex halimus* growing under Cd²⁺ stress. The exposition to Cu²⁺ alone or in combination with NaCl increased significantly the IAA concentration in roots of both species, although to a major extent in *S. fruticosa* (Bankaji et al. 2014). This response is probably related to the induction and growth of new roots that could cope

with stress (Dat et al. 2004). It is interesting to note that there is also an oxygen-requiring step in IAA biosynthesis, the conversion from indole-3-acetaldehyde to IAA catalyzed by an oxidase (Arbona and Gómez-Cadenas 2008). Therefore, data seem to indicate that no oxygen depletion in the culture medium was induced by the stress conditions imposed by Cu^{2+} and NaCl. However, to deeply understand the requirements of oxygen in the hormone biosynthesis in plants intoxicated by different trace elements or different salts in the culture medium, further work is required. Studies in *P. strombulifera* show that in roots of Na_2SO_4 -treated plants the high level of IAA is in relation with increased lateral root formation (Reinoso et al. 2005). However, NaCl treated *P. strombulifera* plants showed low IAA content in the roots. These plants did not show lateral roots formation and the characteristics anatomical and histological of the roots were similar to those registered in the roots of control plants (Reinoso et al. 2004). Thus, IAA levels are related to the lateral roots formation. Finally, these results suggest the involvement of IAA signaling in the physiological responses of *P. strombulifera* roots to salt stress. Therefore, the modulation of IAA levels in roots of halophytic plants may be an attractive approach for conferring protection against salinity conditions.

Polyamines

Polyamines are small organic cations essential for eukaryotic cell growth. They are not phytohormones, but they have been proposed as a new category of plant growth regulators that are purported to be involved in a wide variety of physiological processes (Liu et al. 2007). The biological functions of polyamines (PAs) were initially associated with their ability to bind anionic macromolecules, and thus they were considered to be polycations with unique structural roles. Recent studies showed that PAs also act as regulatory molecules in fundamental cellular processes, including cell division, differentiation, gene expression, DNA and protein synthesis (Igarashi and Kashiwagi 2010; Alcázar et al. 2010). In plants, PAs are implicated in physiological processes including organogenesis, embryogenesis, floral initiation and development, leaf senescence, pollen tube growth, fruit development and ripening. In addition, they have been shown to be an integral part of plant stress response (Bouchereau et al. 1999; Walters 2003; Alcázar et al. 2006). The three main PAs in plants are putrescine (Put), spermidine (Spd), and spermine (Spm). Less common PAs, but frequently found in plants, are diaminopropane (Dap) and cadaverine (Cad).

Stressful conditions alter the PAs levels, particularly Put, with variation depending on type of stress, plant species, and time of exposure (Ali 2000). However, a stress-induced activation of the complete pathway of PA biosynthesis with the accumulation of Spd and Spm is observed relatively

infrequently (Tiburcio et al. 1994). Homeostasis in plants is achieved by modulation of PA biosynthesis, conjugation, catabolism, and transport. However, recent data indicate that such mechanisms are not mere modulators of PA pools but actively participate in PA functions (Tiburcio et al. 2014).

Studies performed in glycophytes have demonstrated that PAs applications and transgenic plants with overproduced PAs showed protective roles of polyamines under abiotic stress conditions, while reduced *in vivo* PA levels result in decreased stress tolerance (Alcázar et al. 2011; Alet et al. 2012). Thus, protective roles have been proposed for PAs in stress tolerance of glycophytic plants (Minocha et al. 2014, Liu et al. 2015, Pál et al. 2015); they regulate cation transport across plant membrane (Pottosin et al. 2014), control senescence and programmed cell death (Del Duca et al. 2014), act as free radical scavengers (Alcázar et al. 2010) and directly or indirectly regulate gene expression (Lutts et al. 2013). Such processes may occur separately, or be combined in a unified strategy to minimize membrane damage, promote cell growth, and enhance cell survival in response to stress (Liu et al. 2007).

In halophytes, accumulation of PAs seems to be a very important factor for their protection and tolerance to salinity. Shevyakova et al. (2006) found that the diamine oxidase (DAO)- H_2O_2 -peroxidase system in leaves and roots of the halophyte *Mesembryanthemum crystallinum* is involved in the regulation of free PAs and conjugated forms of PAs levels under salinity. In addition, PA conjugates per se can be used as electron donors in reactions of H_2O_2 -detoxification. In the halophyte *P. strombulifera* an important accumulation of PAs under salt stress (NaCl and Na_2SO_4) was found. Put was the major PA accumulated. Na_2SO_4 -treated plants mainly accumulate Put, Spd and Spm in roots at -1 MPa (Reginato et al. 2012), in correlation with higher H_2O_2 and malondialdehyde (MDA) levels in these plants (Reginato et al. 2014). NaCl-treated plants showed high Put level in leaves, whereas Na_2SO_4 -treated plants presented low Put level. These low Put levels were directly correlated with inhibition of shoot growth in Na_2SO_4 -treated plants at -1.9 and -2.6 MPa, and possibly associated with a general metabolic alteration caused by SO_4^{2-} anion (Reginato et al. 2014). These results in *P. strombulifera* showed a role for Put in NaCl tolerance in this halophyte. Alternatively, the low Spd level in *P. strombulifera* leaves suggested a rapid degradation of this amine to Put, as part of an interconversion pathway well known in animals and also characterized in higher plants (Reginato et al. 2012). Biosynthesis of uncommon PAs such as 1,3 Diaminopropano (Dap), Cadaverina (Cad), and others, has been associated with the capacity of some organisms to grow or function under extreme conditions (Flores 1991). In *P. strombulifera* accumulation of Dap was much higher in leaves than in roots, with maximal values at low (-1.0 MPa) and moderate (-1.9 MPa) salinity for all treatments (Reginato et al. 2012). Dap result from the catabolism of PAs by the

presence of polyamine oxidases (PAOs) acting on Spd. The view of PA catabolism has shifted from a mere mechanism for regulating PA levels to a participative metabolic pathway in response to different types of abiotic, biotic, and developmental signals. Duhazé et al. (2002) reported accumulation of Dap and Put by catabolism of Spd in various halophytic species of the genus *Limonium*. The specific effect of Dap is poorly understood, but may involve biosynthesis of uncommon PAs and/or β -alanine, via an oxidative deamination pathway in some species (Cohen 1998). Cad was found in *P. strobilifera* mainly in roots and its levels significantly increased in response to Na_2SO_4 (Reginato et al. 2012). The diamine Cad (1.5-diaminopentane) is a lysine catabolite which also influences plant growth and development (Tomar et al. 2013). Cad in roots has been associated with cell elongation and formation of adventitious roots, similarly to Put (Shevyakova et al. 2001; Carrizo et al. 2001). Under stress conditions, Cad accumulation in plants has been proposed to compensate a decrease in the content of the Put-family PAs; its accumulation in roots of Na_2SO_4 -treated *P. strobilifera* may be a stress symptom rather than an adaptative response (Reginato et al. 2012).

