

Review Article

Investigation of the Genetic Basis of Wheat Resistance to Salt Stress

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Abstract

This article explores the genetic factors and mechanisms underlying wheat's resistance to salt stress. One of the key strategic food crops that significantly contributes to the security of the world's food supply is wheat. Abiotic stressors, including salt, elevated temperatures, and drought, create an adverse environment that reduces wheat yield and production capacity. In any stage of plant development, salt stress may result in irreversible losses of yield potential in a variety of agricultural crops, such as wheat, barley, and rice. Salinity stress induces osmotic and ionic stresses, which lead to the transfer of considerable amounts of Na⁺ ions into plant cells and an increase in Na⁺ concentration in the cytoplasm and vacuoles. This process can eventually lead to cell death and disrupt metabolic processes. Soil salinity significantly limits wheat production by reducing plant water absorption and inducing nutritional deficits due to ion toxicity, leading to diminished plant growth and yield. Considering the essential role of wheat in global food security, investigating salt tolerance in wheat and creating salt-tolerant breeds is crucial for maximising the use of saline-alkaline soils and guaranteeing sustained food production.

Keywords: wheat, salt stress, salt tolerance, genetic mechanisms, abiotic stress, ion toxicity

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1. Introduction

Global crop production is in danger because of soil salinity, a crucial abiotic stress factor that lowers agricultural productivity. Climate change, geological and hydrological circumstances, and human activity, particularly excessive irrigation, are the primary drivers causing soil salinity. Consequently, the management of salinization becomes more challenging, and the extent of saline land areas may continue to grow [1]. Wheat (*Triticum aestivum*) is a necessary agricultural crop that is cultivated worldwide and is an essential food in numerous countries. Nevertheless, it is difficult to achieve this demand due to the limited availability of agricultural land and unfavorable climatic conditions. Research indicates that an economic yield, spike indicators, grain mass, and seed number decrease significantly with each unit increase in salinity in both salt-sensitive and salt-tolerant wheat varieties. Excessive accumulation of primarily Na⁺ and K⁺ ions in plant cells is the outcome of soil salinization, which eventually culminates in severe ion toxicity. Furthermore, secondary stress factors like oxidative damage and osmotic stress are produced by salt stress and can interfere with metabolic activities. This review summarizes recent research on the molecular regulatory mechanisms of salt tolerance in wheat and aims to form a theoretical basis for improving breeding efforts by discussing the potential of new technologies to increase salt tolerance in wheat. The high toxicity of salt ions in the soil disrupts the formation of photosynthetic pigments due to the inhibition of the biosynthesis of various chlorophyll components. In wheat, chlorophyll content (CC), relative water content (RWC), normalized difference vegetation index (NDVI), and membrane stability index (MSI) are significantly reduced under the influence of soil salinity.

As salinity levels increase, the amount of water reaching the roots decreases, resulting in poorer nutrient uptake by wheat plants through the root system. In response to salinity stress, changes occur in key physiological functions, including protein synthesis, energy production, and lipid metabolism, during the embryonic stages of the plant. As a result of the drastic weakening of plant growth, the synthesis of toxic metabolites and molecular damage can occur, which ultimately leads to the destruction of the plant [2]. To combat stress, plants re-regulate their metabolism, both enzymatic and non-enzymatic antioxidant mechanisms.

In order to mitigate the osmotic stress induced by salinity, plants synthesise and accumulate metabolically compatible solutes, including proline, carbohydrates, and betaines. Proline functions as an osmoprotectant, assisting plants in maintaining a tissue water potential that is lower than that of the soil. This process, in the end, maintains the turgor pressure that is essential for growth [3]. In addition to maintaining osmotic balance, these compatible solutes also have an antioxidant function, helping to stabilize subcellular structures and regulate intracellular redox potential under stress conditions.

