

Review

## Physio-Chemical and Molecular Characterization of Salinity Stress in Wheat: Mitigation Approaches and Future Perspectives

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## Abstract

Wheat constitutes the backbone of global food supplies, and its production is directly linked to the food and nutritional security of the mounting population. Wheat is vulnerable to abiotic stresses like heat, salinity, and drought. These abiotic stresses tend to reduce the food security of the increasing population by reducing wheat production and nutritional quality. Among abiotic stresses, salinity stress (SS) has emerged as the most prevailing stress in modern high-input wheat farming systems, as it severely hampers crop growth by inducing numerous physiological, biochemical, and molecular alterations. Different genomic approaches, proteomics tools, phenomics, transcriptomics, and metabolomics approaches have been applied to overcome the adverse impacts of salinity stress and increase wheat productivity on a per unit land area basis. In this study, the adverse effects of salt stress on wheat have been objectively elaborated, along with highlighting conceivable mechanisms to deal with salt stress, as well as ion and hormonal management alternatives enabling wheat to mitigate its deleterious impacts.

## Keywords

Antioxidant; genomics; hormone; physiology; salt stress; wheat

## 1. Introduction

Wheat (*Triticum aestivum* L.) is a major cereal crop cultivated globally in a wide range of agroecologies on 15 billion hectares worldwide [1, 2]. It is grown at various altitudes and latitudes, commonly cultivated up to 3000 m above sea level and between 27° S to 40° S latitudes and 30° N to 60° N altitudes. It can also tolerate various humidity levels and temperatures, ranging from tropical to temperate climates, and receive 250–2000 mm of rainfall annually [3]. As a staple crop, it is widely grown in Asia, especially in China, India, Pakistan, and Nepal [4]. In Pakistan, over 40% of the total land is used for winter wheat sowing annually [5]. Wheat is an essential cereal crop and a basic source of protein and calories worldwide. Many scientists stated that approximately 83% of the global population depends on wheat grain for their calorie requirements, while 85% rely on it for protein intake [6].

Various abiotic stresses, such as salinity, drought, nutrient shortages or excesses, and heavy metal toxicity, affected the plants [7]. Among abiotic stresses, salt stress (SS) is an emerging threat to agricultural soils and wheat farming systems globally [8]. Wheat production in arid and semi-arid regions is decreased due to water scarcity and increasing salt concentration in the soil [9]. Globally, it is estimated that salinized soils are expanding by about 8 million hectares (Mha) annually, contributing to a total affected area of approximately 397–434 Mha, which accounts for more than one-third of the world's irrigated land [10]. In Pakistan alone, roughly 40,000 ha of arable land have become unsuitable for cultivation due to salinity [11]. Salinity stress drastically reduces yield due to

less germination and seedling infection, followed by a decrease in plant population per unit area [12].

Salinity affects various plant activities, including physiological, biochemical, and morphological processes, as well as seed germination, development, nutrient uptake, and water uptake. The uptake of nutrients and water is restricted by salt deposition on the roots' surface [13]. Increasing salt stress concentration is a severe constraint on the production of many crops worldwide due to the combined effects of specific ion toxicity and high osmotic potential. Increasing soil salinity can drastically reduce seedling growth and seed germination [14]. Many scientists conclude that salt stress makes early seedling growth and germination the most sensitive stages [15]. The soil salinity directly impacts the establishment of seedlings throughout the early phases of plant growth, which is critical for high yield [16].

## **2. Effects of SS on Wheat**

The germination of wheat is adversely affected by SS, resulting in a reduced number of germinated seeds and a longer time required to complete full germination [17]. The SS reduces plant growth; however, different crop cultivars have varying tolerance and adaptation to saline environments. Many researchers have examined that crop establishment has three main stages: germination, emergence, and early seedling growth, which are particularly sensitive to SS [18]. Salt toxicity not only affects wheat production but also disturbs metabolic functions in plants through ion toxicity, uptake of essential mineral nutrients, deficiency of water potential of cells, and membrane integrity. Sodium chloride (NaCl) is a commonly used soluble salt. The accumulation of sodium ions ( $\text{Na}^+$ ) in plant tissue is one of the most harmful impacts of salinity. The increasing concentration of sodium has inhibited the uptake of crucial micronutrients such as Potassium (K) and Calcium (Ca) from the soil [19]. The basic objectives of this article are to study the effect of salt stress on morphological, physiological, and yield-related attributes of wheat to understand the basic phenomenon and how these traits behave under SS and decrease the overall production of the wheat crop and also discuss the recent state of the art novel crop improvement techniques like genomics, phonemics, proteomics, metabolomics, and transcriptomics approaches to decipher the mechanism of SS for developing the salt tolerant wheat cultivars.

### **2.1 Effects of SS on Morphological Traits**

Saline soils inhibit plant growth due to ionic toxicity and osmotic stress, and they decrease the uptake of essential minerals [20]. Root cells may lose water when conditions are severe instead of absorbing it due to the soil solution's hyperosmotic pressure. Water shortages affect various physiological, gene expression, signaling, and biochemical pathways and processes, leading to reduced cell growth, wilting plant elongation, and, ultimately, plant death. These negative impacts of salt stress include water shortage effects [21]. Wheat is contrived at all stages of growth under salt stress situations which consist of leaf area, leaf shape, aging like senescence, waxiness and cuticle tolerance, leaf size, length of root, root fresh weight, root hairs, root area, dry root weight, and root density, morphological characters and vegetative like diameter, plant height, fresh and dry biomass (Table 1). Consequently, it is necessary to recognize wheat's performance at every growth phase to help develop salinity-tolerant cultivars [22]. It is stated that SS reduces leaf area, which, in turn, decreases the photosynthesis rate and leads to reduced biomass production. It has primary

effects and secondary stresses, including oxidative stress, which frequently develop due to excess reactive oxygen species (ROS) [23]. These ROS modify the bases of nucleic acids, create strand breaks, induce inter- and intra-strand crosslinks, and crosslink with proteins. They also cause lipid peroxidation, which increases membrane permeability and fluidity, denatures structural and functional proteins, and results in other biological effects [24]. The SS decreases the leaf water potential of wheat, causing stomata to close due to turgor pressure loss. This reduction in CO<sub>2</sub> conductivity increases oxidative stress, modifies cell wall integrity, and leads to toxic metabolites, eventually causing the plant's death. It also disturbs the photosynthetic activity of plants, which results in low growth and yield production [25].

**Table 1** Effect of the different levels of salt stress on the wheat traits.

| Varieties                  | Level of salt stress                                  | Effects                                                                                                                                                                                                   | References |
|----------------------------|-------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| Inqlab-91 and MH-97        | 15 dSm <sup>-1</sup>                                  | Decrease the rate of transpiration, stomatal conductance, and assimilation rate of CO <sub>2</sub> .                                                                                                      | [26]       |
| Dan-4589                   | 80 mM solution of sodium sulphate and sodium chloride | Enhances the Na <sup>+</sup> and decreases the K <sup>+</sup> ions, as well as the transpiration rate, photosynthesis rate, concentration of CO <sub>2</sub> inside the stomata, and chlorophyll content. | [27]       |
| Kouhdasht, Atrak and Tajan | 16 dSm <sup>-1</sup>                                  | Decrease the weight of 1000 grain and grain yield, K <sup>+</sup> and Ca <sup>2+</sup> content, and increase the Cl <sup>-</sup> and Na <sup>+</sup> ions.                                                | [28]       |
| Caxton                     | 200 mM solution of NaCl                               | Decrease the percentage of germination.                                                                                                                                                                   | [29]       |
| Yangmai 16                 | 0.75% NaCl solution                                   | Increase the accumulation of Na <sup>+</sup> and decrease the Na <sup>+</sup> /K <sup>+</sup> ratio.                                                                                                      | [30]       |
| Jimai 22                   | 100 mM solution of NaCl                               | Increased process of dehydroascorbate reductase (DHAR), SOD, POD, CAT, GR, and APX, etc.                                                                                                                  | [31]       |
| Rasoul                     | 16 dSm <sup>-1</sup>                                  | Decrease the 1000-grain weight and grain yield                                                                                                                                                            | [28]       |

It has been reported that the early maturity of wheat results from salt stress affecting the leaf area and plant height, with the plumule length being the most sensitive growth stage [32]. Wheat showed a considerable decrease in the colonization pattern of roots, flag leaf area, and leaf expansion under SS. SS also decreases leaf size, the number of leaves per plant, and leaf longevity [33]. The first significant organ is the root, and a strong root system can assist wheat plants by sustaining growth during early phases and extracting water and micronutrients from the soil [34]. The water used for irrigation in agricultural land is often saline, which decreases the yield of crops [35]. It is necessary to understand the mechanisms of tolerance to SS to improve agronomic practices and breeding programs, which can be targeted to impart botanical traits that enable crop plants to withstand saline environments [36].

