



Osmoprotectants: Protective role under various stresses in plants

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Abstract

Plants under adverse environmental conditions try to combat abiotic and biotic stress by making use of adaptive strategies. One such mechanism employs low molecular weight compounds called osmoprotectants that work under various stress conditions. There are different types of osmoprotectants, which for convenience are grouped into various classes, such as sugars (e.g., sucrose, sorbitol, trehalose), sugar alcohols (e.g., *myo*-inositols), amino acids (e.g., proline), polyamines (e.g., spermidine, spermine, putrescine), betaines (e.g., glycine betaine), and. These osmoprotectants defend plants from scavenging ROS (reactive oxygen species) that are generated due to stresses. They activate chaperone-like proteins that help in the maintenance of membrane structures and protein activities. Therefore, it is important to be aware of regulation of osmoprotectant-related genes that confer protection to plants to respond to various stresses. In the present review, we have given a brief account of abiotic stress factors challenging plants and how plants respond to them by citing recent literatures related to role of osmoprotectants.

Keywords: abiotic stresses, reactive oxygen species (ROS), polyamines, mannitol, proline

Introduction

Broadly stress can be any influence adversely affecting an individual or populations and communities. In case of plants, stress limits its productivity and biomass. It not only affects the most basic functions of a plants but also limits its vegetative and reproductive development^[1]. Plants encounter several types of stresses beginning from initial developmental stage till the completion of their lifespan. Scientist from various plant disciplines have divided these stresses into biotic and abiotic. Biotic stresses arise through interactions of phyllosphere as well as rhizosphere of plants with other organisms such as disease-causing bacteria, viruses, fungi, algae, parasitic nematodes and insects^[2-10], while abiotic stresses are result of the interaction among organisms and their physical surroundings. The plants being sessile organisms, run into a diverse type of abiotic stresses such as UV radiations, very high or low temperature, wounding, flooding or drought, salinity, high metal concentrations and nutrient deficiency. Since, these conditions are natural to them, they have their own mechanisms to counter these stress conditions.

Abiotic Stress and Its Effects on Plants

Plants encounter abiotic stresses like high or very low temperatures, excess or scarcity of water, salinity or heavy metal toxicity, nutrient deficiency etc. on day-to-day basis. Such stress conditions have unfavourable effects on the survival of plants, their morphology, physiology, biochemistry, and molecular mechanisms^[2-12].

Plants face never ending harsh situations that are regulated by different environmental conditions. Of all the mentioned abiotic stresses, drought and salinity are of special concerns, since these are causing decline in crop yield in semi-arid and semi-arid regions of the world. Extensive studies have suggested that drought and salinity have the major role in arresting agricultural production throughout the world^[13-20].

1. Stress Due to Salinity

Galvani and coworkers have suggested that almost half of the agricultural land is acutely affected by salinity^[14]. The saline condition is the soil environment may be natural or anthropogenically induced. Due to the natural phenomenon of rocks weathering, different salts such as chlorides of calcium, sodium, magnesium and trace amounts of sulphate and carbonate of salts are added to environment^[13-14, 21]. Besides this, other geogenic processes, inappropriate irrigation practices, dumping of organic, municipal and industrial wastes, fuel combustion, power production, improper agricultural practices of using excessive quantities of chemical fertilizers and pesticides are considered some of the leading causes of salinity^[22-25]. In the present times, majority of farms are suffering from acute salinity issues and this has become one of the most important global environmental concern. The potential negative consequences of these abiotic factors on health of human and animals has alarmed the agronomists. According to the data released by Government of India, approximately 6.74 million hectares area in India is saline and it is estimated that 10% more area is getting added every year to it, and it is projected that by 2050, around fifty percent of agricultural land will be salinity impaired. Hence, in

order to ascertain food security, the GOI has planned to restore 2 million ha of degraded lands, including salt-affected soils, by the year 2030 [26].

