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MINI-REVIEW

The antioxidant system in *Suaeda salsa* under salt stress

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ABSTRACT
Suaeda salsa L. is a typical euhalophyte and is widely distributed throughout the world. Suaeda plants are important halophyte resources, and the physiological and biochemical characteristics of their various organsand their response to salt stress have been intensively studied. Leaf succulence, intracellular ion localization, increased osmotic regulation and enhanced antioxidant capacities are important responses for Suaeda plants to adapt to salt stress. Among these responses, scavenging of reactive oxygen species (ROS) is an important mechanism for plants to withstand oxidative stress and improve salt tolerance. The generation and scavenging pathways of ROS, as well as the expression of scavenging enzymes change under salt stress. This article reviews the antioxidant system constitute of *S. salsa*, and the mechanisms by which *S. salsa*antioxidant capacity is improved for salt tolerance. In addition, the differences between types of antioxidant mechanisms in *S. salsa*are reviewed, thereby revealing the adaptation mechanisms of Suaeda to different habitats. The review provides important clues for the comprehensive understanding of the salt tolerance mechanisms of halophytes.

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Introduction

There exists a set of antioxidant systems responsible for scavenging reactive oxygen species (ROS) in plants.[1,2] Under normal circumstances, these systems can scavenge ROS produced during plant growth, to maintain a state of dynamic equilibrium. Under stress conditions, such as salt stress, the amount of ROS synthesized in plants increases,[3–6] which results in a relatively inadequate antioxidant scavenging capacity and a disequilibrium that leads to oxidative stress.[1,7–10] Plant antioxidant systems can scavenge these ROS to avoid damage by excessive ROS to plants.[11,12] The halophytes have strong ROS scavenging ability, and there is complex relationship between stress resistance and antioxidant ability of halophytes.[13–15] *Suaeda salsa* L. (*S. salsa*) is an annual herbaceous plant of the Suaeda genus, Chenopodiaceae family, which is suitable for saline and alkaline land in the intertidal zone, seaside, lakeside, desert and inland high-salt patches.[16] *S. salsa* can grow in soils with a salt content of 2.5%~3.0% and is a typical salt-tolerant plant,[17–20] which can used as a promising model to underst and salt tolerance and to develop saline agriculture.[21] In recent years, researchers have conducted many studies on the antioxidant system of *S. salsa*and revealed the salt-tolerance mechanisms of Suaeda plants from the perspective of oxidative stress. In this paper, the salt tolerance mechanism of *S. salsa*is reviewed mainly in the context of oxidative stress.

The antioxidant systems in *S. salsa*

Plant antioxidant systems are generally classified into enzymatic defense systems and non-enzymatic defense systems.[1,22,23] The former include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), peroxiredoxin reductase (PrxR) and some ascorbic acid (AsA)-glutathione (GSH) cycle enzymes. Among them, POD includes glutathione peroxidase (GPX) and ascorbate peroxidase (APX), and AsA-GSH cycle enzymes include glutathione reductase (GR), dehydroascorbic acid reductase (DHAR) and monodehydroascorbic acid reductase (MDHAR).[1,24] Non-enzymatic defense systems include AsA, GSH and some thiol-containing low-molecular-weight compounds.[25,26] *S. salsa*scavenges ROS produced by salt stress mainly through the SOD dismutation, CAT pathway, GPX pathway, PrxR pathway and AsA-GSH cycle (Figure 1).

The SOD dismutation

SOD is the first defencein the plant antioxidant system and plays an important role in ROS scavenging. SOD catalyzes the dismutation reaction of two superoxide radicals to form O_2 and H_2O_2. H_2O_2 is then converted to H_2O catalyzed by antioxidant enzymes.[1] Studies have confirmed that under salt stress, the SOD activity of *S. salsa*[27-29] and *S. maritima*[30] increased gradually as the salt treatment increased. This tendency is mainly due tothe activity of SOD, as an inducing enzyme, is affected by the concentration of the substrate superoxide anion. An increase in the degree of salt stress would increase the production of O_2^-, thereby inducing the increase in SOD activity.[20]

The CAT pathway

CAT is an enzymatic scavenging agent based on iron porphyrin as the prosthetic group. This enzyme can promote the rapid decomposition of H_2O_2 into H_2O and O_2. CAT is widely found in plant cells and is one of the key enzymes in the

