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Enhancing Crop Resilience: Breakthroughs in Drought and Salt Stress Tolerance Breeding

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Abstract. In recent years, with the increasing frequency of natural disasters around the world, the pressure on agricultural production is also increasing. Drought and soil salinization caused by natural disasters have become the main obstacles to agricultural development, which have a serious impact on human life and production. Drought changes the growth pattern of crops, affects their metabolic process and stress resistance, and has a significant impact on the growth and yield of crops. Salt stress can cause oxidative damage, which ultimately leads to a substantial decrease in crop yield. Cultivation of drought - and salt-tolerant crops can increase arable land area, ensure food security and high yield, and improve the ecological environment to meet the requirements of sustainable development. This paper mainly discusses how to improve drought and salt tolerance of crops, including how to adapt root system, how to regulate stomatome, how to improve water use efficiency, and how to absorb and transport salt. Moreover, the role of marker-assisted selection (MAS) and CRISPR/Cas9 gene editing technology in the development of drought - and salt-tolerant crops was highlighted. Gene editing technology provides us with accurate methods for crop improvement, but it still faces some challenges, such as the difficulty of co-editing multiple genes and the failure of modification caused by off-target effects. Looking ahead, with the combination of genomics and smart farming technologies, the cultivation of drought - and salt-tolerant crops will continue to advance, helping us to address global challenges such as climate change and soil degradation.

Keywords: Drought tolerance, Salt tolerance, Gene editing, Agricultural sustainability, Stress-resistant crops

1. Introduction

With extreme natural disasters such as global high temperatures, heavy rainfall, floods, and strong typhoons becoming increasingly frequent, agricultural production is facing greater and greater challenges. These disasters often occur together, with droughts and floods alternating, delivering dual biological and non-biological stresses to crops. Drought and soil salinization caused by these natural disasters have become the primary resistance to global agricultural production. Drought directly affects the normal growth and yield of crops by affecting their growth habits, metabolic processes and resistance mechanisms. However, salt stress induces oxidative stress in plants by producing reactive oxygen species (ROS), which damages plant cells and leads to reduced production of target products [1,2]. Soil salinization greatly reduces soil productivity and leads to large-scale desertification, which seriously affects the sustainable development of agriculture and rural economy. In addition to drought and salinization, other environmental stress factors also extensively affect crop yield. With the development of molecular biology technology, researchers can now understand the impact of drought and salinity on crops at the molecular level, and the use of gene editing tools to engineer crops to resist these environmental stresses has become a key task to ensure the sustainable development of agriculture (Figure 1). The development of stress-resistant crops through gene editing technology has become a global agricultural research strategy to cope with increasingly complex environmental stresses.

The stress resistance of crops actually refers to their ability to maintain normal growth and achieve bountiful harvests when facing adverse environmental factors such as drought, floods, salinization, extreme temperatures, and pests and diseases. This ability is mainly determined by the crops' genes as well as their physiological and biochemical processes. Today, crops with strong stress resistance have become an important standard for measuring crop quality. By cultivating such crops, we can not only increase the area of arable land but also ensure food security, improve the ecological environment, protect biodiversity, and ultimately promote sustainable agricultural development [3].

In recent years, there has been significant progress in the breeding of stress-resistant plants, especially in the development of insect-resistant crops (such as genetically modified insect-resistant cotton) and salt-tolerant crops. For example, genetically modified insect-resistant cotton has been widely adopted by over four million small farmers worldwide, with obvious results: not only has the yield per hectare greatly increased, but the use of pesticides has decreased, reducing farmers' exposure to harmful chemicals [4]. A study conducted in Bangladesh in April 2022 showed that the yield of genetically modified insect-resistant cotton increased by 0.81 tons per hectare, and the net profit (2,436 RMB per hectare) was considerably higher than that of conventional cotton (1,624 RMB per hectare) [5]. At the same time, rice breeders have successfully identified, collected, and developed many salt-tolerant rice resources, especially the highly salt-tolerant variety 'Haidao 86' cultivated by Chen and others, which has become a key resource for developing new salt-tolerant rice varieties [6].

