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Functional aspects of WRKYs in stress and growth regulation

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ABSTRACT

The WRKY transcription factor family is one of the largest families of transcription factors, primarily known for its role in regulating plant responses to biotic and abiotic stress conditions. WRKY transcription factors play a crucial role in mediating these responses by participating in plant signal transduction pathways. Numerous studies have highlighted the significance of WRKY in plant responses to various environmental challenges such as pathogen attacks, drought, salinity, and temperature stress. Often, a single WRKY transcription factor can respond to multiple stress factors and may be involved in several regulatory networks. In addition to their role in stress responses, WRKY transcription factors have also been implicated in various aspects of plant growth and development, including seed germination, bud and floral differentiation, panicle development, and leaf senescence. Therefore, the present review aims to summarize the functions of WRKYs in both biotic and abiotic stress responses, as well as in plant development..

KEYWORDS: WRKY, Abiotic, Biotic, Plant development, Gene regulation, Transcription factors

Biotic and abiotic stresses are two fundamental factors that profoundly influence plant growth, development, and survival throughout their life cycle. Biotic stresses mainly arise from pathogenic infections caused by bacteria, fungi, oomycetes, and viruses. In contrast, abiotic stresses encompass a wide range of environmental challenges, including drought, heavy metal toxicity, cold, irradiation, oxidative stress, and heat. The capacity of plants to sense, adapt to, and respond to these diverse stresses is vital for maintaining their physiological balance and ensuring reproductive success (Srivastava et al., 2014; Srivastava et al., 2018). Central to this adaptive capability is the regulation of gene expression by plant-specific transcription factors (TFs), which serve as key modulators of stress-related responses. Prominent among these are the WRKY, AP2/ERF (APETALA2/Ethylene Responsive Factor), and NAC (NAM, ATAF1/2, and CUC1/2) families, all of which play essential roles in orchestrating plant resilience mechanisms (Jiang et al., 2012a). Among them, WRKY transcription factors stand out due to their broad involvement in both stress responses and developmental processes.

Extensive research in Arabidopsis and other plant species has identified numerous transcription factors that have evolved unique plant-specific functions (Reichmann and Ratcliff, 2000). In angiosperms, transcription factors are classified into 58 families based on their DNA-binding domains, with the WRKY gene family ranking as the 7th largest and being widely distributed across the plant kingdom (Zhang et al., 2011; Jin et al., 2014). This widespread distribution underscores their evolutionary significance and functional diversity. Studies on various WRKY transcription factors have revealed their participation in multiple physiological and developmental processes, including trichome and seed development, seed germination, bud and floral differentiation, panicle development, and leaf senescence (Johnson et al., 2002; Miao et al., 2004; Jiang et al., 2009; Liu et al., 2015; Chen et al., 2017; Xiang et al., 2017). These findings highlight the versatile nature of WRKYs as central regulators not only in stress responses but also in guiding key developmental transitions.

Transcription factors operate by modulating gene expression through direct interactions with downstream target genes and transcriptional regulators (TRs), thereby influencing a wide array of biological functions such as growth, development, and activation of signaling pathways during stress and defense responses (Nath et al., 2019). Among the many TF families reported to regulate genes involved in plant defense mechanisms, several, including ERF, MYB, bHLH, bZIP, and NAC, are particularly prominent for their roles in mediating responses to wounding, anaerobic stress, pathogen infection, and UV radiation (Singh et al., 2002). Notably, many of these families are unique to plants and have expanded significantly, reflecting the complex regulatory demands imposed by environmental and biotic challenges. Within these extensive regulatory networks, WRKY proteins are especially noteworthy. They function as indispensable components of gene regulatory systems, orchestrating plant responses to various environmental stresses as well as developmental processes such as seed germination, leaf senescence, flowering, and root development (Geilen et al., 2017; Li

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et al., 2020; Li et al., 2017; Gu et al., 2019; Zhang et al., 2016; Besseau et al., 2012; Li et al., 2016; Grunewald et al., 2012). Their central role in modulating diverse biological processes positions WRKY transcription factors as crucial elements in plant biology. In this context, the present review aims to provide a comprehensive synthesis of current knowledge on the functional roles of WRKY transcription factors, particularly focusing on their involvement in regulating plant responses to biotic and abiotic stresses, as well as their contributions to developmental processes.

