



## Review

# A new perspective of phytohormones in salinity tolerance: Regulation of proline metabolism



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## ARTICLE INFO

## Article history:

Received 19 September 2013

Received in revised form 3 December 2013

Accepted 6 December 2013

## Keywords:

Calcium  
Nitrogen  
Osmolytes  
Phytohormones  
Proline  
Salinity

## ABSTRACT

Salinity is one of the most challenging problems that adversely affects growth and development of plants. Plants adopt various strategies to overcome the adverse effects of salinity stress. In recent years, phytohormones and osmolytes have been involved in reducing the adverse effect of salinity stress. Under salinity stress, osmolyte such as proline maintains cellular homeostasis through osmotic regulation and induces physiological processes favorably. The role of phytohormones under salinity stress is critical in modulating physiological responses that eventually lead to adaptation of plants to an unfavorable environment. The individual role of both proline and phytohormones has been extensively studied, but a comprehensive study on the interaction of phytohormones with proline under salinity stress is lacking. The present review focuses on enhancing our understanding on the mechanism of salinity tolerance via proline and phytohormones with emphasis on phytohormones interaction with proline under salinity stress.

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**Abbreviations:** ACC, 1-amino cyclopropane 1-carboxylic acid; ABA, abscisic acid; ACO, ACC oxidase; ACS, ACC synthase; ATPS, ATP-sulfurylase; AVG, aminoethoxyvinylglycine; BR, brassinosteroids; Ca, calcium; CBL, calcineurin B-like protein; CK, cytokinins; EBL, epibrassinolide; GA, gibberellins; GS, glutamine synthase; GSA, glutamate-semialdehyde; IAA, indole acetic acid; JA, jasmonate; N, nitrogen; NO, nitric oxide; NiR, nitrite reductase; NR, nitrate reductase; NRA, nitrate reductase activity; PAC, paclobutrazol; PDH, proline dehydrogenase; POX, proline oxidase; P5C, pyrroline-5-carboxylate; P5CR, P5C reductase; P5CS, 1-pyrroline-5-carboxylate synthetase; P5CDH, P5C dehydrogenase; ROS, reactive oxygen species; S, sulfur; SA, salicylic acid; SNP, sodium nitroprusside; SOS, salt overly sensitive; OAT, ornithine-delta-aminotransferase.

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## 1. Introduction

The decreasing trend of arable land due to increasing contamination and world's population has resulted in the decrease in food security. It has been projected that the world's population is expected to reach about 9.1 billion by 2050 (about 34% higher than today's population); and to cope with this increasing population food production must be increased by 70% (FAO, 2009). Among abiotic stresses, salinity stress is a major contributor in decreasing the crop productivity. According to the report of FAO (2008), over 6% of the world's land is affected by salinity covering about 400 Mha of the world's land area. Salinization is rapidly increasing on a global

scale and currently affects more than 10% of arable land, which results in a decline of the average yields of major crops greater than 50% (Wang et al., 2009). Salinity stress limits plant development by adversely affecting various biochemical reactions and physiological processes such as photosynthesis, antioxidant metabolism, mineral nutrients homeostasis, osmolytes accumulation and hormonal signaling (Misra and Gupta, 2005; Khan et al., 2012).

The primary effects of salt stress are caused by the presence of ions in rhizosphere limiting extraction of water by roots and reduced plant growth, while the secondary effects are caused by ionic disequilibrium resulting in inactivation of enzymes, nutrient starvation, ionic toxicity in tissues and oxidative stress. Salinity stress induces over production of reactive oxygen species (ROS) (Nazar et al., 2011; Khan et al., 2012) that triggers lipid peroxidation, DNA damage, inhibition of photosynthesis and disturbance in mineral nutrient status (Nazar et al., 2011; Turan and Tripathy, 2012).

For alleviation of adverse effects of salinity stress, several strategies have been adopted and efforts are made to explore mechanisms for salinity tolerance. The accumulation of compatible compounds (osmolytes) is related to improvement of plant tolerance to salt because of its ability to overcome osmotic and water stress and maintain nutrients homeostasis and ion compartmentalization (Nazar et al., 2011; Khan et al., 2012). Among the osmolytes, proline plays an important role in salinity tolerance. Kishore et al. (1995) reported that transformed *Nicotiana tabacum* plants with cDNA encoding 1-pyrroline-5-carboxylate synthetase (P5CS), a regulatory enzyme in proline biosynthesis, from *Vigna* were found more tolerant to salinity and drought stress. *Nicotiana tabacum* plants engineered for higher proline production by removing feedback inhibition of rate limiting enzyme in proline biosynthesis showed increased drought tolerance (Hong et al., 2000). Goudarzi and Pakniyat (2009) have suggested that proline content in *Triticum aestivum* plants in the presence of salinity could be used to select tolerant and susceptible genotype.

