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Influence of salt stress on lipids metabolism, Photorespiration, Photosynthesis and Chlorophyll Fluorescence in crop plants

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Abstract Salt stress presents an increasing threat to plant agriculture. Among the various sources of soil salinity, irrigation combined with poor drainage is the most serious, because it represents losses of once productive agricultural land. Environmental stress due to disordering in cohesions of membrane lipids and proteins. Lipids are among the most prominent constituents of cell membrane which play a fundamental role in cell permeability. Environmental stress due to disordering in cohesions of membrane lipids and proteins. Lipids are among the most prominent constituents of cell membrane which play a fundamental role in cell permeability. Abiotic and biotic stress in living organisms, including plants, can cause overflow, deregulation, or even disruption of electron transport chains (ETC) in chloroplasts and mitochondria. Under these conditions molecular oxygen (O_2) acts as an electron acceptor, giving rise to the accumulation of ROS. Singlet oxygen (O_2), the hydroxyl radical (OH−), the superoxide radical (O_2), and hydrogen peroxide (H_2O_2) are all strongly oxidizing compounds and therefore potentially harmful for cell integrity.

Keywords Ion Homeostasis, Salt Tolerance, Morphological Adaptations

Introduction

Salt stress

Salt stress presents an increasing threat to plant agriculture. Among the various sources of soil salinity, irrigation combined with poor drainage is the most serious, because it represents losses of once productive agricultural land. The reason for this so-called ‘secondary salinization’ (as opposed to primary salinization of seashore salty marshes) is simple: water will evaporate but salts remain and accumulate in the soil. A wide range of environmental stresses such as drought, salinity, alkalinity and pathogen infection are harmful to the plants. Salt stress in soil is one of the major stresses especially in arid and semi-arid regions and can severely limit plant growth and productivity [1]. Salinity is a soil condition by high content of soluble salts. The problem of soil salinity is increasing. Soil salinity stresses plants in two ways: High concentrations of salts in the soil make it harder for roots to extract water, and high concentrations of salts within the plant can be toxic [2]. Reports by the FAO (2005) [3] indicate that 2% of agriculture land is salt affected [4]. Nearly 20% of the worlds cultivated area and nearly half of the worlds irrigated lands are affected by salinity. Processes such as seed germination, seedling growth and vigour, vegetative growth, flowering and fruit set are adversely affected by high salt concentration, that ultimately causing decreased of plant productivity [5]. Adverse effects of salinity on plant growth may be due to ion cytotoxicity and osmotic stress [6]. Metabolic imbalances caused by ion toxicity, osmotic stress and nutritional deficiency under saline conditions may also lead to oxidative stress [7]. Lipids are major components in membrane which has main role in plant cell resistance in proportional to salt stress. Salt stress due to disordering in cohesions of membrane lipids and proteins [8]. Under condition of salinity stress main changes will happen in lipids metabolism and lipid peroxidation was synchronized with increased of the salinity level [8]. Also salt stress caused change in leaf pigment content that terminal photosynthesis level, distillation speed and stomatal transport is changing in salinity stress condition [9].

Ion Homeostasis and Salt Tolerance

Maintaining ion homeostasis by ion uptake and compartmentalization is not only crucial for normal plant growth but is also an essential process for growth during salt stress. Irrespective of their nature, both glycophytes and halophytes cannot tolerate high salt concentration in their cytoplasm. Hence, the excess salt is either transported to the vacuole or sequestered in older tissues which eventually are sacrificed, thereby protecting the plant from salinity stress [10]. Major form of salt present in the soil is NaCl, so the main focus of research is the study about the transport mechanism of Na+ ion and its compartmentalization. The Na+ ion that enters the cytoplasm is then transported to the vacuole via Na+/H+ ant porter. Two types of H^+ pumps are present in the vacuolar membrane: vacuolar type H+-ATPase (V-ATPase) and the vacuolar pyro phosphatase (V-PPase). Of these, V-ATPase is the most dominant H+ pump present within the plant cell. During no stress conditions it plays an important role in maintaining solute homeostasis, energizing secondary transport and facilitating vesicle fusion. Under stressed condition the survivability of the plant depends upon the activity of V-ATPase [11].