2. Effect of Salinity on Plants

Salinity reduces crop yield and productivity significantly by affecting every aspect of plant physiology and biochemistry. The direct undesirable effect of salinity stress on plants is the damage to different physiological phenomenon such as germination of seeds, growth of seedling, plasmolysis, the increased levels of ROS, reduced reproductive development because of induction of Na⁺ and Cl⁻ toxicity [27]. Another report from [28] has also suggested that if there is accumulation of Na⁺ inside the cell, it may drastically change various physiological processes and resulting in reduced growth and plant productivity. Due to salinity stress, 25 % decline in pigment amount, leaf area, and photosynthetic efficiency was shown by Aldesuquy and coworkers [29] while irrigating wheat plants with sea water. The photosynthetic efficiency is also affected because of inhibition of activity of photosystem II (PSII) due to enhanced levels of salt in the cell [30]. It was reported that the PSII and electron transport chain (ETC) is considered to be the major site showing damages caused by salinity stress [31]. An indirect consequence of salinity stress is initiation of hyperaccumulation of ROS like O²⁻ (singlet oxygen superoxide radical), H₂O₂ (hydrogen peroxide) and OH⁻ radical, which damages proteins, lipids and nucleic acids resulting in the death of plant. According to the work of Gill and Tuteja [32], the organelles chloroplasts, mitochondria and plasma membranes of the plant cells are associated to the ETC and are major sites for ROS generation as byproducts of oxygen metabolism. In chloroplasts, PSI and PSII are key sites for ROS generation, whereas in mitochondria, the susceptible locations for generation of O²⁻ on ETC are complex I, ubiquinone and complex III. Due to stress situation, the redox balance of the cell gets disturbed, and the electrons flowing in the ETC, bind to oxygen molecule and lead to generation of ROS [32-33]. Therefore, it is necessary to regulate the level of ROS production so as to avoid undesirable cytotoxicity and oxidative damage. Besides these, at the ionic level, salinity causes osmotic stress, ionic toxicity (Na⁺, Cl⁻ and SO₄²⁻), nutrient deficiency of micro and macro elements and oxidative stress on plants [34]. There are two ways by which plants respond to salinity, first is development of osmotic stress caused due to high levels of sodium (Na⁺) in root, that reduces water potential, and second by undergoing ionic stress caused due to deterioration of nutrient balance [35].

3. Stress Due to Drought

Drought is another abiotic stress that causes huge loss to world food crop productivity. Lately, scarcity of water has been a major contributor to famine and food shortages. The exponentially increasing population is adding to pressure of increasing crop yields that will be possible only with adequate irrigation. More than half of the water resources are already being used to fulfill this requirement but at present, global warming is resulting in higher average mean temperatures and reduced rainfalls that will pose serious threat to the agricultural irrigation needs.

Unlike other natural dangers, drought stress is similar to the salinity stress, and the water holding potential can be diminished by manmade activities that includes increased farming, improper irrigation practices, and over-exploitation of natural resources like forest, ground water and soil erosion.[36]. Water scarcity is a problem of nearly all climatic zones. It includes areas with low and high rainfall. Majorly it is associated with the reduced rainfall received by a region over a period of time. Plants experience draught stress when water available to roots becomes limiting and when the transpiration rate are quite high [37]. Several research works have shown that during salinity stress all the key processes and metabolic pathways such as translation, biosynthesis of photosynthetic pigments and energy molecules, photosynthesis, electron transport rates, and lipid metabolism are adversely affected. [38-39]. Drought deteriorates water balance, membrane permeability, mineral nutrients, and enzymes activities [40].

Response Reaction of Plants to Abiotic Stress Conditions

A plant goes through various changes at molecular, physiological and metabolic levels in response to abiotic stresses. To adapt itself to the stress, several biological, physical and chemical changes takes place in the plant body. Defense mechanisms are activated to re-establish homeostasis and structural organization. At molecular level, expression of several gene families takes place that are responsible for the activation of stress related defense pathways. These genes belong to 3-categories: the first category consists of genes which are related to the protection of membrane and important proteins such as osmoprotectants, free radical scavengers, heat shock proteins, late embryogenesis abundant (LEA) proteins, and chaperons. The second category consists of genes that express ion channels and membrane transporters, and the last category of genes are those that regulate transcription of stress-related genes. Many studies have shown that plant cells accumulate certain proteins like late embryogenesis abundant (LEA) proteins and proteins derived from stress responsive transcription factor genes as means of stress protection [41-44].

Hence, we find that the whole plant machinery gets into work as soon as it starts experiencing stress situation and transcription of several stress related genes initiate. In the present review, we are considering the role of osmoprotectants as a stress nullifier and how it has made the plants adaptive to the varying stress situations. A lot of work with osmoprotectants has been done so far with either traditional methods or by transgenic approach.

Osmoprotectant: A saviour to protect plants from osmotic stress.