Salinity stress impacts the quantitative feature of wheat grain yield. Salinity stress impairs the growth and development of spikelets during the reproductive and maturation stages. Salinity stress has a detrimental impact on the height, spike length, and grain weight of plants. The production of specific bread products from wheat is directly related to grain quality. This property is evaluated based on physical and compositional parameters such as grain hardness (GH), protein content (PC), and moisture content (MC). The effect of salt stress on wheat quality indicators is a relatively understudied area. Therefore, a two-year study was proposed to evaluate the effects of salinity stress on physiological, biochemical, yield, and other quality-related parameters in 20 wheat genotypes of diverse genetic origin, in order to identify parameters that can be used as biomarkers for rapid selection and improvement of salinity-tolerant varieties. In this study, it was hypothesized that the response of wheat quality to salinity stress would differ between genotypes.

2. Effects of Salt on Wheat and Its Physiological Basis

The main stress factors that salt causes in plants are mainly related to ionic toxicity and osmotic stress. The growth of plants is directly influenced by osmotic stress, which restricts the expansion of root ends and leaf cells. The effects of ionic stress on plant growth usually become apparent at later stages. In plants with the ability to transport Na^+ , the effects of ionic stress are often not considered as critical as osmotic stress. The effect of salt stress on aboveground plant growth is observed in two phases: first, a rapid response to an increase in external osmotic pressure, and then a slow response phase to Na^+ accumulation in the leaves. In the first stage, the development of new shoots is weakened, and in the second stage, an accelerated senescence process occurs in older leaves. In particular, in cereal plants, a significant decrease in bushiness and spike number is observed under the influence of salt stress in the initial stage. A decrease in cellular water potential as a result of osmotic stress can limit water use in plants. When exposed to salt stress, a decrease in relative water content (RWC) is observed in both salt-tolerant and salt-sensitive varieties, with a weaker expression in salt-tolerant wheat varieties [4]. Salt stress also stimulates the formation of reactive oxygen species (ROS) such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH). Excessive accumulation of ROS creates oxidative stress, which negatively affects plant growth and development by causing cellular toxicity through damage to membrane lipids and oxidation of proteins [5]. The main source of ROS in plants is NADPH oxidases (NOXs), also known as respiratory burst oxidase (Rboh).

3. Strategies to Improve Salt Tolerance of Wheat

3.1. Breeding

Hybridization, a classic method in plant breeding, has played a significant role in shaping desired characteristics in wheat. The complicated and polygenic trait of salt stress tolerance is regulated by several genes. The selection of salt-tolerant wheat varieties is significantly influenced by a comprehension of the genetic basis of salt tolerance. In order to reduce the adverse effects of salt stress, plants that are tolerant of it apply a range of morphological, physiological, and biochemical strategies, such as ion excretion, the formation of organic osmolytes, the synthesis

of antioxidants, and modifications in nutrition. There are about 350 species in the Triticeae tribe, which includes wheat's wild relatives. There is an enormous amount of genetic variability among its members, in particular when it is related to salt tolerance. Species belonging to the genera *Elytrigia* and *Thinopyrum* are mainly distributed in coastal areas, while *Leymus* species thrive in soils with high salinity and alkalinity. Long wheatgrass (*Thinopyrum ponticum*), a halophyte relative of wheat, is considered one of the plants with the highest salt tolerance and can survive even in conditions of salinity close to seawater. The differences in salt tolerance observed among these species provide favorable opportunities for increasing the salt tolerance of wheat through hybridization and indicate that wild species are a potential source for improving wheat's resistance to salinity. Unlike disease resistance, salt tolerance in wheat is considered more difficult to assess in the breeding process because it is a complex trait controlled by several genes. Since the 1980s, interspecific hybridization techniques have been used to transfer salt-tolerant genes from Triticeae species to common wheat. However, despite the passage of about 25 years since the initial experiments, the new varieties obtained have not yet been widely adopted by farmers due to difficulties related to productivity and ecological adaptation.

3.2. New Breeding Techniques

Although traditional hybridization has achieved significant success, several challenges remain, including the relatively low use of plant chromosomal translocation lines in wheat breeding programs. Furthermore, the integration of desirable traits such as salt tolerance is often limited due to problems such as incompatibility and hybrid sterility in distant hybridization. In order to resolve these challenges, it is necessary to incorporate present molecular biology methodologies, including gene editing, transgenic technologies, and molecular marker-assisted selection, into wheat breeding. These approaches can increase selection efficiency and ensure precise regulation of target traits.