All these studies indicate that polyamines are involved in plant abiotic stress responses, and genetic manipulation of the polyamine biosynthetic and metabolic pathways related genes can be an effective approach for the development of stress tolerant plants.

Conclusions

The understanding of the complex mechanism of salt responses in halophytes could lead to the generation of more salt tolerant crops. In this review, we summarize several findings that broaden our knowledge about phytohormones role in modulating salt stress responses in halophytes. These plants are of significant interest since they are naturally present in environments with an excess of toxic ions. Several studies suggest that halophytes can also tolerate other environmental stresses, and their salt tolerance may, at least partly, rely on common physiological mechanisms. Under these considerations, halophytes are potentially ideal plants to investigate the particular role of each phytohormone more deeply.

From the state of the art, it can be concluded that changes in phytohormone levels in halophytic plant tissues would be an initial process regulating plant growth and development under salinity conditions. Therefore, salinity induced plant responses could be either mitigated or enhanced by exogenous applications or genetic modifications of phytohormone levels. Recently, different mechanisms underlying phytohormone signaling pathways have been described, leading to the elucidation of partial or entire hormonal signaling cascades and their cross-talk. However, most of studies on phytohormone

action are based on exogenous applications and/or genetic manipulation through biotechnological tools applied to glycophytes growing in salinity conditions. Thus, knowledge about how the endogenous hormone levels are affected in halophytes in response to salinity still remains scarce. Further studies should be performed to determinate each phytohormone role and the cross-talk between their signal pathways in halophytes, in order to improve our understanding about the mechanisms by which phytohormones regulate salinity stress responses in these species.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

References

- Abeles FB, Morgan PW, Saltveit ME (1992) Ethylene in plant biology, 2nd edn. Academic Press, New York
- Achard P, Cheng H, De Grauwe L, Decat J, Schoutteten H, Moritz T (2006) Integration of plant responses to environmentally activated phytohormonal signals. *Science* 311:91–94. <https://doi.org/10.1126/science.1118642>
- Achard P, Baghour M, Chapple A, Hedden P, Van der Straeten D, Genschik P, Moretz T, Harberd NP (2007) The plant stress hormone ethylene controls floral transition via DELLA-dependent regulation of floral meristem-identity genes. *Proc Natl Acad Sci U S A* 104: 6484–6489. <https://doi.org/10.1073/pnas.0610717104>
- Adams P, Nelson DE, Yamada S, Chmara W, Jensen RG, Bohnert HJ, Griffiths H (1998) Growth and development of *Mesembryanthemum crystallinum* (Aizoaceae). *New Phytol* 138: 171–190
- Alcázar R, Marco F, Cuevas JC, Patron M, Ferrando A, Carrasco P (2006) Involvement of polyamines implant response to abiotic stress. *Biotechnol Lett* 28:1867–1876
- Alcázar R, Altabella T, Marco F, Bortolotti C, Reymond M, Koncz C, Carrasco P, Tiburcio AF (2010) Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. *Planta* 231:1237–1249. <https://doi.org/10.1007/s00425-010-1130-0>
- Alcázar R, Cuevas JC, Planas J, Zarza X, Bortolotti C, Carrasco P (2011) Integration of polyamines in the cold acclimation response. *Plant Sci* 180:31–38. <https://doi.org/10.1016/j.plantsci.2010.07.022>
- Alet AI, Sánchez DH, Cuevas JC, Marina M, Carrasco P, Altabella T, Tiburcio AF, Ruiz OA (2012) New insights into the role of spermine in *Arabidopsis thaliana* under long-term salt stress. *Plant Sci* 182: 94–100. <https://doi.org/10.1016/j.plantsci.2011.03.013>
- Al-Hakimi AMA, Hamada AM (2001) Counteraction of salinity stress on wheat plants by grain soaking in ascorbic acid, thiamin or sodium salicylate. *Biol Plant* 44:253–261. <https://doi.org/10.1023/A:1010255526903>
- Ali R (2000) Role of putrescine in salt tolerance of *Atropa belladonna* plant. *Plant Sci* 152:173–179. [https://doi.org/10.1016/S0168-9452\(99\)00227-7](https://doi.org/10.1016/S0168-9452(99)00227-7)
- Ali A, Yun DJ (2017) Salt stress tolerance; what do we learn from halophytes? *J Plant Biol* 60(5):431–439. <https://doi.org/10.1007/s12374-017-0133-9>
- Arbona V, Gómez-Cadenas A (2008) Hormonal modulation of citrus responses to flooding. *J Plant Growth Regul* 27:241–250. <https://doi.org/10.1007/s00344-008-9051-x>

