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The review of WRKY transcription factor family functions and its abiotic stress responses in plants

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Abstract. As sessile organisms, plants may encounter various abiotic stresses during their growth, such as low temperatures, high temperatures, drought, and salinity, which can lead to impaired growth, injury, or even death. Transcription factors, as key proteins influencing gene transcription, play a crucial role in plant responses to abiotic stress. Among them, the WRKY transcription factor family is one of the largest in plants and plays a significant regulatory role in plant growth and development. This paper reviews the functions of the WRKY transcription factor family and the current research status on their roles in plant responses to abiotic stress. It discusses how WRKY transcription factors regulate plant hormone signaling pathways and stress signal transduction pathways to enhance plants' ability to cope with abiotic stress.

Keywords: WRKY transcription factor, abiotic stress, signal transduction.

1. Introduction

Plants in natural environments face numerous abiotic stresses such as drought, salinity, and low temperatures, which severely impact their growth and development. As immobile organisms, plants must rely on their own adaptive mechanisms to cope with these challenges. Transcription factors are key regulators of gene expression, and the WRKY transcription factor family plays an essential role in plants' adaptation to stress. By specifically binding to DNA, WRKY transcription factors regulate the expression of downstream genes, thereby influencing physiological processes and enhancing plants' ability to adapt.

With advances in molecular biology techniques, an increasing number of WRKY genes have been identified and cloned, and their roles in plant responses to abiotic stress have gradually been revealed. This paper aims to discuss the functions of the WRKY transcription factor family and review their roles and mechanisms in plants' response to abiotic stress, providing insights for future research.

2. Background

Plants are sessile organisms that may encounter many abiotic environmental conditions during their life process that are detrimental to survival and growth or even lead to injury, destruction, and death. These environmental conditions are known as abiotic stress and may include low temperatures, high temperatures, drought, salinity, ultraviolet radiation, nutrient deficiencies, etc. Plants have evolved various molecular mechanisms involving signal transduction and gene expression to cope with the effects of abiotic stress. Transcription factors are DNA-binding proteins that influence gene transcription through specific interactions with the gene cis-acting elements and are an important component of plant

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evolution. In highly variable environments, transcription factors can regulate the physiological adaptation of plants to the environment[1]. Many transcription factor families have been identified in plants, such as MYB, bHLH, and WRKY.

The WRKY transcription factor family is one of the largest in plants and plays an important regulatory role in plant growth and development. The structure of WRKY transcription factors consists of two parts: the N-terminus contains a conserved WRKYGQK heptapeptide, and the C-terminus contains a C2H2 (C-X4-5-C-X22-23-H-X-H) or C2HC (C-X7-C-X23-H-X-C) type zinc finger structure. In the vast majority of plants, the sequence of WRKY gene family members is conserved. Still, some plants have unique sequences where WRKYGQK can be replaced by WRKYGKK or WRKYGEK, and the "RK" residues can be replaced by "RR, SK, KR, VK, or KK," and the zinc finger structure may also vary[2]. In 1994, after Ishiguro and others cloned the world's first WRKY gene SPF1 from sweet potato[3], with the continuous development of technology, an increasing number of WRKY genes have been identified and cloned. Among them, 74 WRKY gene family members were found in Arabidopsis[4], 109 in rice[5], 45 in barley[6], 83 in maritime pine[7], 81 in tomato[8], 104 in poplar[9], and 136 in maize[10]. Extensive analysis of WRKY transcription factor family members suggests that WRKY transcription factors can modulate plant hormone signaling pathways and abiotic stress signal transduction pathways, inducing the expression of many stress-related genes, thereby enhancing the plant's ability to respond to abiotic stress[11]. AtWRKY40, AtWRKY18, and AtWRKY60 can affect Arabidopsis' response to osmotic and salt stress[12], MaVQ5 and MaWRKY26 are involved in regulating cold stress processes in bananas[13], and overexpression of the OsWRKY71 gene can improve rice's cold tolerance[14]. Currently, regarding the study of the WRKY transcription factor family and plant response to abiotic stress, this article aims to discuss the functions of the WRKY transcription factor family and review the current research status of their roles and mechanisms in plant responses to abiotic stress.

2.1. The WRKY gene family and abiotic stress response

Abiotic stress stimulates interaction between plants and protective proteins, sending signals within the cell through a series of phosphorylation reactions to regulate activation or inhibition of downstream target gene transcription, control the expression of WRKY transcription factors, trigger various physiological and biochemical responses, and thereby respond to stress[15].

2.2. Drought stress

Water is the most significant environmental factor related to plant growth and development, playing a crucial role in plant internal metabolic processes. Drought stress can cause irreversible physiological damage to plant growth, antioxidant systems, and photosynthetic systems. WRKY is an important regulatory factor for plants responding to drought stress.

Studies indicate that the WRKY transcription factor family can directly influence the expression of drought-resistant genes to regulate drought resistance. WRKYTFs can regulate stress-related genes. Transgenic Arabidopsis integrating Iris germanica IgWRKY50 and IgWRKY32 showed significantly higher expression levels of stress-related genes RD29A, DREB2A, PP2CA, and ABA2 than WT after drought treatment[16].