This review summarizes the recent research progress in breeding stress-resistant plants both domestically and internationally, with a particular focus on the current status, challenges, and future development trends in breeding drought-resistant and salt-tolerant crops.

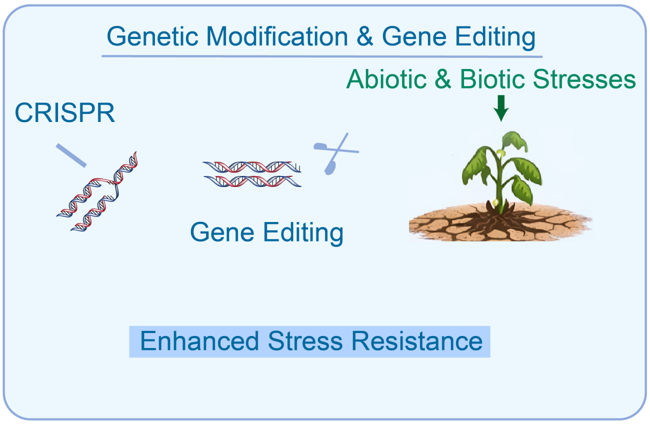

Figure 1. Schematic of gene editing for plants

2. Basic mechanisms of drought and salt-alkaline tolerance crop improvement

2.1. Mechanisms of drought resistance

The depth, size and distribution of plant root systems are mainly influenced by the distribution and content of soil moisture. When soil moisture decreases, different plants will adjust their root growth patterns to adapt to the environment. When water is extremely scarce, root growth, such as elongation, branching and thickening, will be inhibited, especially for plants growing in dry soil, whose root tips may form a cuticle layer to reduce water absorption. Root growth is also affected by the water and nutrient conditions of the plant's above-ground part [7].

Stomatal regulation and leaf structure adaptation play a very important role in plants' response to drought. By regulating stomata, plants can reduce water loss and improve water use efficiency. Plants with strong drought resistance generally have certain special adaptive characteristics, such as smaller and thicker leaves, more trichomes, smaller and denser stomata, thicker cuticles and more developed vascular bundles [7].

Improving water use efficiency is also an important factor for plants to adapt to drought. Photosynthesis directly determines the growth and yield of plants, and most of the exchange of carbon dioxide and water occurs through stomata. The photosynthetic activities in mesophyll cells are very important for regulating water use efficiency. High temperatures reduce surface water and lower the rate of photosynthesis. To adapt to drought stress, plants have evolved three photosynthetic pathways: C_3, C_4 and CAM [8]. Compared with C_3 plants, C_4 plants can more effectively absorb carbon dioxide and fix it separately in mesophyll cells and bundle sheath cells, improving water use efficiency and performing better in dry environments. Finally, CAM plants open stomata at night to absorb carbon dioxide and close them during the day to reduce water evaporation, significantly improving water use efficiency [7].

2.2. Mechanisms of salt-alkaline resistance

In the face of saline-alkali stress, the absorption and transport of salt by plants will be greatly limited. Plants can improve salt tolerance and alleviate ion toxicity caused by excessive Na^+ concentrations in a number of ways, for example, they reduce toxic effects by scavenging Na^+ from roots, regulating Na transport from roots to stems, or storing Na^+ in different parts of the cell [9]. Non-halophytes generally limit sodium absorption by roots, selectively reducing sodium transport to leaves and seeds while enhancing potassium absorption and transport. In contrast, halophytes maintain stability by transferring sodium ions into vacuoles, using ion partitioning mechanisms to regulate ion concentrations within cells.

