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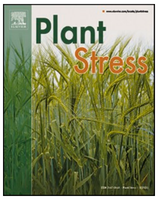

Deciphering the role of WRKY transcription factors in plant resilience to alkaline salt stress

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ABSTRACT

The WRKY gene family consists of unique transcription factors (TFs) found exclusively in plants. These TFs play a crucial role in regulating how plants respond to various abiotic stresses, such as saline-alkaline conditions, temperature fluctuations, drought, UV radiation and others. Scientists have been progressively studying the roles and mechanisms of WRKY in several plant species, including both model plants and essential agricultural crops. This study focus has emerged due to the understanding that alkaline and saline soil stressors considerably impede global agricultural productivity. Multiple research efforts have underscored the significant biological functions of WRKY TFs in assisting plants in coping with various abiotic challenges, particularly in enhancing their ability to withstand alkaline-salt stress. This review aims to investigate the structural capabilities of WRKY TFs and their impact on plant responses to alkaline and salt stresses. Additionally, it seeks to elucidate the role of these TFs in alleviating diverse abiotic and biotic stressors. The objective of this review study is to provide comprehensive insights into the current state of the field and the importance of WRKY TFs in regulating plant responses to salt and alkaline stress.

Introduction

Soil salinization is a widespread environmental problem that presents a substantial risk to agricultural output on a global scale. Alkaline salt stress, one of the various forms of soil salinity, is highly damaging to plant growth and development due to its high pH and the presence of sodium carbonate or bicarbonate. Gaining insight into the molecular mechanisms that drive plant responses to alkaline salt stress is essential for devising methods to enhance crop resilience and guarantee food security in regions impacted by this environmental stress (Shrivastava and Kumar, 2015; Balasubramaniam et al., 2023; Khan et al., 2023). Alkaline-salt soil, referred to as saline-alkali soil, is a kind of soil that has a high pH (usually above 8.5) and a high concentration of soluble salts, mostly sodium salts. This type of soil is frequently found in dry and semi-arid areas where salts build up because evaporation rates are higher than precipitation rates (Zhang and Zeng, 2023). Alkaline-salt soil development is impacted by a number of variables, including an arid or semi-arid environment, the properties of groundwater, geological elements, irrigation techniques, and human activity (Maryol, 2015). The development and persistence of alkaline-salt soil in different regions can be attributed to a variety of factors, including an imbalance between precipitation and evaporation, the presence of shallow groundwater with high dissolved salts, the underlying geology rich in soluble salts, improper irrigation management, and human-induced salt accumulation (Wei et al., 2020). The WRKY family of TFs plays a crucial role in the plant's capacity to adjust and react to salt stress. These transcription factors play a crucial role in initiating and synchronizing the expression of genes that are responsible for the plant's defensive systems against the

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harmful impact of salt stress. The WRKY TFs assist the plant in mounting a well-coordinated and efficient response to the challenges presented by high-salt environments by controlling the transcription of certain genes. This encompasses the initiation of genes accountable for osmotic adjustment, ion homeostasis, and the synthesis of defensive chemicals, all of which are crucial for the plant's endurance and adaptability in the presence of salt stress (Liu et al., 2014; Ullah et al., 2024).