- Arbona V, Argamasilla R, Gómez-Cadenas A (2010) Common and divergent physiological, hormonal and metabolic responses of *Arabidopsis thaliana* and *Thellungiella halophila* to water and salt stress. *J Plant Physiol* 167:1342–1350
- Atzori G, de Vos AC, van Rijsselberghe M, Vignolini P, Rozema J, Mancuso S, van Bodegom PM (2017) Effect of increased seawater salinity irrigation on growth and quality of the edible halophyte *Mesembryanthemum crystallinum* L. under field conditions. *Agric Water Manag* 187:37–46. <https://doi.org/10.1016/j.agwat.2017.03.020>
- Bankaji I, Sleimi N, López-Climent MF, Perez-Clemente RM, Gomez-Cadenas A (2014) Effects of combined abiotic stresses on growth, trace element accumulation, and phytohormone regulation in two halophytic species. *J. Plant Growth Regul.* 33:632–643. <https://doi.org/10.1007/s00344-014-9413-5>
- Black M (2016) The atlas of water: mapping the World's most critical resource, 3rd edn. University of California Press, Oakland
- Boucaud J, Ungar JA (1976) Hormonal control of germination under saline conditions of three halophytic taxa in the genus *Suaeda*. *Physiol Plant* 37:143–148
- Bouchereau A, Aziz A, Larher F, Martin-Tanguy J (1999) Polyamines and environmental challenges: recent development. *Plant Sci* 140: 103–125. [https://doi.org/10.1016/S0168-9452\(98\)00218-0](https://doi.org/10.1016/S0168-9452(98)00218-0)
- Brossa R, López-Carbonell M, Jubany-Mari T, Alegreet L (2011) Interplay between abscisic acid and Jasmonic acid and its role in water-oxidative stress in wild-type, ABA-deficient, JA-deficient, and ascorbate-deficient *Arabidopsis* plants. *J Plant Growth Regul* 30:322–333
- Brown JJ, Glenn EP (1999) Reuse of highly saline aquaculture effluent to irrigate a potential forage halophyte, *Suaeda esteroa*. *Aquac Eng* 20(2):91–111. <https://doi.org/10.1007/s00344-011-9194-z>
- Carrizo C, Pitta-Alvarez S, Kogan M, Giulietti A, Tomaro M (2001) Occurrence of cadaverine in hairy roots of *Brugmansia candida*. *Phytochem* 57:759–763. [https://doi.org/10.1016/S0031-9422\(01\)00127-3](https://doi.org/10.1016/S0031-9422(01)00127-3)
- Catala R, Ouyang J, Abreu IA, Hu Y, Seo H, Zhang X, Chua N-H (2007) The *Arabidopsis* E3 SUMO ligase SIZ1 regulates plant growth and drought responses. *Plant Cell* 19:2952–2966
- Chakrabarti N, Mukherji S (2003) Effect of phytohormone pretreatment on nitrogen metabolism in *Vigna radiata* under salt stress. *Biol Plant* 46:63–66. <https://doi.org/10.1023/A:1022358016487>
- Chen H, Edwards GE (1991) Influence of long photoperiods on plant development and expression of Crassulacean acid metabolism in *Mesembryanthemum crystallinum*. *Plant Cell Environ* 14:271–278
- Chen H, Jones AD, Howe GA (2006) Constitutive activation of the jasmonate signaling pathway enhances the production of secondary metabolites in tomato. *FEBS Lett* 580:2540–2546
- Chen H, Zhang J, Neff MM, Hong SW, Zhang H, Deng XW, Xiong L (2008) Integration of light and abscisic acid signaling during seed germination and early seedling development. *Proc Natl Acad Sci U S A* 105:4495–4500. <https://doi.org/10.1111/j.1365-3040.1991.tb01501.x>
- Chrominsky A, Visscher-Neumann S, Jurenka R (1986) Exposure to ethylene changes nymphal growth rate and female longevity in the grasshopper *Melanaphis sanguinipes*. *Naturwissenschaften* 69:45–66
- Chu (1990) Induction of Crassulacean acid metabolism in the facultative halophyte *Mesembryanthemum crystallinum* by abscisic acid. *Plant Physiol* 93:1253–1260. <https://doi.org/10.1104/pp.93.3.1253>
- Cohen SS (1998) A guide to the polyamines. Oxford University Press, Oxford
- Cornforth JW, Milborrow BV, Dryback G (1965) Synthesis of (±)-abscisic acid. *Nature* 206:715
- Clipson N, Lachno D, Flowers T (1988) Salt tolerance in the halophyte *Suaeda maritima* L. Dum.: abscisic acid concentrations in response to constant and altered salinity. *J Exp Bot* 39:1381–1388
- Danilova MN, Kudryakova NV, Doroshenko AS, Zabrodin DA, Vinogradov NS, Kuznetsov VV (2016) Molecular and physiological responses of *Arabidopsis thaliana* plants deficient in the genes responsible for ABA and cytokinin reception and metabolism to heat shock. *Russ J Plant Physiol* 63(3):308–318. <https://doi.org/10.1134/S1021443716030043>
- Danquah A, de Zelicourt A, Colcombet J, Hirt H (2014) The role of ABA and MAPK signalling pathways in plant abiotic stress responses. *Biotechnol Adv* 32(1):40–52. <https://doi.org/10.1016/j.biotechadv.2013.09.006>
- Dat JF, Capelli N, Folzer H, Bourgeade P, Badot PM (2004) Sensing and signalling during plant flooding. *Plant Physiol Biochem* 42:273–282
- De Smet I, Vanneste S, Inzé D, Beeckman T (2006) Lateral root initiation or the birth of a new meristem. *Plant Mol Biol* 60:871–888. <https://doi.org/10.1007/s11103-005-4547-2>
- Del Amor F, Cuadra-Crespo P (2011) Plant growth-promoting bacteria as a tool to improve salinity tolerance in sweet pepper. *Funct Plant Biol* 39(1):82–90. <https://doi.org/10.1071/FP11173>
- Del Duca S, Serafini-Fracassini D, Cai G (2014) Senescence and programmed cell death in plants: polyamine action mediated by transglutaminase. *Front Plant Sci* 5:120–129. <https://doi.org/10.3389/fpls.2014.00120>
- Dempsey DMA, Vlot AC, Wildermuth MC, Klessig DF (2011) Salicylic acid biosynthesis and metabolism. *The Arabidopsis Book* 9:e0156. <https://doi.org/10.1199/tab.0156>
- Devinar G, Llanes A, Luna V (2013) Abscisic acid and salicylic acid levels induced by different relative humidity and salinity conditions in the halophyte *Prosopis strombulifera*. *Plant Growth Regul* 70(3): 247–256. <https://doi.org/10.1007/s10725-013-9796-5>
- Duan L, Dietrich D, Ng CH, Chan PM, Bhalerao R, Bennett MJ (2013) Endodermal ABA signaling promotes lateral root quiescence during salt stress in *Arabidopsis* seedlings. *Plant Cell* 25:324–341. <https://doi.org/10.1105/tpc.112>
- Duhazé C, Gouzerh G, Gagneul D, Larher F, Bouchereau A (2002) The conversion of spermidine to putrescine and 1,3 diaminopropane in the roots of *Limonium tataricum*. *Plant Sci* 163:639–646. [https://doi.org/10.1016/S0168-9452\(02\)00172-3](https://doi.org/10.1016/S0168-9452(02)00172-3)
- Eganathan PSR, Subramanian HM, Latha R, Srinivasa Rao C (2006) Oil analysis in seeds of *Salicornia brachiata*. *Ind Crop Prod* 23:177–179. <https://doi.org/10.1016/j.indcrop.2005.05.007>
- El Shaer HM (2010) Halophytes and salt-tolerant plants as potential forage for ruminants in the near east region. *Small Rumin Res* 91:3–12
- Ellouzi H, Hamed KB, Hernández I, Cela J, Muller M, Magne C (2014) A comparative study of the early osmotic, ionic, redox and hormonal signaling response in leaves and roots of two halophytes and a glycophyte to salinity. *Planta* 240:1299–1317. <https://doi.org/10.1007/s00425-014-2154-7>
- FAO, (2016) FAOSTAT. Food and Agriculture Organization of the United Nations, Rome, Italy. Web. <http://faostat.fao.org/default.aspx>. Accessed 20 June 2017
- Flores HE (1991) Changes in polyamine metabolism in response to abiotic stress. In: Slocum RD, Flores HE (eds) *Biochemistry and physiology of polyamines in plants*. CRC Press, Boca Raton, pp 213–228
- Flowers TJ, Colmer TD (2008) Salinity tolerance of halophytes. *New Phytol* 179:945–963. <https://doi.org/10.1111/j.1469-8137.2008.02531.x>
- Flowers TJ, Galal HK, Bromham L (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. *Funct Plant Biol* 37:604–612. <https://doi.org/10.1071/FP09269>
- Gharat SA, Parmar S, Tambat S, Vasudevan M, Shaw BP (2016) Transcriptome analysis of the response to NaCl in *Suaeda maritima* provides an insight into salt tolerance mechanisms in halophytes. *PLoS one* 11:e0163485