Non-halophytes generally limit Na uptake by roots and selectively reduce Na transport to leaves and seeds, while enhancing K^+ uptake and transport to maintain their own Na^+ and K^+ balance. However, halophytes maintain cell stability by transferring sodium ions to the vacuole and regulating intracellular ion concentration by ion partition mechanism. Another coping mechanism is osmoregulation. They maintain root turturant pressure by absorbing inorganic ions and reduce sodium uptake, which may inhibit root cell growth and division but is more effective in maintaining healthy cell growth. In addition, plants also synthesize some organic osmotic regulators to increase solute concentration and absorb water from the outside world to further improve their salt tolerance. For example, arginine is an important osmotic regulator that widely exists in plants and plays an important role in osmotic regulation. Studies have shown that arginine can not only help plants regulate osmotic pressure, but also alleviate saline-alkali stress by affecting ion distribution, stabilizing protein structure, and protecting plant photosynthetic system. The addition of arginine can also improve photosynthetic efficiency, energy metabolism and antioxidant enzyme activity, reduce oxidative damage to plants, and further enhance salt tolerance of plants [10,11].

The signal transduction mechanism involved in saline-alkali stress in plants is mainly saline-alkali stress protection pathway, which is mainly regulated by SOS pathway. This pathway involves a series of genes such as SOS1, SOS2, and SOS3. The SOS1 gene encodes a plasma membrane sodium and hydrogen antiporter, which is responsible for removing sodium ions from the cell and maintaining ion balance, and is a key gene for salt tolerance. The interaction between SOS2 and SOS3 can activate the SOS signaling pathway and further enhance plant salt tolerance. The plant hormone abscisic acid (ABA) also plays an important role in response to salinity and osmotic stress [12].

2.3. Intersection of drought and salt-alkaline mechanisms

Studies have shown that the combined pressure of drought and salinity is more severe than either pressure alone, leading to more pronounced ion imbalance and severe difficulties in osmotic regulation, which inhibits plant growth and the antioxidant system. Research on the anatomy of roots has found that under the combined influence of salt, alkalinity, and drought, the morphology, elasticity, and growth direction of root cells will undergo significant changes. To adapt to these pressures, plants will enhance their stress resistance by altering the structure of their aboveground and underground organs [13].

3. Molecular breeding and gene editing for drought and salt-alkaline tolerant crops

3.1. Marker-assisted selection (MAS)

MAS is a breeding technique. It uses genetic markers like single nucleotide polymorphisms (SNPs), simple sequence repeats (SSRs), and amplified fragment length polymorphisms (AFLPs) to identify the genotype differences between individual plants at an early stage of the whole breeding process. Using genetic markers can significantly improve the accuracy and efficiency of selecting high - performance plants. Different from traditional phenotypic selection, MAS have great value for complex traits such as drought tolerance and salt tolerance. These traits are controlled by multiple genes, affected by environmental factors, and it's hard to make a unified evaluation based on their phenotypic performance [14].

Drought and salt tolerance are regulated by multiple genes. The development of molecular genetic markers related to these traits and the establishment of corresponding genetic maps are crucial for breeding efficient salt-tolerant and drought-tolerant plants. Many studies use genome-wide association studies (GWAS) and quantitative trait loci (QTL) maps to identify specific genes related to stress resistance. For example, in rice (Oryza sativa), multiple gene loci related to salt stress have been discovered, including the qSKC1 locus that regulates the ratio of potassium ions to sodium ions, and the Saltol locus that has a significant impact on the salt tolerance of seedlings. The Saltol QTL has become a key marker in the MCS application, significantly improving the efficiency of selecting salt-tolerant varieties [15]. In Zea mays, several QTL related to drought tolerance have been identified by researchers, including genetic genes that control root structure, water evaporation efficiency and other related traits. These QTL and their markers are used in MAS to select drought-tolerant lines [16]. Moreover, the development of new SNP chips and high-density genetic maps has greatly increased the coverage and resolution of markers, making the localization and selection of genes related to complex traits of plants more precise and reliable [14]. Currently, there have been successful studies demonstrating the application of Saltol QTL in the breeding of rice using marker-assisted selection (MAS). For example, by breeding high-yielding plants using Saltol QTL, new cultivars with significant salt tolerance have been sent out while maintaining their agronomic traits [15]. In Triticum aestivum breeding, MAS has been used to integrate multiple QTLs related to water use efficiency, root depth, and drought response. Researchers used SSR markers to select QTLs closely associated with drought stress response, developing stable drought-resistant varieties [17].