STRUCTURE AND CLASSIFICATION OF WRKY TRANSCRIPTION FACTORS: AN INSIGHT

WRKY transcription factors represent a unique and expansive family of plant-specific proteins, with 74 members identified in Arabidopsis, 81 in tomato, and 109 in rice. The family derives its name from a highly conserved amino acid sequence, WRKYGQK, located within a 60-amino-acid-long domain typically found at the N-terminus of these proteins. In addition to this signature WRKY domain, these proteins also feature a zinc finger-like motif at the C-terminus, which is essential for their DNA-binding function (Eulgem and Somssich, 2007; Ross et al., 2007; Huang et al., 2012).

WRKY proteins may contain either one or two WRKY domains, and based on the number of domains as well as the specific type of zinc-finger motif they possess, they are classified into three major groups (Eulgem et al., 2000; Rushton et al., 2010; Bakshi & Oelmüller, 2014). Group I proteins are characterized by the presence of two WRKY domains and a C2H2-type (Cys_2-His_2) zinc-finger motif. In contrast, Groups II and III contain only a single WRKY domain. Group II proteins also have a C2H2-type zinc-finger motif, whereas Group III proteins are distinguished by a C2HC-type (Cys_2-His/Cys) zinc-finger motif. Furthermore, Group II WRKY transcription factors exhibit additional structural diversity and are subdivided into five subgroups: II-a, II-b, II-c, II-d, and II-e. This classification is based on the presence of specific conserved structural motifs beyond the core WRKY domain, reflecting the functional specialization within this family (Ülker & Somssich, 2004; Rushton et al., 2010; Bakshi & Oelmüller, 2014).

WRKYS PLAY ROLE IN PLANT GROWTH AND DEVELOPMENT

WRKY transcription factors play vital roles in various aspects of plant growth and development, including seed germination, ovule formation, flowering, and leaf senescence. In *Arabidopsis*, mutants of both *AtWRKY2* (Jiang and Yu, 2009) and *AtWRKY43* (Geilen et al., 2017) exhibited reduced seed germination in the presence of abscisic acid (ABA). Similarly, overexpression of *OsWRKY17* in *Nicotiana benthamiana* led to decreased germination rates under NaCl and mannitol treatment (Yan et al., 2014). In contrast, increased germination was observed in overexpression lines of *GhWRKY34* (Zhou et al., 2015) and *OsWRKY45* (Qiu et al., 2009) in *Arabidopsis*. Likewise, overexpression of *TaWRKY44* in tobacco (Wang et al., 2015) and *TaWRKY46* in *Arabidopsis* (Li et al., 2020) also enhanced seed germination under mannitol treatment and drought conditions. However, overexpression of *OsWRKY72* in *Arabidopsis* resulted in delayed germination (Song et al., 2010).

Beyond seed germination, numerous WRKY transcription factors have been reported to regulate flowering and senescence. For instance, *AtWRKY75* (Li et al., 2012), *AtWRKY26* (Li et al., 2017), *GhWRKY27*, *GhWRKY91* (Gu et al., 2019), *OsWRKY23* (Jing et al., 2009), *OsWRKY42* (Han et al., 2014), and *TaWRKY7* (Zhang et al., 2016) act as positive regulators of senescence, whereas *AtWRKY54* and *AtWRKY70* act as negative regulators (Besseau et al., 2012). In *Arabidopsis*, *AtWRKY12* and *AtWRKY13* play opposite roles in flowering: *AtWRKY12* promotes flowering under short-day conditions, while *AtWRKY13* delays it (Li et al., 2016). Another WRKY gene, *WRKY71*, has been shown to promote flowering by activating *LFY* and *FT* genes (Yu et al., 2016).