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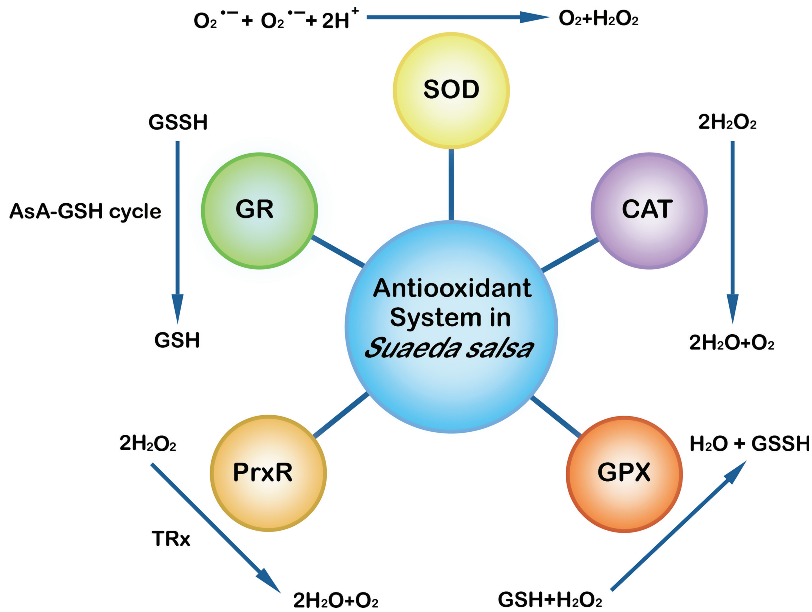

Figure 1. The antioxidant system of *Suaeda salsa*. The superoxide dismutase (SOD) catalyzes the dismutation reaction of two superoxide radicals to form O_2 and H_2O_2, which is then converted to H_2O catalyzed by antioxidant enzymes. The catalase (CAT) is an enzymatic scavenging agent based on iron porphyrin as the prosthetic group, which can promote the rapid decomposition of H_2O_2 into H_2O and O_2. The glutathione peroxidase (GPX) catalyzes the binding of GSH to H_2O_2, generating H_2O and GSSH. Theperoxidase reductase (PrxR) scavenges H_2O_2, using thioredoxin (TRx) as a redox carrier to provide electrons. The glutathione reductase (GR) reduces GSSH to GSH through the AsA-GSH cycle, providing electron donors for the next round of H_2O_2 scavenging.

biological defense system, providing the organism with an antioxidant defence mechanism. When CAT acts on H_2O_2 in plants, two H_2O_2molecules must be bound to the active site of CAT. High concentrations of H_2O_2 can increase the decomposition rate of CAT, so this pathway can effectively scavenge excessive intracellular H_2O_2.[1] Under salt stress, the CAT activities in *S. salsa*[31]and *S. maritima*[30,32] increase, suggesting that this enzymemay play an important role in scavenging H_2O_2 produced by salt stress.

The GPX pathway

GPX is an oxygen radical scavenger. In this pathway, GPX catalyzes the binding of GSH to H_2O_2, generating H_2O and GSSH, and GR then reduces GSSH to GSH, providing electron donors for the next round of H_2O_2 scavenging.[1] Studies have found that salt treatment increasedthe GPX activities in *S. salsa*[31] and *S. fruticosa*[33] leaves. Through a proteomics study, Askari and collaborators found that salt stress could significantly induce the expression of GPX protein in *S. aegyptiaca* leaves.[34]

The PrxR pathway

The PrxR pathway is a central link in the intracellular antioxidant defense system in plants. With its reversible disulfide bonds and thiol changes, thioredoxin (TRx) is used as a redox carrier to provide electrons for PrxR to scavenge H_2O_2.[1] The Prx Q gene expression was up-regulated by NaCl in *S. salsa*, which had a thioredoxin-dependent peroxidase activity, the characteristic of the Prx family.[35] The expression of the PrxR protein in *S. aegyptiaca*was significantly up-regulated by treatment with 150 mmol/L NaCl, indicating that the PrxR protein may play an important role in ROS scavenging under salt stress.[34,36]

The AsA-GSH cycle

The GR plays a role in the production of GSH through the AsA-GSH cycleinthe mitochondria, chloroplast matrix and cytoplasmof plants, and AsA and GSH in the cycle can inhibit lipid peroxidation and scavenge free-radicals.[1]An increase of GR activity promotes the production of GSH content, which can directly scavenge ROS.[37]Treatment of *S. salsa*with 200 mmol/L NaCl increased the AsA and GSH contents in leaves and decreased the H_2O_2content, suggesting that the increase of AsA may be important for the decrease in the H_2O_2content. After treatment of *S. salsa* with 200 mmol/L NaCl for 7 days, the activities of APX and GR in chloroplast matrix and thylakoids were significantly increased, resulting in a decreased H_2O_2content and a decreased membrane lipid peroxidation.[38]