During adverse conditions such as cold, heat or osmotic shock, water or heavy metal stress, plant cells permit the synthesis, inflow, sequestering and accumulation of various solutes for homeostasis^[4]. Different mechanisms are employed by the plant under adverse conditions such as alterations in the its physiology as well as expression of genes related to stress. This leads to the synthesis of array of low molecular weight metabolites like osmolytes or osmoprotectants and other proteins to fight the stress conditions^[41-43, 45-48]. These are inert and non-harmful, small sized molecules are called osmolytes. Earlier, the term osmolyte was used for biomolecules which are produced and amass during osmotic shock to maintain balance in a cell or its surrounding fluid. Recently, the term includes any metabolite or solute that is produced and accumulated in the cell to protect it from the damaging effects of abiotic stress. These are small, soluble, hydrophilic low molecular weight organic and compatible compounds. Unlike inorganic compounds, osmolytes are not toxic at high cellular concentrations and doesn't interfere with the intracellular metabolic activities operating in plants under stress conditions^[49]. Osmolyte biosynthesis and their accumulation is one of the first responses of the host plants to counter the effect of osmotic and oxidative stress. Studies have shown that various signaling pathways like plant hormones, calcium signaling and MAP (mitogen activated protein) kinases control the expression of the osmolyte biosynthesis pathway genes under abiotic stress conditions. Thus, osmolyte accumulation is effect of stress signaling pathways and is mandatory for species survival under stress. During stress condition, various osmolytes belonging to different categories of biomolecules accumulate in notable quantities and are helpful in maintaining ionic balance, osmotic potential, membrane and chromatin structure, free oxygen radical levels and phloem translocated photo-assimilation^[50, 41]. Sometimes due to their importance in protecting against stress like exposure to ultra low temperatures, the osmolytes are also known as cytoprotectants^[51].

1. Types of Osmoprotectants

The osmolytes are grouped into various classes for better understanding of their mode of functioning. The various classes of osmoprotectants include biomolecules such as sugars, amino acids, methylamines, polyols, polyamines and secondary metabolites, which shield plants from the deleterious effects of abiotic stresses and in long run unable them to protect their cells by making them tolerant to specific abiotic stress^[52-54]. In case of salt stress, the common osmoprotectants that are quickly accumulated in affected plants, include amino acids (proline), quaternary amines (betaine, glycine and polyamines), non-reducing sugars (inositol, sorbitol, mannitol, trehalose) and sugar alcohols^[46]. These biomolecules maintain osmotic homeostasis by elevating the water potential. Of these, carbohydrates and sugar alcohols are important osmolytes that are closely linked with a plants normal growth and development during stress responses^[41, 55].

2. Synthesis of osmoprotectants by cells naturally

Osmoprotectants are synthesised in the cell in different cellular compartments such as organelles and different components of cytoplasm. Plants can produce osmoprotectants in a range from 5-50 $\mu\text{mol g}^{-1}$ fresh weight^[56]. Lugan and coworkers^[57] reported that level of osmoprotectants and composition differ with species and under different stresses. The phase of growth of a plant, the type and severity of stress it experiences are important aspects that affect the type, level, structure and localization of osmoprotectants at cellular level.^[58-59] Osmoprotectants are compatible chemicals that are capable of maintaining cell turgor pressure, alleviation of ion toxicity and can replace inorganic salts from the plant cells, which when present at higher concentration produces negative effects on plants and control the cell's osmotic potential and molecular structures^[44].

As the population across the world is increasing, there is high demand for enhanced food production. But due to constant fear of unfavourable environmental conditions, which results in drastic reduction in crop yield, effective strategies must be designed on a regular basis so as to achieve food production goals. Conventional breeding protocols have been successfully used to develop abiotic stress tolerant crop varieties. Some have observed that among the different cultivars of same species, there are lines that have higher concentration of osmoprotectants in comparison to others. Thus, the cultivar with higher concentration of osmoprotectant can be utilized^[60].

Conclusion and Future Prospects

Abiotic stress handling is one of the most important challenges faced by agriculture. Because of this, there is limitation in the choice of crops and their production over large areas, thus can lead to low yield and hence, total crop failures. Abiotic stresses adversely affect the livelihoods of individual farmers and their families as well as national economies and food security. To overcome such situations, it is the need of the hour to improve those plant traits that limits the cop productivity under adverse situations. The enhancement in plant traits can be effectively attained with a indepth knowledge of natural defense mechanisms of plants and understanding the approach to utilize other strategies to enhance the crop yield.

Here, in this review, we have given a brief account of one of the most naturally occurring defence systems in plants, that is osmoprotectants. To summarize, all the previous workers have consensus on that the osmoprotectants take part in improving stress tolerance by a variety of means. They protect the structure of membranes, stabilizes cellular structures by maintaining redox balance, detoxify reactive oxygen species, regulate protein activity and optimizes photosynthetic productivity. Moreover, under various stress the osmoprotectants play a crucial role in activation of defense related response. Understanding the role of each osmoprotectant is thus important to better stress tolerance in crops. The proper knowledge of underlying

mechanisms and pathways of osmoprotectant biosynthesis maybe utilized to optimize the effectiveness of these biomolecules in conferring tolerance or resistance to the abiotic stress. Thus, osmoprotectants in plants are important defense strategy that helps plants to flourish even under adverse environmental situations.

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