



Impact of salinity on photosynthesis and antioxidant system of plants

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Abstract

Abiotic stresses like salinity, drought, and high temperature have undesirable effects on crop productivity and quality, and negative trends in sustainable agriculture. The adverse effects of salinization on plants are evident from negative growth trends from alteration or inhibition of biochemical and physiological processes. The ability of plants to tolerate salt stress is determined by multiple biochemical and molecular pathways. Salt accumulation in soil and water prevents plant growth through two major impacts. Firstly, the existence of salt in the soil solution decreases the capacity of a plant to absorb water, which is referred to as the osmotic or water deficiency of salt stress. This impact relies on the concentration of salt outside the plant and growth inhibition is mainly due to water shortage or osmotic stress, with very little genotypic variation in this trait observed. Secondly, the salt-specific or ion-excess salinity impact, whereby the accumulation of Na⁺ and Cl⁻ ions within the plant leads to toxic impacts on plant biochemistry. Photosynthesis is crucial for the survival of all living biota, playing a key role in plant productivity by generating the carbon skeleton that is the primary component of all biomolecules. Salinity stress is a major threat to agricultural productivity and sustainability as it can cause irreversible damage to photosynthetic apparatus at any developmental stage. This work summarizes the current knowledge of impact of salinity on the key targets of the photosynthetic apparatus under salt stress; and tolerance of PSII to salt stress and its repair; salinity effects on biochemistry of CO₂ fixation and its regulation.

Key words: salinity, photosynthesis, physiology

Introduction

Abiotic stresses like salinity, drought, and high temperature have undesirable effects on crop productivity and quality, and negative trends in sustainable agriculture (Zafar et al., 2021a, Zafar et al 2021b; Manan et al., 2022; Haroon et al., 2022). Salinity in particular is an important limiting factor, causing low yield with inferior quality. Salinity in particular is an important limiting factor, causing low yield with inferior quality (Zafar et al., 2020). Climate change is considered one of the major contributing factors to soil salinization, leading to land degradation and desertification (Zafar et al., 2021c). According to Flowers et al. (1997), high salt concentration is responsible for negative impacts on 7% of total land surface, and 5% of cultivated land. Poor irrigation water quality is another important factor contributing to soil salinization (Rubio et al., 2009). For these reasons, soil salinization is a reported major cause of reductions in the productivity of irrigated and rainfed lands of the world (Razzaq et al., 2020).

Soil salinity affects over 800 million hectares (Munns & Tester, 2008); this accounts for more than 6% of the world's total land area. As most crops are classified as glycophytes, their performance on saline soils is significantly handicapped, resulting in over \$27.3 Bln p.a. penalties to agricultural sector (Qadir et al., 2014). The negative impact of salinity is only going to increase, due to the current climate trends, increasing reliance of agriculture on irrigation, and urbanization rate (Panta et al., 2014). Globally, about 34 MHa of irrigated land is impacted by salinization (Florke, Barlund, van Vliet, Bouwman, & Wada, 2019); 77% of these are in Asia where most of the population lives. The sustainability of the future agriculture and the global food security, therefore, are critically dependent on the efforts of plant breeders to create high yielding staple crop varieties that will incorporate salinity tolerance traits.

The adverse effects of salinization on plants are evident from negative growth trends from alteration or inhibition of biochemical and physiological processes (Zafar et al., 2020). Plants can be classified as glycophytes or halophytes by their ability to survive under high salt concentrations (Wang et al., 2014). Glycophytes are plants that are severely affected by saline conditions both at the cellular and whole-plant level. Under saline conditions, these plants exhibit greater accumulation of solutes, and ionic and osmotic stresses confer nutritional imbalances, which limit the productivity of these plants (Zafar et al., 2021c). The majority of terrestrial plants are glycophytes, including crop plants. Salt stress induces numerous changes in the plants, both morphological and biochemical, with many mechanisms being already identified as adaptations. The effects on the plants are due to osmosis and toxicity of microelements, indirectly due to soil structural problems; salinity might inhibit the growth by affecting the photosynthesis, thus disturbing the mineral uptake and availability. At the cell level, it interferes with passive transport through the cell membrane by changing the electrochemical gradient; decreasing the cellular water content; and influencing the ionic signaling pathways, ion cell performance, and the regulation of the enzymatic activity. Furthermore, the salinity of the soil induces oxidative stress in plants, leading to the production of reactive oxygen species (ROS) that further alter the metabolic activity of the cells. ROS are not only toxic but also interfere with the cell signaling; regulating processes, such as growth; stress response of the cells; and cell death. The tolerance to salinity is complex and genetically controlled, so it may differ from one species to another (Zafar et al., 2021c).

