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Molecular Regulation of Salt Stress Tolerance in Fruit Crops with Special Emphasis on WRKY Transcription Factors

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Abstract

Soil salinity is one of the most severe abiotic stresses limiting fruit crop productivity worldwide. Increasing salinization of agricultural lands due to climate change, irrigation mismanagement, and seawater intrusion has intensified the need for developing salt-tolerant fruit crops. Plants respond to salt stress through complex molecular, physiological, and biochemical mechanisms involving stress perception, signal transduction, transcriptional regulation, and metabolic adjustment. Among the various regulatory components, transcription factors play a pivotal role in orchestrating stress-responsive gene networks. WRKY transcription factors represent one of the largest plant-specific transcription factor families and have emerged as key regulators of plant responses to salinity stress. In fruit crops, WRKY proteins regulate ion homeostasis, osmotic adjustment, reactive oxygen species scavenging, hormonal signaling, and stress-induced gene expression. Recent advances in genomics, transcriptomics, and functional studies have revealed the involvement of WRKY genes in enhancing salt tolerance in several fruit species. This review provides a comprehensive overview of salt stress effects on fruit crops, molecular mechanisms of salt tolerance, structure and classification of WRKY transcription factors, and their specific roles in regulating salt stress responses. Furthermore, recent biotechnological and breeding approaches exploiting WRKY genes for improving salt tolerance in fruit crops are discussed, highlighting future perspectives for developing climate-resilient horticultural systems.

Keywords: *Salt stress, fruit crops, WRKY transcription factors, abiotic stress tolerance, molecular regulation, salinity.*

1. Introduction

Fruit crops contribute significantly to global food security, nutrition, and economic stability, particularly in developing countries. However, fruit production is increasingly threatened by abiotic stresses, among which soil salinity is one of the most damaging. Salinity stress affects nearly 20–30% of irrigated agricultural land globally and is projected to expand further under climate change scenarios. Fruit crops are generally more sensitive to salinity than many annual crops due to their perennial nature, longer growth cycles, and specific physiological requirements.Salt stress adversely affects plant growth and productivity through osmotic stress, ion toxicity, and nutrient imbalance [1]. High concentrations of sodium (Na^+) and chloride (Cl^-) ions disrupt cellular homeostasis, impair photosynthesis, reduce water uptake, and cause oxidative damage. In fruit crops, salinity leads to reduced vegetative growth, poor flowering, fruit drop, inferior fruit quality, and ultimately yield losses. Developing salt-tolerant fruit crops is therefore a priority for sustainable horticulture.

Plants have evolved sophisticated molecular mechanisms to perceive salt stress and initiate adaptive responses. These responses involve signal perception at the plasma membrane, activation of signaling cascades, transcriptional reprogramming, and metabolic adjustments [2]. Transcription factors act as master regulators by controlling the expression of large sets of stress-responsive genes. Among them, WRKY transcription factors have gained considerable attention due to their significant involvement in abiotic stress tolerance.

WRKY transcription factors are plant-specific proteins characterized by the conserved WRKY domain and zinc finger motifs. Initially identified as regulators of pathogen defense, WRKY proteins are now recognized as crucial components in abiotic stress responses, including salinity, drought, heat, and cold stress. In fruit crops, increasing evidence suggests that WRKY genes play essential roles in modulating salt tolerance through regulation of ion transporters, antioxidant systems, hormone signaling pathways, and stress-responsive genes.

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With the advent of high-throughput sequencing technologies, genome-wide identification and functional characterization of WRKY gene families have been reported in several fruit crops such as apple, grape, citrus, banana, and tomato. These studies provide valuable insights into the regulatory networks mediated by WRKY transcription factors under salt stress [3]. This review aims to synthesize current knowledge on the molecular regulation of salt stress tolerance in fruit crops, with special emphasis on WRKY transcription factors and their potential applications in crop improvement.

2. Salt Stress and Its Impact on Fruit Crops

Salt stress affects plants through two major phases: osmotic stress and ionic stress. The initial osmotic phase reduces water availability to roots, leading to decreased cell expansion and stomatal closure. The subsequent ionic phase involves accumulation of toxic Na^+ and Cl^- ions in plant tissues, disrupting metabolic processes.In fruit crops, salt stress manifests as reduced leaf area, chlorosis, necrosis, poor root development, delayed flowering, and reduced fruit set. Salinity also affects fruit size, taste, sugar content, and nutritional quality [4]. Sensitive fruit crops such as citrus, grapevine, and apple exhibit significant yield reductions even at moderate salinity levels.Physiological responses to salinity include reduced photosynthetic efficiency, impaired nutrient uptake, and altered hormonal balance. At the cellular level, salt stress induces oxidative stress by generating excessive reactive oxygen species (ROS), leading to membrane damage, protein oxidation, and DNA damage. Therefore, efficient detoxification of ROS and maintenance of ion homeostasis are critical for salt tolerance.