Although WRKYs are well studied in several developmental processes, fewer studies have focused on their roles in root development. In *Arabidopsis*, *AtWRKY75* is induced under phosphate (Pi) deficiency, and its suppression results in increased lateral root number and length (Devaiah et al., 2007). Conversely, suppression of *AtWRKY46* reduces lateral root formation under osmotic and salt stress (Ding et al., 2015). *AtWRKY23* regulates root development and flavonol biosynthesis (Grunewald et al., 2012). Overexpression of a *GhWRKY6*-like gene in *Arabidopsis* enhanced germination and root length under salt, ABA, and mannitol stress (Ullah et al., 2017). In rice, *OsWRKY74* was shown to enhance root and shoot biomass and improve Pi stress tolerance (Dai et al., 2016). Overexpression of *GhWRKY31* in rice increased resistance against *Magnaporthe grisea* infection but reduced lateral root elongation and formation (Zhang et al., 2007). Additionally, *TaWRKY2* was reported to promote lateral root formation in transgenic wheat by downregulating the ethylene biosynthesis gene *ACS* (Hu et al., 2018).

ROLE OF WRKYS TFs IN ABIOTIC STRESS

WRKY proteins have diverse roles in mediating plant responses to both abiotic and biotic stresses. Abiotic stresses such as drought, radiation, salinity, and cold trigger the activation of several WRKY proteins that contribute to resistance mechanisms. Among these, drought and salt stress are considered two of the most critical abiotic factors affecting plant growth and productivity.

In *Arabidopsis*, mutants of *AtWRKY1* (Qiao et al., 2016) and *AtWRKY63* (Ren et al., 2010) exhibited reduced drought tolerance compared to wild-type plants, while mutants of *AtWRKY46*, *AtWRKY54*, and *AtWRKY70* showed enhanced drought tolerance (Chen et al., 2017). In other plant species, overexpression of *GhWRKY41* (Chu et al., 2015), *OsWRKY30* (Shen et al., 2012), and *OsWRKY47* (Raineri et al., 2015) in *Nicotiana benthamiana* and rice, respectively, improved drought tolerance. Similarly, overexpression of wheat *TaWRKY2* and *TaWRKY19* (Niu et al., 2012), as well as cotton *GhWRKY91* (Gu et al., 2019), enhanced drought tolerance in transgenic *Arabidopsis* lines.

AtWRKY8 was found to be strongly expressed in roots and upregulated under salt stress (Hu et al., 2013). In contrast, rice plants overexpressing *OsWRKY30* (Scarpeci et al., 2013) and *OsWRKY72* (Yu et al., 2010) were more susceptible to salt stress. Recent studies have also shown that overexpression of *PcWRKY33* decreased salt tolerance in *Arabidopsis*, as transgenic plants exhibited impaired Na^+/K^+ homeostasis and reduced activity of ROS-scavenging enzymes (Yin et al., 2024).

Another transcription factor, *OsWRKY63*, negatively regulates cold tolerance in rice by suppressing the expression of *OsWRKY76* (Zhang et al., 2022). *SlWRKY57* has been identified as a negative regulator of salt stress in tomato by repressing the transcription of salt-responsive genes such as *SlRD29B*, *SlDREB2*, and *SlSOS1* (Ma et al., 2023). In soybean, overexpression of *GmWRKY17* enhanced drought tolerance by activating the expression of *GmDREB1D*, a drought-inducible gene (Liu et al., 2023). Similarly, overexpression of *MdWRKY70L* in *Nicotiana tabacum* reduced the accumulation of H_2O_2 and O_2^-, thereby enhancing drought tolerance in transgenic plants (Qin et al., 2022).