Farooq et al., 2020, Farooq et al 2021, Zafar et al., 2022). 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 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 (Parida et al., 2004) as the stress intensifies. Salt accumulation in soil solution reduces water and nutrient uptake. This leads to osmotic stress, ion toxicity, nutrient imbalances and a water deficit. Excessive concentrations of salt ions also injure photosynthetically active leaves, and may lead to chlorosis and early leaf senescence (Hanin et al., 2016). In addition, the supply of carbohydrates, which are needed for cell growth, may be hampered because photosynthesis rates are usually lower in plants exposed to salinity, and especially to sodium chloride (NaCl) (Tuteja et al., 2012). The onset of salt stress and its intensification affect the efficiency of photosynthesis, stomatal conductance and accelerate plant leaf senescence (Zörb et al., 2018). The salt-induced reduction in photosynthesis rate can be caused by partial stomatal closure caused by associated osmotic stress, by non-stomatal limitations caused by an excessive salt build-up and/or ionic imbalance in the leaves or by both limitations (Zafar et al., 2021c). The authors of (Zafar et al., 2020) emphasized that compatible solutes accumulation is necessary to correct the ionic imbalance and the potential water decrease. When NaCl directly hampers leaves and roots the plant will likely suffer from oxidative stress. Oxidative stress generated by an excessive NaCl accumulation affects the integrity of plant cellular membranes, causes electrolyte leakage, and damages chloroplasts (Sahin et al., 2018). Salinity tolerance is highly related to the maintenance of net photosynthetic rates, stomatal conductance and elevated chlorophyll concentration (Zafar et al., 2021c). Excess salt leads to a change in the ionic composition of the stroma of the chloroplasts, which in turn can cause shrinkage of the thylakoids and stacking of adjacent membranes in grana (Ashraf, 2004). An irreversible impairment of the photosynthetic apparatus, associated with a reduction in Rubisco activity, occurs when the stress is prolonged and salt continues to accumulate in the leaves (Tahir et al., 2018). As proposed by (Chaves et al., 2009) under drought stress, the reduction in O₂ in the chloroplasts via the Mehler-peroxidase pathway and possible photorespiration might provide photo-protection by acting as an alternative sink for excess energy in the photosynthetic apparatus. Photorespiration may thus be an alternative sink for light-induced electron flow, and it is often presented as a process that may help consume an appreciable electron flow during periods of restricted CO₂ availability in the chloroplasts and high irradiance (Jallani et al., 2017). According to (Valentini et al., 1995), the ratio J_c/J_o (photosynthetic electron flux density used for RuBP carboxylation/photosynthetic electron flux density used for RuBP oxygenation) is a good indicator of relative rates of carboxylation versus oxygenation and may be directly controlled by the kinetic properties of Rubisco.

Salinity and Physiological and biochemical Attributes

Salt accumulation in soil and water prevents plant growth through two major impacts. Firstly, the existence of salt in the soil solution decreases the capacity of a plant to absorb water, which is referred to as the osmotic or water deficiency of salt stress. This impact relies on the concentration of salt outside the plant and growth inhibition is mainly due to water shortage or osmotic stress, with very little genotypic variation in this trait observed. Secondly, the salt-specific or ion-excess salinity impact, whereby the accumulation of Na⁺ and Cl⁻ ions within the plant leads to toxic impacts on plant biochemistry (Greenway and Munns, 1980). The ionic phase of the growth loss can take some time, in some cases, up to 30 days, to establish and can have impacts on metabolic pathways that are required to provide sufficient energy to drive vital functions in adapting the plant to saline environments (Mittova et al., 2003). This includes the induction of plant proteins and metabolites, compartmentalization of ions at the cellular and tissue levels, the synthesis of compatible solutes, changes in photosynthetic and respiratory pathways, the induction of plant hormones, and alterations in membrane structure. These impacts can ultimately disturb physiological and biochemical homeostasis and lead to yield loss.