## 2.2 Effect of SS on Physiological Processes

The SS disrupts numerous physiological processes of wheat through osmotic and ionic stress. These physiological processes include membrane variability, mineral distribution, changes in plant

development due to calcium dislocation by sodium, and membrane permeability [37]. Many researchers have examined that most physiological traits showed variations among all wheat varieties. The average performance of physiological traits also varied between bread wheat and durum wheat, while bread wheat showed significantly higher  $K^+$  content and lower  $Na^+$  content [38]. It is concluded that SS changes the photosynthetic parameters, including pigment compositions, leaf temperature, leaf water and osmotic potential, leaf relative water content (RWC), and transpiration rate [39]. The accumulation of inorganic ions and low molecular weight organic solutes controls osmotic adjustment in plants imperiled to SS [8]. The pressure potential or turgor pressure is maintained by adjusting osmotic potential, which is essential for normal cell growth and function [40]. Wheat adaptation to SS may be improved by using physiological features related to stress tolerance as a selection criterion. A strong correlation exists between the various physiological reactions of plants to stress and their defense mechanisms, such as changes in water potential and high relative water content (RWC) [41].

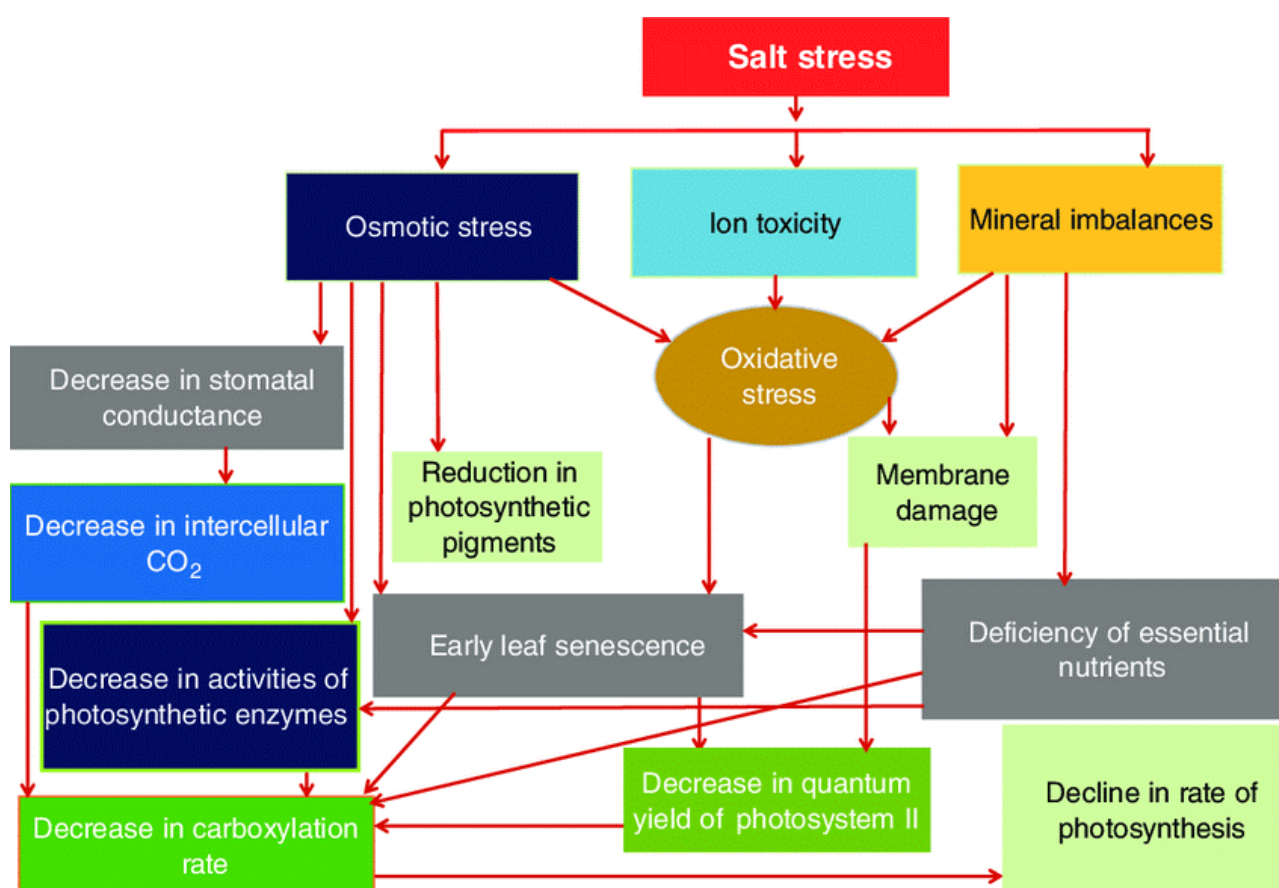
### **2.3 Effects of SS on Economic Yield**

Salinity stress is the leading cause of lower yield and restricting economic use of land resources in both arid and semiarid regions of the World [42]. Under higher salt concentrations, plant development follows a variety of mechanisms. The yield of all the crops decreases due to SS; however, the extent of yield losses may differ between salt-sensitive and salt-tolerant varieties. Furthermore, it also reported that the grain filling period and anthesis stage are extremely sensitive under various abiotic conditions, such as salt stress, and have been considered essential restraints to global wheat production [43]. It is concluded that wheat production decreased due to the decreasing growth attributes of wheat [44]. Many Scientists have reported that crop yield decreases by approximately 7.1% with each unit increase in salinity, up to a level of  $6 \text{ dSm}^{-1}$  [45]. The substantial decline in seeds/spike, thousand seed weight, and economic yield in wheat varieties that are salt sensitive and salt tolerant [46]. Under SS, the number of tillers, shoot-to-root ratio, leaf surface zone, seeds, spikelets, and weight of grain yield all decrease, resulting in lower grain yield [47]. Wheat is destructively affected by increased soil salinity, resulting in a considerable reduction in output. The shape and life processes of cells, tissues, and organs are affected by salinity [48]. Therefore, it is essential to understand that salt stress negatively affects wheat yield. Maintaining superior productivity requires adopting effective mitigation measures to achieve the long-term goal of sustainable food security [33].

### **2.4 Effects of SS on Plant Photosynthesis**

Plant growth and development are inhibited by SS, leading to reduced production [49]. SS has a substantial consequence on seedling growth and seed germination. The reduction in output is observed in several species of plants because SS is typically correlated with a reduction in photosynthetic capacity. Many factors decrease photosynthesis in salt-susceptible plants. However, the exact process of photosynthesis is still undefined [50]. The SS has adverse effects on components of photosynthesis, such as chlorophylls, carotenoids, and enzymes. Variations in that component are influenced by the duration and severity of SS in the crop plant [51]. The photosynthesis rate decreases when ions like sodium and chlorine are added to the photosynthetic pigment, and when water potential is reduced due to high salinity [19]. It is concluded that the rate

of photosynthesis per unit flag leaf area in treated plants is frequently unaffected in SS. When the photosynthesis process is based on chlorophyll rather than leaf area, a reduction in photosynthesis rate is observed because of SS [52]. An essential process in plants that is affected by SS is photosynthesis (Figure 1). Because glutamate is a substrate precursor of chlorophyll and proline biosynthesis, salt increases proline synthesis activity. Reducing chloroplast stromal volume and generating ROS are also thought to play essential roles in inhibiting photosynthesis during water stress, as suggested by SS [53].