Molecular marker-assisted selection combines traditional genetic selection with modern molecular biology methods to produce plant materials with superior genetic properties. This approach, known as marker-assisted selection (MAS), is widely used worldwide to develop various traits in wheat, particularly to improve key economic traits. Several Turkish genotypes and Australian salt-tolerant genotypes were chosen as repeat parents using the MAS approach on the *Nax1* and *Nax2* genes, and four backcrosses were carried out to generate new wheat genetic material. Generation combinations containing salt tolerance genes were obtained as a consequence of this methodology [6].

MAS enables the combination of tolerance components from various genetic sources, facilitates multiple selection in a relatively short time, and allows for early selection of target traits, as salt tolerance in plants typically involves multiple traits and mechanisms. This approach can be considered a significant tool for improving the salinity tolerance of plants. Compared to traditional field evaluation and phenotypic selection, MAS offers a promising approach for the creation of plants with increased salt tolerance. Although numerous QTLs associated with salt tolerance have been identified in various plant species, the development of commercial varieties or breeding lines with improved salt tolerance through MAS remains limited [7].

Due to the complex nature of soil salinity and the difficulties in distinguishing its effects on infiltration processes, it has been difficult to identify reliable loci for salt tolerance and related traits. However, with the gradual increase in data, especially on the wheat genome, QTL mapping has emerged as a crucial tool for uncovering the genetic basis of complex plant traits. The relationship between chlorophyll content and overall biomass characteristics and some physiological parameters suggests that the Na^+ and K^+ accumulation pathways are genetically distinct. Numerous molecular markers linked to genes or QTLs affecting necessary traits have been identified and proposed as potential indirect selection criteria to improve selection efficiency through MAS. Identification of quantitative trait loci (QTLs) remains an effective and reliable approach for studying the genetic basis of salt stress resistance in wheat. QTL mapping allows for the precise localization of genomic regions responsible for traits associated with stress resistance. Research conducted from 1996 to 2022 identified 934 significant quantitative trait loci (QTL) linked to salt stress resistance in wheat. These QTLs covered 21 germination traits, 23 agronomic traits, and 12 ionic traits and were confirmed with $\text{LOD} \geq 3$ in 26 studies. Large-scale genome-wide studies have identified over 500 QTLs associated with salt stress response and have shown that each QTL explains between

8.4% and 40.0% of the phenotypic variation. In a study investigating the genetic basis of wheat seed germination and traits under salt stress conditions, 31 unconditional QTL and 11 conditional QTL associated with 16 candidate genes related to salt stress resistance were identified. Genome-wide association studies (GWAS) have identified significant QTLs associated with chlorophyll content (CC) and specific leaf area (SLA) under salt stress conditions on chromosomes 1B, 2B, 2D, 3A, 3B, 5A, 5B, and 7B. Functional annotation of genes revealed three key candidate genes - TraesCS5A02G355900, TraesCS1B02G479100, and TraesCS2D02G509500, whose expression was significantly increased under salt stress conditions [8].

3.3. Transgenic Technology

Transgenic Technology acts as a crucial optimization strategy in wheat breeding and allows for increased disease resistance, stress tolerance, and yield through the introduction of foreign genes. This technology plays a significant role in creating wheat plants that aim to increase productivity and quality indicators in response to changing environmental conditions and human needs.

3.4. Exogenous Application

The results are occasionally uncertain, and the selection process is time-consuming. Conversely, the most direct method of enhancing salt tolerance in wheat is the exogenous application of specific plant growth regulatory compounds [9]. Examples of these substances include osmoprotectants, signalling molecules, antioxidants, and plant nutrients. Interaction with these foreign compounds leads to the creation of a specific physiological state in the plant, in which various defense mechanisms are activated. Crops are capable of responding to salt stress immediately and effectively as a consequence of this activation. Osmoregulation is a critical adaptive mechanism that enables plants to sustain turgor pressure in stressful environments and enhances their tolerance to drought or salinity at the physiological level. The significant function of osmotic agents is supported by plenty of data from a variety of in vitro and in vivo studies that utilise physiological, biochemical, genetic, and molecular methodologies. These substances, which are involved in enhancing the resistance of plants to both drought and salt stress, include sugars and sugar alcohols (trehalose, D-ononitol, sorbitol, fructose, and mannitol), amino acids (such as proline and exobases), and ammonium compounds (O-choline sulphate, β -alanine betaine, polyamines, glycine betaine, and dimethyl sulfopropionate).