Numerous scientific investigations have underscored the participation of WRKY TFs in facilitating plant reactions to diverse abiotic stressors, such as salt stress (Baillo et al., 2019). The increasing interest in recent years has been directed towards the role of WRKY TFs in conferring plant resistance and tolerance within the context of alkaline salt stress (Wang et al., 2020; Khoso et al., 2022). The stress induced by salty alkali poses significant challenges to agricultural productivity and growth. Plants undergo water stress and exhibit reduced growth due to an osmotic imbalance caused by elevated levels of soluble salts and alkaline soil conditions (Majeed and Muhammad, 2019). In addition, the accumulation of detrimental ions, such as salt and chloride, can directly damage plant tissues and disrupt essential physiological processes. Saline alkali stress not only hinders the availability and absorption of food, but also leads to nutritional imbalances that further restrict the growth of plants (Okon, 2019). Adverse weather conditions can exert a substantial impact on the process of seed germination and the establishment of seedlings, leading to a reduced crop stand and a lower overall plant count (Finch-Savage and Bassel, 2016). Furthermore, the stress might impede several metabolic activities, such as photosynthesis, so reducing the overall yield of the crops. Farmers in saline alkaline areas encounter greater challenges as plants under stress exhibit heightened susceptibility to diseases and pests (Reddy et al., 2004). In order to understand the molecular processes involved in how plants adapt to alkaline salt stress, it is crucial to gain insight into the control of WRKY transcription factor genes and their associated target genes. Controlling the balance of ions and osmotic pressure in plant cells is an important part of the WRKY-mediated signaling pathways that decide how plants react to alkaline salt stress (Rai et al., 2023).

The WRKY6 TF plays a crucial role in modulating root growth under low potassium (LK) stress conditions in Arabidopsis. WRKY6 responds rapidly not only to LK stress but also to various other abiotic stress treatments. Two wrky6 T-DNA insertion mutants exhibited heightened sensitivity to LK treatment, displaying much shorter primary root lengths, lower biomass, and reduced K^+ content in the roots compared to wild-type plants. Conversely, WRKY6-overexpressing lines showed the opposite phenotypes, suggesting that WRKY6 is a TF that regulates root growth under K^+ deficiency conditions. The mechanism by which WRKY6 modulates root growth under potassium deficiency involves the regulation of the potassium channel gene AKT1 expression. WRKY6 has also been shown to directly bind to the promoters of genes involved in the transport of Na^+ and K^+, including HAK5 (high-affinity K^+ transporter) and SOS1 ($\mathrm{Na}^{+/}H^+$antiporter), in Arabidopsis. By adjusting the expression of these ion transport-related genes, WRKY6 overexpression in Arabidopsis can improve resistance to salt stress. Similarly, in rice, WRKY6 has been linked to the control of genes crucial in the plant's response to salt and drought stress. Overexpressing WRKY6 in rice can increase the plant's resistance to abiotic stressors (Yuan et al., 2019; Ahmed et al., 2021). Furthermore, WRKY6 in tomato has been found to play a role in regulating plant responses to various abiotic stresses, including salt stress, by enhancing the expression of genes related to ion homeostasis and transport. These findings suggest a conserved role for the WRKY6 TF in regulating the expression of ion transport-related genes, which can have a significant impact on plant responses to nutrient deficiencies and abiotic stresses, such as potassium deficiency, salt stress, and drought, across different plant species (Hichri et al., 2017). The expression of genes involved in ion transport, such as those encoding Na^+/H^+ exchangers, K^+ transporters, and proton pumps, is thought to be regulated by TFs WRKY11 and WRKY17, which are increased in rice in response to alkaline salt stress. Through regulating the function of these ion transporters, WRKY11 and WRKY17 aid in preserving the proper Na^+/K^+ ratio and avert excessive sodium build-up within the cytoplasm (Hichri et al., 2017; Price et al., 2022). The regulation of genes associated with osmotic stress response and ion transport has been linked to WRKY41 in Arabidopsis. To maintain ion homeostasis under alkaline salt stress, these TFs can alter the expression of genes producing ion transporters, such as $K+$ channels and Na^+/H^+exchangers. In order to maintain cellular water balance and osmotic adjustment, they also regulate the expression of genes involved in the production of compatible solutes and the regulation of aquaporins (Joshi et al., 2022; Khoso et al., 2022). The alkaline environments, elevated concentrations of sodium ions have the potential to disturb the equilibrium of cellular ions, hence inducing detrimental impacts of plant metabolism (Yang et al., 2009). The regulatory part of WRKY TFs in the expression of genes associated with ion transport, including those responsible for producing ion channels and transporters, has been demonstrated (Amin et al., 2021). This regulatory mechanism serves to uphold ion homeostasis and mitigate the adverse consequences of alkaline salt stress.