**Figure 1** Pathway to decrease the photosynthesis rate by oxidative stress in plants under SS [54].

## 2.5 Effect of SS on Wheat Gas Exchange Parameters

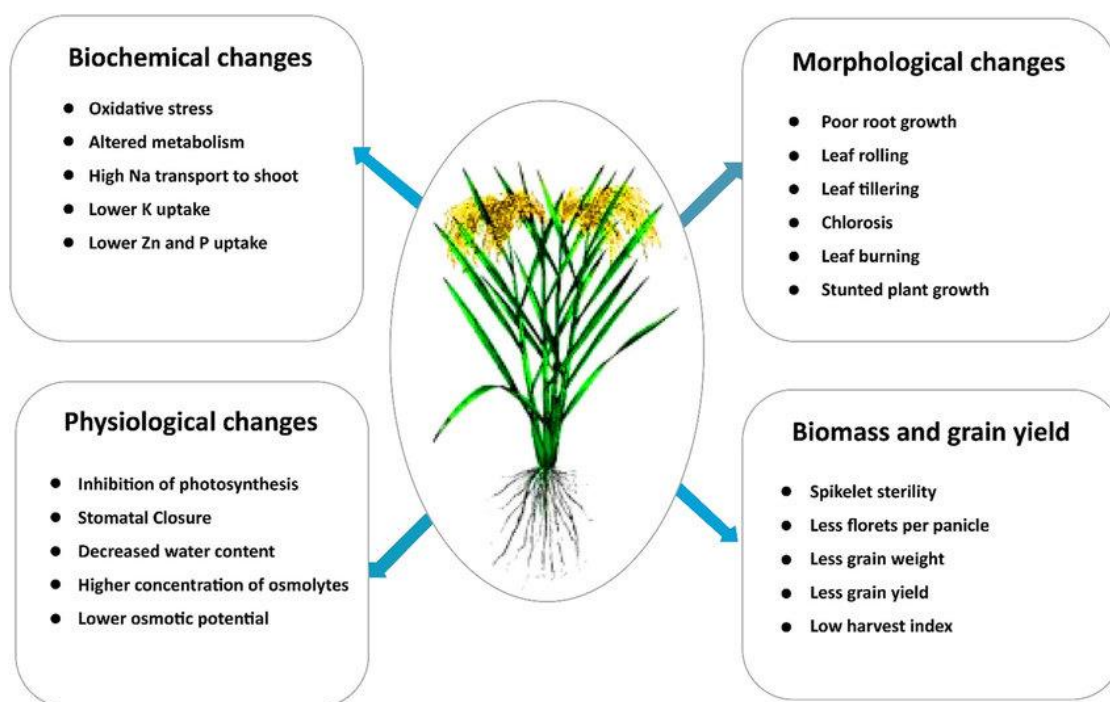
Gas exchange between the atmosphere and plant leaves has a vital role in plant growth and survival in many environmental circumstances [55]. It consists of two main stages: the intake of CO<sub>2</sub> and transpiration. This procedure is regulated by the stomata's conductance from the leaf's surface. Although multiple signal transduction processes contribute to stomata opening and closing, the biophysical aspects and biochemical processes of stomata are not fully observed [56]. The SS inhibits or stunts plant growth due to inflexibility in biochemical and physiological features. Among all the physiological features, gas exchange is one of the most significant traits, whose regulation can enable crop plants to withstand low to medium salinity stress, and substantial changes in these gas exchange characteristics occur due to SS [57]. For instance, plants susceptible to SS indicate a considerable reduction in transpiration rates, stomatal conductance, and water use efficiency [58].

Additionally, the photosynthetic processes of plants are positively correlated with both plant growth and the yield of cereals, including wheat [58]. The variability in plants is related to different gas exchange features under SS that survive within species and the variety of the same species. So, plant gas exchange features can be utilized as a screening method for salt tolerance in crops, as they are significantly associated with plant growth.

## 2.6 Effects of SS on Plant Germination and Growth

Seed germination is a vital stage for the efficacious establishment of vigorous seedlings, which is sensitive to SS than other vegetative growth stages. The toxic ions are accumulated in plants and cause an imbalance of nutrients [59]. The concentrations of essential ions that do not meet the plant's needs are reduced, disrupting the normal physiological processes. High salinity stress slows down the process of seed germination, whereas seed dormancy occurs due to medium to low levels of salinity stress. Higher concentrations of SS can hinder shoot and root elongation by slowing down the water uptake of the plant [60]. Many scientists stated that SS could rapidly inhibit root growth and the capacity to absorb water and essential nutrients from the soil [61]. Like other crops, seed germination and seedling growth in wheat were adversely affected by SS and drought [62].

Kesh et al. [63] found that the percentage of germination, shoot length, and length of root significantly declined with increasing concentrations of NaCl (0–150 mM) in all genotypes of wheat. Osman et al. [64] examined that a higher concentration of SS badly affected plumule growth. Radical dry weight is reduced with a rising level of salinity; under SS level  $8 \text{ dSm}^{-1}$  –  $16 \text{ dSm}^{-1}$  (54% to 91%), radicle dry weight is reduced, also (40% to 85%) plumule dry weight of wheat decrease under SS alternating from  $4 \text{ dSm}^{-1}$  to  $16 \text{ dSm}^{-1}$  as compared to the normal, in dry maize weight of plumule and radical under SS were also detected. The length of the shoot and root is a significant factor for SS because different metabolites are accumulated in plants under SS (Figure 2).



**Figure 2** Effect of SS on morphological, physiological, Biochemical, and yield-related traits [65].



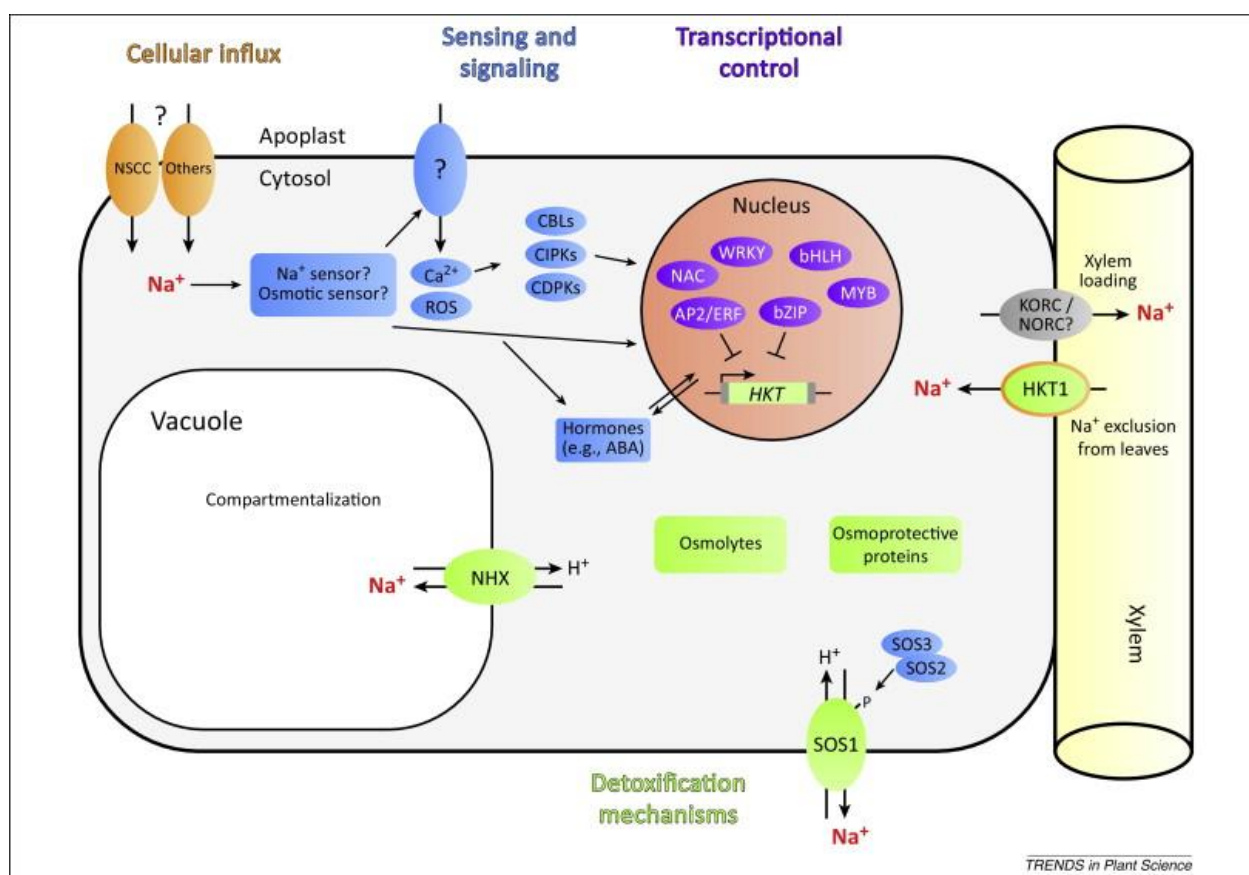
Furthermore, different changes are observed in plants, such as phenolic compounds,  $K^+/Na^+$  ions, chlorophyll contents, soluble sugars, root-to-shoot biomass ratio, and proline under a saline environment. Likewise, total soluble sugar is the main factor of carbohydrate metabolism, plant productivity, and photosynthesis. Under saline conditions, plants are subjected to osmotic and ionic stress, significantly reducing crop growth and development [66].