Crop growth necessitates optimal plant nutrition. Nutrients support plant growth and functionality, and they additionally assist wheat crops in managing the adverse effects of salt stress. Excessive salinity causes nutritional lacks that interfere with normal plant growth and metabolism by increasing the absorption of Cl^- and Na^+ while decreasing the absorption of Zn^{2+} , Ca^{2+} , and K^+ . K, N, phosphorus (P), magnesium (Mg), silicon (Si), selenium (Se), and zinc (Zn) are the crucial nutrients for plants. By stimulating respiratory enzymes, boosting photosynthetic efficiency, and supporting osmotic management, potassium is known to improve wheat's resistance to salt. For regulating the flow and distribution of Na^+ , Cl^- , and mineral ions, external Si application improves wheat growth under salt stress. It is believed to be an effective method of increasing crop tolerance to salt in the field [10]. Additionally, by lowering reactive oxygen species (ROS) under salt stress, Se application may reduce wheat damage.

3.5. Non-Enzymatic Antioxidants and Exogenous Signaling Molecules

Ascorbic acid (AsA), glutathione (GSH), tocopherol, and other non-enzymatic antioxidants are crucial in suppressing ROS levels in plants. Salt stress significantly increases lipid peroxidation, leading to a marked increase in the activity of antioxidant enzymes in plants [11]. Application of AsA to wheat roots increases endogenous AsA levels and catalase (CAT) activity, helping to maintain ion homeostasis and improve photosynthetic potential, thereby reducing the negative effects of salt stress on some wheat varieties.

Correlation analysis and principal component analysis (PCA) were performed to understand the variability in adaptation mechanisms in wheat plants under control and salt stress conditions. The limited success in selecting salinity-tolerant wheat varieties can be attributed to the absence of precise indicators for physiological and

agronomic traits associated with salinity stress, as well as the low genetic diversity present in current wheat genetic resources. Although varieties previously described as salt-tolerant have been used in breeding efforts, the results obtained have been limited due to a lack of understanding of the mechanisms of salt tolerance. Most of the areas prone to saline soils are currently unused. Cultivation of salt-tolerant wheat varieties on saline soils can be of enormous importance in terms of attracting these areas to agriculture and meeting the food needs of the ever-growing population. This will be possible by clarifying the mechanisms behind differences in salt tolerance between different wheat varieties and identifying salt-tolerant genotypes.

4. Conclusion

There are still several necessary questions waiting to be discovered. In addition to the known and putative ion receptors, are there salt receptors in the plasma membrane, cytoplasm, and organelles of plant cells? How do responses to salt stress interact with other environmental stresses? How can plant growth and productivity be linked in salt-affected areas? The degree of damage caused by salt to plants depends on many different factors: the growth stage of the plant, ion levels, genotype, temperature, plant organs exposed to salt, the composition of the saline solution, and the duration of salt exposure. As a result of continuous developments in scientific and technological methods, the genetic and molecular basis of salt tolerance in wheat is increasingly being elucidated.

Wheat's tolerance to salt stress can be greatly increased by the development of novel salinity-tolerant varieties and genetic advancements, and notable progress has been made in this area. A better comprehension of the complex characteristics associated with salinity in wheat has been made possible by the use of current technologies and ongoing advancements in this field. Simultaneously, there is a growing interest in the breeding of wild relatives of wheat and the transfer of beneficial genes from them. Nevertheless, this particular area continues to confront numerous obstacles. Initially, there are several limitations on the genetic transformation of wheat, including a small selection of wheat varieties that can be transformed and a poor transformation efficiency. These limitations prevent the efficient and stable transfer of essential salt stress resistance genes to target varieties. In order to address these challenges, researchers have created growth regulatory factors (GRFs) and their cofactor-interacting factors (GIFs) to improve the regeneration and transformation capabilities of plants.

Author Contributions

The author prepared the concept and methodology, reviewed, and edited the article.

Conflict of Interest

The author declares no conflicts of interest.

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