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Impact of Salinity on Growth and Development of Plants with the central focus on Glycophytes: an overview

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ABSTRACT
Plants are the most flexible organisms of nature, tending to change themselves depending on the environmental conditions they are exposed to. If the conditions are favourable, plants grow smoothly, but if conditions are adverse, they cannot maintain their everyday activities. The conditions that are unsuitable for plants' growth and survival are considered stress. In the present scenario, salinity is one of the detrimental environmental stresses for plants and allied organisms. Salinity stress is a severe environmental constraint to plant growth and plant survival. Excess salt in soil affects plants multitudinously. In the present communication, the authors have reviewed the effects of salt stress on the growth, phenology, and primary and secondary metabolism of glycophytes which are sensitive to salinity and include many economically important crops. Soil salinity affects almost all the events of a plant by inducing osmotic stress, altering the nutrient level and creating toxicity. It also disturbs cell division, genetic circuits and protein synthesis machinery of plants. Salt stress can affect the plant at any stage of life, from germination to seed dispersal. A plant under salt-induced stress shows extensive modification from the ultra-cellular level to the organ level. Most of the impacts of salinity stress in the plant are regulated by the intimate result of the impact. Plants also adopt various morphological, biochemical and physiological modifications to cope with this stressful situation.
KEYWORDS: *Salinity Stress, Glycophytes, Seed Germination, Metabolism, Genetic circuit, Salt tolerance*

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INTRODUCTION

Soil salinization is one of the decisive environmental factors limiting production in crop-growing areas of arid and semi-arid regions worldwide [1, 2]. Salinization accumulates water-soluble salts, gradually transforming fertile lands into infertile soils (barren land). Technically salinity refers to the amount of dissolved mineral salts in water and soil. A soil is considered saline when the soil solution's electrical conductivity (EC) reaches 4 dSm^{-1} (equivalent to 40 mM NaCl). Chemically salts comprise electrolytes of anions (primarily CO_3^{2-}, SO_4^{2-}, Cl^-, NO_3^-, and $HCO3^-$) and cations (primarily Ca^{2+}, K^+, Mg^{2+}, Na^+). Among the salts, sodium chloride (NaCl) is the most important constituent of the saline environment. Salts soluble in the water get deposited in the soil's upper layer, which can be accumulated in the soil over a certain period [3]. Saline soil generates an osmotic pressure of about 0.2 MPa, significantly reducing many plants' growth and productivity, including agriculturally important crop plants [4]. Almost 25% of the agricultural lands in arid and semi-arid regions are affected by salinity stress [5]. Worldwide, the soil of nearly 831 Mha of land is affected by salt [6], within which crop losses caused by irrigation-induced salinity are substantial and are estimated to be equivalent to more than US$ 27 billion per year [7]. Generally, impaired water uptake, germination disruption, stunted growth, photosynthesis retardation, oxidative stress, and yield reduction are the key effects of salinity on crop plants [8]. Thus, salt-tolerant crops are becoming increasingly important in exploiting and utilising saline soil. Salt tolerance may be considered as the ability of plants to grow and complete their life cycle on a substrate containing high concentrations of soluble salt [9].

In recent decades research interests have been focused on salt stress that affects the growth and development of plants, mainly in the stage of seed germination [10, 11]. Soil salinity is dependent on two factors – Primary and Secondary factors. Primary factors include the interaction of natural salts, whereas, Secondary factors include anthropogenic activities. Some of the primary factors include erosion of rock, capillary rise from shallow brackish groundwater, an intrusion of seawater along the coast, salt-laden sand blown by sea wind, impeded drainage etc. [12]. Secondary factors include irrigation without proper drainage, industrial effluents, aberrant misuse of fertilizers and pesticides, deforestation, flooding with saline water, high water table and poor irrigation groundwater, etc. [12]. Salt is an inorganic mineral, primarily of sodium chloride (NaCl), that can dissolve in water. NaCl is the predominant salt causing salinization, the process by which water-soluble salts pile up in the soil. Surprisingly, plants have evolved mechanisms to regulate salt accumulation [13]. In plants, excess salinity causes early short-term responses for perceiving and transducing the stress signal and subsequent long-lasting responses for reconfiguring the transcriptional network to regulate growth and development. At lower concentrations, salinity results delay in germination and growth. The reduction in plant growth under salinity stress is primarily due to high salt concentrations in the apoplasts of growing tissues [14]. There are numerous effects of high salinity on plants (Figure 1): osmotic stress, ionic disbalance and toxicity, nutritional disorganization, oxidative stress, change in metabolic processes, disruption of the membrane, decrease in cell division and expansion, genotoxicity etc. [15-17]. Cumulatively these effects reduce plant growth and development and ultimately threaten the plant's survival [18].

Based on the salinity tolerance level, plants are classified into two groups – Glycophytes and Halophytes. Table 1 highlights some of the main differences between Halophytes and Glycophytes. Glycophytes cannot grow in the presence of high salt levels. Their growth is inhibited or even entirely prevented by 100–200 mM NaCl concentrations, resulting in plant death [19]. In contrast, halophytes can survive in high NaCl concentrations (300–500 mM) because they have developed better salt resistance mechanisms [20, 21]. In addition, halophytes developed structural and functional adaptations, like salt excretion through secretory glands, viviparous germination etc., which enable them to thrive in saline environments [22]. Glycophytes cannot develop such adaptations and thus cannot withstand high levels of salt stress. About 98% of economically important plants are glycophytes and are intolerant to salt, therefore unable to grow successfully in saline soils [23]. Most glycophytes are highly susceptible to soil salinity even when the soil EC is 4 dS m^{-1} [24]. However, some are moderately tolerant to salinity up to a mild salt concentration. There are variations in tolerance in glycophytes; several keep away from salinity while others avoid or defend against salinity, and some endure salinity.

Halophytes	Glycophytes
Plants that can complete their whole life cycle at salt concentrations higher than 200 mM NaCl are considered Halophytes.	Plants that can complete their whole life cycle at salt concentrations lower than 40 mM NaCl and disturbed by higher salt concentration are considered Glycophytes.
Usually, they can tolerate concentrations of 300–500 mM NaCl or even more [17, 25].	Most of them are unable to survive in salt concentration 100–200 mM NaCl [25].
Halophytes show several morphological and anatomical adaptations to cope up with the situation. Most halophytes possess glands and bladders, which actively excrete excess salts [26].	Glycophytes lack any such specialized morphological or anatomical feature to cope up with the salt stress situation.
In most halophytes, osmotic regulation is mediated by the increase in concentrations of Na^+ and Cl^- in the tissue [27, 28].	In glycophytes, tolerance to salinity is controlled by the exclusion of these ions from tissues [28, 29].
Their metabolic process may be tolerant to salt stress in comparison to glycophytes [30].	Their metabolic process is halted or inhibited during salt-induced stress [30].
Halophytes have a capacity for osmotic adjustment in that the plants accumulate osmolytes such as glycine betaine and proline that maintain the osmotic balance disrupted by the presence of ions in the vacuole [31].	The capacity for osmotic adjustment in glycophytes is comparatively less [31].
'Controls' in Na^+ influx strategy in roots to lower Na^+ accumulation in halophytes is more active [32].	'Controls' in Na^+ influx strategy in roots to lower Na^+ accumulation in glycophytes is less active than halophytes [32].
Halophytes can maintain high metabolic activity even at inhibitory concentrations of intracellular Na^+ and possess enhanced antioxidant mechanisms [33].	Glycophytes cannot maintain their normal metabolic activity even with very minute salt stress [33].

Table 1: Differences between Halophytes and Glycophytes

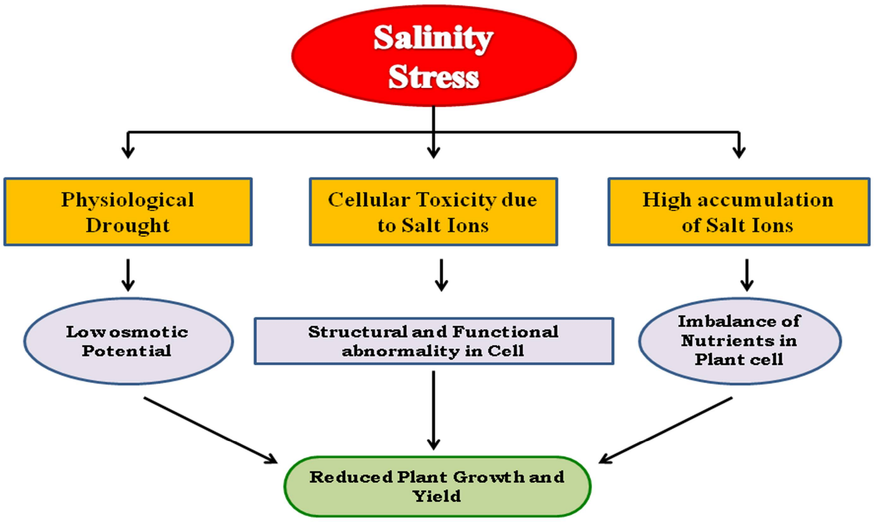

Figure 1: Schematic representation of the impact of salinity on plants

ABSORPTION OF SALT INSIDE THE PLANT AND ITS MOVEMENT

Transport of salts from soil to plant is quite complex as a plant, or its organelles, can interact with several ions of its saline habitat. Many recent studies also reveal that soil salinity is a multi-salt rather than a single-salt system. Besides, salt absorption and salt movement in the plant body are influenced by factors like temperature, oxygen level and various inhibitors on metabolism and ion uptake. In the case of most glycophytes, the root is the organ that absorbs ions from the saline rhizosphere. Entry and association of ions with the root cells may occur through several physical processes, including diffusion, ion exchange, Donnan equilibria, mass flow and adsorption [34, 35]. The movement of salt or ions across the cell membrane is an active process dependent on metabolic energy. In this process, a carrier molecule of the cell membrane transports an ion against the electrochemical potential gradient. In addition, salt/ions can enter the root through non-selective cation channels (NSCCs), which transport ions across the plasma membrane [36, 37]. For the last few decades, many researchers have studied NaCl-induced stress, particularly on plant mechanism(s) by which Na^+ and Cl^- enter roots. Ion uptake can occur in many plant species via the symplastic and apoplastic pathways [38, 39]. The salt entry into the root system activates numerous signal cascades that produce ionic tolerance by limiting salt ions like Na^+ influx into the root and reducing its translocation [40]. After the entry of ions into the cortical cell, accumulated ions subsequently move through the symplast to the stele by diffusion. Finally, they leak out of the stellar parenchyma cells into the xylem [41].