Plants encountered several obstacles that influenced their growth and development during their whole life cycle. Numerous transgenic clones have been created, exhibiting enhanced characteristics, and a subset of these clones have undergone field testing, rendering them suitable for environmental release. The genetic stability of genetically altered forests has been further substantiated through field studies. Genetically engineered plant development has focused on various tree species (Zhang et al., 2014; Garg et al., 2023). The development of agriculture is hampered and food security is put in threat by salinized soil, which lowers seed germination rates and limits crop growth. One of the major negative environmental variables influencing agricultural production and food security is soil salinization (Ahmed and Ambinakudige, 2023). Environmental adaptation in plants is facilitated by the development of complex signaling pathways, which often include signal transducers, receptors, secondary signals, and plant hormones (Liu et al., 2023a). During periods of abiotic stress, TFs are crucial in the signal transduction pathways. Through their ability to affix themselves to a variety of cis-elements and exert control over the expression of a group of genes that are connected to one another, TFs contribute to the establishment of plant resistance. Commonly discovered structural components within TFs encompass the DNA-binding domain, the transcriptional regulation domain, the nucleotide lipid structure (NLS), and the oligomerization site. The regulatory actions of WRKY TFs are controlled by the collective functioning of numerous structural domains, which are temporal, geographic, and mechanism-dependent (Jia et al., 2018).

In order to exert an influence on cellular shape, developmental trajectory, and regulatory mechanisms, a multiplicity of TFs play an essential part in the regulation of a greater number of genes (Strader et al., 2022). Plants generate and transmit a diverse range of signals that stimulate TFs in reaction to both biotic and abiotic stimuli. The stressors encompass salt, drought, low temperature, hot temperature, and infections, among others. When transcription factors TFs attach to certain cis-acting sites, they activate RNA polymerase and transcribed complexes, which eventually leads to gene products beginning to react to the signal. This marks the beginning of the process by which particular genes generate transcription and expression (Zuo et al., 2023). In light of this, target genes that TFs regulate may allow plants to react appropriately to environmental stimuli. Despite the fact that (MYB, bZIP, AP2/EREBP, and NAC) are families of TFs that have linked to adversity (Ma et al., 2019; Sun et al., 2023). Within the field of plant stress responses, the WRKY TF family has been the subject of a significant amount of study. There are a number of biological processes that are significantly impacted by the WRKY family, which is a unique superfamily of TFs that may be found in higher plants and algae. This family is particularly important in the management of both biotic and abiotic stimuli (Li et al., 2023a).

A complex family of proteins noted for their unique structural characteristics is referred to as the WRKY TFs. At the core of the WRKY structure is the DNA binding domain located at the N-terminus (Wang et al., 2023c). This domain contains a conserved hetapeptide sequence, with WRKYGQK being the canonical motif. Nevertheless, several variations in this particular sequence have been detected, including WRKYGKK, WRKYGMK, WSKYGQK, WKRYGQK, WVKYGQK, and WKKYGQK. Modifications in the DNA binding domain have likely to affect both the specificity and the degree of interaction that occurs between WRKY proteins and the DNA sequences that they are attempting to bind to (Shah et al., 2021). The zinc-finger structure that may be found at the C-terminus of WRKY proteins is a structure that works in conjunction with the DNA binding domain. It has been noticed that there are two prevalent forms of zinc-finger motifs: CX29HXH and CX7XX24HXC. There are variances among the various groups of WRKY proteins, despite the fact that the bulk of WRKY proteins contain zinc-finger motifs of the C_2H_2 and C_2HC types. The number of WRKY domains and the characteristics of their zinc-finger motifs are examined in order to differentiate between Group I, Group II, and Group III. This is done in order to distinguish between the three groups. Group I typically consists of one C_2H_2 zinc-finger structure and two WRKY domains, whereas groups II and III each have one WRKY domain within their respective structures. A notable distinction can be made between the zinc-finger structure found in group II and that found in group III, which demonstrates the presence of structural variation within the WRKY protein family (Eulgem et al., 2000; Phukan et al., 2016; Goyal et al., 2023).