### **3. Effects of SS on Biochemical Traits**

#### **3.1 Antioxidant Responses under SS**

Secondary messengers or signaling molecules, such as the mitogen-activated protein kinase (MAPK) pathway, carry signals to the nucleus through redox reactions, promoting tolerance against various abiotic stresses through different cellular mechanisms [67]. In the adaptation process of plants in response to environmental stimuli, ROS play a significant role as signal transduction molecules that adjust several pathways during their adaptation to SS [68]. Additionally, these are important for triggering various essential natural processes, including cell differentiation and cellular proliferation [69]. It is also concluded that SS increases the production of ROS, which initiates numerous damages and physiological disruptions in crop plants [70]. Moreover, these ROS play a significant role as signal transduction molecules in influencing responses to environmental stresses, pathogen infection, various developmental stimuli, and programmed cell death. However, these also cause oxidative damage to cells under SS [71]. Genetic studies have found that respiratory burst oxidase homolog (Rboh) genes encode plasma membrane-associated NADPH oxidases and are the major producers of signal transduction-associated ROS in cells. This happens when ROS production continuously increases, known as the "oxidative burst" [72]. Ion poisonousness, synthesis of ROS, and high osmotic stress develop in plants due to SS [73]. ROS accumulates in the cells due to environmental stress. After accumulation in the cell, it can directly damage the plants by oxidative stress, resulting in a reduction retarding growth and grain yield. Plants protect their cells from damage because they have antioxidant mechanisms to manage ROS. This balance between the purification and production of ROS is determined by antioxidants, like enzymatic and nonenzymatic [74]. Enzymatic antioxidants are Catalase (CAT), glutathione peroxidase (GPX), superoxide dismutase (SOD), peroxiredoxins (Prxs), ascorbate-glutathione (AsAGSH), dehydroascorbate reductase (DHAR), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and ascorbate peroxidase (APX) [75]. Nonenzymatic antioxidants are cellular redox buffers, such as ascorbate (Asa), tocopherol, Glutathione (GSH), carotenoids, and phenolic compounds [76]. It has been concluded that ROS can be both harmful and beneficial in plants subjected to SS. When ROS levels in the cell exceed the capacity of scavenging systems, cells enter the oxidative zone, resulting in variation and cell damage, which can lead to cell death (Figure 3). The cells are in the reduced zone when ROS levels are decreased, which affects cell division, organogenesis, stem cell maintenance, and biotic and abiotic responses [77]. The ROS involved as an indicating molecule in processes such as development and growth, stomatal conductance, programmed cell death (necrosis), hormonal signaling, cell cycle, regulation of gene expression, and senescence has been extensively explored [78]. In wheat, it was detected that soaking seeds with  $H_2O_2$  increases the tolerance of seedlings under drought conditions [79]. Furthermore,  $H_2O_2$  pretreatment with aluminum in wheat decreases ROS accumulation in the plant [79]. The exogenous  $H_2O_2$  treatment protects the wheat seedlings from damage by SS [80].



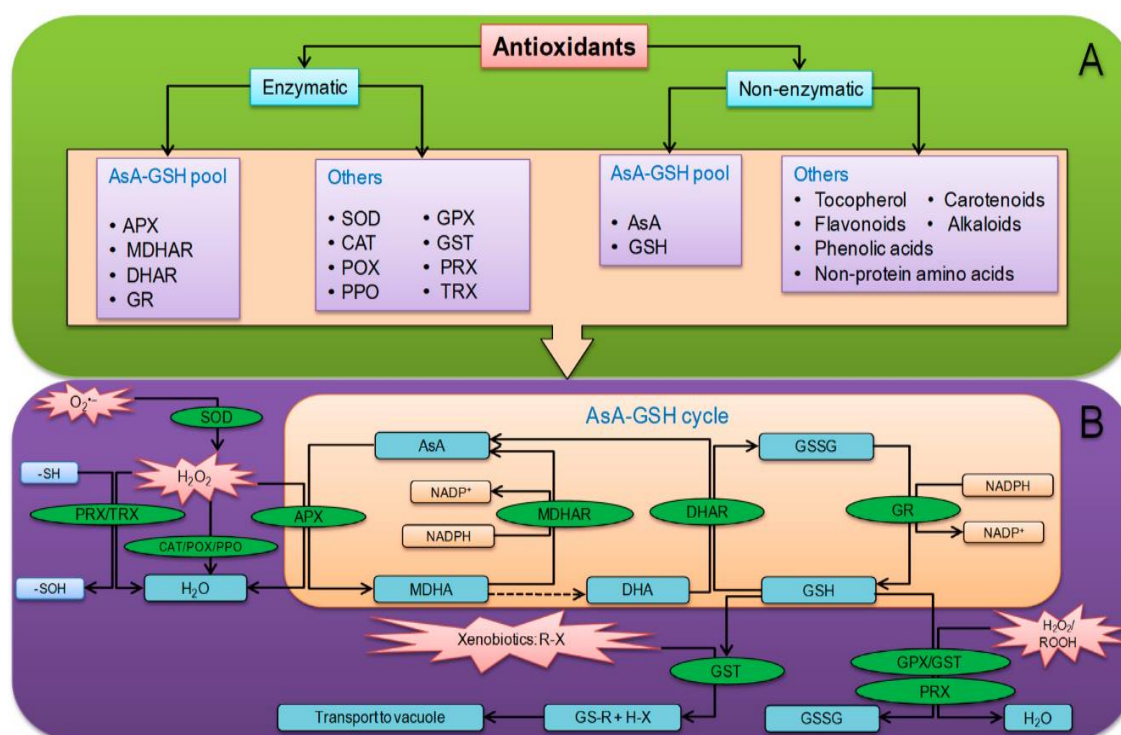


**Figure 3** Detoxification mechanism of plants by using the pathway of cellular influx, sensing and signaling molecules and transcriptional control [81].

### 3.2 Role of Non-Enzymatic Antioxidants to Cope with SS

Under ionic, oxidative, and osmotic stresses, which result in growth retardation of crop plants by disrupting plant functions and different growth phases [82]. The ROS are produced under oxidative stress. These ROS interact with proteins, lipids, nucleic acids, and cell enzymes and ultimately cause cell death [83]. There is a balance between the amount of ROS production and scavenging under normal circumstances. However, during extreme environmental stress, the stability is disturbed, producing oxidative stress in plant cells [84]. Phenolic compounds can act as non-enzymatic antioxidants or oxygen-free radical scavengers. Phenolic compounds are soluble cell elements that change the environment in response to abiotic stress. Similarly, the deposition of phenolic compounds in salt-tolerant plants is considered a mechanism for reducing ROS synthesis and protecting cell membranes from damage caused by SS [85].

Non-enzymatic antioxidant anthocyanin not only inactivates free radicals but also inhibits anthocyanin deposition in epidermal layers, effectively reducing oxidative stress and enabling plants to perform their functions efficiently [86]. Under SS, plants protect themselves against the harmful effects of oxidative stress by developing defense mechanisms. ROS scavenging is the primary mechanism against abiotic stresses [87]. The detoxification process of non-enzymatic reduced substances, such as Asa, GSH, and enzymatic antioxidants, is essential for ROS scavenging [88]—the complex non-enzymatic ROS scavenging, including Asa, tocopherol, and GSH (Figure 4). The non-enzymatic antioxidant process provides a strategy to increase plant tolerance under SS [89].



**Figure 4** Comparison between enzymatic and non-enzymatic antioxidant (A), defence mechanism in plant under various abiotic stresses by utilizing the enzymatic and non-enzymatic antioxidant (B) [90].

### 3.3 Role of Ion Pumps, Calcium, and Potassium Ions in Maintaining Homeostasis

The SS has repressive effects on wheat phenological aspects such as leaf number, leaf rate, and expansion [91]. Potassium is a macronutrient essential for physiological processes such as regulating osmotic pressure, stomata movement, and activating enzymes in plants [92]. The increase in K concentration under SS could ameliorate the harmful effect of SS on the growth and yield of the plants [93]. Additionally, K application expressively increased dry shoot and root weights, K and Na ratio, chlorophyll a and b contents, emergence percentage, and osmotic potential in wheat crops under SS [94]. A fundamental requirement for normal growth under SS is the control of ion concentration and homeostasis. Despite their nature, plants can survive under high salt concentrations in the cytoplasm of their cells. The plant can prevent SS by storing surplus salt in older tissues that will eventually be eliminated or excess salt in vacuoles [95].

In the cytoplasm,  $Na^+$  enters and then moves to the vacuole via transmembrane  $Na^+/H^+$  antiporters. The proton motive force created by proton pumps in the tonoplast stimulates the entry of  $Na^+$  across the tonoplast membrane [96]. In plants, salinity results in ion instability and hyperosmotic stress. Under hyperosmotic stress, the deposition of inorganic ions ( $K^+$ ,  $Cl^-$ , and  $Na^+$ ) in the cytoplasm maintains the external osmolarity to prevent osmotic imbalance and support growth [97]. Under SS, two wheat varieties demonstrated that the restoration of shoot sap osmolarity ranged from 87% to 100%, mainly  $K^+$ ,  $Na^+$ , and  $Cl^-$  absorption [98]. Potassium (63%) contributed the most to the osmotic adjustment in shoot cells. However, in hyperosmotic stress conditions, K alone cannot maintain the osmotic adjustment, and the concentration of  $Na^+$  and  $Cl^-$  masks the requirement for plants to overcome salinity stress [99].