SALINITY STRESS AND AGRICULTURE

Although salts are a common and indispensable component of soil, and some are essential nutrients for plants, excess salt in soil and/or water may destroy plants and the ecosystem. Soil salinization is an unavoidable phenomenon, yet there is no suitable technique to resist soil salinity. Many agricultural practices, like applying fertilizers, pesticides etc., are responsible for accelerating soil salinity. Besides, all irrigation waters, whether from canals or underground pumps, contain some dissolved salts [42]. Along with natural factors of salinity, other factors enhance the salinity of the irrigated land. Soil salinity limits the yield of crops and creates a problematic situation of food crisis [4, 20]. At low salt concentrations, yields are mildly affected or not affected at all [43], but yield moves towards zero at high salinity. Plants are the most flexible organisms in the biological kingdom, with the potential to change them by any kind of stress, like salinity stress. Salinity is the cumulative result of a complex accumulation of micro-stress on different cellular organelles and their components [44]. Most of a plant's activities are influenced by the inception and progression of salt stress. At the initial exposure to salinity, plants experience water stress, and with long-term exposure to salinity, plants experience ionic stress and ionic toxicity. These effects reduce plant growth, and stunted development and survival is hampered.

Salinity is detrimental to the various processes of crop plants, such as seed germination, seedling growth, vegetative growth, flowering and fruit set. Ultimately, it causes diminished crop yield and product quality, thereby causing a loss of economy [45]. To cope with these stressful situations, different plant species adopt different mechanisms like membrane system adjustment, cell wall modifications, variations in cell division, cell cycle, hormonal regulation and alteration in metabolism operating in either isolation or synchronization. The plant response to salinity is complex but presumably includes some mechanism to report increasing levels of ions, either in the external medium or within the cell. Numerous morphological, physiological and biochemical modifications occur in plants due to exposure to salinity.

Salinity can affect plants at any stage of their life cycle. Adverse effects of salinity on seed germination, plant species growth and development have been extensively investigated in different corners of the earth. Undoubtedly, plants have undergone a complex and diverse evolutionary response to salinity through cell, organ and whole plant processes [46]. The most common effects in plants under saline stress are toxicity, diminished CO_2 assimilation and enhanced generation of reactive oxygen species [47].
It is well known that salinity has a tremendous negative influence on various ecologic glycophytes crops. Based on the salt tolerance, glycophytes are classified into four subgroups Sensitive, Moderately Sensitive, Moderately Tolerant and Tolerant. Almost 99% of crop plants reduce yields under salinity stress. Salt-sensitive plants are highly affected by salt stress, but all glycophytes face yield loss up to a certain level. Excess salinity harms all crop plants' growth phases, from germination to maturation. Plants often show leaf yellowing, wilting, and stunted growth under salt stress [48]. Saline soil reduces both the quality and quantity of the crop plant. Yield loss also depends on various crops and other agricultural conditions. In some varieties, a reduction is found in the whole plant, including economic parts, whereas in others, only non-economical parts are affected. A decrease in root biomass has been reported in broccoli and cauliflower under salinity stress [49]. Irrigation with saline water has been shown to enhance the occurrence of blossom-end rot in tomatoes, pepper fruits, and eggplants, a nutritional disorder related to Ca^{2+} deficiency [50].

IMPACT OF SALINITY STRESS DURING SEED GERMINATION

Seed germination and seedling establishment are the most vulnerable stages in all plants' life cycles, including glycophytes. Salinity-responsive features account for the majority of seed germination and seedling growth. Salinity may be either inhibitive to germination, without loss of viability, or a delaying factor at stress levels where germination is not repressed [51, 52]. During seed germination and seedling growth, plants remain weak and thus easily affected by adverse conditions like salinity. Germination usually occurs in surface soils, which gather soluble salts due to the soil's evaporation and capillary push of water content, thereby decreasing numerous factors along with phytohormones and ROS signalling [53]. All the germination events, from the imbibition of water to the seedling establishment, are adversely affected by increased salinity levels (Table 2). Salt stress declines the germination rate and delays seeds' emergence in various plants. It also induces changes in the structure and metabolism of seeds. Structural changes may occur at sub-cellular, cellular, tissue, and organ levels [54, 55], affecting the rate of essential metabolisms like respiration, transport of materials, and induction of new tissues in the germinating seeds or seedlings. Salinity influences several structural changes in germinating seeds and seedlings. Most common cellular symptoms include changes in the shape of the cell; lignification and thickening of the cell wall; loss of intercellular spaces; the reduced size of plasmalemma and contraction of plasmalemma away from the cell walls; disaggregation of intra-membranous particles; reduced and damaged mitochondrial apparatus; formation of small pro-vacuoles instead of the single large vacuole; diffusion and condensation of chromatin material in embryo; the abnormal size of cortical cell in mesocotyl; constriction of cortical tissue of mesocotyl; increased lignification of secondary tissues; induction of endodermis with Casparian band; suberin lamellae close to root base; earlier development and differentiation of secondary xylem in hypocotyls [54-59].
The impact of salinity on the plant is variable in species or even varieties. It also depends on the intensity of salinity, duration and coexistence of other stresses. Certain internal factors like the thickness of the seed coat, the permeability of the seed coat, the amount and nature of reserve food material in endosperm etc., also interfere with the result. Seed germination of different plant species is influenced by salt concentration in different ways, but seeds suffer osmotic stress in all cases. Such osmotic stress either completely inhibits germination at higher levels or induces a state of dormancy at lower levels [60-62], even reducing the proper circulation of absorbed water into different tissues of germinating seeds, including testa and embryonic tissues. For any spermatophytic plant, including glycophytes, rehydration of cells in the dormant seed is the prime condition for germination. After the influx of sufficient water, all the arrested metabolic activities are triggered in the rehydrated seed, which culminates in the emission of a radicle. Such metabolic activities are affected by salinity either entirely or partially (Table 3). Most metabolic disorders in germinating seeds caused by salinity stress are due to ionic imbalance or ionic toxicity. Under salinity stress, embryonic cells and rehydrated seed cells accumulate toxic ions, hampering diverse metabolic processes. Among the toxic ions, the most significant one is Na^+ ions. Rehydrated seeds inevitably take up Na+ ions in massive amounts, which are unfavourable for numerous enzymatic processes that deal with germination [63]. Other ions also show an inhibitory effect on several processes associated with seed germination. Some lead to altered or reduced synthesis of macromolecules and micromolecules and slow their mobilization towards developing tissues [63]. It is also found that the influx of more Na^+ ions in the cellular matrix decreases the entry of mineral ions like K^+ ions, which in turn decreases the efficiency of many enzymes related to the germination process

because most of them use K^+ ions as a cofactor. Also, the K^+ ion participates in many cellular functions in germinating seeds, including charge balancing and osmoregulation [64]. Therefore, the lack of sufficient K^+ ions results in an imbalance in cellular homeostasis. Salinity also causes the accumulation of different metabolites in germinating seeds, and a few of them, like soluble sugar, proline, soluble proteins etc., are beneficial to cope with the situation [57, 65]. However, some of them, like phenolic compounds, disturb the normal metabolic processes of seed germination [66].

Hydrolytic breakdown of stored food reserve is hampered; even the movement of food from source to sink, i.e. storage tissue to developing embryo axes, is limited due to saline stress [67, 68]. The α-amylase enzyme essential for seed germination is inhibited due to salt stress [60]; thus, starch-to-sugar conversion occurring during germination is also affected. The harmful effect of salinity increases osmotic pressure, which restricts water absorption into the seed. Germinating seeds under salt stress exhibit a lowered and delayed production of radicle and plumule [69-71]. The impact of salinity on the seedling stage is variable with species. The capacity of seedlings to cope with salinity is principally related to the greater transport of ions to shoot from roots. Exogenous NaCl inhibits seed germination by mediating the biosynthesis of ABA and GA; and importantly, ABA biogenesis inhibitors, such as fluridone (FLUN), might be a potential plant growth regulator that could be used to enhance seed germination under salinity stress conditions [72].

