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Mechanisms of plant responses to salinity stress

Abstract. *Environmental stress is a major area of scientific interest because it limits the productivity of both plants and crops. Anthropogenic activities have exacerbated the issue even more. As a result, salt stress appears to be a significant barrier to plant and crop productivity. Salinity has a variety of effects on plants, including osmotic effects and ion-specific toxicity, as well as proline accumulation and sulphur assimilation. Plants known as halophytes have a high salt tolerance, allowing them to survive and thrive in extremely saline conditions. The study of halophytes aids our comprehension of important adaptations required for survival in high salinity environments. Therefore, enhancing plant salt tolerance as well as increasing agricultural yield and quality of crops in saline lands is of vital importance. Here, we look at what we know about how salinity affects plant metabolism and how plants deal with it.*
Keywords: *salt stress, Salicornia and Sarcocornia Plants, sulfur assimilation, proline accumulation, reactive oxygen species (ROS), halophyte plants.*

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Introduction

Over time, plants have developed several adaptation strategies to changing environmental conditions such as temperature, light, mineral concentrations, water, and other abiotic, biotic factors. One of the oldest and most significant worldwide abiotic pressures impacting agricultural output is soil salinity. According to the Food and Agricultural Organization (2008), salt affects around 6% of the world's total land surface or roughly 800 million hectares of land (http://www.fao.org/ag/ag1/ag11/spush/). Furthermore, by 2050, it is estimated that roughly half of all arable land would be damaged by salt stress [1,2]. As a result, there is a pressing need to develop approaches to mitigate the negative impacts of salt stress and to implement measures to boost crop yield in saline environments. Salinity has an impact on a variety of physiological processes in cell metabolism, including photosynthesis, protein synthesis, energy, and lipid metabolism, as well as causing growth reduction. Plant growth is influenced by ionic and osmotic effects, nutritional imbalances, and oxidative stress. For sustainable crop production, it is therefore vital to understand the physiological processes and molecular mechanisms that plants use to build salt resistance [3,4].

Salt Stress: Consequences and Mechanism of Detoxification

Plants are affected by soil salinity in two ways. High salt concentrations in the soil make it difficult for roots to draw water, and high salt concentrations in the plant can be hazardous [6,7].

Salt stress causes plants to accumulate excessive amounts of sodium (Na^+) and chloride (Cl^-), disrupting the vital nutrient balance. Plants adapt to salt stress to maintain a suitable K^+/Na^+ ratio in the cytosol. Furthermore, excessive formation of reactive oxygen species (ROS) that obstruct physiological activities is an inescapable consequence of elevated Na^+ and Cl^- buildup in plants. High levels of reactive oxygen species (ROS) can oxidize photosynthetic pigments, proteins, lipids, and nucleic acids [8,9]. In transgenic cabbage plants and salt-tolerant cultivars, controlling ROS generation and scavenging in the chloroplast has been demonstrated to be critical for salinity tolerance [9,10]. ROS serves as a stress signal, triggering acclimation and defense systems that, in turn, mitigate stress-related oxidative damage [11–13]. H^2O^2 generated by apoplastic polyamine oxidase has recently been demonstrated to alter salinity stress signaling in tobacco and to play a role in the plant response balance between stress tolerance and cell death [14,15]. DNA damage from excessive ROS generation includes base deletion, pyrimidine dimers, cross-links, strand breakage, base modification, and activation of programmed cell death [16]. As a result, plants have numerous detoxification systems to protect cellular components from ROS [17].

Plant salt tolerance systems can be classified as either low-complexity or high-complexity. Changes in various metabolic pathways are involved in low-complexity processes. Selective ion accumulation or exclusion, control of ion uptake by roots and transport into leaves, ion compartmentalization at the cellular and whole-plant levels, synthesis of compatible solutes, changes in membrane structure, induction of antioxidative enzymes, and other changes are examples of these changes [18,19]. Changes that protect major processes like photosynthesis and respiration, such as water use efficiency, and those that preserve important features like cytoskeleton, cell wall, or plasma membrane–cell wall interactions [5,20], as well as chromosome and chromatin structure changes, such as DNA methylation, polyploidization, amplification of specific sequences, or DNA elimination [21,22], are examples of high-complexity mechanisms. Low-complexity mechanisms are thought to be triggered in a coordinated manner to safeguard higher-order processes [23].