The process of evolutionary study has led to the discovery that the WRKY proteins that are classified as belonging to group II, specifically categories I, IIa + IIb, IIc, IId + IIe, and III, have been found to be WRKY proteins, do not have a common evolutionary inheritance. This suggests a complex evolutionary history involving gene duplication and divergence. In addition to the core DNA binding domain and zinc-finger motifs, certain WRKY proteins also feature additional structural elements such as leucine zipper structures, glutamate enrichment domains, and proline enrichment domains. These diverse structural features likely contribute to the functional versatility of WRKY proteins in regulating various biological processes in plants (Rushton et al., 2008; Wang et al., 2023b). In addition, some WRKY proteins have leucine zipper structures, glutamate enrichment domains, and proline enrichment domains (Singh et al., 2002; XU et al., 2023).

The primary reason for saline stress is the presence of a significant quantity of soluble salts, particularly sodium chloride, in the soil. Saline stress has a number of negative effects on plants, the most significant of which are ion toxicity, osmotic stress, and nutrient deprivation. The presence of high salt concentrations in the soil may lead to osmotic stress because it reduces the amount of water that is available to plant roots. Ion toxicity happens when too many salt ions, such Na^+ and Cl, build up in plant tissues and mess with cellular functions (Li et al., 2019). Due to competition between salt ions and vital minerals, nutrient shortage, in particular K^+ and Ca_2^+ deficits, occurs. On the other hand, alkaline stress is characterized by a high pH of the soil, usually above 8.5, brought on by an excess of basic cations such Ca_2^+, Mg_2^+, and CO_{32}, it is the opposite (Wali et al., 2022). Alkaline stress's high pH has a direct impact on the stability of proteins, membrane integrity, and metabolic activities, which can affect plant growth and development. Due to competition between salt ions and vital minerals, nutrient shortage, in particular K^+ and Ca_2^+ deficits, occurs. While alkaline stress is characterized by high soil pH, usually above 8.5, brought on by an excess of basic cations such Ca_2^+, Mg_2^+, and CO_{32}, it is the opposite (Kumari et al., 2022). Because of its high pH, alkaline stress has a direct influence on the stability of proteins, the integrity of membranes, and the metabolic activities, which can affect plant growth and development. Crops growing in alkaline soils experience both high pH stress and $CO3^{2-}/HCO_3$- stress, which is typically associated with $NaHCO_3$ or Na_2CO_3 presence. Therefore, knowledge of the saline-alkaline stress response may aid in increasing the salt tolerance of crops (Wu et al., 2020).

Effects of saline-alkali and salt on plant morphology and physiology

Plant respiration, photosynthesis, and the entire process of growth and development are all significantly influenced by abiotic stresses such as severe dryness, high salt and alkalinity levels, and other similar factors. The plant's stress may impede its capacity to uptake water and vital nutrients, which are needed for sustaining cellular functioning and supporting the energy-generating processes of photosynthesis and respiration. Consequently, plants that frequently encounter elevated salt concentrations tend to have diminished rates of respiration, leading to decreased oxygen intake and carbon dioxide release. This is a result of the cellular machinery's challenge in maintaining homeostasis and providing the required energy for growth and development. Excessive alkalinity, which is marked by a high concentration of hydroxide ions and increased pH levels, can negatively impact the physiological functions of plants. High alkalinity can impede the accessibility and uptake of vital nutrients, including iron, manganese, and boron, which are needed for the optimal operation of the photosynthetic apparatus. This disturbance has the potential to cause a reduction in the plant's capacity to absorb and utilize light energy, leading to a decrease in the effectiveness of photosynthesis and adversely affecting the overall development and productivity of the plant. In addition, the high pH of alkaline soils can modify the availability and solubility of other minerals, worsening the pre-existing nutritional imbalances in the plant and impeding its capacity to perform vital metabolic functions like respiration and photosynthesis.