Table 1. Effects of Salt Stress on Growth, Physiology and Yield of Major Fruit Crops

Fruit crop	Sensitivity to salinity	Major physiological effects	Impact on yield and quality
Apple	Moderate to high	Reduced photosynthesis, ionic imbalance, oxidative stress	Reduced fruit size, yield decline
Citrus	Highly sensitive	Leaf chlorosis, Na^+ and Cl^- toxicity	Poor fruit set, inferior fruit quality
Grapevine	Moderate	Altered water relations, reduced stomatal conductance	Reduced berry size and sugar content
Banana	Highly sensitive	Root damage, reduced nutrient uptake	Severe yield losses
Tomato	Moderately tolerant	Osmotic stress, ROS accumulation	Reduced fruit number and weight

Table 2. Major Molecular Mechanisms Involved in Salt Stress Tolerance in Plants

Mechanism	Key components	Functional role under salt stress
Ion homeostasis	SOS pathway, NHX, HKT transporters	Na^+ exclusion and compartmentalization
Osmotic adjustment	Proline, glycine betaine, sugars	Maintenance of cell turgor
Antioxidant defense	SOD, CAT, APX, POD enzymes	Detoxification of reactive oxygen species
Hormonal regulation	ABA, JA, ethylene	Stress signaling and stomatal control
Transcriptional regulation	WRKY, NAC, MYB, bZIP	Regulation of stress-responsive genes

Table 3. Classification and Structural Features of WRKY Transcription Factors

WRKY group	Number of WRKY domains	Zinc finger motif	Functional relevance
Group I	Two	C_2H_2	Broad stress and developmental regulation
Group II	One	C_2H_2	Abiotic and biotic stress responses
Group III	One	C_2HC	Stress adaptation and signal transduction

Table 4. WRKY Transcription Factors Reported to Confer Salt Stress Tolerance in Fruit Crops

Fruit crop	WRKY gene	Stress response	Major functional role
Apple	MdWRKY9	Salt stress	Enhances antioxidant defense and ion balance
Grape	VvWRKY genes	Salt and drought stress	Regulation of stress-responsive genes
Citrus	CsWRKY genes	Salinity stress	Modulation of ion transport and ABA signaling
Tomato	SlWRKY genes	Salt stress	Improved growth and stress tolerance
Banana	MaWRKY genes	Salinity stress	ROS scavenging and osmotic adjustment

Table 5. WRKY-Mediated Regulatory Pathways in Salt Stress Tolerance

Regulatory pathway	WRKY involvement	Physiological outcome
ABA signaling	Activation of ABA-responsive genes	Improved stomatal regulation
ROS signaling	Induction of antioxidant enzymes	Reduced oxidative damage
Ion transport regulation	Control of Na^+/K^+ transport genes	Maintenance of ionic balance
Stress gene expression	Binding to W-box elements	Enhanced stress tolerance

Table 6. Biotechnological Approaches Targeting WRKY Genes for Salt Tolerance Improvement

Approach	Description	Application in fruit crops
Transgenic overexpression	Overexpression of WRKY genes	Enhanced salt tolerance
CRISPR/Cas genome editing	Targeted modification of WRKY genes	Precise trait improvement
Marker-assisted breeding	Selection of favorable WRKY alleles	Accelerated breeding programs
Omics-based approaches	Transcriptomics and proteomics	Identification of key WRKY regulators

Table 7. Advantages of Targeting WRKY Transcription Factors for Salinity Tolerance

Aspect	Advantage
Gene regulation	Controls multiple downstream genes
Stress specificity	Rapid response to salinity stress
Breeding potential	Useful markers for stress tolerance
Sustainability	Reduced dependency on chemical inputs

3. Molecular Mechanisms of Salt Stress Tolerance in Plants

Salt tolerance in plants is governed by multiple molecular mechanisms, including ion homeostasis, osmotic adjustment, antioxidant defense, and stress signaling pathways. Key components include ion transporters such as SOS1, NHX, and HKT proteins, which regulate Na^+ exclusion, compartmentalization, and transport.Signal transduction pathways involving calcium signaling, mitogen-activated protein kinases (MAPKs), and phytohormones such as abscisic acid (ABA) play central roles in stress perception and response. ABA accumulation under salt stress triggers stomatal closure and induces expression of stress-responsive genes [5]. Transcriptional regulation is a crucial step in these adaptive responses. Several transcription factor families, including NAC, MYB, bZIP, DREB, and WRKY, coordinate the expression of downstream target genes involved in stress adaptation. Among these, WRKY transcription factors have emerged as key regulators due to their broad involvement in stress-responsive gene networks.