- Gómez-Cadenas A, Zentella R, Walker-Simmons MK, Ho TH (2001) Gibberellin/abscisic acid antagonism in barley aleurone cells: site of action of the protein kinase PKABA1 in relation to gibberellin signaling molecules. *Plant Cell* 13:667–679. <https://doi.org/10.1105/tpc.13.3.667>
- Gong Q, Li P, Ma S, Rupassara SI, Bohnert HJ (2005) Salinity stress adaptation competence in the extremophile *Thellungiella halophila* in comparison with its relative *Arabidopsis thaliana*. *Plant J* 44:826–839. <https://doi.org/10.1111/j.1365-313X.2005.02587.x>
- Guo W, Cong Y, Hussain N, Wang Y, Liu Z, Jiang L (2014) The remodeling of seedling development in response to long-term magnesium toxicity and regulation by ABA-DELTA signaling in *Arabidopsis*. *Plant Cell Physiol* 55:1713–1726. <https://doi.org/10.1093/pcp/pcu102>
- Guo D, Zhou Y, Li HL, Zhu JH, Wang Y, Chen XT, Peng SQ (2017) Identification and characterization of the abscisic acid (ABA) receptor gene family and its expression in response to hormones in the rubber tree. *Sci Rep* 7:451–457. <https://doi.org/10.1038/srep45157>
- Guralnick LJ, Ku MSB, Edwards GE, Strand D, Hockema B (2001) Induction of PEP carboxylase and crassulacean acid metabolism by gibberellin acid in *Mesembryanthemum crystallinum*. *Plant Cell Physiol* 42:236–239. <https://doi.org/10.1093/pcp/pce020>
- Hao L, Zhao Y, Jin D, Zhang L, Bi X, Chen H, Xu Q, Ma C, Li G (2012) Salicylic acid altering *Arabidopsis* mutants response to salt stress. *Plant Soil* 354:81–95. <https://doi.org/10.1007/s11104-011-1046-x>
- Hauser F, Horie T (2010) A conserved primary salt tolerance mechanism mediated by HKT transporters: a mechanism for sodium exclusion and maintenance of high K⁺/Na⁺ ratio in leaves during salinity stress. *Plant Cell Environ* 33:552–565. <https://doi.org/10.1111/j.1365-3040.2009.02056.x>
- Hedden P, Thomas GS (2012) Gibberellin biosynthesis and its regulation. *Biochem J* 444:11–25. <https://doi.org/10.1042/BJ20120245>
- Horvath E, Szalai G, Janda T (2007) Induction of abiotic stress tolerance by salicylic acid signalling. *J Plant Growth Regul* 26:290–300. <https://doi.org/10.1007/s00344-007-9017-4>
- Igarashi K, Kashiwagi K (2010) Modulation of cellular function by polyamines. *Int J Biochem Cell Biol* 42(1):39–51. <https://doi.org/10.1016/j.biocel.2009.07.009>
- Iqbal M, Ashraf M, Jamil A (2006) Seed enhancement with cytokinins: changes in growth and grain yield in salt stressed wheat plants. *Plant Growth Regul* 50:29–39
- Iqbal M, Ashraf M (2010) Changes in hormonal balance: a possible mechanism of pre-sowing chilling-induced salt tolerance in spring wheat. *J Agron Crop Sci*. <https://doi.org/10.1111/j.1439-037X.2010.00434.x>
- Iqbal N, Nazar R, Khan MIR, Masood A, Khan NA (2011) Role of gibberellin in regulation of source-sink relation under optimal and limiting environmental conditions. *Curr Sci* 100:7–10
- Jain M, Khurana JP (2009) Transcript profiling reveals diverse roles of auxin-responsive genes during reproductive development and abiotic stress in rice. *FEBS J* 276:3148–3162. <https://doi.org/10.1111/j.1742-4658.2009.07033.x>
- Jurado S, Abraham Z, Manzano C, López-Torrejón G, Pacios LF, Del Pozo JC (2010) The *Arabidopsis* cell cycle F box protein SKP2A binds to auxin. *Plant Cell* 22:3891–3904. <https://doi.org/10.1105/tpc.110.078972>
- Kang D-J, Seo Y-J, Lee J-D, Ishiri R, Kim K-U, Shin D-H, Park S-K, Jang S, Lee I (2005) Jasmonic acid differentially affect growth, ion uptake and abscisic acid in salt tolerance and salt sensitive rice culture. *J Agron Crop Sci* 191:273–282. <https://doi.org/10.1111/j.1439-037X.2005.00153.x>
- Ke-fu Z, Mingliang L, Jiayao L (1986) Reduction by GA3 of NaCl-induced inhibition of growth and development in *Suaeda ussuriensis*. *Aust J Plant Physiol* 13:547–551. <https://doi.org/10.1071/PP9860547>