Limitations in the activity of photosynthesis induced by salinity exposure is a major physiological impact of salt exposure, reducing photosynthesis both in the short- and long-term. Coupled with the loss of photosynthetic activity, changes in plant respiration have also been extensively observed. These two processes are linked through the concept of carbon-balance, where an estimate of photosynthesis-fixed carbon minus respiratory carbon results in net assimilated carbon for plant growth. Under saline conditions, a slowing of respiration has been observed in some cases, but the impacts on the net carbon status of the plant remains limited due to a significant decrease in photosynthesis (Schwarz and Gale, 1981). However, other experiments have shown that specific respiration rates are either increased (Che-Othman et al., 2020) or are unaffected (Koyro et al., 2006). This coupled to the observation that generally the rate of photosynthesis decreases, indicates that respiratory variation may be essential in determining the differences in yield between salt stressed and non-stressed crop varieties. For example, a susceptible variety of wheat may show a dramatically enhanced rate of respiration under salt conditions, while the tolerant variety retains respiratory homeostasis, as a result the tolerant variety allocates less of its fixed carbon to respiration and more to growth (Kasai et al., 1998).

The disadvantage of elevated respiration rates is that carbon is spent on respiration instead of being assigned to the synthesis of new tissue, thereby restricting growth under a saline environment (Flowers et al., 2015). Mitochondrial respiration during salt exposure is needed to produce more ATP, which provides energy for metabolic processes such as ion exclusion, synthesis of compatible solutes and detoxification of ROS (Munns and Tester, 2008). When mitochondrial respiration is disrupted, this also disrupts the balance between ROS production and scavenging leading to the over accumulation of ROS, which requires greater respiration to detoxify (Jacoby et al., 2010). Additionally, the ability of a plant to exclude Na⁺ ions is linked to its root respiration rate (Malagoli et al., 2008) and it has been shown that respiratory homeostasis in leaves is associated with salt tolerance in wheat (Jacoby et al., 2013), however, this is yet to be verified in a larger range of species. The greater energy-use efficiency of a plant reduces the need to increase respiration and subsequently this will lower the production of ROS. The changing abundance of metabolites that are components of the metabolic pathways that drive respiration can play an important role in plant salinity tolerance and these compounds can serve as a repository of energy or act to adjust osmotic potential in crops exposed to salinity.

Inactivation of photosystems I and II and CO₂ fixation system by NaCl

The ability to control transport of Na⁺ across cellular membranes plays a critical role in the salt-induced inhibition of PSII activity. Increased Na⁺ levels in leaf apoplastic space results in a time- and dose-dependent inhibition of PSII activity in the intact mesophyll cells (Percey et al., 2014). These cells were able to maintain optimal photosynthetic performance when exposed to salinity for more than 24 hours while isolated chloroplasts showed declines in both the relative electron transport rate (rETR) and the maximal photochemical efficiency of PSII (Fv/Fm) within the first hour of treatment (Percey, McMinn, et al., 2016). The rETR was much more sensitive to salt stress compared with Fv/Fm, with 40% inhibition of rETR observed at apoplastic NaCl concentration as low as 20 mM. This reduction in rETR was accompanied by reductions in the amount of light required to saturate the photosystems (Percey, McMinn, et al., 2016). Interestingly, the impact of salinity on rETR and maximal photochemical efficiency of PSII was about two-fold more pronounced in isolated chloroplasts from glycophyte species (peas and broad beans) compared with their halophytic counterparts. The decrease in PSII activity correlated with K⁺-efflux from a cell, implying essentiality of K⁺ homeostasis for chloroplast operation (Pottosin & Shabala, 2016). Also, Na⁺ and Cl⁻ entry into the stroma can be critical for grana formation, inducing grana unstacking and thylakoid membranes disturbance, hence, eventually reducing PSII activity (Bose et al., 2017).