### 3.4 Hormones' Function and Their Response to SS in Wheat

The osmotic adjustment, hormonal signal transduction, mineral nutrients, programmed cell death, and cell elongation are among the key roles of ROS (Table 2). This pathway is also influenced by ROS and calcium ions, as well as regulators and hormones like ethylene (ET), brassinolide (BRs), indole-3-acetic acid (IAA), methyl jasmonates (MeJA), polyamines (PAs), abscisic acid (ABA), and salicylic acid (SA) [100]. Some plant species produce phytohormones like ABA, which aid the plant in closing its stomata, reducing water loss through transpiration [101]. All agronomic indices of wheat, including fresh and dry weight, emergence percentage, and photosynthetic pigments, were lowered by NaCl concentration [102]. SA favors plant growth in both saline and non-saline circumstances [103]. ABA, a plant stress hormone, is key in signaling between the various plant developmental processes and adaptive responses to SS [104]. ET, a receptor mutant, *etr1-1*, showed increased sensitivity to SS, including early seedling establishment, seed germination, and early seedling developmental processes [105]. IAA (Auxin), a plant hormone, is essential for adaptable plant development and growth. Its presence, auxin maxima, is closely linked to newly formed plant structures. For example, auxin contributes to organogenesis, cell elongation, apical dominance, and vascular tissue development. JA is a critical signaling molecule in plants for various developmental and defensive functions [106]. IA has a significant role in regulating plant growth. It can also restrict apical dominance, cell elongation, and vascular tissue development [105, 107].

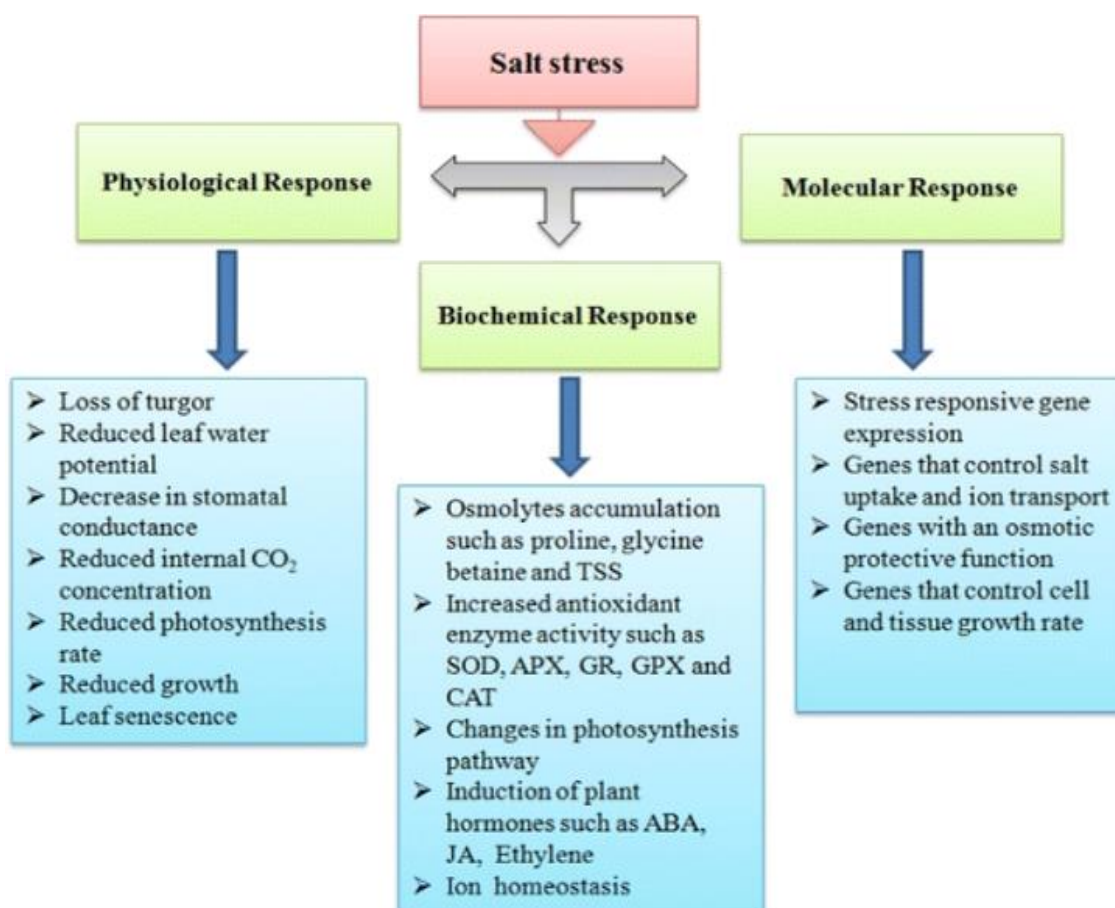
**Table 2** Role of hormones under SS to increase the plant activities.

| Varieties           | Dose of SS                      | Dose of Hormones                                    | Effects on Plant Traits                                                                                                           | References |
|---------------------|---------------------------------|-----------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------|------------|
| Inqlab-91<br>MH-97  | 15 dSm <sup>-1</sup>            | Auxin ( $4.89 \times 10^{-4}$ ) mM                  | Increase the assimilation rate of CO <sub>2</sub> , productive tillers, growth, and grain yield                                   | [20]       |
| Inqlab-91<br>MH-97  | 150 mM NaCl                     | Auxin ( $4.89 \times 10^{-4}$ ) mM                  | Increased germination percentage, Improved ion homeostasis, and Increased shoot dry weight                                        | [108]      |
| Giza-168<br>Sohag-3 | 50, 100, 150, and 200 mM (NaCl) | 150 mg L <sup>-1</sup> quantity of Gibberellic acid | Enhanced pigment of photosynthesis, content of proline, carbohydrate, protein, grain weight, and amino acid                       | [109]      |
| MH-97<br>Inqlab-91  | 15 dSm <sup>-1</sup>            | 100, 150, and 200 mg L <sup>-1</sup> cytokinins     | Increased germination percentage enhanced the growth of early seedlings, including root dry weight and shoot dry weight           | [110]      |
| MH-97<br>Inqlab-91  | 15 dSm <sup>-1</sup>            | 100, 150, and 200 mg L <sup>-1</sup> cytokinins     | Increased height of plant, biomass of shoot dry weight, increased productive tillers, grain yield, and 1000-grain weight          | [111]      |
| Mehran-89           | 0.13 M NaCl                     | ABA ( $10^{-6}$ M)                                  | Increased germination percentage, and root and shoot biomass                                                                      | [112]      |
| PUNJAB-85           | 100 mM NaCl                     | 10 mM ABA                                           | Increased root length and plant height, improved shoot and root dry weight, Increased chlorophyll content, decreased uptake of Na | [113]      |

### **3.5 Effects of SS at the Genetic and Molecular Level**

Proline is a proteinogenic amino acid that finds its use in the biosynthesis of proteins [107]. To impart tolerance against SS, proline performs a vital function. Proline content and 26 kDa protein were observed, indicating a high level in wheat, which induced salt-responsive genes that protect the plant during salt tolerance [114]. Many proteins and genes have been acknowledged in different SS-induced plant functions. These proteins and genes are 25 kDa protein P150, Bnd22, RAB 21 kDa, 27 kDa protein, 26 kDa protein, fibronectin, and vitronectin [115].

The TaAOC1 gene in wheat scrambles the Allene Oxide cyclase enzyme in Arabidopsis, increasing JA levels and allowing the plant to withstand high salt [116]. This indicates that JA has a beneficial influence on salinity tolerance. Transgenic expression of TAOC1 in the ABA-sparse mutant had the same salt tolerance and physical appearance as in the sufficient type, implying that ABA presence does not influence TAOC1 gene expression [117]. The MYC2 mutant background, on the other hand, affects TAOC1 expression and salt tolerance. MYC2 stimulates the AOC-catalyzed branch in the biosynthesis of jasmonates. At the same time, ABA does not affect the production of jasmonates in response to SS. The 26 kDa protein content significantly increased in wheat, indicating it is induced by a salt-responsive gene to protect the plant in the SS environment [118]. qRT-PCR is used to analyze TaDi19A expression in the leaves and roots of wheat plants exposed to various environmental stresses and hormone treatments [119]. The basic function of that gene (HKT) is to regulate the equilibrium between K and Na ions in the cell under SS [120]. Over-expression of AtMYB44 reduces transpiration and improves drought and salt tolerance [36]. The expression of betaine aldehyde dehydrogenase (BADH) genes is induced by salt and cold stress environments. Inducing betaine maintains the osmotic pressure, keeping the enzymes active for metabolism [121]. Mannitol is a sugar alcohol that acts as a significant carbon source, scavenger, and coenzyme regulator of ROS in osmoregulation (Figure 5). Under SS, transporter genes play a critical role in maintaining ionic equilibrium [122]. The nuclear factor Y (NF-Y) gene family functions under the SS environment and is involved in various regulatory functions of plant development [123].