The regulation of TFs plays a crucial role in the intricate and structured mechanisms by which plants adapt to various abiotic stimuli present in their surroundings (Singh et al., 2002; Dong et al., 2023). One of the main consequences is a decrease in stomatal conductance, which causes plants to have smaller openings in their stomata, resulting in a reduced diffusion of CO_2 into the leaves. The scarcity of CO_2 directly hampers the Calvin cycle, which is the phase of photosynthesis that does not depend on light. This is because CO_2 is the main substance used for carbon fixation. In addition, exposure to saline-alkali stress can lead to a decline in the chlorophyll levels in plant leaves, which in turn reduces the ability of plants to capture light energy during the light-dependent stage of photosynthesis. The reduction in chlorophyll levels hampers the overall effectiveness of the light-dependent processes (Fang et al., 2021). Moreover, saline-alkali stress has the potential to disturb the activity and functionality of vital photosynthetic enzymes, including Rubisco, which plays a critical role in the conversion of CO_2 into organic substances. The inhibition of these enzymes greatly decreases the speed of carbon fixation and the total productivity of photosynthesis (Pang et al., 2016). Saline-alkali stress can trigger oxidative stress, resulting in the production of ROS that can harm the photosynthetic machinery, particularly the chloroplasts responsible for photosynthesis. This oxidative stress additionally impairs the effectiveness of the photosynthetic mechanism (Lu et al., 2022). Saline-alkali stress significantly affects the respiratory systems of plants. It has the potential to damage the structure and hinder the function of plant mitochondria, which are the organelles responsible for cellular respiration. This can result in a decrease in the efficiency of ATP synthesis and an elevation in the formation of ROS (Zhanwu et al., 2014). In addition, saline-alkali stress can hinder the function of several respiratory enzymes, including those associated with the TCA cycle and the electron transport chain. This leads to a reduced rate of cellular respiration and energy generation (Yang et al., 2023). Furthermore, saline-alkali stress can disturb the equilibrium between carbohydrate metabolism and other metabolic pathways, resulting in an imbalance in the availability of respiratory substrates, which in turn contributes to the decreased efficiency of the respiratory process (Bidalia et al., 2019).

Importantly, salt-alkali stress has a considerable impact on the growth and development of plants, as well as their physiological and biochemical processes. When plants are subjected to saline-alkaline stress, the information about the stress is initially received at the roots, and it is gradually sent to the portions of the plant that are above ground. After then, the information is transmitted to the regions of the plant that are lower. There are a number of important characteristics that govern the response of plant seedling biomass to salt-alkaline stress. Some of these parameters include the root surface area, the number of root tips, the leaf area, and the photosynthetic rate. However, there are many more key parameters as well (An et al., 2021; Ying et al., 2023). Plants can change their morphology after prolonged exposure to saline-alkali stress in order to more effectively adapt to the environment. Reports indicate that halophytes exhibit various morphological and anatomical adaptations in response to salinity. There are several observed alterations, including increased succulence, leaf pubescence, modifications in the quantity and dimensions of stomata, the presence of a multilayered epidermis, thickened cuticles, early lignification, stopping differentiation, and changes in the diameter and number of xylem vessels (Öztürk et al., 2023; Wang et al., 2023f).

Saline-alkaline stress in soil increases sodium ions, causing increased osmotic pressure in plant cells, leading to physiological dehydration and osmotic stress. To address this, plant cells synthesize and accumulate organic substances like proline, soluble proteins, betaine, sugar, polyols, and polyamines. These molecules are essential for maintaining water potential stability, altering water's characteristics, increasing internal osmotic potential resilience, supporting protein folding stability, and protecting large molecules' structure for osmoregulation. Sorghum seedlings modify the synthesis of small molecules like proline and soluble proteins to adapt to saline-alkaline conditions, preserving their physiological functioning and enduring unfavorable environmental conditions (Sun et al., 2019). Wheat was subjected to salt-alkali stress, which resulted in increased amounts of proline, soluble sugar, and polyol (particularly sorbitol). This was a response to the salt-alkaline conditions that were unfavorable (Guo et al., 2015). The complex balance of ions inside cellular structures can be upset by the elevated concentration of sodium ions in the soil during saline-alkaline stress, which can have number of negative effects on plant physiology (Fig. 2) (Hasegawa, 2013).