Evidence has also emerged that Na⁺ toxicity per se cannot fully explain inhibitory effects of salinity of PS machinery operation. For example, Zhang et al. (2018) used JIP-test and 820 nm light reflectance curves (Δ MR/MR0) to study effects of different types of sodium salt (NaCl, Na₂SO₄, NaHCO₃ and Na₂CO₃) at an equivalent Na⁺ concentration on PSII and PSI activity in sorghum. All salts inhibited electron transport from Q_A to Q_B at the PSII acceptor side. However, while all salts demonstrated the inhibition of PSII activity, the effect of alkaline salts was greater than the one of neutral salts. Also, NaCl stress showed no changes in PSI activity whereas other sodium salts showed PSI inhibition, likely due to higher pH values (Zhang et al., 2018). The effect of NaCl on PSII appears to be dependent on a cell's ability to modify the composition of thylakoid membrane proteins and efficiency of energy transfer from PSII light-harvesting antenna complex to RC (Jajoo, 2014; Kan et al., 2017; Sudhir & Murthy, 2004).

Salinity tolerance is known to be associated with a ploidy level (Chao et al., 2013; Shabala, 2019). Yan et al. (2015) showed that salt-induced photoinhibition of photosystems was found in autodiploid but not tetraploid honeysuckle (*Lonicera japonica*) plants. At the same time, in both type of plants salinity elevated NPQ, which can dissipate the excess excitation light energy into heat lowering generation of ROS and thus providing photoprotection (Wobbe, Bassi, & Kruse, 2016).

The dark reactions of photosynthesis are also affected by salinity (Bahmani, Noori, Darbandi, & Akbari, 2015; Meng et al., 2016). In addition to decreased CO₂ availability for photosynthetic carbon assimilation caused by stomatal closure, many key photosynthetically-related enzymes are inactivated (Table 1). This inhibition leads to the accumulation of NADPH that can induce excitation pressure and hence the generation of ROS in PSI. The accumulation of ROS, in turn, induces inhibition of biosynthesis of photosynthetic proteins, specifically D1 protein (Nishiyama et al., 2001; Nishiyama, Allakhverdiev, & Murata, 2006). This inhibition compromises an ability of photodamaged PSII for recovery (Murata et al., 2007). In addition, salt stress inhibition of the rate of D1 degradation can also manifest itself.

The classical view dominated in the literature from early 80ies was that photosynthetic enzymes in halophytes and glycophytes are equally sensitive to elevated Na⁺ levels (e.g. Osmond & Greenway, 1972). More recent findings question this notion (Bose et al., 2017). Chloroplastic fructose-1,6-bisphosphatase (FruP₂ase) purified from cultivated rice (*Oryza sativa*) was more sensitive to NaCl *in vitro* than that from the close halophytic relative *Porteresia coarctata* (Ghosh, Bagchi, & Majumder, 2001), largely as a result of the mutation in five amino acid residues in FruP₂ase gene. As a result, FruP₂ase activity in *Porteresia* was not inhibited by treatment as high as 500 mM NaCl (Chatterjee et al., 2013). Moreover, in a halophyte species *Kalidium foliatum*, application of 500 mM NaCl even increased Rubisco activity (Gong et al., 2018). Also, although *in vitro* effects of salinity on Rubisco activity is not different between glycophytes and halophytes (Osmond & Greenway, 1972), the latter demonstrate the higher extent of attachment of Rubisco activase to the thylakoid membrane (Li, Zhang, Lu, Wen, & Lu, 2011; Sengupta & Majumder, 2009; Wicwarz, Gubernator, Kruk, & Niewiadomska, 2015). This ensures restoration of Rubisco active form in the close proximity of PSI thus improving efficiency for CO₂ fixation in an ATP limiting environment (Chen, Wang, Mi, Chen, & Xu, 2010).

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