**Figure 5** Comparison of physiological, biochemical, and molecular traits response in plants under SS [124].

#### 4. Crop Management under SS

##### 4.1 Seed Priming and Nutritional Management under SS

Seed priming (SP) is a simple and inexpensive method for boosting seed viability under many abiotic stresses, such as salt stress [125]. During the early stages of germination, but before radical projection, pre-sowing controlled hydration, known as SP, regulates and enhances pre-germination metabolic activity [126]. The SP practices increase the seed germination percentage, seedling emergence, growth, and yield traits. Seed priming with CaCl<sub>2</sub> or KCl enhanced the performance of the seedlings in terms of growth, development, and yield [127]. Many scientists demonstrated that the germination rate, time taken to complete germination, root length, and seed vigor were all significantly improved by seed priming. Germination performance improved when low-vigor seeds were primed [128]. Plant nutrients are vital for obtaining an optimal yield, but an inadequate supply of essential nutrients due to poor soil fertility will decrease crop production worldwide [129]. It is reported that 60% of soil worldwide is nutrient-deficient; however, suitable soil nutrient levels are required to attain maximum production [130]. Nutrients are necessary to decrease the effects of different abiotic stresses, including SS. Plants consume numerous nutrients like magnesium (Mg) and nitrogen (N) in the photosynthetic activity, phosphorus (P) for adenosine triphosphate (ATP) generation, and K for enzyme activation and stomatal regulation [131]—salt-tolerant variety development with applicable agronomic experiences under SS conditions that improve crop

production. Various opportunities exist for genetic diversity in gene banks, providing adequate support to develop a salt-tolerant variety with high yield compared to current cultivars [132]. In the gene pool, the basic genetic makeup of several crop species is present, which supports breeders in developing salt-tolerant varieties. Also, plant breeders develop salt-tolerant varieties specifically for rice and wheat crops [114]. During the development of salt-tolerant varieties, genetic and physiological characteristics also play a significant role in achieving maximum yield at the harvesting stage [133]. Agronomic traits such as leaf number, number of tillers, plant height, root length, shoot length, leaf area, germination percentage, leaf water content, root dry weight, RWC, shoot dry weight, as well as physiological traits such as stomatal conductance, chlorophyll content,  $K^+/Na^+$  or  $Ca^{2+}/Na^+$  discrimination,  $Na^+$ , and  $Cl^-$  exclusion, photosynthesis rate, and leaf water relations have all been considered as evaluating of salt susceptible cultivars under controlled conditions [134]. SE El-Hendawy et al. [135] reported that agronomic and physiological traits provide selection criteria for salt-tolerant wheat genotypes in field environments.

#### **4.2 Mechanisms of SS Tolerance**

In response to SS, wheat cultivars tend to change at the cellular and organ level [136]. Salinity is regarded as one of the most essential abiotic pressures that has reduced global output [137]. Plants use a diversity of methods, such as osmotic adjustment, ionic balance, synthesis of PAs and nitric acid production, interaction of oxidative stress and antioxidant enzyme, osmoprotectants, and suitable solutes biosynthesis, to survive under SS environments [138].

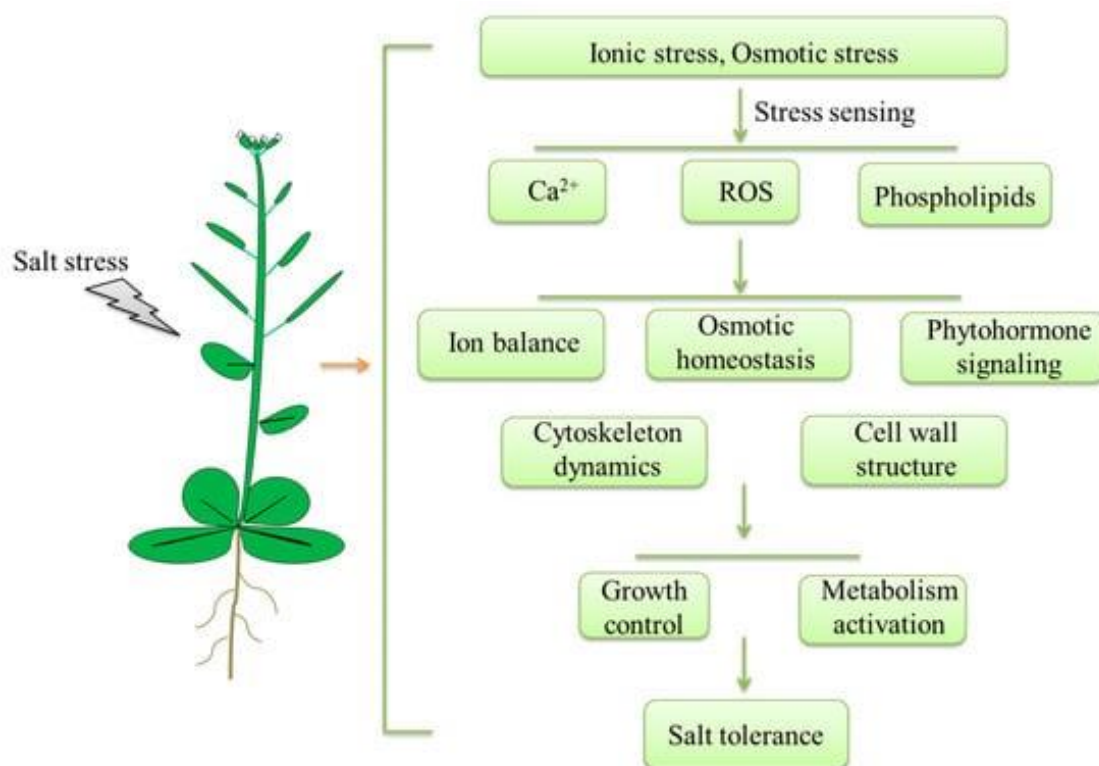
#### **4.3 Osmotic Adjustment**

Plants tend to utilize osmoregulation to diminish the negative consequences of SS [19]. Polyols, sugars, amino acids, and quaternary ammonium compounds are organic chemicals that plants store to reduce osmotic potential [139]. Osmoregulation triggers the defense mechanism against antioxidant species [140]. Osmotic adjustment is a process in which a cell's water potential is reduced without a corresponding reduction in cell turgor pressure due to the accumulation of solutes by cells. The addition of large amounts of both organic and inorganic solutes can cause an osmotic adjustment in plants under SS. In rare circumstances, solute buildup exceeds the limits of cytoplasmic content regulation, resulting in growth retardation [141]. Cell wall elements play a crucial role in any plant's metabolic function. These metabolic processes, including protein metabolism, energy production, respiration, and nucleic acid synthesis, play a vital role in the growth of the cell and make up a substantial portion of its biomass [142]. The accumulation of Na and K ions in the leaf blade is a primary factor in the destruction of chlorophyll, leading to a significant imbalance in the index measuring chlorophyll content. Low chlorophyll content reduces photosynthesis, which leads to seedling growth. Additionally, it negatively impacts the photosynthate that plants need to survive in stressful environments [85, 143]. Increasing salinity-induced stress reduces the osmotic potential of the soil solution, significantly reducing the amount available to the plants [144].



#### 4.4 Ionic Balance

Ionic balance is a critical development that adjusts ion flux to maintain a low concentration of  $\text{Na}^+$  ions while increasing the concentration of  $\text{K}^+$  ions [145]. Regulating internal  $\text{Na}^+$  and  $\text{K}^+$  ion balance is critical for performing numerous functions in the cytosol and maintaining membrane potential and cell volume [146]. The plants maintain excess salt and homeostasis by primary and secondary active transport, and  $\text{Na}^+$  and  $\text{K}^+$ , positively charged ions, accumulate in the tonoplast membranes and plasma membrane, respectively (Figure 6). It is concluded that several  $\text{K}^+$  genes are affected by SS. The excess  $\text{Na}^+$  ions are segregated in the vacuole to protect the cytosol from the harmful effects of sodium ions and ion toxicity [147]. High levels of  $\text{Na}^+$  result in their accumulation in plant cells during SS and eventually reach toxic levels, affecting ion homeostasis [148]. By eliminating  $\text{Na}^+$  from the cytoplasm, plants tend to maintain low levels of  $\text{Na}^+$ .  $\text{Na}^+/\text{H}^+$  antiporters, which transport  $\text{Na}^+$  in exchange for  $\text{H}^+$ , are mainly used to accomplish this [149]. The  $\text{Na}^+$  is transported to the apoplast by plasma membrane-localized  $\text{Na}^+/\text{H}^+$  antiporters, and vacuole-localized  $\text{Na}^+/\text{H}^+$  antiporters maintain  $\text{Na}^+$  compartmentation in vacuoles. During SS, the salt overload sensitive (SOS) regulatory system modifies the activity of  $\text{Na}^+/\text{H}^+$  antiporters to control ion homeostasis [150].