Salt Tolerance in Halophyte Plants

Plants may be split into two types based on their resistance to salinity: glycophytes and halophytes. Halophytes are a kind of halophyte that can complete their life cycle at a salt concentration of at least 200 mM NaCl and makeup around 1-2% of the world's flora [24,25]. Some of the more extreme halophytes termed halophytes, can grow and produce biomass at seawater salinities. *Suaeda fruticosa*, which grows in association with *Arthrocnemum macrostachyum*, was reported to exhibit its highest biomass production rate at 400–600 mM NaCl, with little mortality when grown at up to 1000 mM NaCl [26,27].

Halophytes are phylogenetically varied plant species that belong to a variety of plant families, including both dicots and monocots. They are plants that live in one of two types of natural habitats: (1) habitats with high levels of brackish water in the soil that frame coastal lines in both tropical (e.g., mangrove ecosystems) and temperate (e.g., arid and semi-arid inland regions where annual evaporation rates exceed precipitation); and (2) arid and semi-arid inland regions where annual evaporation rates exceed precipitation. Salts are released from basal rocks in these areas, rising to the top layer of soil by capillary action, where they precipitate and induce soil salinization. There are very limited opportunities to use halophytic plant species as crops although there are occasional outliers, such as *Salicornia* from the *Chenopodiaceae* family [28,29].

***Salicornia* and *Sarcocornia* Plants**

Salicornia and Sarcocornia, genera that naturally survive in coastal salt marshes from the Arctic to the Mediterranean and are frequently subjected to daily tides, are promising prospects for the establishment of novel halophytes as crop species.

On the sea coasts, salt-tolerant species of both genera are commonly referred to as "pioneer plants" [30–32]. *Salicornia* is a novel vegetable crop that can be watered with saltwater or very saline water. *Salicornia* is a salt-tolerant plant that can be watered with water that contains as much salt as saltwater [33,34]. The perennial *Sarcocornia* differs from the annual *Salicornia* by its distinct perennial growth habit [30,35] and floral arrangement peculiarities [32,36]. Both genera contain succulent shoots that may be utilized to grow green crops, but the yields and nutritional value of each are different [37,38].

Salicornia is a vegetable with leafless shoots that resemble green asparagus that has been introduced to the European market. The young fleshy tips of this green vegetable are in high demand in gourmet kitchens, not only because of their salty flavor, but also because of their high nutritional content in terms of minerals, antioxidants, and vitamins like vitamin C and β-carotene [33,38]. Importantly, a halophyte crop must be capable of high-yield production under salty circumstances to be economically viable [34,39].

Involvement of Sulphur Containing Compounds in Salt Tolerance

Mineral nutrient levels are important for crop yield and quality. The mineral nutrition and sustainability of crops are both complicated in a saline environment. Reports on the effect of the interaction between salinity level and mineral nutrients on salt tolerance are available [29,40]. For example, an adequate supply of sulfur (S) has been shown to enhance growth and photosynthetic activity to a great extent, and to protect against the negative effects of salt stress on barley crops [41]. Through S-N mediated metabolite synthesis of antioxidant defense compounds in Olieferous brassicas cultivars, plant N and S supply played an important role in plant growth, development, and productivity [42].

Sulphur is found in a wide range of compounds, such as polysaccharides, iron-sulphur clusters, lipids, as well as a broad variety of biomolecules such as vitamins (e.g biotin and thiamine), cofactors (e.g CoA and S-adenosyl- methionine) peptides (e.g glutathione and phytochelatins), secondary products (allyl cysteine sulphoxides and glucosinolates) and the S containing amino acids cysteine and methionine [43,44]. Thiols can react with a wide range of agents, including free radicals, reactive oxygen species, and cytotoxic electrophilic organic xenobiotics, thanks to cysteine residues. As a result, sulphur metabolism is critical in plant stress responses [45–47].

Plants with high antioxidant levels have a better ability to scavenge ROS and so deal with higher salt concentrations [15,48]. As a result, increased antioxidant compound synthesis can be exploited as a future selection factor in crop breeding for salt tolerance [49]. Reduced glutathione (GSH) is one of the antioxidants involved in scavenging ROS and maintaining steady-state ROS levels.