Morphological Adaptations of Plants to Salinity

Irrigation with saline water has different effects on plant growth according to different effects and mechanisms in (1) glycophyte vs. halophyte plants, as well as between different species of the same family and genus, and even between cultivars; (2) different salt levels in the irrigation water and (3) the time of exposure to such stress (short-term assays vs. long-term assays). Munns (1992) [12] concluded that the salts absorbed by plants do not control growth directly, but that they do influence turgor, photosynthesis and/or the activity of specific enzymes. Demonstrating the complexity of salt stress, this author developed a model showing a two-phase effect of salinity on plant growth. Growth is first reduced by a decrease in the soil water potential (osmotic phase) and, later, a specific effect appears as salt injury in leaves, which die because of a rapid increase in salt in the cell walls or cytoplasm when the vacuoles can no longer sequester incoming salts (ionic phase). Munns (1992) [12] found that this salt accumulation in the old leaves accelerates their death and thus decreases the supply of carbohydrates and/or growth hormones to the meristematic regions, thereby inhibiting growth. The fact that plant growth is limited by a reduction in the photosynthesis rate and by an excessive uptake of salts affects the production of specific metabolites that directly inhibit growth. The anatomy of the root system (length, root diameter, etc.) determines root performance, enabling plants to acquire water and nutrients and thereby increase the replacement rate of plant water lost [13]. Optimum root systems can support shoot growth and improve plant yields, since roots serve as an interface between plants and the soil [14]. A proliferated root system would therefore appear to be better for plants, for it allows them to penetrate deeper layers of soil to acquire water and nutrients. Recent studies, however, have shown that species with other root features, including small roots, can be more advantageous for shoot development [15]. For example, just a few roots in moist soil can provide amounts of water independent of the root number. Other root characteristics, such as the number and diameter of xylem vessels, width of the root cortex, number of root hairs, and the suberin deposition in both the root exodermis and endodermis, also determine the permeability of roots to water [16].

Lipids metabolism

Environmental stress due to disordering in cohesions of membrane lipids and proteins [17]. Lipids are among the most prominent constituents of cell membrane which play a fundamental role in cell permeability [18]. Under condition of stress main change will happen in lipids metabolism [19]. Total lipids content in Canola (Brassica napus L.) with increasing NaCl levels was decreased [18]. Increasing soil salinity levels strongly influence the essential lipids biosynthesis [20]. In other hand, lipid peroxidation was synchronized with increased of the salinity level which had a relation with plants such as Wheat [21], Tomato [22] and Purslane [8, 23] was reported. Mono galactosyl diglyceride (MGDG) is main glycerol lipid in leaf was effect of intensive stress imposing, was reduced that is express of chloroplast membrane destructions [8]. Low unsaturation lipids degree limited the membrane fluidity band restricted permeability to Na and Cl ions [24]. Phospatidic acid (PA) is a common phospholipids that is a major constituent of cell membranes. PA is the smallest of the phospholipids. They have long been recognized as of importance during germination and senescence, and they appear to have a role in response to stress damage and pathogen attack [25]. PA (Figure 1) is lipid signals in plants that normally PA only constitutes a minor proportion of the cellular lipid pool but in responses to stress PA levels can increase significantly [26]. PA has been implicated in intracellular signaling that formed in response to salt stress has been suggested to function as a signaling molecule guiding the plants accumulation responses to salt stress. PA can bind and affect the activity of various signaling proteins, including protein kinases and phosphatases. Also, PA has been suggested to regulate the activity of vacuolar pump upon high salt treatment which may help maintain the protein gradient. Salinity stress has been shown to increase PA levels in the green algae chlamydomonas, Tomato, Tobacco and Alfalfa. DGPP (Diacylglycerolpyrophosphate) increased in response to salinity stress, that was found for various dicots and green algae chlamydomonas. DGPP functions to PA signaling and function as a phospholipids second messenger in ABA signaling in salt stress. Diacylglycerolpyrophosphate (DGPP) is the phosphorylated product of PA which is produced by a novel enzyme, Pa kinase. DGPP is a minor lipid, present in very low amounts, but in response to salinity stress its levels have been found to increase in Chlamydomonas, Tomato, Alfalfa and Arabidopsis [26]. Salinity stress has been shown to affect inositol triphosphate (IP3) and phosphatidylinositol bisphosphate (PIP 2) levels in Arabidopsis and Tobacco cells [27]. The accumulation of PIP 2 in response to salt stress seems to be typical for osmotic stress but no other stresses have been shown to increase PIP 2 in plants cells, including Arabidopsis, Tobacco pollen and various green algae [26].

