

Halophytes-Miracle Plants to Survive in Extreme Saline Environment

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Abstract

Halophytes are the plants which have capacity to survive in the highly salt affected soils. This ability against high salt is mainly because of two mechanisms – salt tolerance and salt avoidance. The mechanism of salt tolerance includes adaptations such as shedding, secretion and succulence whereas salt avoidance composed of excretion of Na⁺, reduction of Na⁺ influx and compartmentalization. Along with these mechanisms, salt tolerance or avoidance may be linked with various metabolic processes such as ROS generation and detoxification pathways, signal transduction, osmoregulation or ion homeostasis through osmoprotectants and differential expression of salt-responsive genes and transcription factors. Therefore, the elucidation of such metabolic pathways linked with salt tolerance and identification of salt-responsive genes or promoters from various halophytes may be studied for the genetic engineering of crop plants for salt tolerance using various molecular or advanced breeding techniques.

Keywords: Halophytes; Salt Tolerance; Salt Avoidance

Introduction

Salt affected soils alone have assumed significant global dimension, as about 1000 million ha area in more than hundred countries is affected by this menace. Besides, rapid salinization and alkalization of land in the irrigated landscape is inflicting unacceptable environmental damages. Poor quality ground water, shrinking biological diversity and threat of the global climatic change have added new dimensions to the already complex problem of rational management of soil and water in salt affected environment. Overcoming salt stress is a main issue to ensure agricultural sustainability

and continued food production. In salt marshes, coastal plants do not just survive at certain salinity levels, but they also grow and reproduce vegetatively and sexually and generally there is distinct species zonation from lower to upper parts of the salt marshes [1]. Ranked along an elevational gradient, plant species from the lower marsh have often been found more salt and flood tolerant than plants from the middle and upper marsh [2,3]. But why do most of lower salt marsh species (halophytes) not occur at the upper marsh or on less saline and non-saline inland sites? Generally it is assumed that they are outcompeted by faster growing non-halophytes, i.e. glycophytes. It does not appear that a reduced relative

growth rate is causing halophytes to be outcompeted by glycophytes in non-saline environments but some other factors might be involved. Flowers et al defined this as an obligate requirement for high ion concentrations for optimal growth [4]. That is, these halophytes do not just tolerate high salinity levels (i.e.400–600 mMNaCl, representing sea water level salinity) in hydroponic culture, they also require considerable salinity levels (i.e.200–300mM NaCl which is 35–55% sea water salinity) to attain optimal growth. Based on the salt demand, halophytes can be obligate and facultative halophytes [5]. Obligate halophytes consistently require salt for their growth, but facultative halophytes have the ability to grow on the soil devoid of salt. The salt tolerant mechanisms of halophytes are unique from the glycophytes i.e. salt-sensitive. Therefore, the novel and advanced mechanisms are hard to study only with the model plants such as Arabidopsis. Along with the glycophytes a number of halophytes (such as Suaeda, Atriplex, Thellungiella halophila, Cakile maritima and Suaeda maritima) are now being studied as model halophyte to explore salt tolerant mechanisms. In this review, we present a short study to understand the molecular and physiological mechanism of halophytes which can be explored further for developing salt tolerance crops.

Mechanism of Salt Tolerance

Halophytes mainly use two approaches against high salinity, salt avoidance and salt tolerance [6]. Under the approach salt tolerance, halophytes follow three mechanisms to survive i.e. excretion of Na⁺, reduction of Na⁺ influx and compartmentalization [6-8]. A study was conducted on grass and non-grass halophytes, namely, Dichanthium annulatum, Suaeda nudiflora, Sporobolus marginatus, Urochondra setulosa and Aleuropus lagopoides collected from Rann of Kuchh, Bhuj, Gujarat and established in blocks filled with sandy and moist soil in a screen house under natural conditions at ICAR-CSSRI, Karnal. The salinity levels were maintained at EC 15, 25 and 35 dSm⁻¹. Surprisingly, it was observed that these halophytes have the property of desalinization which may be beneficial for waste lands in salt affected areas. Salt crystals were clearly visible on leaf surface in Urochondra growing in saline conditions with hardening and folding of leaves suggesting that accumulated salt in shoot/leaves is excluded from the plant system through transpiration. After three years of plantation, the soil pH reduced from 9.5 to 9.15 and 10.0 to 9.6 in sodic conditions and soil salinity significantly reduced from EC 15 to 13.2; 25 to 23.4 and 35 to 32.4 dSm⁻¹ respectively [9]. This property of Urochondra, how the roots

compartmentalize excess Na ions to shoot and then finally exclusion through leaf surface, needs further molecular evaluation through identification of genes for Na exclusion mechanism.