The response of *S. salsa*to salt stress

The effects of different salt concentrations on the*S. salsa* antioxidant system

Salt stress can lead to increased ROS in plants and thus cause oxidative stress, and the ability to scavenge stress-induced H_2O_2effectively is crucial to stress resistance.[39,40]*S. salsa* can reduce the production of ROS free radicals and the oxidative stress by increasing the activities of antioxidant enzymes.[41,42]Hence, under salt stress, the activities of various enzymes and the content of non-enzymatic substances involved in the H_2O_2 scavenging process would reflect the salt-stress resistance ability of *S. salsa*. Studies have revealed that the effects of salt-stress treatment on the POD activity in *S. salsa* in different habitats were different.[21]Upon salt treatment, the POD activity in *S. salsa* in the intertidal habitat was significantly higher than that in the saline-alkali habitat. With the increase of NaCl concentration, the GR and GSH in *S. salsa* leaves showed an increase first and then a decrease. Similarly, the GST expression in leavesof *S. salsa*also showed a tendency to increase first and then decrease. Some investigators have studied the organ-specific response and the activity of plasma membrane H^+-ATPase in callus by studying vacuole H^+-ATPase in the NaCl-treated *S. salsa*shoots and roots.[43,44] Cheng and collaborators found that salt stress could improve the cold resistance of *S. salsa*,[45] improve seed vigor,[46] promote seed maturation[47](e.g., salt and nitrate would promote dimorphic seed production and seed germination[48]) and possibly affect the yield and salt tolerance of *S. salsa*.[49]

Effects of different combined treatments of waterlogging and salt on*S. salsa* antioxidant systems

Using greenhouse control simulation experiments, some papers reported the effects of different groundwater depth and salt concentration on the activities of antioxidant enzymes in multiple Suaeda populations and revealed the mechanism of synergistic regulation of antioxidants in Suaeda caused by waterlogging and salt stress.[50–52]With waterlogging stress and an increase in salt concentration, the SOD activity increased nearly three fold, and with decreased waterlogging stress, the SOD activity decreased, indicating that waterlogging and salt stress had a positive interaction with SOD and that both salt stress and waterlogging stress could increase the SOD activity. Although the trend of CAT changes under salt stress conditions was similar to that of SOD, the CAT activity decreased during waterlogging stress.[31,53,54]Under waterlogging and salt stress conditions, MDA content increased with an increase in salt concentration, indicating that when *S. salsa* is subjected to the dual stress of waterlogging and high salinity, the membrane system of the cells is severely damaged.[54–57]Based on the changes in water depth at different times, *S. salsa*in coastal saline-alkali soils could adjust the oxidative stress scavenging system to adapt to different environments. The different responses of SOD and CAT to waterlogging stress may be adaptive mechanisms by which *S. salsa* maintains long-term survival in different water and salt environments.[54]

The regulation of antioxidant system in *S. salsa* under some other stresses

Liu and collaborators found that mercury exposure inhibited plant growth of *S. salsa* and induced significant metabolic responses and increased activities of antioxidant enzymes including SOD and POD.[58]And after exposure to environmentally relevant lead and zinc for 15 days, the expression levels of CAT genes were significantly upregulated in *S. salsa*.[59]Under chilling stress, the SOD and APX activity in *S. salsa* increased first and then declined, while the production of ROS ($O_2.^-$ and H_2O_2) decreased first and then increased.[60]Co-expression of the *S. salsa GST* and *CAT1*genes in transgenic rice resulted in greater increase of CAT and SOD activity following both salt and paraquat stress.[61]These studies indicated that different stresses could synergistically regulatethe antioxidant system of *S. salsa*.

The antioxidant abilities of different *S. salsa*ecotypes

*S. salsa*can be divided into two ecotypes, red-violet and green, depending on the color of the leaves. The former is affected by high salt, low temperature and waterlogging, while the latter is mainly affected by salt stress and drought stress.[21,56]The two ecotypes of *S. salsa*also have different antioxidant pathways. The contents of reduced GSH and AsA and the activities of SOD and APX in the red-violet ecotype of *S. salsa*were higher than in the green ecotype, while the POD and CAT activities were lower than in the green ecotype. By analysing four antioxidant enzymes, it was found that there were differences in the antioxidant enzyme profiles in the leaves of the two ecotypes of *S. salsa*. The expression levels of SOD and APX in the red-violet ecotype of *S. salsa*leaves were higher than those in the green ecotype, while the CAT and POD expression levels in the leaves of the green ecotype of *S. salsa*were higher than those in the red-violet ecotype.[62] The activity and isoenzyme expression of the antioxidant enzymes in the leaves were different between the two ecotypes of *S. salsa*, suggesting that they relied on different antioxidant enzymes for ROS scavenge.