3.2. Gene editing technologies

The application of gene editing technology provides a powerful tool to solve the limitations of traditional breeding methods in the breeding of drought and saline-alkali resistant crops. With the rapid development of gene editing technologies such as CRISPR/Cas9, TALEN (transcription activator-like effector nuclease) and ZFN (zinc finger nuclease), crop genomes can be modified at the molecular level to improve drought and saline-alkali resistance genes, thereby effectively improving crop tolerance to adverse environments.

CRISPR/Cas9 system is an efficient gene editing technology based on sgRNA guidance. It can achieve precise double strand breaks at specific gene sites, and gene knockout, insertion or replacement can be performed through the cell's own repair mechanism. In drought and saline-alkali resistance crop breeding, CRISPR/Cas9 can effectively knock out the suppressor genes related to water stress and salt stress or activate and overexpress beneficial genes related to drought and saline-alkali resistance. For example, in rice, knockout of salt tolerance (DST) genes by CRISPR/Cas9 system significantly improved plant tolerance to salt stress and increased rice yield [18]. In wheat, dehydration response element-binding protein 2 (TaDREB2) and ethylene response factor 3 (TaERF3) were edited by CRISPR/Cas technology, resulting in enhanced drought tolerance [19].

TALEN is a technology that uses a specific DNA-binding domain to direct gene editing by FokI nucleases. ZFN technology combines zinc finger protein and FokI nuclease, which can precisely recognize and cleave specific positions of DNA, so as to achieve gene knockout or mutation. Compared with CRISPR/Cas9 and TALEN, ZFN is more complex to develop, but it can provide high specificity and efficiency of gene editing in multiple crops. These two gene editing methods have been gradually replaced by CRISPR/Cas9 system due to their editing efficiency and operation difficulty. By knocking out the gene of fatty acid desaturase (FAD) by TALEN, soybean varieties rich in oleic acid and low in linoleic acid have been bred, and the shelf life and thermal stability of soybean oil have been improved [20]. Previous studies showed that insertion of the PAT cassette by ZFNs disrupted the endogenous ZmIPK1 gene in maize, which changed the inositol phosphate profile in growing maize seeds and improved the herbicide resistance in maize [21].

CRISPR/Cas9, TALEN and ZFN have their own advantages and disadvantages. CRISPR/Cas9 system has become the main technology for gene editing of drought - and saline-resistant crops due to its simple operation, high efficiency and wide application. TALEN has excellent targeting accuracy and low off-target rate, and is suitable for studies with high requirements for gene editing. ZFN technology has unique advantages in dealing with complex traits and multi-gene regulation. With the continuous progress and optimization of technologies, these gene editing technologies are expected to play a greater role in the molecular breeding of drought and saline-alkali resistant crops in the future, further improve the resilience of crops, and provide strong support for global agriculture to cope with climate change.

Table 1. Typical examples of CRISPR/Cas9 for improving crop drought and salt-alkaline tolerance

Plant Species	Gene Edited	Technique Used	Trait Improved	Reference
Rice	DST gene (Dehydration Stress Tolerance)	CRISPR/Cas9	Salt tolerance	[18]
Rice	OsRR22 (Response regulator gene)	CRISPR/Cas9	Drought tolerance	[22]
Zea mays	ARGOS8 (promoter variants)	CRISPR/Cas9	Drought tolerance	[23]
Tomato	SlLBD40	CRISPR/Cas9	Drought tolerance	[24]
Arabidopsis	AITR1–6 (multiple transcription factors	CRISPR/Cas9	Drought & Salt tolerance	[25]

4. Development and application of genetically modified crops

In the agricultural field, especially in the cultivation of drought-resistant and salt-tolerant crops, the application of gene editing technology has significantly enhanced the environmental adaptability of crops. By introducing stress-resistant genes from external sources into the genome of target crops, researchers have successfully developed transgenic crops that can withstand drought and saline-alkali environments. These crops not only increase agricultural productivity but also provide effective solutions to global climate change and land degradation.