- Kendrick MD, Chang C (2008) Ethylene signaling: new levels of complexity and regulation. *Curr Opin Plant Biol* 11:479–485. <https://doi.org/10.1016/j.pbi.2008.06.011>
- Khan MA, Gul B, Weber DJ (2000) Germination responses of *Salicornia rubra* to temperature and salinity. *J Arid Environ* 45:207–214. <https://doi.org/10.1006/jare.2000.0640>
- Khan MA, Ansari R, Gul B, Li W (2009) Dormancy and germination responses of halophyte seeds to the application of ethylene. *C R Biol* 332:806–815. <https://doi.org/10.1016/j.crvi.2009.05.002>
- Kim H, Hwang H, Hong JW, Lee YN, Ahn IP, Yoon IS, Yoo SD, Lee S, Lee SC, Kim BG (2012) A rice orthologue of the ABA receptor, OsPYL/RCAR5, is a positive regulator of the ABA signal transduction pathway in seed germination and early seedling growth. *J Exp Bot* 63:1013–1024
- Koyro HW, Lieth H (2008) Global water crisis: the potential of cash crop halophytes to reduce the dilemma. In: Lieth H, Garcia SM, Herzog B (eds) *Mangroves and halophytes: restoration and utilization*. Tasks for vegetation science, vol 43. Springer, Dordrecht, pp 7–19
- Koyro HW, Khan MA, Lieth H (2011) Halophytic crops: a resource for the future to reduce the water crisis? *Emir J Food Agric* 23:1–16
- Krishnamurthy P, Mohanty B, Wijaya E, Lee D, Lim T, Lin Q, Xu J, Loh C, Kumar P (2017) Transcriptomics analysis of salt stress tolerance in the roots of the mangrove *Avicennia officinalis*. *Sci Rep* 7:10031
- Kudoyarova GR, Vysotskaya LB, Cherkozyanova A, Dodd IC (2007) Effect of partial rootzone drying on the concentration of zeatin-type cytokinins in tomato (*Solanum lycopersicum* L.) xylem sap and leaves. *J Exp Bot* 58:161–168
- Kuznetsov V, Kruglova AG, Molodyuk OI, Karyagin VV, Mescheryakov AB, Ragulin VV, Rakitin V, Kholodova FVP (2003) Hormonal regulation of crassulacean acid metabolism (CAM) and inter-organ stress signal transduction. *Phytohormones in Plant Biotechnology and Agriculture*, Kluwer Academic Publishers, Dordrecht, pp 95–203
- Lange M, Knop N, Lange T (2011) Stamen derived bioactive gibberellin is essential for male flower development of *Cucurbita maxima* L. *J Exp Bot* 63:2681–2691
- Li ZR, Li G, Qin P (2010) The prediction of ecological potential for developing salt-tolerant oil plants on coastal saline land in Sheyang Saltern. *China Ecol Eng* 36:27–35. <https://doi.org/10.1016/j.ecoleng.2009.09.006>
- Lieth H (2000) Cashcrop halophytes for future halophyte growers. EU concerted action project IC 18CT96-0055, final meeting at the beginning of the EXPO 2000. Institute of Environmental Systems Research, University of Osnabrück, Germany. ISSN 09336-3114-20
- Liu J, Kitashiba H, Wang J, Ban Y, Moriguchi T (2007) Polyamines and their ability to provide environmental tolerance to plants. *Plant Biotechnol* 24:117–126. <https://doi.org/10.5511/plantbiotechnology.24.117>
- Liu JH, Wang W, Wu H, Gong X, Moriguchi T (2015) Polyamines function in stress tolerance: from synthesis to regulation. *Front Plant Sci* 6:827–830. <https://doi.org/10.3389/fpls.2015.00827>
- Llanes A, Bertazza G, Palacio G, Luna V (2013) Different sodium salts cause different solute accumulation in the halophyte *Prosopis strombulifera*. *Plant Biol* 15:118–125. <https://doi.org/10.1111/j.1438-8677.2012.00626.x>
- Llanes A, Masciarelli O, Ordoñez R, Isla MI, Luna V (2014) Differential growth responses to sodium salts involve different ABA catabolism and transport in the halophyte *Prosopis strombulifera*. *Biol Plant* 58:80–88. <https://doi.org/10.1007/s10535-013-0365-6>
- Lutts S, Hausman JF, Quinet M, Lefèvre I (2013) Polyamines and their roles in the alleviation of ion toxicities in plants. *Ecophysiology and responses of plants under salt stress* Springer, New York, NY, pp 315–353
- Macková J, Vasková M, Macek P, Hronková M, Schreiber L, Santrucek J (2013) Plant response to drought stress simulated by ABA application: changes in chemical composition of cuticular waxes. *Environ*