Phytohormones have also been shown to influence salinity tolerance through modulating several physiological processes and biochemical mechanisms (Fatma et al., 2013). Their role in salinity stress is critical in modulating physiological responses that lead to adaptation of plants to an unfavorable environment. The role of phytohormones such as ethylene (Iqbal et al., 2013; Khan et al., 2012), gibberellins; GAs (Iqbal et al., 2011a), abscisic acid; ABA (Gurmani et al., 2013), cytokinins; CK (Wu et al., 2013), salicylic acid; SA (Nazar et al., 2011; Khan and Khan, 2013; Khan et al., 2013), nitric oxide; NO (Uchida et al., 2002), jasmonates; JAs (Khan and Khan, 2013) and brassinosteroids (Sharma et al., 2013) in stress tolerance has been reported. However, the mechanisms involved by phytohormones for salinity tolerance vary widely. The present review focuses on the involvement of phytohormones in salinity tolerance through regulation of proline metabolism in the light of available literature.

## 2. Involvement of proline in salinity tolerance

Proline plays a protective function against salinity stress in plants (Kishor et al., 2005; Verbruggen and Hermans, 2008). It acts as a compatible osmolyte, enzyme protectant, free radical scavenger, cell redox balancer, cytosolic pH buffer and stabilizer for subcellular structures (Kishor et al., 2005; Verbruggen and Hermans, 2008) to bring about salinity tolerance. Proline synthesis in plants occurs mainly from glutamate, which is reduced to glutamate-semialdehyde (GSA) by the P5CS enzyme, and spontaneously converted to pyrroline-5-carboxylate (P5C). P5C reductase (P5CR) reduces the P5C intermediate to proline. The catabolism of proline occurs in mitochondria via the sequential action of

proline dehydrogenase or proline oxidase (PDH or POX) producing P5C from proline, and P5C dehydrogenase (P5CDH), which regenerates glutamate from 5C. Glutamate plays a central role in overall nitrogen (N) homeostasis. Alternatively, proline can also be synthesized from ornithine, which is transaminated first by ornithine-delta-aminotransferase (OAT) producing GSA and P5C and then converted to proline.

The accumulation of free proline under salinity stress as reported in *Pisum sativum* (Najafi et al., 2006), *Brassica juncea* (Rais et al., 2013) and *Triticum aestivum* (Ashfaq et al., 2014). The proline accumulation is possible due to increase in the enzymes of its synthesis or decrease in the enzymes of its oxidation. Amini and Ehsanpour (2005) have shown that higher level of proline content under salinity stress in stem and leaf that was due to the expression of genes encoding enzymes of proline synthesis such as P5C or decrease in enzymes of proline oxidation such as PDH. In salt stress conditions, P5CS1 is induced and PDH is repressed (Kishor et al., 2005). In potato, the over-expression of the P5CS gene from *Arabidopsis* stimulated synthesis of proline under salt stress and improved salinity tolerance (Hmida-Sayari et al., 2005).

Proline functions as an osmolyte for the intracellular osmotic adjustment and its accumulation plays a critical role in protecting photosynthetic activity in *Opuntia streptacantha* plants under salt stress (Silva-Ortega et al., 2008). They observed that the *Osp5cs* gene of *O. streptacantha* was induced by salt stress at 9 and 11 days of salt treatment. Proline accumulation in response to water stress and salinity is preceded by a rapid increase of the mRNA level of P5CS controlling the rate-limiting step of glutamate-derived proline biosynthesis (Strizhov et al., 1997). Proline is involved in the synthesis of key proteins that are necessary for stress responses (Khedr et al., 2003). They reported that dehydrins are induced by proline to levels that are comparable to those under stress conditions. Similarly, *salt* gene of rice is induced both by proline and by NaCl, drought and ABA (Garcia et al., 1997). Banu et al. (2009) have shown that proline and betaine provided a protection against NaCl-induced cell death by decreasing the level of reactive oxygen species (ROS) and lipid peroxidation as well as improvement of membrane integrity by increasing antioxidant gene. Hoque et al. (2007) reported that exogenous proline mitigated the detrimental effects of salt stress more than exogenous betaine by increasing antioxidant enzyme activities.

## 3. Revisiting the role of phytohormones in salinity tolerance

Phytohormones are endogenous growth regulators that regulate germination, growth, metabolism, or other physiological activities and mechanisms of tolerance of plants to salinity stress. They are critical in modulating physiological responses under salinity stress (Khan et al., 2013). The present section deals with the role of phytohormones in salinity tolerance.

Auxins are known to regulate salinity stress effect in plants. A molecular link between auxin signaling and salt stress has been established by Jung and Park (2011). They suggest that a membrane bound transcription factor (NTM2) incorporates auxin signal in seed germination which modulates seed germination under salinity stress. Similarly, Park et al. (2011) observed that overexpression of IAA30 gene of NTM2 mediates salt signaling pathway. Tirkayi (2007) observed that signaling *arx1* gene provides protection to *Arabidopsis thaliana* under salt stress. Fang and Yang (2002) reported that auxin responsive gene (*AtMEKK1*, *AtRSH3*, *Cat1*, *Fer1*) expressions were down-regulated and NIT1, NIT2 were induced in *Arabidopsis thaliana* to alter the level of IAA and to interact with salt stress responses.

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