Research findings indicate that increased levels of NaCl have a notable impact on the leaf area to plant height ratio in three distinct plant species: *Phaseolus vulgaris*, known for its susceptibility to salt, and *Gossypium hirsutum*, which exhibits a certain tolerance to salt (SIKDER et al., 2020) The ratio of leaf area to plant height is significantly reduced in these three plant species when exposed to elevated amounts of sodium chloride, with the exception of the salt-resistant *Atriplex patula* being an exception (Khalil, 2020). In comparison to the other species, the leaf thickness of the salt-tolerant species *A. patula* was greater. This was determined by the anatomical structure of the leaves. The larger epidermal and mesophyll layers, in addition to the higher succulence of the leaf, were thought to be responsible for this phenomenon (Palchetti et al., 2021). In addition, the measurements of stomatal and mesophyll conductance demonstrated that salt stress slowed down the rate of photosynthesis and decreased the amount of carbon dioxide that was present in chloroplasts (Wang et al., 2018b). Additionally, throughout salt stress, the anatomical structure of the *Populus euphratica* plant exhibited alterations in vessel development and inhibition of xylem differentiation, thereby enhancing the plant's capacity to withstand salinity (Ge et al., 2022). Additionally, research conducted on cotton and *Leymus chinensis* has revealed that plants are capable of adapting to salt-alkali stress through the elongation of their specific roots and root ratio (Wang et al., 2018a). The findings of a study investigating the cotyledon node zone in the halophyte plant *K. sieversiana* indicate that this zone potentially influences the plant's tolerance to different concentrations of saline and alkalinity. An exposure to salt and/or alkali results in a reduction in the amounts of sodium and chloride in the xylem fluid that is acquired from the cotyledon node zone located above. The cotyledon node zone is characterized by a selective restriction of ion mobility, and this restriction occurs under both acidic and basic circumstances. This may be an exceptional method by which halophyte plants withstand alkali and salinity (Wang et al., 2019). In brief, plants that are resistant to salt demonstrate increased resilience by modifying their above-ground and below-ground organ systems, so producing a suitable morphological structure to efficiently endure unfavorable circumstances.

The vacuolar membrane contains *NHX1* and the cell membrane contains *NHX7* (SOS1), which are ion antiporters. By removing and storing sodium ions from cells, they lessen the negative consequences that they can cause. This system helps plants lessen the negative effects of sodium ions. Calcium-dependent SOS2/SOS3 kinases control the activity of these antiporters (Bahmani et al., 2015). The transport of Na^{+} is facilitated by H^{+-}ATPase and H^{+-}VPPase present in both cell and vacuolar membranes. Saline-alkaline stress enhances the activity of H^{+-}ATPase and H^{+-}VPPase, which aids in the transportation of sodium ions from the cytoplasm to the apoplast and vacuole (Ye et al., 2019). There is a strong correlation between the amount of potassium that is present in plants and the regulation of osmosis, membrane potential, and enzyme activity in those plants (Hasanuzzaman et al., 2018). Plants require a high K^{+} to Na^{+} ratio in the cytoplasm to support proper growth and development. The cytoplasm undergoes an inflow of Na+ ions during saline-alkali stress, which lowers the membrane potential below its initial value. As a result, this causes the $K^{+/}\mathrm{Na}^{+}$ ratio to become unbalanced by activating K^{+} outflow channels such as NSCC, GORK, and SKOR (Falhof et al., 2016). More evidence shows that certain K^{+} channel proteins, like *Arabidopsis* K^{+} transporters (AKT1) and high-affinity K^{+}transporters (HKTs), are very important for plants to be able to take in K^{+}. HKTs represent a distinct category of Na^{+}/K^{+-} specific type II transport proteins. Under some conditions, Type II HKTs have the ability to transport Na^{+} ions, although they exhibit a preference for K^{+} ions. The HAK/KUP/KT family of K^{+} transporters, which includes HAK5 as well as KUP7, and the shaker family of K^{+} channels, which includes AKT1, often have an effect on how much potassium is absorbed (Cotsaftis et al., 2012; Li et al., 2018). Recent research indicates that HAK/KUP/KT family members are linked to $K+$ absorption and stress responses in tea plants. Plants overexpressing the HAK gene are salt-tolerant, but low K^{+} and Na^{+} simultaneously suppress HAK synthesis, reducing transporter functionality and making plants susceptible. This is primarily due to Na^{+} ion depolarization (Bacha et al., 2015; Yang et al., 2020). The absorption of $K^{+}$is limited by PM H^{+-}ATPase's enzymatic activity, which generates a pmf across the PM and transports protons out of the cell, allowing HAKs to take in K^{+}ions (Pottosin and Dobrovinskaya, 2014; Falhof et al., 2016). *Arabidopsis* seedlings overexpressing *PutAKT1* absorb more K^{+} and accumulate less Na^{+}, demonstrating its role in salt stress resistance due to increased cytoplasmic K^{+}/Na^{+}ratios (Ardie et al., 2010; Su et al., 2019). Polyamines modify K^{+} channels in root and guard cells, facilitating Na^{+} translocation and affecting K^{+}mobility (Pottosin et al., 2021).