- Exp Bot 86:70–75. <https://doi.org/10.1016/j.envexpbot.2010.06.005>
- Macri F, Vianello A, Pennazio S (1986) Salicylate-collapsed membrane potential in pea stem mitochondria. *Physiol Plant* 67:136–140. <https://doi.org/10.1111/j.1399-3054.1986.tb02434.x>
- Manousaki E, Kalogerakis N (2011) Halophytes: an emerging trend in phytoremediation. *Int J Phytoremediation* 13:959–969. <https://doi.org/10.1080/15226514.2010.532241>
- Marin E, Jouannet V, Herz A, Lokerse AS, Weijers D, Vaucheret H, Nussaume L, Crespi MD, Maizel A (2010) miR390, *Arabidopsis* TAS3 tasiRNAs, and their *AUXIN RESPONSE FACTOR* targets define an autoregulatory network quantitatively regulating lateral root growth. *Plant Cell* 22:1104–1117. <https://doi.org/10.1105/tpc.109.072553>
- Martineau B, Houck CM, Sheehy RE, Hiatt WR (1994) Fruit-specific expression of the *A. tumefaciens* isopentenyltransferase gene in tomato: effects on fruit ripening and defense-related gene expression in leaves. *Plant J* 5:11–19
- Miersch O, Neumerkel J, Dippe M, Stenzel I, Wasternack C (2008) Hydroxylated jasmonates are commonly occurring metabolites of jasmonic acid and contribute to a partial switch-off in jasmonate signaling. *New Phytol* 177:114–127. <https://doi.org/10.1111/j.1469-8137.2007.02252.x>
- Minocha R, Majumdar R, Minocha S (2014) Polyamines and abiotic stress in plants: a complex relationship I. *Front Plant Sci* 5:175
- Misra N, Saxena P (2009) Effect of salicylic acid on proline metabolism in lentil grown under salinity stress. *Plant Sci* 177:181–189. <https://doi.org/10.1016/j.plantsci.2009.05.007>
- Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651–681. <https://doi.org/10.1146/annurev.arplant.59.032607.092911>
- Nakashima K, Yamaguchi-Shinozaki K (2013) ABA signaling in stress-response and seed development. *Plant Cell Rep* 32:959–970. <https://doi.org/10.1007/s00299-013-1418-1>
- Nambara E, Marion-Poll A (2005) Abscisic acid biosynthesis and catabolism. *Annu Rev Plant Biol* 56:165–185
- Navarro L, Bari R, Achard P, Lison P, Nemri A, Harberd NP, Jones JDG (2008) DELLAs control plant immune responses by modulating the balance of jasmonic acid and salicylic acid signaling. *Curr Biol* 18:650–655. <https://doi.org/10.1016/j.cub.2008.03.060>
- Nir I, Shohat H, Panizel I, Olszewski N, Aharoni A, Weiss D (2017) The tomato DELLA protein PROCERA acts in guard cells to promote stomatal closure. *Plant Cell* 12:3186–3197. <https://doi.org/10.1105/tpc.17.00542>
- Nishiyama R, Watanabe Y, Fujita Y, Le DT, Kojima M, Werner T, Vankova R, Yamaguchi-Shinozaki K, Shinozaki K, Kakimoto T (2011) Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *Plant Cell* 23:2169–2183. <https://doi.org/10.1105/tpc.111.087395>
- Ozfidan-Konakci C, Uzilday B, Ozgur R, Yildiztugay E, Sekmen AH, Turkan I (2016) Halophytes as a source of salt tolerance genes and mechanisms: a case study for the salt Lake area, Turkey. *Funct Plant Biol* 43:575–589. <https://doi.org/10.1071/FP15288>
- Pál M, Szalai G, Janda T (2015) Speculation: polyamines are important in abiotic stress signaling. *Plant Sci* 237:16–23
- Panda BB, Badoghar A, Das K, Panigrahi R, Kariali E, Das S (2015) Compact panicle architecture is detrimental for growth as well as sucrose synthase activity of developing rice kernels. *Funct Plant Biol* 42:875–887. <https://doi.org/10.1071/FP14363>
- Pearce S, Huttly AK, Prosser IM, Li YD, Vaughan SP, Gallova B, Phillips AL (2015) Heterologous expression and transcript analysis of gibberellin biosynthetic genes of grasses reveals novel functionality in the GA3ox family. *Plant Biol* 15:130–135. <https://doi.org/10.1186/s12870-015-0520-7>
- Pedranzani H, Racagni G, Alemano S, Miersch O, Ramirez I, Peña-Cortes H, Taleisnik E, Machado-Domenech E, Abdala G (2003) Salt tolerant tomato plants show increased levels of jasmonic acid. *Plant Growth Regul* 41:149–158. <https://doi.org/10.1023/A:1027311319940>
- Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. *Curr Opin Plant Biol* 14:290–295. <https://doi.org/10.1016/j.pbi.2011.02.001>
- Pieterse CMJ, Leon-Reyes A, Van der Ent S, Van Wees SCM (2009) Networking by small-molecules hormones in plant immunity. *Nat Chem Biol* 5:308–316. <https://doi.org/10.1038/nchembio.164>
- Poljakoff-Mayber A, Lerner HR (1994) Plants in saline environment. In: Pessaraki M (ed) *Handbook of plant and crop. Stress* Marcel Dekker, New York, pp 65–96
- Pospišilová J (2003) Participation of phytohormones in the stomatal regulation of gas exchange during water stress. *Biol Plant* 46(4):491–506. <https://doi.org/10.1023/A:1024894923865>
- Potters G, Pasternak TP, Guisez Y, Jansen MAK (2009) Different stresses, similar morphogenic responses: integrating a plethora of pathways. *Plant Cell Environ* 32:158–169. <https://doi.org/10.1111/j.1365-3040.2008.01908.x>
- Pottosin I, Velarde-Buendía AM, Bose J, Zepeda-Jazo I, Shabala S, Dobrovinskaya O (2014) Crosstalk between reactive oxygen species and polyamines in regulation of ion transport across the plasma membrane: implications for plant adaptive responses. *J Exp Bot* 65:1271–1283
- Reginato M, Abdala G, Miersch O, Ruiz O, Moschetti E, Luna V (2012) Changes in the levels of jasmonates and free polyamines induced by Na₂SO₄ and NaCl in roots and leaves of the halophyte *Prosopis strombulifera*. *Biologia* 67:689–697. <https://doi.org/10.2478/s11756-012-0052-7>
- Reginato M, Castagna A, Furlán A, Castro S, Ranieri A, Luna V (2014) Analysis of the oxidative damage in the halophyte *Prosopis strombulifera* salinized with NaCl and Na₂SO₄. Role of polyphenols as antioxidant protection. *AoB Plants* 6(Special Issue: Physiology and ecology of halophytes plants living in salt-rich environments). <https://doi.org/10.1093/aobpla/plu042>
- Reinbothe C, Springer A, Samol I, Reinbothe S (2009) Plant oxylipins: role of jasmonic acid during programmed cell death, defence and leaf senescence. *FEBS J* 276:4666–4681. <https://doi.org/10.1111/j.1742-4658.2009.07193.x>
- Reinoso H, Sosa L, Ramírez L, Luna V (2004) Salt-induced changes in the vegetative anatomy of *Prosopis strombulifera* (Leguminosae). *Can J Bot* 82:618–628. <https://doi.org/10.1139/b04-040>
- Reinoso H, Sosa L, Reginato M, Luna V (2005) Histological alterations induced by sodium sulphate in the vegetative anatomy of *Prosopis strombulifera* (Lam.) Benth. *World J Agric Sci* 1:109–119
- Rejeb IB, Pastor V, Mauch-Mani B (2014) Plant responses to simultaneous biotic and abiotic stress: molecular mechanisms. *Plants* 3:458–475. <https://doi.org/10.3390/plants3040458>
- Rivero RM, Gimeno J, Van Deynze A, Walia H, Blumwald E (2010) Enhanced cytokinin synthesis in tobacco plants expressing PSARK:IPT prevents the degradation of photosynthetic protein complexes during drought. *Plant Cell Physiol* 51:1929–1941. <https://doi.org/10.1093/pcp/pcq143>
- Russell DW, Conn EE (1967) The cinnamic acid 4-hydroxylase of pea seedlings. *Arch Biochem Biophys* 122:256–258. [https://doi.org/10.1016/0003-9861\(67\)90150-6](https://doi.org/10.1016/0003-9861(67)90150-6)
- Ryu H, Cho YG (2015) Plant hormones in salt stress tolerance. *J Plant Biol* 58:147–155. <https://doi.org/10.1007/s12374-015-0103-z>
- Sachs T (2005) Auxin's role as an example of the mechanisms of shoot/root relations. *Plant Soil* 268:3–19. <https://doi.org/10.1007/s11104-004-0173-z>
- Sairam RK, Tyagi A (2004) Physiology and molecular biology of salinity stress tolerance in plants. *Curr Sci* 86:407–421