GSH is a tripeptide that is present in high amounts throughout the cell [50,51]. During H_2O_2 breakdown by GSH, the ratio of GSH to its oxidized form, glutathione disulfide (GSSG), is critical for maintaining redox balance in the cell [51–53]. Several plants, including tomato, wheat, and the halophyte *Myrothamnus flaberllifolia* [51,54,55], have been found to benefit from maintaining a high GSH/GSSG ratio.

The activity rates of serine acetyl transferase (SAT) and O-acetyl serine thiol lyase (OASTL) rise in plants subjected to salinity stress, promoting a greater rate of cysteine biosynthesis, which results in enhanced GSH production for defensive responses to salt stress-induced ROS [3]. Many studies have been reported in which S assimilation was improved to generate glutathione. *Brassica napus* treated with saltwater conditions boosted its S assimilation rate and cysteine and GSH production significantly [51,56]. Salt stress has been linked to changes in S assimilation enzymes in broccoli, and *Arabidopsis* [41,47,57] found that salt stress impacted root thiol concentration via modifying the rate of S assimilation. Transgenic techniques have also proven successful in improving plant salt tolerance capability by modifying S metabolism. Increased resistance to oxidative stress was shown when the sulfate transporters, ATP-sulfurylase, Cys, OAS, and GSH were overexpressed [46,58]. Thus, employing genetic engineering to change the regulation of S partitioning and manipulate the production of S-containing molecules in plants might be a viable strategy for enhancing salt tolerance [59,60].

Regulation of Sulfur Assimilation

The absorption of inorganic sulfate by the sulfate transporters SULTR 1,2 is generally the first step in plant sulfur metabolism, and it is fueled by the proton motive force provided by ATPase [60,61].

Sulphate reduction activation is the most common pathway for assimilation, and it occurs in plastids [44,62]. The adenylylation of sulfate, mediated by ATP sulfurylase (ATPS), generates adenosine 5′-phosphosulfate, which starts the sulfate reduction pathway (Fig 1). (APS). The plastidic enzyme APS reductase then converts APS to sulfite (APR). Sulfite reductase also converts the hazardous sulfite to sulfide (SiR). Sulfide is then integrated into cysteine in a process mediated by the enzyme OAS-TL [60,63]. Sulfide is combined with O-acetylserine (OAS), which is catalyzed by SAT.

Most sulfur compounds are generated from cysteine, which is the major intermediate [see Fig 1 and [62]]. Cysteine can also be used as a precursor for the production of methionine, which is then integrated into proteins or transformed into S-adenosyl methionine (SAM) by SAM synthetase after a reaction with ATP. The two principal S products, cysteine, and methionine, need interactions with both N and C metabolism. The coordinated actions of S, N, and C metabolism in plants are believed to improve salt stress tolerance and aid the S assimilatory reduction route for salt stress control in plants [4].

As previously mentioned, sulfate assimilation in plants is highly documented. However, only scarce information exists on sulfate assimilation in halophytes exposed to salinity. Thus, not much is known about the behavior of the biochemical and molecular components of sulfate assimilation in halophytes [40,64].