Plant WRKY TFs: roles and regulation

Inducible expression of WRKY TFs is seen in response to particular stimuli. TF expression patterns are often classified into two main categories: constitutive and inducible. Numerous factors, including infections, signal molecules, temperature, drought, and mechanical stress, have been shown to affect the regulation of WRKY gene expression. Furthermore, WRKY TFs play a significantly important role in a variety of physiological processes that occur in plants. The second-largest assemblage of TFs in the *Arabidopsis* senescent leaf transcriptome is referred to as WRKY TFs (Gu et al., 2019; Rivero et al., 2022). It has reported by Gu et al., 2019 that *GhRipen2–2* plays regulatory functions in the processes that control leaf senescence and as a result of the fact that its expression was significantly elevated throughout the process of leaf senescence and was boosted by *GhWRKY27*. As potential members of a regulatory network that combines internal and external inputs to control the commencement and advancement of leaf senescence, WRKY53, WRKY54, and WRKY70 have been investigated. It is possible that WRKY30 is working in conjunction with these three genes. (Besseau et al., 2012). The finding of *SlWRKY28*-induced regulation of the enzyme gene in the ROS scavenging pathway has demonstrated that it has the potential to serve as a technique for transgenic lines to improve their resistance to alkaline salt. The identification of *SlWRKY28* TFs involved in the regulation of alkaline salt tolerance holds significant theoretical and practical importance (Wang et al., 2020). The WRKY family has a number of regulatory mechanisms. When WRKY proteins interact with W-box elements, they change the transcriptional activity of downstream target genes, either by turning them on or off. Moreover, it possesses the capacity to form protein complexes alongside supplementary active constituents, augmenting transcription binding activity. Engaging with conserved W-box cis-acting areas that are positioned within the promoter region of the target genes is necessary for WRKY TFs to be able to stimulate the expression of downstream genes (Phukan et al., 2016).