Germination event	Impact of Salinity on the event	Reference
Imbibition	Reduced hydration of seed coat, cotyledon and embryonic tissues.	[73, 74]
Immobilization and active metabolism	Reduced water uptake. Disaggregation of intermembrane particles. Leakage of solutes. Reduced mobilization of reserve material. Inhibition of Enzymes associated with the metabolism of carbohydrates and fatty acid. Alternative protein synthesis. Production of osmotically active solutes.	[75] [76]; [74] [77, 78] [79].
Emergence and elongation of embryonic tissues	Delayed and reduced emergence of radicle and plumule. Reduced elongation of embryonic tissues	[71, 80, 81]
Establishment of seedlings	Reduced growth and vigour of seedling; Enhanced seedling mortality.	[78, 82]

Table 2: Impact of salinity on different stages of the seed germination process

Metabolites	Effect of Salinity on different metabolites associated with Germination
Carbohydrates	Reduction in endospermic α-amylase activity in a concentration-dependent manner [83].
	Promotion of cotyledonary α-glycosidase activity [84].
	Accumulation of osmotically active sugars [65].
	Increase in the levels of total soluble sugars, sucrose and glucose concentrations in the cotyledons [85].
Amino Acids and Proteins	Progressive accumulation of free proline [74].
	Inhibition of methionine and leucine uptake and incorporation into proteins chain [86].
	Toxic to the protein phosphatase and protein kinase-specific activities [87].
	Changes in protein phosphorylation-dephosphorylation [76].
	De novo synthesis of four new heat-shock proteins during stress and seven during recovery [79].
Lipids	Reduction in the activity of glyoxysomal catalase, malate synthase, and iso-citrate lyase [88].
	Reduction in the utilization of total lipids and triacylglycerol [88].
	Increase in linolenic acid and linolenic acid-rich TAGS [89].
Nucleic acids	The decrease in DNA contents [90].
	Reduced incorporation of the precursors of nucleic acids biosynthesis [57].
	Condensed chromatin material [91].
	Inhibition of RNase activity [92].
	Hydrolysis of RNase [93].
Other Organic compounds	Increase in betaine aldehyde dehydrogenase enzyme activity [94].
	Increased betaine contents [73].
	The decrease in soluble amino nitrogen [94].
	Induction of putrescine synthesis with the activation of arginine decarboxylase [95, 96].
	Significant increase in spermidine [95, 96].
	Accumulation of total polyamines [95, 96].
Minerals	Reduced levels of macro-and micronutrients [97].

Table 3: Impact of salinity on different metabolites associated with germination

Under salt stress, rehydrated or germinating seeds of glycophytes accumulate some metabolite which is beneficial to the germination events and seedling development. These metabolites may be beneficial for germination, first by reducing osmotic inhibition and second by providing substrates for the growth of embryonic tissues [74, 96]. In addition to natural compounds, some external chemical has also been employed by different researchers to alleviate the adverse effects of salt (Table 4).

Chemical Compound	Role in the alleviation of salt stress During Germination and Seedling development
Sugars	Promotes seed germination; Providing substrates for the growth of embryonic tissues and promote seedling growth [73].
Proline	Osmoprotection of cells of germinating seed, enhancement of hypocotyl growth, promoting seedling growth [73, 96].
Polyamines	Enhancement of salt tolerance; Stimulating germination by their endogenous biosynthesis; Promoting seed germination [73, 95, 96].
Glutamine and Glutamic Acid	Enhancing glutamine synthase and glutamine synthetase activity and counteracted growth inhibition due to salt [96].
Thiourea	Reversal of salt-inhibited germination [95].
Fusicoccin	Counter inhibiting decreased water potential enhancing protein synthesis; promoting seedling growth [55, 98].
Auxins	Breaking dormancy; eliminating osmotic inhibition; enhancing water uptake [99].
Gibberellin	Breaking dormancy; Counteracting inhibition of α-amylase activity in the seed; promotion of seedling growth and development [99].
Cytokinin	Enhancing protein synthesis; promoting radicle emergence; offsetting salt damage; increased water uptake [100-104].
Ethylene	Enhancing endogenous synthesis and stimulate germination (Wang et al., 2020).
Calcium	Buffering of Na^+ toxicity; Promotion of membrane activity of germinating seed; Enhancing germination and emergence of plumule [55, 96, 105-107].
Potassium	Eliminating ionic toxicity, Enhancing germination, and promote the growth of radicles [96].
Magnesium	Reducing Na^+ toxicity and promote the growth of radicles [96].
Nitrate	Reversal of salt inhibited germination and enhancement of seed germination and seedling emergence [108].
Ammonium	Enhancing protease activity and solubilization of endospermic protein [109].

Table 4: Role of different compounds in the alleviation of salt stress During Germination and Seedling development

Impact of Salinity Stress during the Growing Stage

Generally, mature plants react to salinity by a reduction in growth, but there are numerous quantitative differences in the degree of response. Under salinity, a mature plant may show changes in physiological and biochemical attributes [110]. Different studies have shown considerable variations in salt response between species of the same genus, between cultivars, or within varieties. These variations are intimately correlated with differences in the translocation of different salt ions, especially Na^+ and Cl^- in plant portions above the ground. Though inhibition of growth by salt-induced stress is the most evident effect, it is not a simple phenomenon that similarly affects all types of plants or organs. For example, in glycophytes, salinity stress causes two phasic responses [4]. Stomatal openings are shut off, and the enlargement of the leaf is repressed in phase I, which takes place in a short time, i.e. minutes or a few days.

In contrast, in phase II, toxic ions accumulate, particularly in older leaves, causing premature senescence, reduced yield and death of the plant, as seen in Figure 2 [5]. Up to a certain salinity level, all glycophytic plants appear normal but may have abnormal characteristics in roots, stems, leaves, flowers and fruits. Most glycophytes under salt-induced stress show more or less typical symptoms in the mature plant body viz stunted growth-restricted lateral shooting, reduction in the size of leaves, fruits and seeds [111]. In the case of crop plants, it downgrades both the yield and quality. High salinity can affect plants in multiple ways. Salt-affected soils are characterized by high electrolyte content and extraordinarily acidic or basic pH conditions and are unfavourable for most glycophytes. Such kind of soils usually has less biological activity because of both the osmotic and ionic effects on most living entities, including plants. Besides salt-affected soil lacking carbonaceous substrates, this is also unsuitable for plants.

Initially, salinity stress is detected by the root system of the plant. Salinity induces growth inhibition in roots but is less affected than other plant parts. Salt stress was shown to influence root system architecture (RSA). The rate of lateral root emergence, as well as the primary root vector angle and straightness, were found to be affected by salt stress [112]. A recent study on *Lycopersicon esculentum* found that the general root architecture was substantially modified in response to salinity, especially for the position of the lateral roots in the soil [113]. It is also found that specific concentrations can stimulate root growth while inhibiting shoot growth [114]. In glycophytic plants, the initial effect due to salinity is the interference in water absorption. The soil-root osmotic gradient is the driving force responsible for water absorption by the plant. In typical (non-saline) soil, the osmotic contribution to water retention is relatively small, but in saline soil, it may be considerably higher, causing reduced water availability for glycophytes [8, 115, 116]. Ionic stress arises due to the disproportionate influx of Na^+ ions via the root cell, distorting the Na^+/K^+ and Na^+/Ca^{2+} equilibrium [117].

High salt depositions in the soil generate low water potential in the root zone, making it difficult for the plants to pump water. As a result, plants face osmotic stress. On the other hand, a plant under salinity stress immediately closes its stomata and prevents excess water loss. When grown in salt, most plants accumulate some Na^+ in their roots even though it is excluded from the shoots. But due to this activity, plants accumulate excess ions like Na^+, Cl^- etc. and hence face ionic stress. Thus salts interfere with plant growth through two major processes: initially, the growth slows due to osmotic stress, as the water uptake by the root is impaired; subsequently, the old leaves pile up salt to a toxic level leading to its death [4]. This salinity-induced stress can halt the growth of organs or entire plant growth as the plant focuses its energy on conserving water and improving ionic balance. Significant net alterations in Na^+, K^+, and H^+ fluxes in roots were caused by salt stress. A study on *Triticum aestivum* [118] has shown that although salt shock could cause a net Na^+ influx in roots, net Na^+ fluxes were not visible after the shock.

An insufficient water supply causes many structural and metabolic dysfunctions in plant parts and the entire plant. Like other stresses most common symptom of salinity-induced stress is stunted growth of plants. It is a common phenomenon in almost all glycophytes. Undoubtedly, stunted growth is directly dependent on the abnormality of cellular structure and metabolism. In many glycophytic plants, salinity remarkably reduced both K^+ and Na^+ proportions in the root while enhancing those in the stem [119]. The root is the plant organ that faces salt stress at the beginning. Salinity affects the severe damage of roots in the parenchymatous tissues, as indicated in the cortex and pith [120]. It is yet uncertain whether structural impairment of root anatomy is directly due to salinity. Still, ion and osmotic stress induced by the gathering of salt within cells might contribute to cellular abnormality or distortion or even cell death—salinity-induced structural changes of the xylem and phloem in the stele [121]. Few xylem vessels with smaller sizes were noticed in the roots of stressed glycophytes; on the other hand, salinity enhances xylem deformity in leaves. Initially, both effects seem problematic, but the latter increases resistance to water transports to the leaf and helps diminish the plant's overall water loss. Salinity may cause earlier tissue ageing, as seen by earlier differentiation of the xylem (lower down in the root) and more extensive lignification of the xylem elements [122].