4. WRKY Transcription Factors: Structure and Classification

WRKY transcription factors are defined by the conserved WRKY domain containing the amino acid sequence WRKYGQK and a zinc finger motif. Based on the number of WRKY domains and zinc finger types, WRKY proteins are classified into three major groups: Group I, Group II, and Group III.Group I WRKYs possess two WRKY domains, while Group II and III contain a single WRKY domain. Group II is further subdivided into several subgroups based on phylogenetic analysis. WRKY proteins bind to W-box elements (TTGACC/T) in the promoter regions of target genes to regulate transcription.Genome-wide analyses have identified large WRKY gene families in fruit crops, indicating their evolutionary expansion and functional diversification [6]. Differential expression patterns of WRKY genes under salt stress suggest their involvement in stress-specific regulatory networks.

5. Role of WRKY Transcription Factors in Salt Stress Tolerance

WRKY transcription factors regulate salt stress tolerance through multiple mechanisms. One key role is the regulation of ion homeostasis by controlling genes involved in Na^+ transport and compartmentalization. Certain WRKY proteins modulate the expression of SOS pathway genes, thereby enhancing Na^+ exclusion and reducing cytosolic toxicity [7]. WRKY factors also play a critical role in antioxidant defense by regulating genes encoding enzymes such as superoxide dismutase, catalase, and peroxidases. Enhanced antioxidant capacity helps mitigate oxidative damage under salinity stress.

Hormonal signaling pathways, particularly ABA signaling, are closely associated with WRKY-mediated stress responses. Several WRKY proteins act as positive or negative regulators of ABA-responsive genes, influencing stomatal behavior and stress adaptation.In fruit crops, WRKY genes have been shown to confer salt tolerance when overexpressed. For example, MdWRKY9 in apple has been reported to enhance salt tolerance by improving antioxidant activity and maintaining ion balance. Similar findings have been reported in grapevine, citrus, and tomato, highlighting the conserved role of WRKY transcription factors across species.

6. WRKY Transcription Factors in Fruit Crops under Salt Stress

Functional studies in fruit crops have demonstrated that WRKY transcription factors are differentially expressed in response to salt stress. Transcriptome analyses reveal that several WRKY genes are rapidly induced upon salt exposure, indicating their role in early stress signaling.In apple, WRKY genes regulate salt tolerance by modulating ROS scavenging systems and stress-responsive gene expression. In grapevine, specific WRKY members are associated with enhanced salt and drought tolerance. Citrus WRKY genes have been implicated in ion transport and stress signaling, while tomato WRKYs contribute to improved growth and yield under saline conditions [8].These findings suggest that WRKY transcription factors act as central nodes in stress regulatory networks and represent promising targets for genetic improvement of fruit crops.

7. Biotechnological and Breeding Approaches Targeting WRKY Genes

Advances in molecular biology and biotechnology offer new opportunities to exploit WRKY transcription factors for improving salt tolerance in fruit crops. Genetic engineering approaches, including overexpression and gene editing using CRISPR/Cas systems, enable precise manipulation of WRKY genes.Marker-assisted selection and genomic selection strategies can also be employed to identify and incorporate favorable WRKY alleles into breeding programs [9-11]. Integration of omics approaches such as transcriptomics, proteomics, and metabolomics provides a comprehensive understanding of WRKY-mediated stress responses.

8. Future Perspectives

The significant progress, challenges remain in translating laboratory findings into field applications. Functional redundancy among WRKY genes and their complex regulatory interactions require further investigation. Future research should focus on understanding WRKY networks at the systems level and their interaction with other transcription factors [12]. The conventional breeding with molecular and genomic tools will accelerate the development of salt-tolerant fruit crops.

Harnessing WRKY transcription factors holds great promise for enhancing resilience of horticultural systems under increasing salinity stress.

9. Conclusion

Salt stress poses a major threat to fruit crop productivity worldwide. WRKY transcription factors play a crucial role in regulating molecular and physiological responses to salinity stress in fruit crops. Through modulation of ion homeostasis, antioxidant defense, and hormone signaling, WRKY proteins enhance plant tolerance to saline conditions. Advances in genomics and biotechnology provide valuable tools to exploit WRKY genes for crop improvement. A deeper understanding of WRKY-mediated regulatory networks will facilitate the development of salt-tolerant fruit crops, contributing to sustainable horticulture and food security under changing climatic conditions.

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