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Salt tolerance and salinity effects on plants: a review

Asish Kumar Parida[a], Anath Bandhu Das[a,b,*]

[a]National Institute for Plant Biodiversity Conservation and Research, Nayapalli, Bhubaneswar 751015, Orissa, India
[b]Regional Plant Resource Centre, Nayapalli, Bhubaneswar 751015, Orissa, India

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Abstract

Plants exposed to salt stress undergo changes in their environment. The ability of plants to tolerate salt is determined by multiple biochemical pathways that facilitate retention and/or acquisition of water, protect chloroplast functions, and maintain ion homeostasis. Essential pathways include those that lead to synthesis of osmotically active metabolites, specific proteins, and certain free radical scavenging enzymes that control ion and water flux and support scavenging of oxygen radicals or chaperones. The ability of plants to detoxify radicals under conditions of salt stress is probably the most critical requirement. Many salt-tolerant species accumulate methylated metabolites, which play crucial dual roles as osmoprotectants and as radical scavengers. Their synthesis is correlated with stress-induced enhancement of photorespiration. In this paper, plant responses to salinity stress are reviewed with emphasis on physiological, biochemical, and molecular mechanisms of salt tolerance. This review may help in interdisciplinary studies to assess the ecological significance of salt stress.

Keywords: Antioxidative enzymes; Compatible solutes; Ion homeostasis; Photosynthesis; Salt stress

1. Introduction

Salinity is the major environmental factor limiting plant growth and productivity (Allakhverdiev et al., 2000b). The detrimental effects of high salinity on plants can be observed at the whole-plant level as the death of plants and/or decreases in productivity. Many plants develop mechanisms either to exclude salt from their cells or to tolerate its presence within the cells. During the onset and development of salt stress within a plant, all the major processes such as photosynthesis, protein synthesis, and energy and lipid metabolism are affected. The earliest response is a reduction in the rate of leaf surface expansion, followed by a cessation of expansion as the stress intensifies. Growth resumes when the stress is relieved. Carbohydrates, which among other substrates are needed for cell growth, are supplied mainly through the process of photosynthesis, and photosynthesis rates are usually lower in plants exposed to salinity and especially to NaCl.

Salinity stress biology and plant responses to high salinity have been discussed over two decades (Flowers et al., 1977; Greenway and Munns, 1980; Ehret and Plant, 1999; Hasegawa et al., 2000; Zhu, 2002) and it has been over a decade since salinity tolerance in marine algae has been covered (Kirst, 1989). These reviews covered organismal, physiological, and the then-known biochemical hallmarks of stress and the bewildering complexity of plant stress responses. We summarize in this review physiological, biochemical, and molecular mechanisms of salt tolerance with the salient features of salinity stress effects on plants. In this review, much research information about cellular, metabolic, molecular, and genetic processes associated with the response to salt stress, some of which presumably function to mediate salt tolerance, has been gathered.

*Corresponding author. National Institute for Plant Biodiversity Conservation and Research, Nayapalli, Bhubaneswar 751015, Orissa, India. Fax: +91-674-2550274.
E-mail address: a_b_das@hotmail.com (A.B. Das).

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2. Salt tolerance of plants

Salt tolerance is the ability of plants to grow and complete their life cycle on a substrate that contains high concentrations of soluble salt. Plants that can survive on high concentrations of salt in the rhizosphere and grow well are called halophytes. Depending on their salt-tolerating capacity, halophytes are either obligate and characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% sea water or facultative and found in less saline habitats along the border between saline and nonsaline upland and characterized by broader physiological diversity which enables them to cope with saline and nonsaline conditions.

2.1. Mechanism of salt tolerance

Plants develop a plethora of biochemical and molecular mechanisms to cope with salt stress. Biochemical pathways leading to products and processes that improve salt tolerance are likely to act additively and probably synergistically (Iyengar and Reddy, 1996). Biochemical strategies include (i) selective accumulation or exclusion of ions, (ii) control of ion uptake by roots and transport into leaves, (iii) compartmentalization of ions at the cellular and whole-plant levels, (iv) synthesis of compatible solutes, (v) change in photosynthetic pathway, (vi) alteration in membrane structure, (vii) induction of antioxidative enzymes, and (viii) induction of plant hormones (Fig. 1). These are discussed under separate headings.

Salt tolerance mechanisms are either low-complexity or high-complexity mechanisms. Low-complexity mechanisms appear to involve changes in many biochemical pathways. High-complexity mechanisms involve changes that protect major processes such as photosynthesis and respiration, e.g., water use efficiency, and those that preserve such important features as cytoskeleton, cell wall, or plasma membrane–cell wall interactions (Botella et al., 1994) and chromosome and chromatin structure changes, i.e., DNA methylation, polyploidization, amplification of specific sequences, or DNA elimination (Walbot and Cullis, 1985). It is believed that for the protection of higher-order processes, low-complexity mechanisms are induced coordinately (Bohnert et al., 1995).

2.2. Ion regulation and compartmentalization

Ion uptake and compartmentalization are crucial not only for normal growth but also for growth under saline conditions (Adams et al., 1992b) because the stress disturbs ion homeostasis. Plants, whether glycophyte or

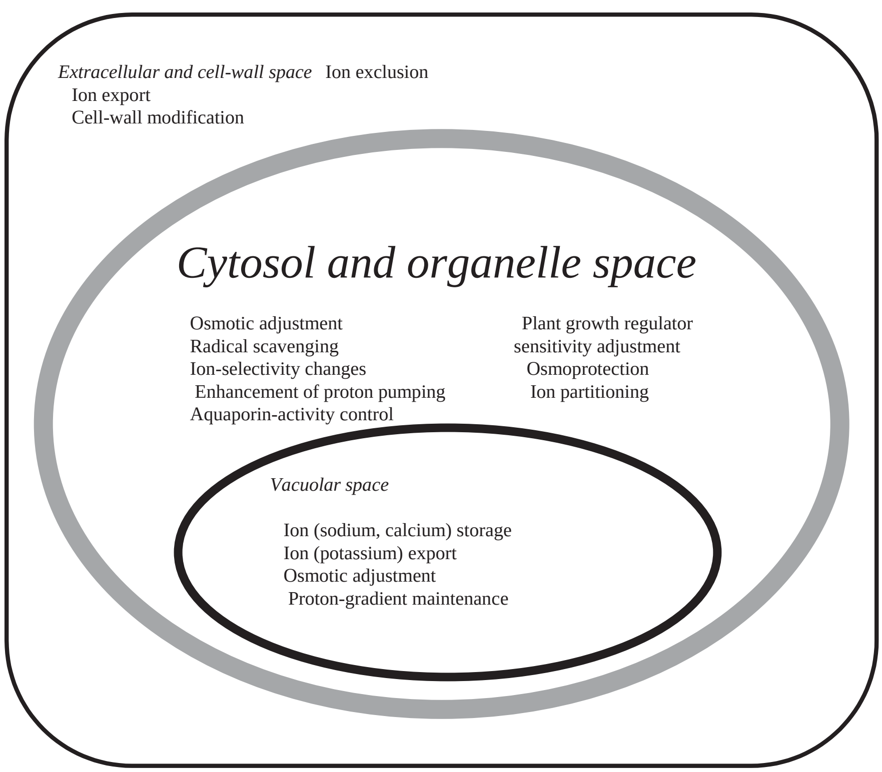

Fig. 1. Biochemical functions associated with tolerance to plant salt stress. The schematic presentation of a plant cell includes three compartments that are defined by the plasma membrane and tonoplast (reproduced from Bohnert and Jensen, 1996).