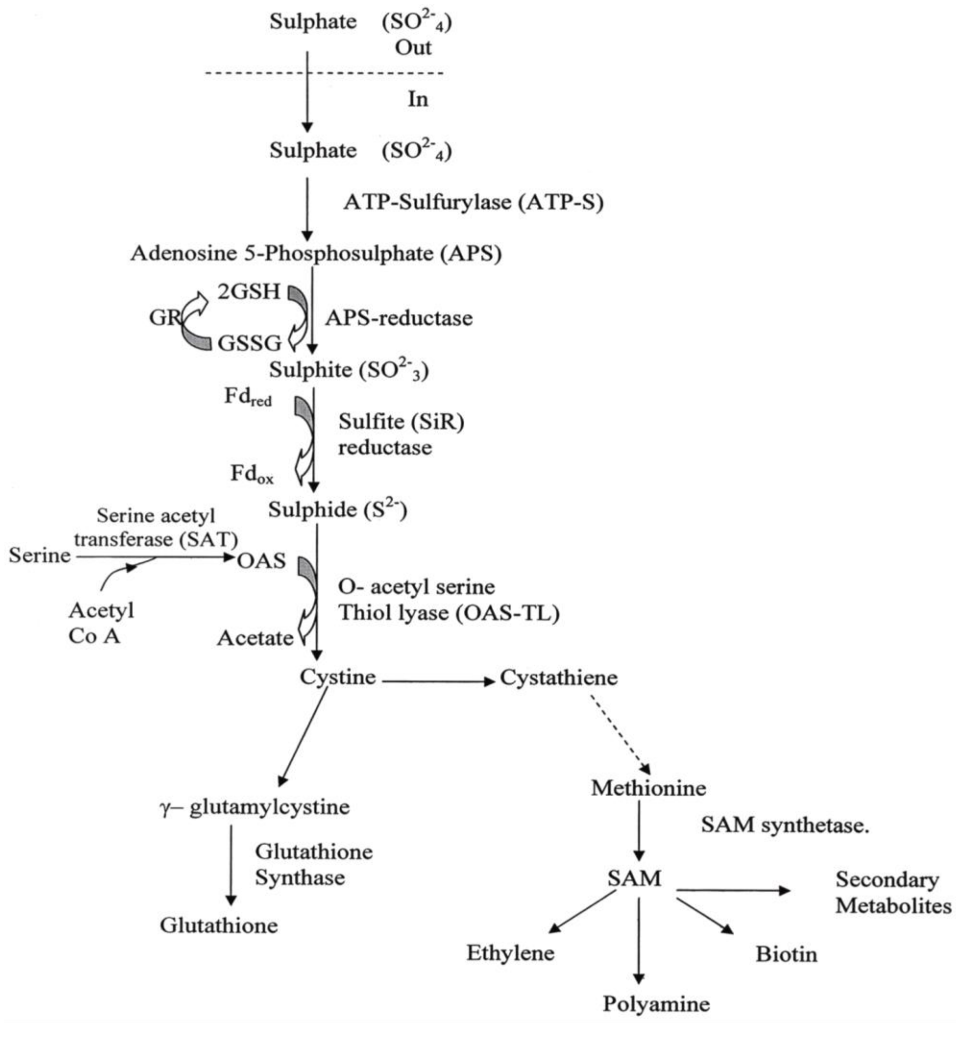

Figure 1. Schematic representation of the sulfate reduction pathway [3]

Mechanisms of proline stress protection

The accumulation of proline is one of the most critical changes in the metabolism of plants when they are under a lot of salt stress. [65].

In plants, intracellular proline levels have been discovered to expand by>100-fold under stress. Proline accumulation in plants happens throughout the presentation on different stresses, including salt, drought, UV radiation, and oxidative stress [66]. Under stress conditions (e.g., drought, salinity), proline accumulation for plants includes complementary regulation of pyrroline-5-carboxylate synthetase (P5CS) and proline dehydrogenase (PRODH). Over higher plants, biosynthesis from claiming proline happens using two pathways relying upon the relative accessibility of the elective substrates, glutamate (Glu) and ornithine (Orn). The Glu pathway starts for P5CS by reducing Glu with ATP and $NAD(P)H^{+}H^{+}$ to glutamate-semialdehyde (GSA), which transforms to pyrroline-5-carboxylate (P5C) spontaneously. For proline biosynthesis, the Orn pathway needs to be mostly acknowledged as an elective pathway. Orn is transaminate by ornithine-d-aminotransferase (OAT), which produces GSA and P5C, which is then subsequently reduced to proline by pyrroline-5-carboxylate reductase (P5CR) [67]. P5CS activity (Glu pathway) expanded upon salt stress treatment, same time OAT action (Orn pathway) remained unchanged, implying that the Glu pathway instead of the Orn pathway assumes an additional huge part on proline amassing throughout osmotic regulation in salt stress [65].

During salt stress, proline was shown to protect Complex II of the mitochondrial electron transport chain, stabilizing mitochondrial respiration.

Under specific conditions, the P5C–proline cycle can deliver electrons will mitochondrial electron transport without producing glutamate and, under specific conditions, could produce more ROS in the mitochondria [68]. Proline catabolism is, therefore, a critical regulator for cell division ROS equalization and impacts various extra regulatory pathways. The certainty that proline might go about as a signaling molecule and also impact protection pathways, and control complex metabolic and developmental processes offer extra chances for plant improvement [5,68].

In the halophyte species, proline might have been sequestered will vacuoles in non-stressed plants, while in salt-stressed plants, a high proline content might have been distinguished in the cytosol, suggesting the vitality of de novo proline biosynthesis and also transport for proline accumulation [7].