With the onset of salt stress, the earliest visible response of the plant is usually a reduction followed by a cessation of leaf blade expansion and early senescence of the leaf as salinity intensifies [123]. Numerous studies showed the negative effect of salinity on leaf area, length and number with the increase in salt concentration. Salinity affects not only external morphology but also internal morphology and the cellular matrix of leaves. Leaves are more vulnerable than roots to Na^+ simply because Na^+ and Cl^- accumulate higher in shoots than in roots [61]. It also induces the synthesis of certain toxic compounds in the cytoplasm of leaf cells. Such accumulated toxic salts are then transported in the leaf apoplast, leading to dehydration, turgor loss, and death of leaf cells and tissues [124]. Initially, salt taken up by the plant concentrates in the old leaves. Then continued transport of salt into transpiring leaves over a long period eventually results in very high Na^+ and Cl^- concentrations, and finally, the young leaves die [125]. However, the salt taken up by the plant does not directly inhibit the growth of young leaves [126]. Because during salt stress, rapidly elongating cells continuously accommodate the salt within their expanding vacuoles [125]. Salinity-induced crop yield reduction occurs due to several physiological and biochemical dysfunctions in plants under salinity stress [127]. Due to the presence of salts in the soil, plants confront problems obtaining water from the soil, negative osmotic potential, and a high concentration of potentially toxic sodium carbonate and chloride ions [128]. Salt stress can induce osmotic and ionic stresses in plants. It also reduces the plant's ability to take up water, resulting in an abnormality in both cellular and metabolic processes [129]. Some specific leaf damage symptoms may be recognized at high salinity, such as colour change, succulence, necrosis, and leaf tip burn due to Na^+ or Cl^- ions [130, 131].

Several reports have shown that salinity decreases the number of nodes per plant, flowers per node, and the number of fruits and seeds [132]. It also retards the rate of bud development [4]. Microsporogenesis and elongation of stamen filament are inhibited; the escalation of apoptosis in certain tissue types, abortion of ovules and senescence of fertilized embryos occur under saline conditions, thereby affecting reproductive development [133]. Salinity can also reduce seed yield by decreasing physiological performance and accelerating the seed-filling period [134, 135].

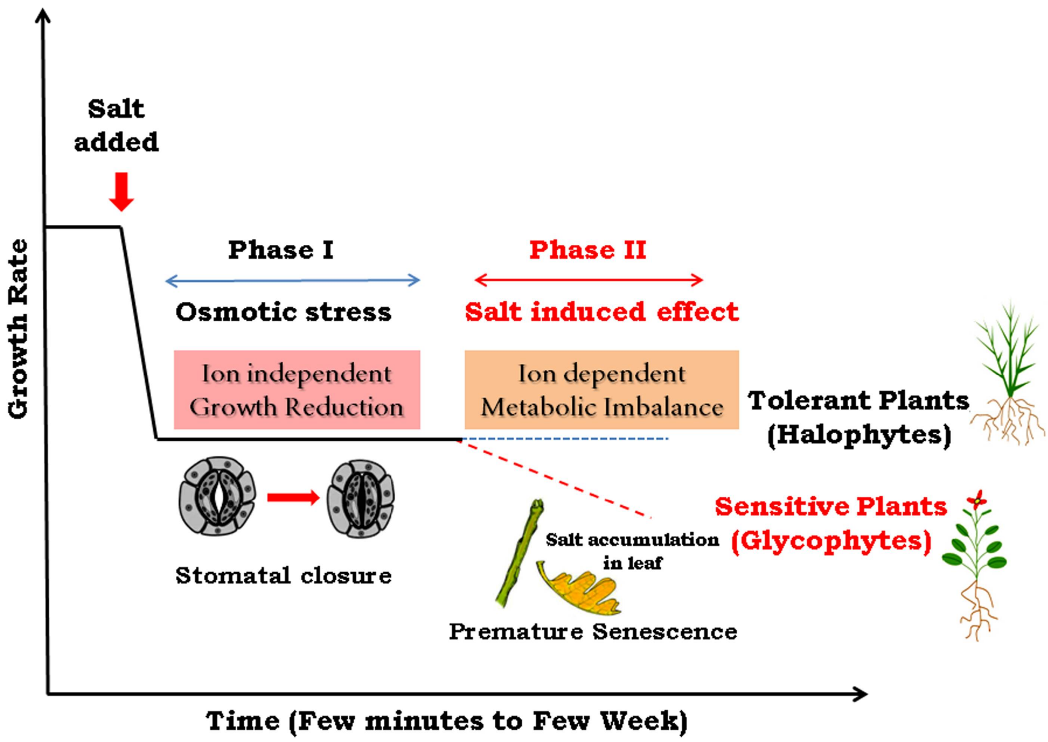

Figure 2: Two-phase response in plants under salinity stress [Modified from [136]]. Phase – I: During this phase, both glycophytes and halophytes tolerate salinity induced osmotic stress by the closure of stomata. Phase – II: During this phase, halophytes tolerate themselves up to level but glycophytes face some irreversible damage due to salt-induced ionic toxicity and after a certain level it leads to death

EFFECT ON PRIMARY METABOLISM

When a plant is exposed to salinity, almost all fundamental processes within the plant are drastically influenced, which can lead to the plant's death. Some of the significant effects of salinity on the morphology of plants include leaf relative water content, dry leaf weight, shoot length, number of leaves, number of branches, total leaf area, root architecture etc. In contrast, major salt-influenced physiological characteristics are stomatal conductance (g_s), transpiration rate (T_R), net photosynthetic (P_n), the yield of photosystem II (ΦPsII), intercellular CO_2 concentration (CO_{2int}) etc. [137]. At initial conditions, salinity results in two types of stresses-hyperosmotic stress and hyperionic stress [138]. Excess accumulation of Na^+ during salt stress disrupts protein and nucleic acid structure by interfering with hydrogen bonding and polar contacts [139]. The effect of salinity stress is usually more pronounced on the shoot system than the root system [140]. If the stress condition prevails, it results in a decline in photosynthetic yield in many plants. Salinity is initially affected by decreasing or perhaps total arrests of plant growth caused by the diminished osmotic potential that restrain roots' absorption of water and nutrients. The high salt concentration causes salt ions accumulation in cells that frequently create toxicity, which is manifested in plants by chlorosis and necrosis of the leaf tissues [16, 131]. It was found in several studies that chlorophyll content was reduced with increasing salinity. Salinity retards the concentrations of Chl a, Chl b and total chlorophylls [141]. It also affects the chloroplast structure. The reduction in chlorophyll biosynthesis is probably due to the inhibitory effect of the accumulated ions of various salts on the biosynthetic metabolism [142]. The entire chloroplast is also disorganized due to salinity stress, as the salt destabilizes the chloroplast membrane. Chloroplasts are usually more sensitive to salinity than other organelles [143].

(i) Absorption

The absorption of water and minerals is the keystone physiological process of all plants. Plants can usually take up water and essential minerals as they have higher water pressure in the soil under normal conditions. But when the soil's salinity increases, the soil's osmotic pressure becomes higher than in plant cells, and cells cannot uptake enough water. To cope with this situation, plants decrease their turgor and close their stomata to conserve water. Accumulation of Na^+ ions or similar ions may gradually decrease the uptake of many essential cations such as K^+, Mg^{2+} or NH_4^+. As a result, the Ca^{2+}/Na^+ ratio in the root zone is also decreased. In addition, it affects membrane properties due to the displacement of membrane-associated Ca^{2+} by Na^+, leading to the rupture of membrane integrity and selectivity [144]. A significant amount of membrane depolarization occurs when positively charged Na^+ crosses the plasma membrane. Such depolarization makes the passive uptake of many essential cations thermodynamically impossible and, at the same time, dramatically increases the efflux of some of them. It has also been reported that plants accumulate some osmotically active compounds due to such stress to lower the osmotic potential [145]. Higher concentrations of Na^+ in the cytoplasm disrupt the uptake of other ions into plant cells, adversely affecting many metabolic pathways [146]. It has been shown that soil salinity increases P, Mn, and Zn and decreases K and Fe concentrations in plant tissues [147]. Due to salinity, the osmotic potential of cell sap changes to maintain a constant water potential gradient between leaf and soil. Plant salinity stress can be characterized by slowing shoot and root growth, reduced photosynthesis, and the reallocation of respiration from growth to maintenance [148-152].

(ii) Transpiration and Stomatal activity

Reduction in stomatal aperture is the most prominent and instant assessable response against salinity. Under optimal conditions, plants typically lose 95–98% water from the leaf surface via stomatal pores in a process termed stomatal transpiration. A small amount of water loss also occurs through the leaf cuticle, even when the stomata are fully closed. The latter is called residual (cuticular) transpiration. Most glycophytic plants under salinity stress show a rapid reduction of the stomatal aperture and its activity, decreasing a considerable deduction of transpiration. Salinity disturbs stomatal conductance rapidly and transiently due to interruption in water relations and sharply the local synthesis of short-lived ABA in roots [153] and soon after relocating into leaves through the xylem. When ABA binds with membrane receptor molecules of guard cells, it activates Ca^{2+} channel proteins of both cell membrane and tonoplast, triggering an influx of Ca^{2+} ions into the cytosol. Due to this, a rapid rise of Ca^{2+} ions occur in guard cells. High Ca^{2+} ion concentration inhibits K^+ channel proteins activity though it keeps normal Cl^- channel proteins activity [154]. Jiang et al., 2019 [155] identified the first molecular component required for salt-induced $[Ca^{2+}]_I$ elevation, MOCA1, and revealed a biochemical function of GIPCs (Glycosyl inositol phosphorylceramide sphingolipids in the plasma membrane) as monovalent-cation sensors. According to this study, Na^+ ions bind to GIPCs and depolarize the cell-surface potential to gate Ca^{2+} influx channels.