While in salt avoidance approach, halophytes include adaptations such as shedding, secretion and succulence. Salt secreting structures such as salt glands and salt hairs are distributed in halophytes as in case of halophyte Urochondra setulosa and the secretion process is a complex mechanism. In some halophytes, shedding of the old leaves is another strategy to avoid the salt toxicity when grown under the high salt concentrations. Proline accumulation was 10.59 folds increase in at EC 35 dSm⁻¹ and 6.85 folds at pH 9.0 + EC 20 dSm⁻¹ was observed in U. setulosa. Salt crystals are clearly visible on leaf surface, suggesting that accumulated salt in shoot/leaves is excluded from the plant system through transpiration [10,11]. It has been reported that proline levels, contents of the soluble sugar in leaves and roots of I. Halophila exhibited basically an enhancement under salt stress conditions and the ratio of K⁺ to Na⁺ was also greater than 1 [12].

The key mechanisms of salt tolerance is linked with ROS (Reactive oxygen species) generation and detoxification pathways, signal transduction, osmoregulation or ion homeostasis through osmoprotectants and differential expression of salt-responsive genes and transcription factors [13,14]. The effect of severe salinity stress is shown to be as a result of oxidative damage to cells, including membrane lipids, proteins, and nucleic acids through excessive production of reactive oxygen species [15]. ROS detoxification includes the antioxidative enzymes such as catalase, peroxidase, superoxide dismutase which play a protective role in scavenging toxic radicals [16]. Halophytes maintain a high cytosolic K⁺/Na⁺ ratio by salt sequestration into cell vacuoles through transporters. In S. marginatus higher Na⁺ accumulation was observed in shoots than root, however in case of U. setulosa, the Na⁺ concentration increased both in root and shoot.

Another key mechanism of halophytes to cope with the salt stress is the accumulation of osmoprotectants such as proline content, glycine betaine, polyphenols, soluble sugars and inorganic ions [17-19]. In our studies also, a significant increase in total soluble sugars was observed in all the grass spp [9]. The major osmoprotectants, proline accumulated 4-10 folds at EC 35 dSm⁻¹ and 6-8 folds at combined stress of pH 9.0 + EC 20 dSm⁻¹.

The most common strategies for salt tolerance among halophytes and glycophytes are compartmentalization of Na⁺, inhibition of Na⁺ influx and Na⁺ efflux. These strategies mainly regulated by multigene family and governed by antiporters. Under the control of non-specific promoter CaMV35S, the transporters encoding genes (NHX, HKT, SOS etc.) of glycophytes showed tolerance range of 150-250 mM NaCl whereas halophytic genes showed tolerance range up to 400 mM NaCl [20]. Halophytes, at the molecular level, regulate stress-responsive genes via ABA-dependent or ABA-independent regulation mechanism to impart salt tolerance. Generally, halophytic salt tolerance is a complex network which includes the interactions of a number of physiological responses caused by the several genes and gene products.

Is there a new perspective for a successful saline agriculture? Can we suggest a viable strategy for future engineering of improved salt tolerance? To test the applicability of this hypothesis to halophyte evolution, it is necessary to perform halophyte/glycophyte promoter swaps and to compare the activities of the corresponding promoter, to check for possible differences in tissue-specificity patterns. Unfortunately, such studies are still in incubation. To select the proper transgenes, it is indispensable to learn more about the mechanisms underlying salt tolerance in halophytes. Mainly, two main approaches are being used to improve salt tolerance either to exploit the natural genetic variations, through direct selection in stressful environments or through mapping quantitative trait loci and subsequent marker-assisted selection; or the generation of transgenic plants to introduce novel genes or to alter expression levels of the existing genes to affect the degree of salt stress tolerance. Several investigators have used candidate gene cDNAs from halophytic species for over-expression in *A. thaliana* or other glycophyte hosts, and observed a significant alleviation of salt stress in the transgenic hosts, proving that the genes in question do contribute to the salt tolerance of the halophytic source species. The important question is whether the genes in question contribute more to salt tolerance in the halophyte than the orthologous genes do in glycophytes. As a first step in the identification of 'real' salt tolerance genes, i.e. the genes that produce the difference in salt tolerance between halophytes and glycophytes, extensive transcriptomic comparisons are therefore urgently needed. In view of the probable variation in the nature and the tolerance potentials of the mechanisms in halophytes, it is desirable to have a number of genetically accessible halophyte model species from different monocotyledonae and dicotyledonae families.

Halophytes are considered as amazing plants whose potential against high salt concentration are yet to be revealed. In brief, salt tolerance in a halophyte involves the formation of osmoprotectants, changes in ion homeostasis, induction of antioxidants, activation of crosstalk genes and the developments of salt bladders or salt glands. A single species of halophyte cannot be considered as a model species as different halophytes use a different mechanism to respond to salt stress. Hence, the isolation and identification of salt-responsive genes and promoters from various halophytes can be explored for the genetic engineering of crop plants for salt tolerance using transgenic approach.

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