The mechanisms by which proline alleviates anxiety could be classified into two broad categories. One possibility is that organisms gather proline by increasing proline biosynthesis, with proline acting as an osmolyte, a chemical chaperone, and a direct scavenger of OH^{-} or O^{-2}. A second system relies ahead on dynamic proline metabolic flux and linkages with different metabolic pathways. Proline metabolic flux prompts cell insurance by helping maintain cellular energy and $NADP^{+}$/NADPH balance, enacting indicating pathways that push cell survival, What's more helping should different pathways for example, such those tricarboxylic acid cycle and GSH biosynthesis [66,67]

Conclusion

In the future, soil salinity will continue to be a danger to agricultural productivity and food security. The most efficient strategy to solve his environmental problem is to cultivate salt-tolerant crops. Under salt stress, sulfate needs for metabolic adaption responses are increasing, indicating the importance of sulfur-containing metabolites. Sulfur-containing compounds have two functions in plants: they serve as structural components for a variety of cellular components as well as for cellular interaction with the environment as signaling molecules. Changes in ROS and ROS-related enzymes are also early stress indicators. Early identification of salinity stress impact may be possible using molecular and oxidative stress. Still, each stress signature has its limitations, whether they are morphological, physiological, oxidative, or molecular changes in plants. Chlorophyll content, proline accumulation, stress protectants, and membrane stability are all investigated using physiological and biochemical markers. These physiological markers, especially changes in plants' levels of proline, are important for making plants more resistant to salt.

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Тұздылық стресіне өсімдіктердің жауап беру механизмдері

Аңдатпа. Экологиялық стресс ғылыми қызығушылықтың негізгі саласы болып табылады, өйткені ол өсімдіктердің де, дақылдардың да өнімділігін шектейді. Антропогендік белсенділік бұл мәселені одан әрі ушықтырды. Нәтижесінде, тұзды стресс өсімдіктер мен дақылдардың өнімділігіне айтарлықтай кедергі келтіреді. Тұздылық өсімдіктерге әртүрлі әсер етеді, соның ішінде осмотикалық әсер және ион-спецификалық уыттылық, сонымен қатар пролиннің жиналуы және күкірттің ассимиляциясы. Галофиттер деп аталатын өсімдіктер тұзға жоғары төзімділікке ие, бұл оларға тұзды стресс жағдайында өмір сүруге және өсуге мүмкіндік береді. Галофиттерді зерттеу жоғары тұздылық жағдайында өмір сүру үшін қажет маңызды бейімделулерді түсінуге көмектеседі. Сондықтан өсімдіктердің тұзға төзімділігін арттыру және тұзды жерлерде дақылдардың өнімділігі мен сапасын арттыру өте маңызды. Мұнда біз тұздылықтың өсімдіктер алмасуының әртүрлі аспектілеріне және оның өсімдіктерге төзімділік стратегиясына әсері туралы түсінігімізді қарастырамыз.

Түйін сөздер: тұзды стресс, *Salicornia* және *Sarcocornia* өсімдіктері, күкірттің ассимиляциясы, пролиннің жиналуы, оттегінің белсенді формалары (ОБФ), галофитті өсімдіктер.

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Механизмы ответа растений на солевой стресс

Аннотация. Экологический стресс является основной областью научного интереса, поскольку он ограничивает продуктивность как растений, так и сельскохозяйственных культур. Антропогенная деятельность еще больше усугубила эту проблему. В результате солевой стресс, по-видимому, является серьезным препятствием для продуктивности растений и сельскохозяйственных культур. Соленость оказывает различное воздействие на растения, включая осмотический эффект и ионоспецифическую токсичность, а также накопление пролина и ассимиляцию серы. Растения, известные как галофиты, обладают высокой солеустойчивостью, что позволяет им выживать и процветать в чрезвычайно засоленных условиях. Изучение галофитов способствует пониманию важных адаптаций, необходимых для выживания в условиях высокой солености. Поэтому повышение солеустойчивости растений и повышение урожайности и качества сельскохозяйственных культур на засоленных землях имеют жизненно важное значение. Здесь мы рассмотрим наше понимание влияния солености на различные аспекты метаболизма растений и стратегии его толерантности у растений.

Ключевые слова: солевой стресс, растения *Salicornia* и *Sarcocornia*, ассимиляция серы, накопление пролина, активные формы кислорода (АФК), галофитные растения.

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