Simultaneously efflux of Cl^- ions from the cytosol of guard cells increases the pH of the cytosol and triggers depolarization of the plasma membrane. In existing circumstances, K^+ is effluxed through Guard Cell outward and rectifies the GORK channel, triggering loss in turgidity in the guard cell; thus, finally, stomatal closure occurs [156]. Under severe stress conditions, when stomata are closed and stomatal transpiration is reduced to nearly zero, the difference in residual transpiration becomes a significant factor in determining water use efficiency. It improves plant performance under stress conditions [157]. Plants try to sustain the usual rates of transpiration in the saline environment. This is a typical indicator of salt tolerance since transpiration is linked to standard rates of CO_2 absorption required for photosynthesis [158]. Due to the reduction in transpiration rate, leaf temperature significantly increases [159].

Photosynthesis

Photosynthesis is the most fundamental physiological process of plants. Salinity has many direct and indirect effects on photosynthetic processes. Almost all plants show a reduction in photosynthetic yield. Photosynthesis involves various components such as Photosynthetic pigments (Chlorophylls, Carotenoids, Phycobillins etc.), Photosystems (PS-I and PS-II), Electron transport systems and Carbon fixation pathways. This reduction has been primarily attributed to salt damage of the photosynthetic tissue, to stomata and consequent restriction of the availability of CO_2 for carboxylation or acceleration of senescence [160]. The reduction in photosynthesis takes place under stress due to a reduction in stomatal conductance, which hinders the availability of CO_2 for its fixation in the leaves [161]. Numerous studies have demonstrated that salt-induced inhibition in photosynthesis is accompanied by stomatal closure under short-term salt exposure and non-stomatal limitations under long-term salt exposure [162]. It is thought to be caused by reduced CO_2 availability due to decreased stomatal conductance [163]. Some researchers assume that alterations in photosynthetic metabolism occur during an increase in salinity [164]. Under salinity, plants may adopt different strategies to modulate carbon balance and energy allocation for tissue [165]. Clustering of chloroplasts takes place, and alteration of the ultrastructure occurs of the assimilating organs under salinity [166], which comprise enlargement of thylakoid membranes, without any grana, and swollen mesophyll cells [167]. Another vital factor is the reduction in chlorophyll concentrations in the chloroplast. It may be due to the inhibitory effect of the accumulation of ions of different salts on the biosynthesis of the various fraction of chlorophyll [142]. The decline of chlorophyll a and chlorophyll b amounts with the application of NaCl was reported in many plants. This is due to the increased activity of destructive enzymes called chlorophyllase [168]. However, in many plants, the increase or decrease of Chlorophyll a, chlorophyll b, chlorophyll a/b and carotenoid contents is dependent on the exposure time of salt [169]. The deposition of NaCl in chloroplasts of higher plants is enhanced by salt stress; the growth rate is also affected, which is linked with the reduction of electron transport activity of photosynthesis [170]. In most of the higher plants, the activity of Photosystem – II is inhibited by salt stress [171, 172]; however, there are few dissimilar results [173, 174]. Though, it is yet to clarify whether these low photosynthetic rates are responsible for the reduced growth in salinized plants or if stunted plants control assimilation through negative feedback of a reduced sink activity.

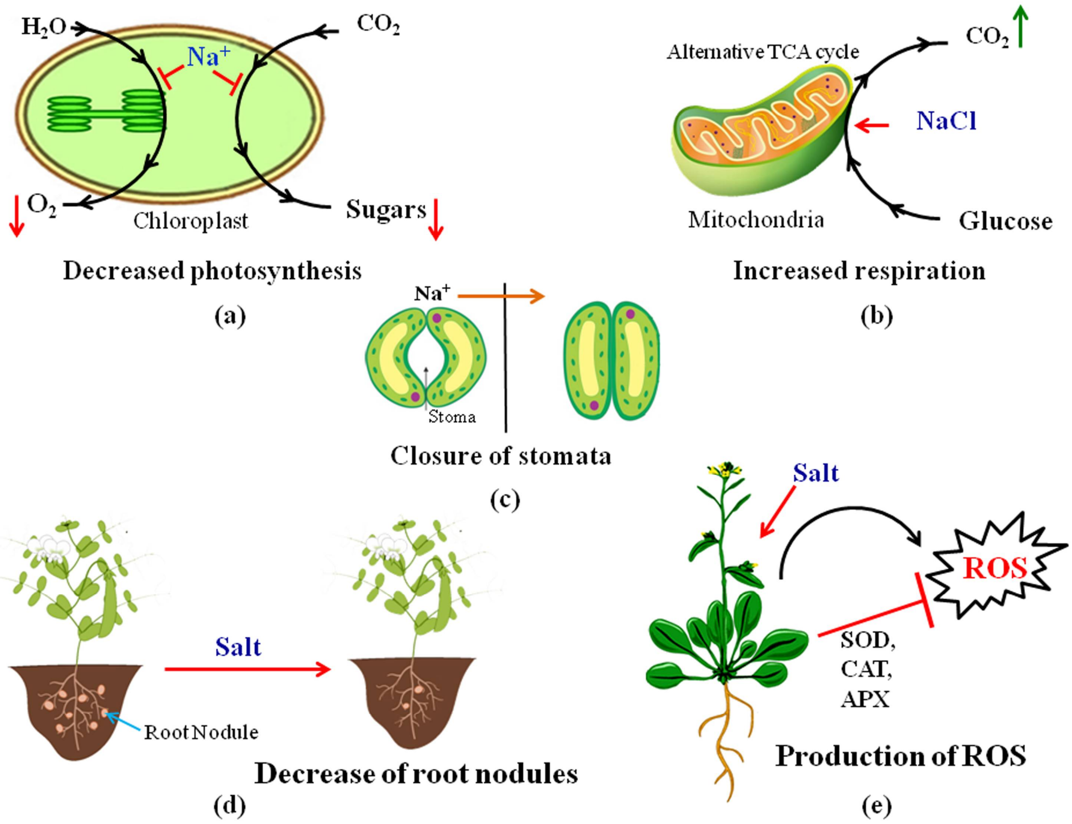

Figure 3: Effect of salinity on primary metabolism and physiological functions of plants. (a) Na^+ diminishes the photosynthetic ability by altering the proton-motive force and reducing the efficiency of CO_2 fixing enzymes. (b) NaCl increases cellular respiration by increased the activity of alternative TCA cycle pathways. (c) Na^+ induces stomatal closure to reduce water loss. (d) Salinity causes a decrease in the number, volume and weight of root nodules. (e) Salinity causes the accumulation of a measurable amount of Reactive oxygen species (ROS) such as hydroxyl radicals, hydrogen peroxide, and superoxide anions in plant cells. To combat ROS, plants have developed an efficient antioxidative defence mechanism among these enzymes; superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) are notable

Respiration

Excess salt in the soil increases cellular respiration and has been seen to cause membrane instability and changes in membrane permeability [175]. It has been reported that increasing salt concentration accelerates respiration in the root and stem. Scarcity of the pyruvate carrier and pyruvate dehydrogenase subunits takes place under salinity, which reduces the activity of the cyclic operation of the TCA cycle to supply reductants for respiration [176]. Previous research has shown that mitochondrial respiration is essential during plant salt stress because it provides ATP and reductants that fuel adaptive processes, including ion exclusion, compatible solute synthesis, and reactive oxygen species (ROS) detoxification [4]. A decline in aconitate and citrate abundance accompanies the decrease in pyruvate utilization. Multiple studies have reported that salt-stressed plants exhibit changes in the ratio of carbon dioxide (CO_2) released over oxygen (O_2) consumption (respiration quotient), potentially indicating that mitochondria oxidize a diverse range of substrates under salinity [177-179]. Zidan and Elewa, 1995 [65] noted that the rate of respiration increases sharply with the increase in sodium chloride (NaCl) level. These might involve the increased activity of alternative TCA cycle pathways under salinity stress [180, 181]. Plant species also adopt different strategies in utilizing carbon sources for energy metabolism through the TCA cycle in saline environments. Salt stress also increases the activity of an alternative pathway along with the cytochrome pathway [182].

Nodulation and Nitrogen Fixation
Salinity interferes with nodulation and nitrogen fixation in many leguminous plants. In legumes, the bacteria, especially *Rhizobium* sp., live on the roots called nodules. Within these nodules, the bacteria do nitrogen fixation, and N_2 is converted into NH_3, which the plant ultimately absorbs. Salinity may impact the *Rhizobium* symbiosis directly by decreasing infection and nodule development (e.g., by decreasing the number of root hairs) as well as nitrogen fixation capacity in legumes and indirectly by limiting accessible carbon [183]. In several experiments, it was found that salinity caused a decrease in the number, volume and weight of nodules in a plant like Chick Pea, Cow Pea, Mung Bean, Soyabean etc. [184-186]. At a specific level of salinity, nodule formation is completely inhibited. There are several reasons behind this inhibition; firstly, the salinity results in shrinkage of root hairs; secondly, the root hair matrix becomes unsuitable for colonization of *Rhizobium* and similar microorganisms; and thirdly, salt can cause irreversible damage to leghaemoglobin. Under salt-induced stress, reduced N_2-fixation in nodules is followed by a decrease in the activity of H_2O_2 scavenging enzymes such as catalase and ascorbate peroxidase, as well as antioxidant levels such as ascorbic acid [187]. However, in some cases, especially in salt-tolerant legume – salt-tolerant microbial strain association, nodule formation remain normal, but nitrogen fixation is absent [110, 188]. Salinity induces premature senescence of already-formed nodules. A decrease in rhizobial colonization and shrinkage under a saline environment around the root zone causes premature senescence of earlier-formed nodules [186]. Salinity also reduces nodule respiration, nitrogen fixation and root hair formation, which may cause less survival of the plants in stressed conditions [187]. Nodule senescence is a complex and regulated process that includes changes in leghemoglobin content, structural changes in nodule cells, decreased nitrogenase activity, changes in the lifestyle of microorganisms and growth capacity, and many more [189].