Bt cotton is a typical example of a transgenic crop. By introducing the Cry gene of Bacillus thuringiensis, Bt cotton gained insect resistance, effectively reducing the use of pesticides and improving the health of the crops. Recent studies have also found that Bt cotton has very good drought resistance characteristics. Under drought conditions, Bt cotton has higher water use efficiency due to improved root growth and enhanced water uptake due to gene editing, and is able to maintain better growth status in the environment with little water [26].

Drought-resistant maize is also widely used in transgenic crops. By using gene editing technology to transfer genes related to water stress, such as ARGOS8 gene or ZmPL1 gene, drought resistance traits of maize have been significantly improved [23,27]. Gene editing technologies such as CRISPR/Cas9 have been widely used in maize breeding. By precisely modifying drought-resistant genes, researchers have successfully improved maize traits under drought conditions. Drought-resistant maize could effectively cope with water shortage by enhancing root growth and improving water absorption and use efficiency.

5. Challenges and future trends in breeding drought and salt-alkaline tolerant crops

Gene editing technology, with CRISPR and other tools as the core, provides a precise and efficient breeding way for breeding crops adapted to extreme environments. However, humans still face multiple challenges in the cultivation of salt-alkali and drought resistant crops. Most stress resistance traits are regulated by complex gene metabolism networks. It is difficult to achieve a substantial improvement in comprehensive stress resistance by gene editing only for a single target, and the precise control of multi-gene collaborative editing is still a major problem. Off-target effects caused by gene editing may lead to abnormal crop growth. The genome complexity of polyploid crops such as potato also further reduces the efficiency of gene editing. The public also has misunderstandings about gene-edited crops, and the differences in regulatory policies for genetically modified crops around the world also restrict the large-scale promotion of breeding and editing technology. In addition, the stability of stress resistance traits in the field is easily affected by environmental changes, the high cost of technology development, and the great uncertainty of the effects of drought and saline-alkali resistance also hinder the popularization of transgenic crops in agricultural production.

In the future, molecular breeding researchers will conduct in-depth studies in the fields of plant stress response mechanism, epigenetic regulation and memory of stress response, and molecular network regulation. In the field of applied basic research, we will focus on gene discovery and molecular breeding of broad-spectrum disease resistance, crop insect resistance (especially borers and aphids), high and low temperature resistance, and drought resistance, and a number of new crop varieties with multi-resistance will be commercialize.

From the end of the 20th century to the beginning of the 21st century, with the cross-integration of omics, systems biology, synthetic biology and computational biology, modern biological breeding technologies emerged, among which the most representative technologies include whole-genome selection, gene editing and synthetic biology. With the support of interdisciplinary collaborative innovation, drought - and salt-tolerant crop breeding will continue to develop. Corresponding agricultural technologies, such as precision irrigation engineering technology under automatic monitoring and control conditions, sprinkling irrigation, drip irrigation, micro-irrigation and seepage irrigation, implement real-time precision irrigation according to soil moisture and crop water demand during different growth periods of different crops, which can greatly save water resources, improve the effective utilization rate of water resources, and effectively help drought and saline-alkali resistant crop breeding.

6. Conclusion

In today's society, soil salinity has become a serious threat to plant growth and global food security. Research on crop salt-alkali tolerance mechanisms and high-throughput screening of crops, combined with precise breeding technologies, will become an important development direction in the future. Further in-depth research is still needed to improve the stress resistance of plants. For future climate change and soil degradation issues, the breeding of drought and salt-alkali resistant crops will need further development, particularly in the areas of genetic resource exploration, breakthroughs in breeding technology, and the integration of agricultural management practices. With the development of intelligent technologies such as the Internet of things, big data, cloud computing, and 5G, genetic breeding technology and intelligent agriculture technology will continue to evolve and integrate. Agricultural production is gradually becoming green, standardized, digital, networked and intelligent. The cultivation of drought and saline-alkali resistant crops will play an important role in global food security and environmental protection [25]. The use of advanced genome screening and molecular editing technologies, coupled with ecological agricultural management practices, can help to develop more effective multi-stress tolerant varieties and practical application strategies, and provide an important stable foundation for breeding crops that can cope with global environmental changes.

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