Interaction between WRKY TFs and Associated Abiotic Stress Factors

In the abscisic acid (ABA)-dependent stress response, mitogen-activated protein kinases (MAPKs) play crucial roles in transducing downstream signals, whereas in biotic stress responses, wound-induced protein kinase (WIPK) and salicylic acid (SA)-induced protein kinase (SIPK) are key components (Li et al., 2011). Some MAPKs are activated under both biotic and abiotic stress conditions; for instance, in *Arabidopsis*, *MPK3*, *MPK6*, and *MPK4* are involved in both pathways (Danquah et al., 2014). In rice, *WRKY30* enhances drought tolerance by interacting with MAPK cascades. A point mutation at the serine (Ser) residue in the Ser-Pro site of *WRKY30* leads to a drought-sensitive phenotype (Shen et al., 2012) (Figure 1). These results suggest the importance of MAPK-mediated phosphorylation in the drought tolerance activity of *OsWRKY30*. Overexpression of *AtWRKY34*, a pollen-specific transcription factor, under its native promoter led to the phosphorylation of the *WRKY34* protein by *MPK6* and *MPK3* (Guan et al., 2014). In vivo studies further demonstrated that mutations at the phosphorylation site of *WRKY34* impaired its function (Guan et al., 2014). These signaling studies provide valuable insights that could contribute to the development of a variety of stress-tolerant transgenic crops.

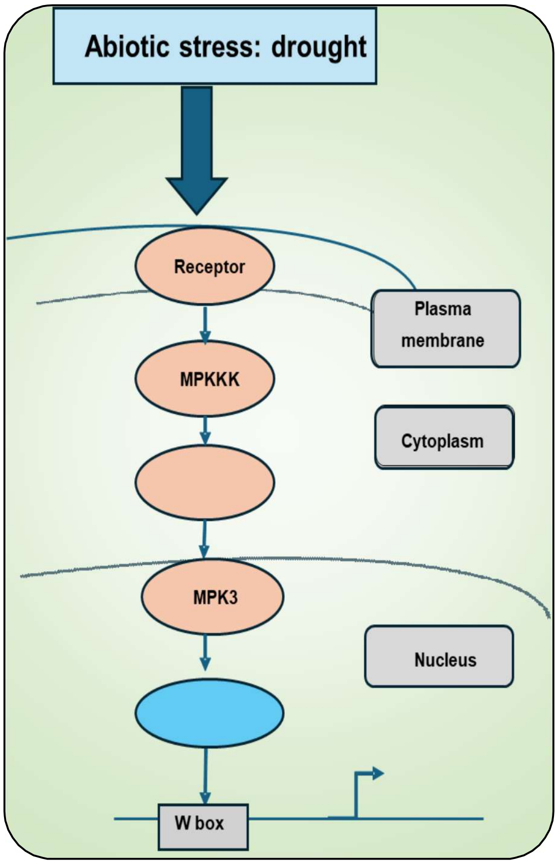

Figure 1. MAPK pathway induces *OsWRKY30* transcription factors activity during drought stress.

ROLE OF WRKY TFs IN BIOTIC STRESS

In *Arabidopsis*, *AtWRKY28* and *AtWRKY75* have been shown to confer resistance against oxalic acid and fungal infections by regulating the jasmonic acid (JA)/ethylene (ET) signaling pathway (Chen et al., 2013). The *atwrky33* mutant exhibited heightened susceptibility to *Botrytis cinerea*, which was associated with salicylic acid (SA)-mediated repression of the JA pathway (Birkenbihl et al., 2012). Similarly, overexpression of *AtWRKY61* in *Arabidopsis* (Gao et al., 2016) and *GhWRKY15* in tobacco (Yu et al., 2012) enhanced resistance to viral infections. In contrast, the rice genes *OsWRKY62* and *OsWRKY76* function as negative regulators of biotic stress responses. Double mutants of these genes showed increased susceptibility to *Magnaporthe oryzae* and *Xanthomonas oryzae* pv. *oryzae* (Xoo) (Liu et al., 2016), whereas overexpression of *OsWRKY71* increased resistance to Xoo in rice (Liu et al., 2007). *GhWRKY70*, similar to *OsWRKY62* and *OsWRKY76*, also negatively regulated tolerance to *Verticillium dahliae* in transgenic *Arabidopsis* by upregulating SA-associated genes and downregulating JA-associated genes (Xiong et al., 2019). *AtWRKY48* has also been reported to negatively affect basal resistance to virulent *Pseudomonas syringae* (Xing et al., 2008). More recently, WRKY genes in potato, such as *ScWRKY023* and *ScWRKY045*, were found to be induced in response to wounding, while during viral infection, *ScWRKY016* and *ScWRKY045* were downregulated (Villano et al., 2020).