Effect on Secondary Metabolism
To combat salinity stress, plants adopt combinations of diverse pathways. Salinity stress involves changes in various physiological and metabolic processes, depending on the severity and duration of the stress, and ultimately inhibits crop production [126, 190]. Enhanced salt stress causes a significant decrease in the number of amino acids such as cysteine, arginine, and methionine (around 55% of total free amino acids in the plant), but proline, proteinogenic amino acid concentration increases [191]. Due to salinity, the plant cells accumulate a measurable amount of Reactive Oxygen Species (ROS) such as hydroxyl radicals, hydrogen peroxide, and superoxide anions which can severely damage cell organelles and biomolecules like polysaccharides, proteins, lipids and nucleic acids [192-198]. These ROS are usually generated in the cytoplasm, mitochondria, chloroplastid and apoplastic space and impart phytotoxic reactions such as lipid peroxidation, protein degradation, DNA mutation etc. Still, it is also proven that they can accelerate oxidative damage to the cell [199-204]. Salinity-induced ROS formation can lead to oxidative damage in various cellular components such as proteins, lipids, and DNA, interrupting vital cellular functions of plants [205]. To combat ROS, plants have developed an efficient antioxidative defence mechanism, which acts through the synthesis of metabolites and activation of a complex enzymatic system [206]. Among these enzymes, superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) stand out [207]. Salinity affects different aspects of carotenoid and flavonoid metabolism in *Solanum nigrum.* The potential antioxidant properties of carotenoids and flavonoids and their related vital genes may be efficiently involved in the restriction of salt-induced oxidative damage [208]. Similarly, Cuong et al., 2020 [209] showed that salinity enhances phenylpropanoid accumulation and their related gene expression in wheat sprouts.

Effect on Cellular Organelles
Salinity significantly modifies the structure and metabolic activities of almost all cellular organelles, cytosol and cell wall. It can indirectly affect cell wall properties by altering gene expression; however, some salt ions, such as Na^+, can also physically interact with the cell wall components directly and modifies their chemical properties. Under salinity stress, Na^+ ions enter the cortical root cells through Voltage Independent Non-Selective Cation Channels, which in turn induce depolarization of plasma membrane and activation of Depolarization Activated Non-Selective Cation Channels (DA-NSCCs) and allow further Na^+ influx [36]. Cell surface area and nuclear size decrease at high salinity, consistent with signs of plasmolysis [210]. Plasma membranes are the primary site of salinity injury where ROS interact with unsaturated fatty acids leading to the peroxidation of essential lipids and reducing the membrane's fluidity [211].

In most cases, damage caused by Na^+ on higher plants is not only due to increased intracellular Na^+ levels but also predominantly by the disruption of cytoplasmic K^+/Na^+ homeostasis on account of Na^+ competing with K^+ for binding sites at the cell membrane and depolarization-induced K^+ efflux [146]—depolarization of cell membrane results in leakage of K^+ ions. In addition, when plants are under excess salinity, the dividing cells rapidly elongate, and the excess salts modify the cell wall's metabolic activities, causing the deposition of various materials [142]. Thus, the elasticity of the cell wall gradually decreases. Due to this modification, the secondary cell walls become rigid, and consequently, the turgor pressure efficiency in cell enlargement is also decreased [142].

Most of the studies reveal that chloroplast is highly affected during salt stress. High salinity has multiple effects on chloroplasts, including reduced CO_2 uptake due to stomatal closure, reduced photosynthetic efficiency, thylakoid membrane damage, oxidative stress, impaired osmotic and ionic homeostasis, and disrupted protein synthesis and turnover [212]. In addition, salinity affects the strength of the forces bringing the protein-lipid complex pigment into the chloroplast. As the chloroplast is a membrane-bound structure and its stability depends on the membrane integrity, which under high salinity conditions seldom remains intact due to which reduction in chlorophyll may occur [213]. It is also pointed out that salt affects the ultrastructure of the chloroplasts due to the enlargement of the thylakoids and starch grains [214]. Electron microscopic studies on the thylakoid structure showed that thylakoids get disorganized and cells' starch content decreases when salt exposure [215, 216]. Maintenance of optimal K^+ and Cl^- concentrations within the chloroplast is pivotal for pH regulation, volume regulation, thylakoid stacking, electron transport properties, and, eventually, photosynthetic efficiency [217-219]. Under the saline condition, when Na^+ reaches a threshold value, it decreases the level of K^+ and disturbs the activity of the chloroplast. Hyper-accumulation of sodium ions can additionally compromise plant growth by reducing the rate of photosynthesis if the ions are not compartmentalized at the cellular or intercellular level.

A study on the leaves of sweet potatoes showed that salinity also initiates vacuole development, swelling in the endoplasmic reticulum and mitochondria, the decline in mitochondrial cristae, and formation of vesicles and fragments in the tonoplast and degradation of the cytoplasm [167]. In addition, Na^+ can enter vacuoles by activating Na^+/H^+ antiporters energized by a proton motive force (PMF) established by vacuolar proton pumps [220].

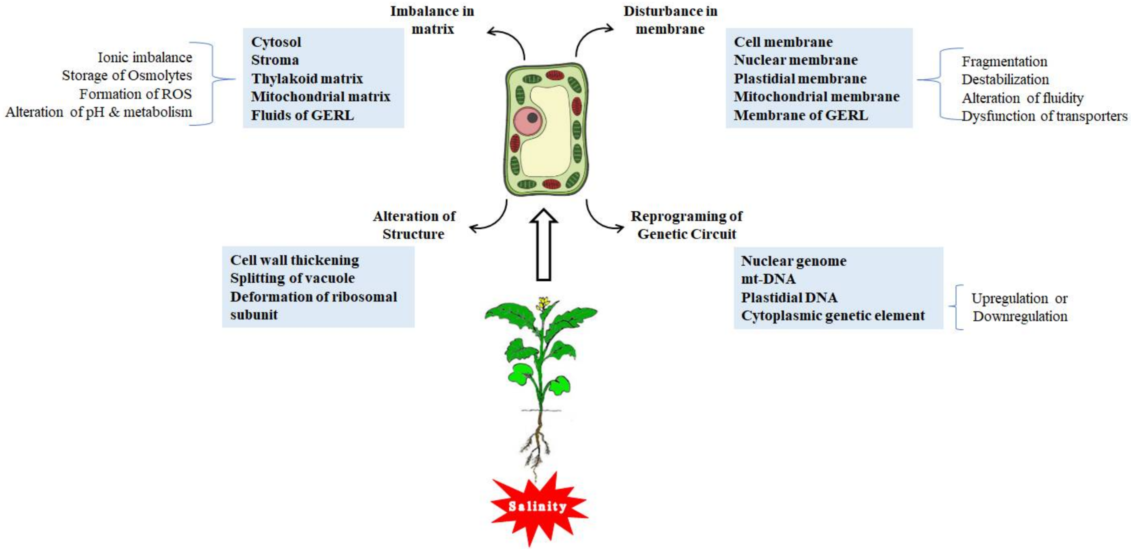

Figure 4: Effect of salinity on major cell organelles. (a) Salinity destabilizes the cell membrane. (b) Salinity imbalance Genetic circuits. (c) High salt concentration splits large vacuole into many small pro-vacuoles. (d) High salt concentration and Na^+ ions destabilize the thylakoid membrane and damage the pigment structure. (e) High salinity results in swelling of mitochondrion but declines the number of its functional unit-cristae (f) Hyper-accumulation of salt increases the rigidity of the cell wall but decrease its elasticity

In response to osmotic stress, plants produce osmolytes like glycine betaine, trehalose or proline, which protect them from dehydration or protein denaturation. However, oxidative stress – an outcome of ionic stress- produces different enzymatic or non-enzymatic antioxidants, which protect plants from the harmful effects of ROS [221]. Under salinity, the cytoplasm accumulates several low molecular weight compounds and maintains osmotic and ionic balance in the vacuole. The accumulation of soluble carbohydrates in plants has been widely reported as a response to salinity, despite a significant decrease in the net CO_2 assimilation rate [222]. Many cytoplasmic proteins are also induced by salinity which can cause alterations in the cytoplasmic viscosity of the cells [16]. Amino acids (including Imino acids), amides etc., have also been reported to accumulate in plant cells under mild salt stress. Proline is accumulated in massive amounts among the amino acids as it contributes substantially to the cytoplasmic osmotic adjustment [223]. Proline accumulation is a late adaptive response in plant tissues under salt stress, and proline production has been proposed to have a multi-component effect on stress tolerance [224]. Carillo et al., 2008 [225] reported that proline typically ranges from 0.5 - 1.0 µmol/g is regarded as unstressed, and 1.0 to 50 µmol/g is regarded as stressed. Recent discoveries indicate that proline is essential in plant growth and differentiation across the lifecycle. It is a crucial determinant of many cell wall proteins that plays essential roles in plant development [226]. Proline also plays a pivotal role in protein synthesis. Thus, due to abnormal proline content, the plant faces multidirectional impacts. Although amides generally accumulate in salt-stressed plants to a lesser extent than other nitrogen-containing compounds [227]. Some osmoprotective compounds are also found in the cytoplasm of some crop plants under salt stress. The most common compounds are glycine betaine, β-alanine betaine and proline betaine [145]. The high amount of proline in the cell will increase the phenol compounds through the biosynthetic pathway of proline–linked pentose phosphate, enhancing shikimate and phenylpropanoid synthesis [228]. Proline and glycine betaine also participate in chlorophyll reconstruction, activating the Krebs cycle and constituting an energy source [229]. Some polyhydric alcohols also play a vital role during salt stress [230]. Some enzymatic and non-enzymatic antioxidants play roles in protection under salt stress [145]. GABA, a non-proteinogenic amino acid, usually increases abundance during plant stress [181]. Earlier studies on the roles of GABA in plant stress adaptation were usually related to pH regulation, nitrogen storage, carbon metabolism, and its role as an osmolyte during osmotic stress [181].