Researchers compared the antioxidant systems of the two different ecotypes of *S. salsa*in the intertidal habitat and found that the major antioxidant enzymes in the two ecotypes were not identical.[63] Under natural conditions, the H_2O_2content in the leaves of the green ecotype of *S. salsa*was significantly higher than that in the red-violet ecotype, and the activities of the antioxidant enzymes were not significantly different between these two ecotypes. Wang and collaborators found that the content of betacyanin in *S. salsa*increased under salt stress.[64]The content of betacyanin in the red-violet ecotype of *S. salsa*was higher than in the green ecotype, and the concentration of exogenous H_2O_2 was significantly negatively correlated with the content of betacyanin in leaves. These findings indicate that betacyanin may be involved in regulating the ROS levels as a non-enzymatic antioxidant agent in *S. salsa*, thereby reducing stress-induced oxidative damage.

The activity of extracts in *S. salsa*

The activity of flavonoid extracts in *S. salsa*

Flavonoids are a class of plant secondary metabolites with extensive biological activities, including antioxidant, anticancer, anti-inflammatory, anti-allergy, hypoglycemic, hypolipidaemic, immunomodulatory, antibacterial, anti-drug and anti-cardiovascular disease activities.[65] Some researchers obtained crude flavonoids from *S. salsa*using 65% ethanol, which were subjected to polyamide column chromatography to obtain refined flavonoids. The total content of flavonoids was determined by spectrophotometry, and the antioxidant properties were studied using the nitrogen blue tetrazolium (NBT) method, which showed that the flavonoids in *S. salsa* have an inhibitory effect on the autoxidation of lard.[47,66]Wang and collaborators obtained ten flavones from the 95% ethanol extract of the leaves and stems of *S. salsa*, and found that luteolin could clear DPPH and ·OH, with IC50 values 2.89 and 36.7 μg/mL, respectively.[67]In addition, these flavonoids all have strong inhibitory effects on *Escherichia coli* and *Staphylococcus aureus*, with the total flavonoid extracts during the flowering period having the greatest inhibitory effect on the bacteria. Studies have also demonstrated that the total flavonoids in *S. salsa*extracts could scavenge hydroxyl radicals and oxygen free radicals, and inhibit α-amylase and lipase activities.[68]

The activity of other extracts in *S. salsa*

Except for flavonoids, some other compounds from *S. salsa* have various activities, which can be used as industrial and pharmaceutical materials. Li and collaborators comprehensively analyzed the metabolic response of *S. salsa* under salinity from the perspective of omics, demonstrating that secondary metabolites, such as quercetin, 2,4-dihydroxybenzoicacid, isorhamnetin and 2-hydroxygenistein, may play an important role as antioxidants and regulatory substances.-[69]Wang and collaborators isolated ten known metabolites from *S. salsa* using 95% ethanol, and found one of the compounds, (−)-syringaresinol-4-O-β-D-glucopyranoside, showed moderate cytotoxic activity against four carcinoma cell lines, determined by the MTT colorimetric method.[70]

Perspective

A large number of researches have been conducted on the antioxidant effects of *S. salsa*, which laid the foundation for revealing the antioxidant mechanism of Suaeda plants and provided important clues for a comprehensive understanding of the salt tolerance mechanisms of euhalophytes. The activity of the enzymes in the antioxidant system is closely related to plant metabolism during stress. However, at present, the production and detection technologies of various ROS forms have not been perfected, and the research on plant scavenging mechanisms needs to be developed. The analysis of ROS generation and properties in halophytes and the action of plant antioxidant systemsis not only important for understanding the physiological metabolism of plants *per se*, but also has profound significance for improving the stress tolerance of transgenic plants through the bioengineering of antioxidant genes. Therefore, the study of the salt tolerance mechanisms in halophytes, including their antioxidant systems, needs to be strengthened, and in-depth investigations of secondary stress caused by salt stress in Suaeda plants also need to be conducted. Combined with the analysis of stress-induced transcriptional regulation and energy metabolism, the osmotic regulation mechanisms and the antioxidant mechanisms should be clarified and the salt-tolerance mechanisms of Suaeda plants systematically elucidated, laying the foundation for genetic engineering of plant salt-tolerance.

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