One well-characterized example of WRKY transcription factor involvement in biotic stress responses is *AtWRKY33* in *Arabidopsis* (Figure 2). *AtWRKY33* plays a pivotal role in mediating plant defense mechanisms during pathogen attack. Under normal, non-infected conditions, *AtWRKY33* forms a regulatory complex with mitogen-activated protein kinase 4 (*MPK4*) via its interaction with the substrate *MKS1*, contributing to the regulation of pattern-triggered immunity (PTI) (Qiu et al., 2008). However, upon infection with the bacterial pathogen *Pseudomonas syringae*, *MKS1* undergoes phosphorylation, triggering the disassembly of the complex. This phosphorylation event leads to the release of both *MKS1* and *AtWRKY33*. Once released, *AtWRKY33* translocates to the nucleus, where it activates the transcription of *PAD3* (*Phytoalexin Deficient 3*), a gene encoding an enzyme crucial for the biosynthesis of antimicrobial phytoalexins (Qiu et al., 2008). Through this mechanism, *AtWRKY33* directly contributes to strengthening the plant's defense response against pathogenic invasion.

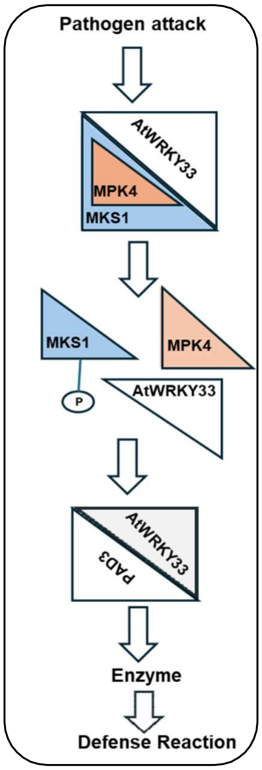

Figure 2. *AtWRKY33* roles during pathogen infection

CONCLUSIONS AND FUTURE PROSPECTS

As one of the largest and most functionally diverse transcription factor families, WRKY transcription factors play indispensable roles in regulating both plant development and stress responses. Over the years, accumulating evidence has demonstrated that WRKY proteins are not limited to developmental processes but are also integral components of complex regulatory networks that modulate plant responses to a wide range of biotic and abiotic stresses. These include processes such as seed germination, leaf senescence, flowering, and root development. Despite extensive studies, the precise molecular mechanisms and modes of action through which WRKY transcription factors exert their regulatory functions remain only partially understood. Recent advances in genomic and transcriptomic technologies have significantly expanded our ability to identify and characterize *WRKY* gene families across diverse plant species, offering valuable insights into their functional roles and mechanisms of action. In particular, elucidating their downstream target genes, interaction partners, and self-regulatory feedback loops is essential for a comprehensive understanding of the transcriptional networks governing plant stress responses and development.

Looking ahead, future research should also address the influence of epigenetic modifications and non-coding RNAs in regulating WRKY transcription factors. Integrating these layers of regulation could provide a more holistic view of how WRKYs function under varying environmental conditions. Such insights hold considerable potential for the development of stress-resilient crops, ultimately contributing to improved agricultural productivity and sustainability.

Conflicts of Interest: The author declares no conflicts of interest.

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