Increasing soil salinity levels strongly influence essential lipids biosynthesis, metabolism, and peroxidation. Salinity dramatically reduces the total lipid content in many plants. Among the lipids, Mono galactosyl diglyceride (MGDG), the main glycerolipid of leaves, is highly affected by intensive salt stress. Salinity also disturbs the normal metabolism of another lipid – Phosphatidic acid. In turn, it shows multitudinous effects including cell membrane destability, increased susceptibility against the pathogen, abnormal vacuolar pump, abnormal signalling, etc. [231-233].

All plants have evolved a cellular mechanism of salt stress survival by avoiding or tolerating salt stress. Plants either dominate during salt stress or ion disequilibrium or alleviate the consequent secondary effect caused by stresses [234]. The ability of plants to tolerate salinity depends on the interaction between salinity and environmental factors such as soil, water, and climatic conditions. These adaptations even include metabolic activities and genetic modifications. Plant responses to salinity have been divided into two main phases – Ion-independent Growth Reduction and Ion-dependent Metabolic Imbalance (Figure 2). An ion-independent growth reduction takes place within minutes to days and causes stomatal closure and inhibition of cell expansion, mainly in the shoot [19, 235, 236]. Whereas ion-dependent metabolic imbalance takes place over days or even weeks and pertains to the build-up of cytotoxic ion levels, slows down metabolic processes, causes premature senescence, and ultimately cell death [4, 237]. The magnitude of the effect of salinity varied with the plant species, type and level of salinity. Interspecies, intra-species and inter-cultivar variations, and even individual lines differ at different ontogenetic stages to salt tolerance, which provides scope for the selection of genotypes for salt tolerance [238].

Compound	Role in the alleviation of salt stress in mature plant
Glucose	Limit the accumulation of Na^+ and stimulate the uptake of K^+, thereby maintaining ion homeostasis under salt stress [239].
Sucrose, fructose	ROS scavenging and osmoprotection [240].
Trehalose	Osmoprotection [241]; Regulation of sugar metabolism [242]; stabilization of plasma membranes and photosynthetic pigments [243].
Pyruvate	Energy metabolism [244, 245].
Proline	Providing organic nitrogen during stress [243]; Osmoprotection of cells [246, 247]; Assists in stimulating the expression of salt-stress-responsive proteins [248].
Alanine	Precursor for protein and nitrogen-containing compounds and acts as a signalling molecule [249-252].
Glutamate	Precursor for other amino acids [240, 249, 250].
GABA	Osmoprotection, Growth regulation, Nitrogen and Carbohydrate metabolism [251, 253, 254].
Leucine	Osmoprotection [245].
Aspartate	Precursor for other amino acids [240, 255].
Cyclitols	Acts as an osmoticum [255].
α- AB	Osmolyte [255].
Myoinositol	Osmotic adjustment [256].

Pinitol	Osmoprotection [256, 257].
Polyphenols	Antioxidant activity [252, 258].
Ascorbic Acids	Eliminates free radicals [259, 260]; Membrane protection [261]; Countering the inverse effects of salt stress on membrane integrity, pigments biosynthesis and net photosynthetic rate [262].
Glutathione	Counteracts the damage of principal cellular components due to ROS generation [263].
Tocopherols	Reduce ROS levels in photosynthetic membranes and restricts the extent of lipid peroxidation thru decreasing lipid peroxyl radicals [264]; Minimize oxidative damage [265].
Polyamines (Putrescine, Triamine spermidine and Tetra-amine spermine)	Alteration of gene expression for the biosynthesis and/or accumulation of osmotically active solutes maintenance of membrane integrity, better photosynthetic efficiency, drop-in ROS generation and accumulation of Na^+ and Cl^- ion in different organs [266-268].
Abscisic acid	Regulation of stomatal movement, biosynthesis of storage proteins and lipids and leaf senescence [269].
Indole Acetic Acid	Decreasing salt-mediated injuries [270, 271].
Gibberellic acids	Decrease the inhibitory effect of salt stress on growth traits, increase photosynthetic pigments, RWC and enzymatic activity [270, 272].
Jasmonic acid	Osmoprotection, Stomatal regulation and enhancing proline accumulation [273, 274].
Salicylic acid	Salt tolerance by restoring membrane potential and checking salt-induced K^+ loss [275]; enhancement of synthesis of Chlorophyll and carotene (Car); Maintenance of membrane integrity [276] and membrane permeability [277].
Brassinosteroids	Salt tolerance [278]; Alleviates the injurious effect on nuclei and chloroplasts [278].
Calcium	Alleviating the adverse effect of NaCl-induced salt stress [279].
Potassium	Retaining water content as well as cell turgidity by maintaining ionic balance [280].
Nitric oxide	Inhibits lipid peroxidation by countering with lipid radicals [281-283]; Influences K^+ and Na^+ homeostasis [281, 284].
Hydrogen peroxide	Stress signals transduction [285, 286]
Selenium	Resistance again salt stress; Reduce NaCl-induced lipid peroxidation [287]; Counteract the inimical effect of salt stress by regulating Superoxide Dismutase and Peroxidase [288]; Enhance Proline accumulation [289].
Silicon	Counteract the salt stress [290]

Table 5: Role of different metabolites in the alleviation of salt stress in mature plant

GENETIC CIRCUIT AND PROTEIN SYNTHESIS IS DISRUPTED BY SALINITY STRESS

Plants respond to saline stress by various cellular processes that involve stress sensing, diverse signalling pathways and changes in gene expression, controlled and modulated by transcription factors [4, 291]. It is found that salinity delays the synthesis of nucleic acids and RNAase associated with different metabolic processes. Besides, the protein synthesis machinery is sensitive to NaCl [292], and increased protein synthesis ability has been reported to contribute to salt tolerance. Due to low K^+ levels, protein synthesis is inhibited because K^+ is an essential element in protein synthesis as it binds tRNA to the ribosomes [293]. Salinity affects *de novo* protein synthesis, and the synthesis of ribosomes itself is required for protein synthesis and closely correlates with growth [20, 291]. Many ribosomal proteins have been reported to be up– or down-regulated under various stress conditions, including salinity stress [294]. Salt stress affects the cell cycle and differentiation. Salinity arrests the cell cycle transiently by reducing the expression and activity of cyclins and cyclin-dependent kinases that result in fewer cells in the meristem, thus limiting growth [133, 295]. Regulation of gene expression in salinity stress includes a wide array of mechanisms plants use to up-regulate or down-regulate the production of specific gene products, i.e. protein or RNA [205]. It has been long considered that it is implausible that one gene alone determines plant salinity tolerance, so a proper strategy to obtain salt-tolerant varieties is to pyramid several genes contributing to salinity tolerance [296, 297]. In a study on *Capsicum annum,* it was shown that salt tolerance is intimately associated with ABA signalling under salinity; it forms a network between different genes and physiological traits to generate the complex response [298]. Salinity also causes the accumulation of unfolded proteins, and the degradation of such nonfunctional proteins is important for plant salt tolerance [299-301].

Genes enhanced or activated	Plants under Saline Stress	References
AtHELPS	*Arabidopsis*	[302]
AtSKIP	*Arabidopsis*	[303]
JcDREB	*Arabidopsis*	[304]
mt1D	*Arabidopsis*	[305]
PeJRL	*Arabidopsis*	[306]
DcHsp17.7	Carrot	[307]
SOS1	Eggplant	[308]
IbMYB1	*Ipomoea batatas*	[309]
PSP68	Pea	[310]
S6PDH	Persimon	[311]
StCYS1	Potato	[312]
StDREB2	Potato	[313]
StDWF4	Potato	[314]
StZFP1	Potato	[315]
HSPC025	Rice	[316]
OsHSP23.7	Rice	[317]
OsHSP71.1	Rice	[317]
OsHSP80.2	Rice	[317]
OsHSP17.0	Rice	[317]
OsHSP23.7	Rice	[317]
OsFBA1	Rice	[318]
OsFBL7	Rice	[318]
mTERF	Rice	[318]
PDH45	Rice	[319]
PSP68	Rice	[320]
PRP	Rice	[316]
SAG	Rice	[316]
imt1	Tobacco	[321]
PDH45	Tobacco	[322]
AtNHX1	*Brassica*	[323]
SOS1	*Brassica*	[323]
SOS2	*Brassica*	[323]
SOS3	*Brassica*	[323]
TaHKT1;5	Wheat	[324]
TaSOS1	Wheat	[324]
TaPUB1	Wheat	[118]