Photorespiration

Photorespiration can act as a sink for excess reducing power, thereby preventing the over-reduction of the photosynthetic electron chain. In addition, the photorespiratory pathway serves to convert phosphoglycolate (2PG) to 3-phosphoglycerate (3PGA), which can be metabolised to either regenerate RuBP or to make complex sugars and other carbon-based organic metabolites. These effects can be even more important considering that different stress conditions can increase photorespiratory rates. Drought and salinity, for example, trigger a decrease in stomatal conductance, thus decreasing the CO_2:O_2 ratio and increasing photorespiration [28]. Under salinity conditions, the photorespiratory pathway can prevent photo-oxidative damage by continuously recycling CO_2 for the chloroplast from the decarboxylation of glycine in the mitochondria. In addition, glycerate, produced inside the peroxisome, can be imported into the chloroplast and enter the Calvin cycle. These mechanisms keep the Calvin cycle working and prevent ROS generation in the electron transport chain, providing substrates for the chloroplast and decreasing the risk of photoinhibition under environmental stress conditions. The stimulation of glycolate oxidase activity by salinity in pea leaf peroxisomes from salt-tolerant plants suggests that photorespiration can act as a molecular mechanism in NaCl-tolerance [29]. In C3 plants, both CO_2 fixation and photorespiration are the major sinks of electrons from PSII (4 electrons are required for CO_2 or O_2 reacting with Rubisco). In some salt-tolerant plants, increases in catalase activity have been recorded after an NaCl challenge, such as those described in tomato plants and myrtle, suggesting increased photorespiratory activity. CAT has been found predominantly in leaf peroxisomes, where it chiefly functions to remove H_2O_2 formed in photorespiration or in the _-oxidation of fatty acids in the glyoxysomes. The increase in CAT activity in salt-tolerant plants may suggest an involvement of photorespiration in the NaCl stress response. A correlation between CAT activity and photosynthesis has been described, since an increase in CAT reduces the photorespiratory loss of CO_2 [30]. Another protective mechanism for the photosynthetic machinery is the water-water cycle. This cycle can be defined as the photoreduction of molecular oxygen to water in PSI by the electrons generated in PSII from water. In this cycle, half of the electrons generated in PSII are used for the photoreduction of dioxygen to superoxide in PSI, and the other half are used for the regeneration of ascorbate [31].

Antioxidant Regulation of Salinity Tolerance

Abiotic and biotic stress in living organisms, including plants, can cause overflow, deregulation, or even disruption of electron transport chains (ETC) in chloroplasts and mitochondria. Under these conditions molecular oxygen (O_2) acts as an electron acceptor, giving rise to the accumulation of ROS. Singlet oxygen ($1O_2$), the hydroxyl radical (OH−), the superoxide radical (O_2), and hydrogen peroxide (H_2O_2) are all strongly oxidizing compounds and therefore potentially harmful for cell integrity. Antioxidant metabolism, including antioxidant enzymes and nonenzymatic compounds, play critical parts in detoxifying ROS induced by salinity stress. Salinity tolerance is positively correlated with the activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidise (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR) and with the accumulation of nonenzymatic antioxidant compounds. Gill et al. (2013) [32] has recently reported a couple of helicase proteins (e.g., DESD-box helicase and OsSUV3 dual helicase) functioning in plant salinity tolerance by improving/maintaining photosynthesis and antioxidant machinery. Kim et al. (2013) [33] showed that silicon (Si) application to rice root zone influenced the hormonal and antioxidant responses under salinity stress. The results showed that Si treatments significantly increased rice plant growth compared to controls under salinity stress. Si treatments reduced the sodium accumulation resulting in low electrolytic leakage and lipid peroxidation compared to control plants under salinity stress. Enzymatic antioxidant (catalase, peroxidase, and polyphenol oxidase) responses were more pronounced in control plants than in Si-treated plants under salinity stress.

Photosynthesis and Chlorophyll Fluorescence

Salt stress affects photosynthesis both in the short and long term. In the short term, salinity can affect photosynthesis by stomatal limitations, leading to a decrease in carbon assimilation. This effect can produce rapid growth cessation, even after just a few hours of salt exposure. In the long term, salt stress can also affect the photosynthetic process due to salt accumulation in young leaves and decreases in chlorophyll and carotenoid concentrations even in halophyte plants [34]. The photosynthesis rate (PN) can drop due to stomatal closure (gs), and/or other non-stomatal limitations, like the disturbance of the photosynthetic electron chain and/or the inhibition of the Calvin Cycle enzymes, such as Rubisco, phosphoenol pyruvate carboxylase (PECP), ribulose-5-phosphate kinase, glyceraldehyde-3-phosphate dehydrogenase or fructose-1,6-bisphosphatase . A drop in gs can prevent excess water loss by transpiration, whereas proper regulation of the photosynthetic process can minimise the generation of ROS in PS II ($1O_2$) and in the reducing side of the PSI (O_2 and H_2O_2) [34].

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