**Figure 6** Mechanism of salt tolerance in plants under ionic stress and osmotic stress [151].

#### 4.5 Osmoprotectants and Suitable Solutes Biosynthesis

Osmoprotectants are non-toxic compounds that consist of amino acids, PAs, sugars, and quaternary ammonium compounds. In a stressful environment, it maintains enzymes and cellular structures, acts as a scavenger of ROS and metabolic signals under abiotic stress [152]. Compatible



solutes or low molecular mass compounds accumulate in the cytoplasm to accommodate the ionic imbalance because they do not disrupt normal metabolic processes in the vacuoles [153]. Osmolytes are known to perform the functions of osmotic balance, enabling continuous water inflow (or decreased outflow) and protecting structures, with deposition proportionate to the change in external osmolality within species-specific constraints [154]. For instance, proline, glycine betaine (GB), sugars, and polyols are among these suitable solutes [155]. A sizeable portion of all assimilated CO<sub>2</sub> is made up of polyols, which also play the roles of compatible solutes, scavengers of oxygen radicals, and low-molecular-weight chaperones, brought on by SS [156]. Acyclic (like mannitol) and cyclic polyols are two types of polyols (e.g., pinitol). To manage with SS, mannitol, a sugar alcohol, may be used as a suitable solute [153]. Osmotic adjustment and osmoprotection are two difficult-to-differentiate mechanical functions of polyols. They function as osmolytes, aiding in cytoplasmic water retention and the sequestration of salt to the vacuole or apoplast during osmotic adjustment. These osmolytes interact with membranes, protein complexes, or enzymes to protect cellular structures. These compounds have hydrogen-bonding properties that enable them to safeguard macromolecules from the negative consequences of a higher ionic concentration in the environment [157].

#### **4.6 Interaction of Oxidative Stress and Antioxidant Enzymes**

Interestingly, a range of environmental conditions, such as soil salinity, drought, high temperature changes, and heavy metals, hurt plants either directly or indirectly through increasing ROS synthesis [158]. The potential of the many types of ROS to oxidatively damage proteins, DNA, and lipids is a typical pattern. These cytotoxic characteristics of ROS provide for the vast array of enzymatic and non-enzymatic detoxification mechanisms that have evolved in plants [159]. Since the balance between oxidative and antioxidative capacities determines the fate of the plant, oxidative stress is essentially a controlled process. The antioxidant defense system provides adequate protection against free radicals and active oxygen under non-stressful environments. As a result, the antioxidant defense system's efficiency increases. The term "antioxidant" generally refers to a diverse group of chemicals that protect cells against damage that may otherwise be caused by exposure to particular highly reactive substances. The antioxidants can inhibit other molecules from oxidizing. Transferring electrons from a substance to an oxidising agent is a necessary step in the chemical process of oxidation [160].

#### **4.7 Synthesis of Polyamines and Nitric Acid Production**

Nitric oxide (NO) and PAs are considered essential signaling molecules in plants, playing a wide range of roles in controlling the adaptive responses of plants to challenging environmental situations. They are known to trigger a variety of cell signaling pathways, and their interaction helps plants cope with unfavorable environmental conditions [161]. NO, a small gaseous molecule that regulates a number of plant growth and developmental processes, acts as a quick signaling molecule during a range of stress reactions and induces the expression of a number of redox-regulated genes [162]. In addition to regulating essential antioxidant enzymes, it scavenges lipid and superoxide radicals to prevent lipid peroxidation [163]. The reciprocal relationship between PAs and NO improves tolerance to SS. Research supports the correlation between NO and the diverse stress

levels carried by PAs. ABA biosynthesis is enhanced by upregulated NO generation via PA signaling, which also plays a significant role in abiotic stress tolerance processes [164].

## **5. Approaches to Improve Salinity Tolerance in Wheat**

### **5.1 Conventional Methods to Improve Tolerance in Wheat under SS**

Among prevalent techniques to offset the adverse effects of SS, screening of salt-tolerant genotypes is one of the biologically viable and economical ways to increase crop yield [165]. Meanwhile, SS reduces the growth and production of the crop; an appropriate selection standard is needed to define the comparative salt tolerance [166]. A particular expression of plants' substantial tolerance to salinity is a significant indicator of their genetic potential to withstand the effects of salinity contamination, which is an essential feature in agriculture [167]. The developed high-yielding varieties (HYVs) performed poorly in some soils due to iron, zinc, and manganese toxicity, salinity, acid sulphate toxicity, aluminum toxicity (for upland wheat and rice), iron deficiency, and nutrient inequities [168]. The link between international and national sequencers and the effectiveness of native breeding initiatives may be examined when variations from external sources outcompete those from local breeding efforts. However, concerns over genetic susceptibility, as well as the risks associated with genetic consistency and massive monocultures, have become increasingly prominent [169]. Stress is defined as an abiotic factor that affects an organism, while cultivars represent the organism's response. Salinity resistance can be categorized into two categories: "evasion" and "tolerance" [170]. Screening conditions are vital for the effective selection of breeding methods. In the first generations, screening under stress situations can be excellent for selecting stress-tolerant lines. However, due to climatic fluctuations worldwide, these lines may not consistently perform over time. Breeding programs assess their resources in certain regions where drought stress and high temperature stress are major issues; nevertheless, stress is not always continuous due to indecisive weather patterns. This is especially true for stresses like salinity or frost, which are highly variable and heterogeneous [171]. The procedure of multiplication and multiyear trials at specific points in the production testing stages might aid the identification of salinity-tolerant germplasm. Breeding programs must be developed to improve cycle time, a key component in producing abiotic-tolerant cultivars, to speed up the cultivar development process. In comparison to traditional breeding strategies, the ability to develop and select wheat populations in different locations, seasons, or years in Mexico allows wheat generations to improve earlier. Strategy for wheat breeding is also looking at implementing a fast generation improvement scheme in a field-based screen house to encourage or boost varietal development [172]. Increasing genetic successes in grain production under abiotic stress, such as water stress, heat stress, and SS, by shortening breeding cycles, is the most effective approach; yet, it remains underutilized. Incorporating genomic predicted breeding values into selection could significantly improve the breeding technique.

### **5.2 Omics-Based Approaches**

Recently, genomics approaches (Whole-genome sequencing, QTL mapping, marker-assisted selection, genome editing using CRISPR/Cas, etc.), transcriptomics techniques (RNA-sequencing to reveal changes in gene expression in response to SS), and proteomics have been employed to develop salt-tolerant cultivars of field crops, including wheat. The use of *in vitro* tissue culture

techniques for cell line selection has received significant attention recently. The presence of a selective agent in the callus initiation media, such as NaCl, could improve the chances of recovering salt-tolerant plants [173]. Many investigations have found that cultures acquire salt tolerance after being exposed to a stress agent for multiple passages [174]. Other studies have reported that using the initial subculture to assess salt tolerance is the best option, as cumulative exposure to SS may enhance adaptation to salinity. In contrast, plants regenerated from long-term culture may not exhibit improved tolerance [175]. Plant tissue culture techniques offer a viable and practical method for creating salt-tolerant plants. The production of fertile and genetically stable salt-tolerant regenerants in durum and bread wheats, as well as other species, has been previously reported [176]. Biological and cellular processes, such as plant development, genome structure, and interactions with the environment, are the objectives of plant molecular biology. These in-depth multidimensional studies require examination linking together the entire genetic, functional, and structural elements. The term "omics" refers to these comprehensive research initiatives [177]. Due to the complicated genetic makeup of salt tolerance, conventional breeding has achieved only moderate success. Recent developments in "omics" technology, including transcriptomic, genomics, metabolomics, and QTL omics, can identify the essential biomolecules and genes governing salinity tolerance [178].

### **5.3 Genomic-Based Approach**

Genomics-assisted breeding includes subsequent introgression and genomic mapping, which are used to increase tolerance in wheat varieties. QTL mapping, or quantitative trait loci, is a significant technique for demonstrating different complex traits on a genetic basis that is controlled by multiple genes. Polygenes controlled the abiotic stresses like SS and showed a quantitative inheritance [179]. There is also apparent genotypic diversity in salinity tolerance of crops like wheat and rice, which is related to leaf mortality caused by excessive salt accumulation in the leaves [180]. Plant genetic resources (PGRs) have been collected, conserved, and evaluated for a long time to supply plant breeders with different genetic materials, expand the genetic base, and develop new crop varieties to counteract climate change [181]. The environment heavily influences several genes and genotype and environment ( $G \times E$ ) interaction, which control salt tolerance, a quantitatively inherited trait [182]. The availability of molecular markers made it possible to conduct mapping studies, primarily using microsatellites or simple sequence repeats (SSRs), and, more generally, single-nucleotide polymorphisms (SNPs). Salt tolerance-related traits have been widely mapped using QTL mapping and other mapping techniques such as association mapping and Bulk-seq/QTL-seq (using extreme, i.e., low and high performing, bulks) [183].