Table 6: List of some genes associated with salt resistance

FUTURE PERSPECTIVE

Salt stress causes immense loss of biodiversity and agricultural productivity worldwide. To gain normal growth functioning, the plant must facilitate its detoxification, prevent damage, re-establish its homeostasis, and resume normal metabolism. Conventional selection and breeding techniques have been used to improve salinity tolerance in many plants, including crop plants [83], but it has been fruitless in many cases. As salinity impacts any native vegetation and the wildlife that depends on it for survival, biodiversity loss escalates. The ability of seeds to germinate at high salt concentrations in the soil is crucial for the survival of many plant species. It isn't easy to develop a salt-tolerant variety of any plant without sufficient knowledge of the mechanisms controlling salt tolerance because the effect of salinity varies within species, varieties or genotypes according to the level of salinization. As salinity tolerance is a complicated polygenic crop parameter, it is also very tedious to predict salinity tolerance based on a specific trait [325]. Earlier, attempts to develop salt-resistant cultivars were of limited success due to the multigenicity of the trait and the lack of availability of suitable donors containing beneficial alleles for salinity tolerance. Therefore, plant biologists aimed at overcoming severe environmental stresses need to be quickly and fully implemented. Most researchers of the present era have opined that the most effective and feasible way to minimize the detrimental effects of salinity on crop production is to enhance the salinity-tolerant ability [326, 327]. The multigenic nature of salt tolerance confirmed that the development of salt-tolerant genotypes of any plant needs a collective approach of conventional, molecular, genomic, and transgenic techniques. Recombinant DNA Technology and plant breeding are often accustomed to increasing salt-tolerant varieties efficiently but are time-consuming [328]. Microbial technology is one of the most desired strategies for crop productivity at present and future [329]. Biotic approaches for overcoming salinity-related issues have been gaining much attention for a few decades. Plant Growth Promoting Rhizobacteria (PGPR), Plant Growth Promoting Fungi (PGPF), Actinomycetes, Mycorrhizal fungus (VAM) etc., probably cause growth improvement through different mechanisms under salinity conditions. Therefore, biopriming, i.e. use of plant growth-promoting rhizobacteria to promote speedy, consistent, and enhanced crop establishment, enhances harvest quality and yield [330]. Genetic engineering approaches and biotechnology would help manipulate the osmoprotectant biosynthetic pathways for accumulating such molecules that act by scavenging ROS, reducing lipid peroxidation, and maintaining protein structure and functions [247, 331]. Latef and Chaoxing, 2014 [332] validated that PGPR inoculation on pepper seeds exhibited higher morphological parameters such as plant height, greater root length, larger leaf size, and increased dry matter in saline soils. Another study showed that inoculating some Plant Growth Promoting Bacillus isolates under salt stress conditions reduces oxidative stress by increasing plant growth parameters with increased antioxidant enzymes in *Pisum sativum* [328]. Beneficial microbes such as endophytes, PGPR, PGPF, VAM etc. are also capable of reducing salt stress in plants through the production of ROS scavenging enzymes, modulating osmotic adjustment, enhancing uptake of K^+ to counteract Na^+, and modulation of signalling pathways, etc. [333-335]. The combination of *Azospirillum brasiliense* and *Azotobacter chroococcum* has been reported to improve chlorophyll content and vegetative growth in coriander growing under saline stress [336]. Some microbes can produce IAA for plant growth, ACC-deaminase for reducing ethylene levels in stress, and exo-polysaccharides for chelating Na^+ [333, 337-339]. Mutualistic interaction of arbuscular mycorrhiza fungi (AMF) residing in the root endosphere of many terrestrial plants can mitigate salinity stress and promote continued growth [340, 341]. Anoshee and Farzami Sepehr, 2016 [342] pretreatment with *Glomus mosseae* resulted in the induction of salinity tolerance in *Lycopersicum esculentum*. Interaction of AMF with plants could alleviate salt stress-induced reduction in plant health, productivity, leaf area, and biomass with improved root-to-shoot dry mass ratio [343-346]. Under salinity, mycorrhizal fungi not only enhance plant growth but also alter physiological processes in plants, such as promoting osmolyte accumulation, acquisition of nutrients like N, P, and K^+, enhancement of antioxidant enzyme activities and photosynthetic capacity while decreasing Na^+ induced damages and MDA contents [347, 348]. AMF can inhibit the influx of Na^+ ions, maintain the normal non-toxic concentration of Na+ ions, and continue photosynthesis and other metabolisms [349].

Molecular genetics and plant transformation advances have made it feasible to assess biotechnological strategies based on activated signal cascades, engineered biosynthetic pathways, targeted gene or protein expression or alteration of the natural stress responsiveness of genes for the development of salt-tolerant crops [16]. Plant salinity tolerance greatly depends on signalling processes, adaptation mechanisms, and the efficiency of energy consumption of the plant species exposed to salt. Each of these can interact to provide great complexity in the response and the resulting levels of tolerance [350]. Therefore, discovering the molecular mechanism and exploring new strategies conferring salt stress to different wild and cultivated plants will help breed salt-tolerant crop cultivars. To date, with the help of omics technology, many processes have been found to become dominant at the molecular level in plant salt response, including salt signal perception and transduction, membrane dynamics, detoxification of ROS, uptake/exclusion of salt ions and compartmentalization, alteration of genetic circuits protein translation and/or turnover dynamics, cytoskeleton/ cell wall dynamics, carbohydrate and energy metabolism, and so on. Priming is another physiological method that improves seed performance and provides faster and more synchronized germination. Different seed priming techniques are effectively used to alleviate the negative effect of salt on the seed. Halo priming - a pre-sowing seed treatment with inorganic salts like KNO_3, $CaCl_2$, KCl, NaCl, $NaNO_3$, $MnSO_4$, $MgCl_2$ etc. is easy, low cost and low-risk technique and an alternative approach to overcome the salinity problem in agricultural lands [351]. Seed priming with nanomaterials provides a sustainable, practical and scalable tool for improving crop tolerance to stress during the critical seedling development stage [352]. Foliar applications of nanoparticles are among the novel approaches to facilitating plants' developmental processes under salinity stress [353]. TiO_2 nanoparticles, Ag nanoparticles, Zn nanoparticles, silica nanoparticles etc., are some of the widely used nanoparticles to alleviate the negative effect of salinity and allied stressful situations in agriculturally essential crop plants [347, 353-356].

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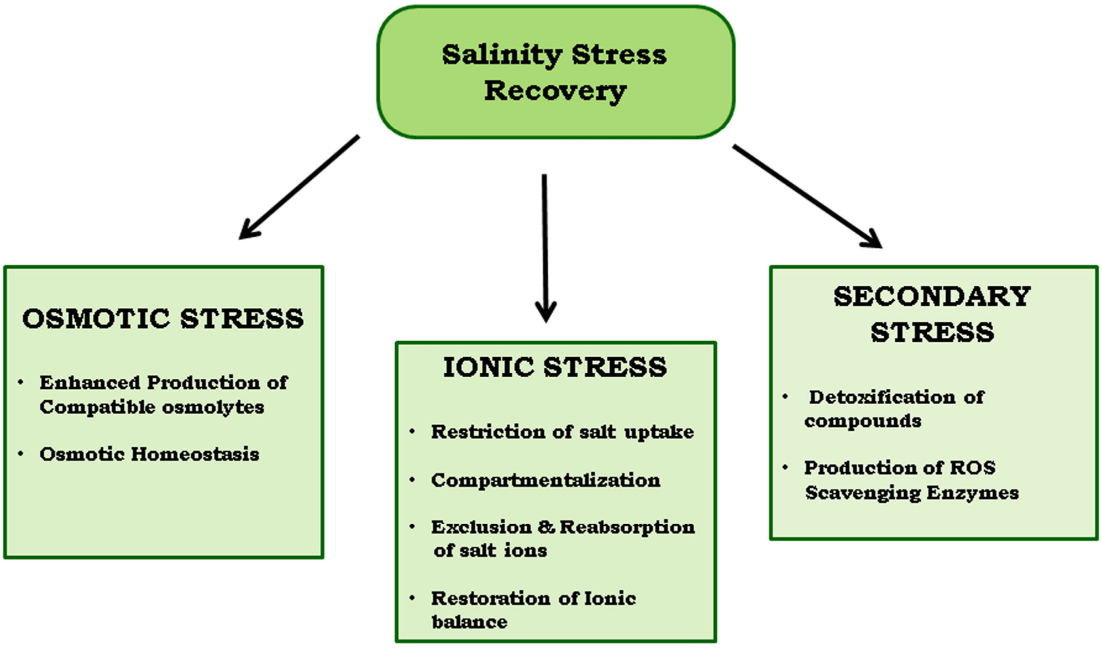

Figure 5: Different mode of stress recovery in plants under salinity stress

CONCLUSION

In the present decade, salinity has gained a global concern due to its adverse effects on crops and other economically important plants. Most crop plants are glycophytes and can tolerate salinity to a limiting degree by using various physiological mechanisms. However, in the past few decades, massive uncontrolled anthropogenic activities have led to elevating salinity; presently, it is a grave issue. In the coming decade, it will be a significant threat to the food security of the entire world because high salinity causes rapid death of almost all glycophytes. The investigators believe that soil salinity is an unavoidable and irresistible phenomenon and that the only way to overcome the problem is to develop salt-resistant or salt-tolerant crop varieties. Extensive research through cytogenetical, biochemical and molecular analysis has elucidated that among various salinity responses, mechanisms of salinity tolerance, strategies controlling ion uptake, transport and balance, osmotic regulation, hormone metabolism, fundamental and secondary metabolism and stress signalling play pivotal roles in the understanding of plant adaptation in response to salinity stress. Plants resistant to salinity stress will grow well by inducing the production of secondary metabolites and avoiding the toxic effects caused by the ions [357]. Scientists, plant breeders and genetic engineers worldwide are trying to develop salt-resistant crop varieties through transgenic and genetic recombination technology. However, there is still a shortage of knowledge about the mechanism and strategy of salt resistance.

Author Contribution

Both authors listed have made a substantial, direct and intellectual contribution to the work and approved it for publication. In addition, AKS and SS had the idea for the article; AKS performed the literature search and data analysis, AKS drafted, and SS critically revised the work.

Conflicts of interest
NO

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