- Sakakibara H (2006) Cytokinins: activity, biosynthesis, and translocation. *Annu Rev Plant Biol* 57:431–449
- Sakakibara H, Kasahara H, Ueda N, Kojima M, Takei K (2005) Agrobacterium tumefaciens increases cytokinin production in plastids by modifying the biosynthetic pathway in the host plant. *Proc Natl Acad Sci U S A* 102:9972–9977
- Samiullah A, Bano A (2011) Evaluation of oxidative stress tolerance, growth responses, osmolites and phytohormonal estimation in selected halophytes. IACSIT Press, Singapore
- Sasaki-Sekimoto Y, Taki N, Obayashi T, Aono M, Matsumoto F, Sakurai N, Masuda T (2005) Coordinated activation of metabolic pathways for antioxidants and defence compounds by jasmonates and their roles in stress tolerance in Arabidopsis. *Plant J* 44:653–668
- Shah J, Chaturvedi R, Chowdhury Z, Venables B, Petros RA (2014) Signaling by small metabolites in systemic acquired resistance. *Plant J* 79:645–658. <https://doi.org/10.1111/tpj.12464>
- Shen X, Wang Z, Song X, Xu J, Jiang C, Zhao Y, Zhang H (2014) Transcriptomic profiling revealed an important role of cell wall remodeling and ethylene signaling pathway during salt acclimation in Arabidopsis. *Plant Mol Biology* 86:303–317
- Shevyakova N, Rakitin V, Duong D, Sadomov N, Kuznetsov V (2001) Heat shock-induced cadaverine accumulation and translocation throughout the plant. *Plant Sci* 161:1125–1133. [https://doi.org/10.1016/S0168-9452\(01\)00515-5](https://doi.org/10.1016/S0168-9452(01)00515-5)
- Shevyakova N, Rakitin V, Stetsenko L, Aronova E, Kuznersov V (2006) Oxidative stress and fluctuations of free and conjugated polyamines in the halophyte *Mesembryanthemum crystallinum* L. under NaCl salinity. *Plant Growth Regul* 50:69–78. <https://doi.org/10.1007/s10725-006-9127-1>
- Siegal ML, Bergman A (2002) Waddington's canalization revisited: developmental stability and evolution. *Proc Natl Acad Sci U S A* 99:10528–10532. <https://doi.org/10.1073/pnas.102303999>
- Silverman P, Seskar M, Kanter D, Schweizer P, Metraux JP, Raskin I (1995) Salicylic acid in rice (biosynthesis, conjugation, and possible role). *Plant Physiol* 108:633–639. <https://doi.org/10.1104/pp.108.2.633>
- Sosa L, Llanes A, Reinoso H, Reginato M, Luna V (2005) Osmotic and specific ion effects on the germination of *Prosopis strombulifera*. *Ann Bot* 96:261–267. <https://doi.org/10.1093/aob/mci173>
- Szepesi A, Csiszar J, Gemes K, Horvath E, Horvath F, Simon ML, Tari I (2009) Salicylic acid improves acclimation to salt stress by stimulating abscisic aldehyde oxidase activity and abscisic acid accumulation, and increases Na⁺ content in leaves without toxicity symptoms in *Solanum lycopersicum* L. *J Plant Physiol* 166:914–925. <https://doi.org/10.1016/j.jplph.2008.11.012>
- Taji T, Seki M, Satou M, Sakurai T, Kobayashi M, Ishiyama K, Shinozaki K (2004) Comparative genomics in salt tolerance between Arabidopsis and Arabidopsis-related halophyte salt cress using Arabidopsis microarray. *Plant Physiol* 135:1697–1709. <https://doi.org/10.1104/pp.104.039909>
- Takeuchi K, Gyohda A, Tominaga M, Kawakatsu M, Hatakeyama A, Ishii N, Hashimoto M (2011) RSOsPR10 expression in response to environmental stresses is regulated antagonistically by jasmonate/ethylene and salicylic acid signaling pathways in rice roots. *Plant Cell Physiol* 52(9):1686–1696. <https://doi.org/10.1093/pcp/pcr105>
- Tao JJ, Chen HW, Ma B, Zhang WK, Chen S, Zhang JS (2015) The role of ethylene in plants under salinity stress. *Front Plant Sci* 6:1059
- Tari I, Simon LM, Deer KA, Csiszar J, Sz B, Gy K, Szepesi A (2004) Influence of salicylic acid on salt stress acclimation of tomato plants: oxidative stress responses and osmotic adaptation. *Acta Physiol Plant* 26S:237
- Thomas JC, Bohnert HJ (1993) Salt stress perception and plant growth regulation in the halophyte *Mesembryanthemum crystallinum*. *Plant Physiol* 103:1299–1304. <https://doi.org/10.1104/pp.103.4.1299>
- Tiburcio AF, Besford RT, Capell T, Borrell A, Testillano PS, Risueño MC (1994) Mechanisms of polyamine action during senescence responses induced by osmotic stress. *J Exp Bot* 45:1789–1800. <https://doi.org/10.1093/jxb/45.12.1789>
- Tiburcio A, Altabella T, Bitrián M, Alcázar R (2014) The roles of polyamines during the lifespan of plants: from development to stress. *Planta* 240:1–18. <https://doi.org/10.1007/s00425-014-2055-9>
- Todaka D, Zhao Y, Yoshida T, Kudo M, Kidokoro S, Mizoi J, Toyooka K (2017) Temporal and spatial changes in gene expression, metabolite accumulation and phytohormone content in rice seedlings grown under drought stress conditions. *Plant J* 90:61–78. <https://doi.org/10.1111/tpj.13468>
- Tognetti VB, Müllenbock P, Van Breusegem F (2012) Stress homeostasis—the redox and auxin perspective. *Plant Cell Environ* 35:321–333
- Tomar PC, Lakra N, Mishra S (2013) Cadaverine: a lysine catabolite involved in plant growth and development. *Plant Signal Behav* 8. <https://doi.org/10.4161/psb.25850>
- Tsonev T, Lazova G, Stoinova Z, Popova L (1998) A possible role for jasmonic acid in adaptation of barley seedlings to salinity stress. *J Plant Growth Regul* 17:153–159. <https://doi.org/10.1007/PL00007029>
- Ungar IA (1978) Halophyte seed germination. *Bot Rev* 44(2):233–264. <https://doi.org/10.1007/BF02919080>
- Valenzuela CE, Acevedo-Acevedo O, Miranda GS, Vergara-Barros P, Holuigue L, Figueroa CR, Figueroa PM (2016) Salt stress response triggers activation of the jasmonate signaling pathway leading to inhibition of cell elongation in Arabidopsis primary root. *J Exp Bot* 67(14):4209–4220. <https://doi.org/10.1093/jxb/erw202>
- Ventura Y, Wuddineh WA, Myrzabayeva M, Alikulov Z, Khozin-Goldberg I, Shpigel M, Samocha TM, Sagi M (2011) Effect of seawater concentration on the productivity and nutritional value of annual Salicornia and perennial Sarcocornia halophytes as leafy vegetable crops. *Sci Hortic* 128:189–196. <https://doi.org/10.1016/j.scienta.2011.02.001>
- Wang H, Liang X, Wan Q, Wang X, Bi Y (2009) Ethylene and nitric oxide are involved in maintaining ion homeostasis in Arabidopsis callus under salt stress. *Planta* 230:293–307
- Walters DR (2003) Polyamines and plant disease. *Phytochem* 64:97–107
- Wasternack C (2014) Action of jasmonates in plant stress responses and development-applied aspects. *Biotechnol Adv* 32:31–39. <https://doi.org/10.1016/j.biotechadv.2013.09.009>
- Wasternack C, Hause B (2013) Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in *annals of botany*. *Ann Bot* 111:1021–1058. <https://doi.org/10.1093/aob/mct067>
- Weber H, Vick B, Farmer E (1997) Dinor-oxo-phytodienoic acid: a new hexadecanoid signal in the jasmonate family. *Proc Natl Acad Sci U S A* 94:10473–10478
- Wi SJ, Jang SJ, Park KY (2010) Inhibition of biphasic ethylene production enhances tolerance to abiotic stress by reducing the accumulation of reactive oxygen species in *Nicotiana tabacum*. *Mol Cells* 30:37–49
- Wilmoth JC, Wang S, Tiwari SB, Joshi AD, Hagen G, Guilfoyle TJ, Reed JW (2005) NPH4/ARF7 and ARF19 promote leaf expansion and auxin-induced lateral root formation. *Plant J* 43(1):118–130. <https://doi.org/10.1111/j.1365-313X.2005.02432.x>
- Wochok ZS, Sluis CJ (1980) Gibberellic acid promotes Atriplex shoot multiplication and elongation. *Plant Sci Lett* 17:363–369. [https://doi.org/10.1016/0304-4211\(80\)90169-8](https://doi.org/10.1016/0304-4211(80)90169-8)
- Woodward AW, Bartel B (2005) Auxin: regulation, action, and interaction. *Ann Bot* 95(5):707–735. <https://doi.org/10.1093/aob/mci083>
- Wu L, Zhang Z, Zhang H, Wang XC, Huang R (2008) Transcriptional modulation of ethylene response factor protein JERF3 in the oxidative stress response enhances tolerance of tobacco seedlings to salt, drought, and freezing. *Plant Physiol* 148:1953–1963