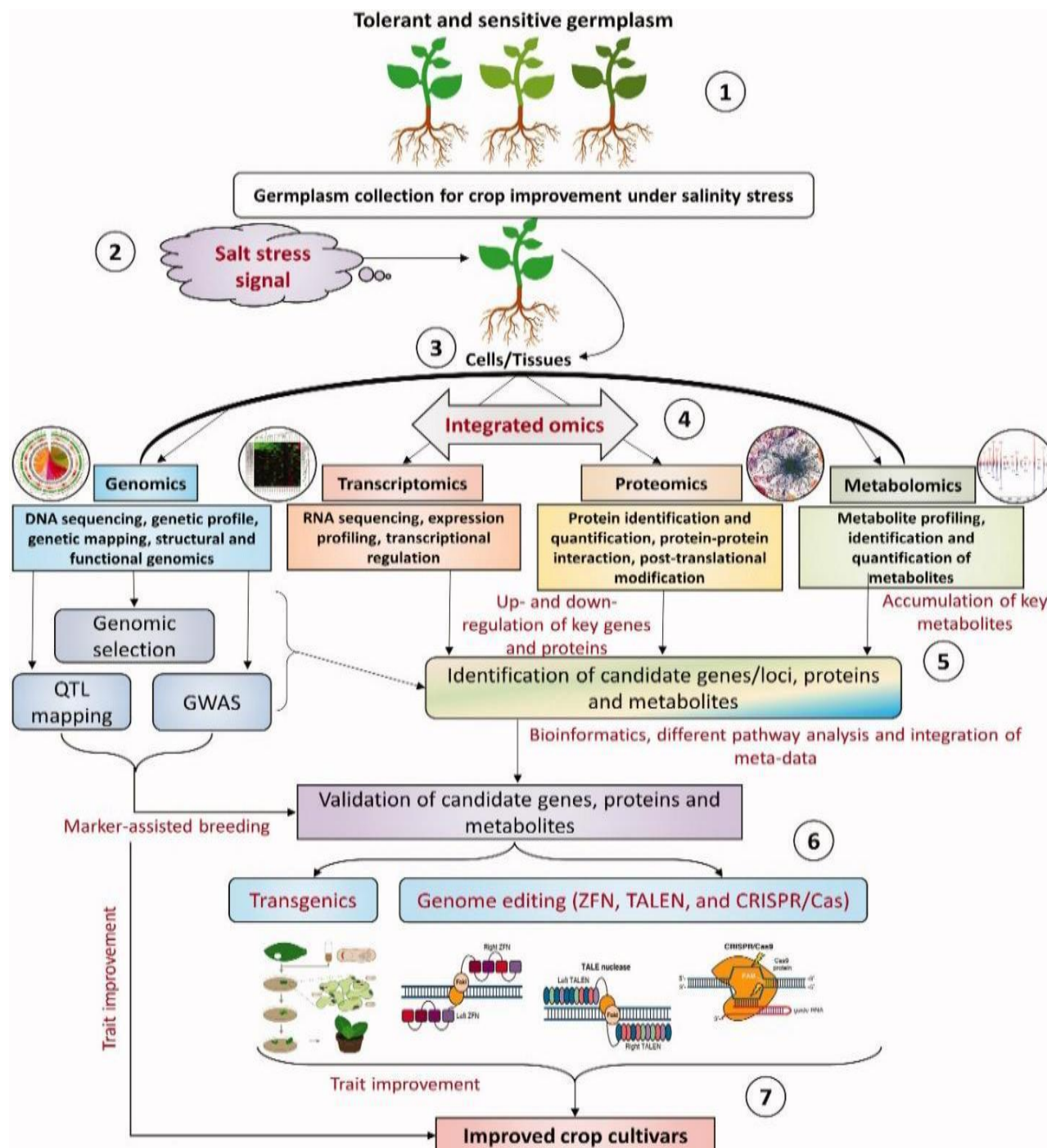
### **5.4 Proteomics Approach**

Proteomics helps by detecting protein modulations and pathway alterations, in capturing insights about salt-stress tolerance. The salt-stress response and defence biomarkers in wheat included phosphor proteomics such as cp31BHv, betaine-aldehyde dehydrogenase (BADH), cytosolic (GS1), Cu/Zn superoxide dismutase (SOD), MAT3, leucine aminopeptidase 2 (LAP2), and 2-Cys peroxiredoxin BAS1 [184]. It has been revealed that the overexpression of ion transporter proteins (for example, malate transporter), tubulin, profilin, retinoblastoma, casparian strip membrane protein, and xyloglucan endotransglycosylase improves salt tolerance. Three genes,

TraesCS4B01G254300.1, TraesCS6A01G336500.1, and TaABCF3—encoding OPAQUE1, NRAMP-2, and transporter genes, respectively—improved SS tolerance by balancing the shoot  $\text{Na}^+/\text{K}^+$  ratio, specific energy fluxes for absorption, dissipation, and shoot  $\text{Na}^+$  uptake [185].

### **5.5 Metabolomics Approach**

The SS can induce numerous changes in a plant's protein, transcript, and other biochemical disruptions. Frequently, a plant responds to SS biochemically without changing its transcriptional or protein expression [186, 187]. These biological molecules are also known as metabolites, and metabolomics is the study of metabolites [186]. Metabolomics identifies and analyzes significant alterations in plant cells following stress detection. Due to its remarkable qualities, which include its ability to alter many structures and functions, the study of metabolites has recently gained popularity in modern scientific research [188]. MDA, glutathione, and ascorbate, three important metabolites involved in stress resistance, were up-regulated under SS during the early growth stage (Figure 7). Other stress-responsive metabolites that have shown induced accumulation after salinity include cinnamyl alcohol dehydrogenase (CAD), cinnamoyl-CoA reductase (CCR), and 3-ketoacyl-CoA synthase [189].



**Figure 7** Pathway of Omics approaches to improve crop cultivars after sensing the SS picture, modified from [190].

## 5.6 Phonemics Approach

Nondestructive imaging provides a significant advancement in understanding growth in response to environmental factors, such as varying water availability, across a vast number of genotypes with comparably little effort. This is due to the dynamic nature of plant growth [191]. Remote sensing for high-throughput phenotyping (HTP), in the scientific and agricultural productive systems, is becoming more effective in breeding and improving the germplasm evaluation procedures [192]. Due to numerous challenges, such an evaluation should test transpiration in a large number of plots

and the field phenotyping response of plants to SS. Plant transpiration evaluation has relied chiefly on surrogate attributes, which has probably led to an overdependence on the surrogates [193].

### **5.7 Transcriptomic Approach**

In wheat, many transcriptomic approaches have been employed using different parts of plants, such as roots, shoots, stems, and leaves, to recognize SS tolerance. Salt tolerances in wheat cultivars have been increased by the signal transduction module gene and the diacylglycerol kinase encoding gene [194]. The SS-resistant gene, TaMYB73, was increased in roots but significantly suppressed in leaves when exposed to SS. However, in Arabidopsis, the gene's overexpression increased stress tolerance [195]. Previously, it has been established that xyloglucan, expansin, dehydrins, endotransglycosylase/hydrolase, and peroxidases are root-growth-enhancing genes to improve SS tolerance. The study also discovered 10,805 unigenes in 'Kharchia Local' roots at anthesis, and SS increased the expression of AP2/ERF transcription factors (TFs), MYB, WRKY, NAC, and bHLH [196].

## **6. Future Perspectives and Conclusion**

Wheat is the primary cereal crop around the world. However, SS is a primary hazard to the worldwide production of wheat, nutritional security, and food because its concentration is continuously increasing in the soil. SS adversely influence plant growth, seed germination, ATP production, photosynthesis, turgor pressure, ionic imbalance, nutrient uptake, hormonal imbalances, and yield. Wheat crop demonstrates an extensive array of physiological, molecular, and morphological responses under SS. However, wheat crops employ various mechanisms, such as salt tolerance, ion homeostasis, osmotic protection, and the addition, absorption, and transport of ions, osmoprotectants, and suitable solutes. They also rely on the biosynthesis of suitable solutes, interaction between oxidative stress and antioxidants, synthesis of polyamines, and nitric oxide production to cope with SS. Under abiotic stress, including SS seed priming, crop germination percentage, seedling emergence, growth, and yield traits, as well as nutritional management, are enhanced. Plants use numerous nutrients, such as nitrogen for photosynthetic activity, K for enzyme activation, and phosphorus for ATP production, to decrease the effects of SS. Plants protect their own cells from damage because they have antioxidant mechanisms to manage additional reactive oxygen species (ROS). Plant breeders use different omics (genomics, phonemics, proteomics, metabolomics, and transcriptomics) approaches to understand the mechanism of SS because salinity has complex genomic behavior. The molecular and physiological mechanisms are crucial for breeders to develop salt-tolerant wheat cultivars. These mechanisms provide a selection criterion for screening of salt-tolerant cultivars in wheat. In contrast, more understanding is still needed in several areas, particularly with regard to the physiological basis of the partitioning of assimilate from plant sources to sinks. Additionally, more research is required to understand how root-shoot signaling affects nutrient and water intake in wheat plants subjected to SS. Additionally, exogenous application of osmoregulators, nutrients, ions, and hormonal management can also help to improve salt tolerance in wheat cultivars. All these approaches hold promising potential to overcome the adverse effects of SS on wheat crops and may contribute to enhanced wheat productivity, thereby ensuring food security.

## Author Contributions

M.Z., A.S., Q.A., B.A., Y.N., J.I., F.C., M.E., H.A., and D.A wrote the initial draft. M.S.I., M.A.I., D.R., Ö.K., and A.E.S. reviewed and edited the manuscript. A.E.S. and Ö.K. funding acquisition.

## Competing Interests

The authors have declared that no competing interests exist.

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