Improving the efficiency of ROS scavenging is of great significance for enhancing plant drought resistance. WRKY TFs can regulate the expression of genes related to antioxidant enzymes and use the ROS scavenging system to reduce the content of reactive oxygen species in plants. By constructing PtWRKY2 overexpressing Arabidopsis lines, it was found that PtWRKY2 can significantly improve the survival rate of Arabidopsis under high-temperature stress. By conducting a comprehensive transcriptome analysis, it was found that PtWRKY2 may reduce ROS accumulation by enhancing the expression of antioxidant enzyme-encoding genes and thus improve plant survival rates[17].

In addition, WRKY transcription factors (TFs) control gene expression via the abscisic acid signaling pathway, impacting plant drought resistance. Abscisic acid plays a key role in regulating plant drought resistance. When plants are suffering from drought stress, ABA accumulates in the leaves and enhances

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the drought tolerance of terrestrial plants by inhibiting stomatal opening, increasing protective enzyme activity, and other means. Transgenic Arabidopsis overexpressing GhWRKY70 exhibited greater sensitivity to ABA-induced stomatal closure and higher expression levels of ABA biosynthesis-related genes[18]. XsWRKY20 from Xanthoceras sorbifolium can enhance the ability to cope with drought stress by integrating ROS homeostasis and ABA signaling pathways to regulate ABA signaling and antioxidant enzyme-related genes[19]. The ABA-mediated stomatal closure and other signaling pathways in Arabidopsis are specifically regulated by AtWRKY63[20]. Moreover, WRKY transcription factors can negatively regulate plant tolerance to drought stress. OsWRKY114 downregulates the transcription levels of ABA signaling pathway genes OsPYL2 and OsPYL10, and their expression decreases under drought stress to improve drought resistance[21].

2.3. Salt stress

There are large areas of saline-alkali land in arid and semi-arid regions, where it is difficult to grow crops. Enhancing crop resistance to salt stress is crucial for improving crop productivity. High concentrations of ions cause osmotic pressure imbalance within the plants, leading to metabolic disturbances and inhibited growth and development. Additionally, salt stress can induce oxidative stress, generate reactive oxygen species, affect photosynthesis, and limit plant growth. WRKY transcription factors play a key regulatory role in plants' response to salt stress.

GmWRKY54 of Glycine max inhibits the expression of STZ by positively regulating the dreb2a-mediated pathway in response to salt stress[22]. FcWRKY70 promotes the expression of arginine decarboxylase, enhancing plant salt tolerance[23]. Different WRKY genes exhibit various functions in plants; some are positive regulators, such as IbWRKY47, which significantly enhances salt tolerance in sweet potato[24], and MdWRKY55 in apple, which regulates salt stress response by forming a complex with MdNHX1, and its overexpression significantly improves salt tolerance in apple[25]. Conversely, some are negative regulators, such as CmWRKY17, which makes chrysanthemums more sensitive to salt stress[26], and the expression of the CaWRKY27 gene is induced by salt stress, with its overexpression making Arabidopsis and tobacco more sensitive to salt stress[27].

WRKY transcription factors also help plants cope with salt stress by regulating ions' homeostasis and antioxidant enzyme activities in plants. Sorghum SbWRKY50 regulates ion balance in plants by controlling the expression of SOS1 and HKT1[28]. Additionally, WRKY genes are also involved in signaling pathways such as ABA and H2O2, further regulating plant salt tolerance. For instance, GmWRKY13 reduces salt stress tolerance by up-regulating the expression of ABI1, while ZmWRKY17 inhibits tolerance to high salinity through exogenous ABA treatment[29].

2.4. Low-temperature stress

The impact of low-temperature stress on plant growth is significant. Plants that have been exposed to low temperatures see modifications in their cell structure and osmotic regulating chemicals, which account for 58% of the changes. Additionally, the expression and response mechanisms of related cold-resistant genes also change. WRKY transcription factors participate in the regulation of plant response to low-temperature stress through different signal transduction pathways. For example, PlWRKY70 of peony is widely expressed in buds and rapidly reaches peak levels 4 or 8 hours after low-temperature stress treatment[30]. WRKY contributes in the plant response to low-temperature stress via many pathways. Four LcWRKYs in loofah are considerably increased under low-temperature stress, and they contain methyl jasmonate, salicylic acid, and abscisic acid-responsive elements, all of which play essential roles in low-temperature stress[31]. In cockscomb grass, VbWRKY32 expression is upregulated after low-temperature stress, which upregulates the transcription levels of cold-responsive genes, increases antioxidant activity, maintains membrane stability, enhances osmotic regulation capacity, and increases plant low-temperature resistance[32]. In rice under low-temperature stress, the MADS-Box TF OsMADS57 and its interacting protein OsTB1 synergistically activate the transcriptional regulation of OsWRKY94, preventing tillering by inhibiting the transcription of the organ development gene D14[33].

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3. Conclusion and Prospect

One of the biggest transcription factor families, the WRKY family, is essential to the regular functions of plant life. The intricate and varied roles of WRKY TF members have been thoroughly uncovered by growing amounts of study, and it is now evident how important WRKY transcription factors are to plants' reactions to abiotic stress. However, there are many members of WRKY transcription factors, and the regulatory pathways are very complex, so further research is needed on the molecular mechanisms and functions in regulating important biological functions. Grain is the lifeline of the national economy. Nowadays, the global climate is unstable, with frequent extreme disasters. Global crops will face more abiotic stress. Saline-alkaline disasters, droughts, and extremely high or low temperatures can all have an additional impact on crop development. In order to identify resistance genes, enhance planting techniques, and other aspects of crop science, we must investigate the roles and mechanisms of WRKY transcription factors in greater detail. This is a great benefit to improving crop yield and quality.

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