- Wu H, Zhang Z, Wang J, Oh D, Dassanayake M, Liu B, Huang Q, Sun H, Xia R, Wu Y, Nan Wang Y, Yang Z, Liu Z, Zhang W, Zhang H, Chua J, Yan C, Fang S, Zhang J, Wang Y, Zhang F, Wang G, Lee S, Cheeseman J, BoLi Y, Min J, Yang L, Wang J, Chu C, Chen S, Bohnert H, Zhu J, Wang X, Xie Q (2012) Insights into salt tolerance from the genome of *Thellungiella salsuginea*. PNAS 30:12219–12224. <https://doi.org/10.1073/pnas.1209954109>
- Xu ZY, Kim DH, Hwang I (2012) ABA homeostasis and signaling involving multiple subcellular compartments and multiple receptors. Plant Cell Rep 32(6):807–813. <https://doi.org/10.1007/s00299-013-1396-3>
- Yalpani N, León J, Lawton MA, Raskin I (1993) Pathway of salicylic acid biosynthesis in healthy and virus-inoculated tobacco. Plant Physiol 103:315–321. <https://doi.org/10.1104/pp.103.2.315>
- Yoshikawa H, Honda C, Kondo S (2007) Effect of low-temperature stress on abscisic acid, jasmonates, and polyamines in apples. Plant Growth Regul 52:199–206. <https://doi.org/10.1007/s10725-007-9190-2>
- Zanten M, Voesenek LACJ, Peeters AJM, Millenaar FF (2009) Hormone- and light-mediated regulation of heat-induced differential petiole growth in *Arabidopsis thaliana*. Plant Physiol 151:1446–1458. <https://doi.org/10.1104/pp.109.144386>
- Zia S, Egan TP, Khan AK (2008) Growth and selective ion transport of *Limonium stocksii* Plumbaginaceae under saline conditions. Pak J Bot 40:697–709