The self-promoters of most WRKY TFs have a substantial abundance of W-box components, which enables them to attach to their own promoters and create networks of self- or cross-regulation (Rama Devi et al., 2022). In the plant *Capsicum frutescens*, for example, the *CaWRKY6* gene can make *CaWRKY40* more active, which makes the plant better able to handle high temperatures and humidity. The topic of discussion is Maxim Glycine. In addition, the *GmWRKY27* protein forms a collaboration with *GmMYB174* to restrict the expression of *GmNAC29*, while also directly inhibiting the function of the downstream *GmNAC29* promoter. Hence, this system enhances the plant's ability to withstand drought and salt stress (Cai et al., 2015; Noman et al., 2019). In *Petroselinum crispum*, the *PcWRKY1* promoter exhibits the capacity to interact with both its own sequence and the *PcWRKY3* promoter when pathogenic bacteria are present. The initiation of transcription is facilitated through a process known as self-negative feedback regulation and cross-regulation, which involves additional WRKY proteins. The demonstration of this phenomena has been achieved by employing chromatin immunoprecipitation (ChIP) investigations (Wang et al., 2023d). Moreover, this study represents the inaugural investigation into the tissue specificity and stress response profiles of two distinct wild potato cultivars. One notable finding of the research was the identification of eleven WRKY genes that were solely expressed in leaves, while six WRKY genes were exclusively expressed in flowers. In addition, it has been noted that the potato genes *StWRKY016, StWRKY045*, and *StWRKY055*, which are leaf-specific, have a significant impact on enabling plant adaptation to stress generated by increased temperature. Further investigation into *AtWRKY25* has provided additional insights. The down-regulation of two genes implicated in the oxidative stress response has been observed with exposure to elevated temperatures. Additionally, the expression levels of *AtWRKY25* genes that are triggered by high temperatures have reduced (Zhang et al., 2017; Villano et al., 2020).

A particular type of cis-regulatory element called the W-box attaches to DNA and is the main mechanism, that WRKY proteins use to exert their influence over the expression of genes. WRKY proteins are responsible for regulating transcription, which can either stimulate or suppress the expression of genes farther down the gene chain (He et al., 2016). Research on WRKY TFs has found the W-box, a short DNA sequence, in the promoter region of many genes. A number of different experimental techniques, including gel electrophoresis, random binding site selection, yeast one-hybrids, and transfection, were utilized in order to achieve this goal. A number of genes that are related with defensive processes are among the genes that *CaWRKY6* and *CaWRKY40* frequently target. These genes include *CaHIR1, CaDEF1, CaPO2, CaHSP24*, and others. It has been proven in previous research that *CaWRKY6* belonging to pepper, the IIb subgroup exhibits the capacity to interact with and stimulate the promoter area of *CaWRKY40*. An additional observation that has been made is that WRKY TFs have the ability to directly interact with the expression of their own genes as well as the expression of other genes. Efficiency in regulating leaf senescence is adversely affected by the interaction between *AtWRKY53* and the *AtWRKY42* promoter in Arabidopsis (Hussain et al., 2019; Wang et al., 2023b).

The interplay between WRKY TFs and phytohormones

A significant aspect in the plant's capacity for adaptation is the WRKY family of TFs, plays a crucial role in the plant's molecular response to saline-alkaline and salt concentrations. Osmotic adjustment, ion homeostasis, and antioxidant defense are some of the stress-responsive pathways that are controlled by WRKY TFs, which are responsible for controlling the activity of genes that are responsible for some of these processes. One example of this is the WRKY63 TFs found in *Arabidopsis*, responsible for stimulating the expression of the P5CS gene, which ultimately leads to increased proline synthesis and a greater tolerance to osmotic stress of the plant (Jiang and Deyholos, 2009). Similarly, the WRKY8 TF in rice also leads to an increase in the expression of the betaine aldehyde dehydrogenase (BADH) gene, which in turn leads to an increase in the accumulation of glycine betaine and an improvement in the plant's ability to tolerate salt (Wai et al., 2020). By boosting the expression of genes that encode enzymes such as SOD, CAT, and GST, WRKY TFs, such as WRKY20 in *Arabidopsis* and WRKY31 in tomato, have the potential to boost the antioxidant capacity of the plant. This is accomplished by increasing the expression of genes. The oxidative stress that is caused by this activity is somewhat reduced (Hussain et al., 2021; Asaf et al., 2023).

Phytohormones are a class of signaling chemicals synthesized by plants, which play a vital part in the regulation of numerous physiological processes such as growth, development, and stress. The coordination of a plant's defensive systems and adaptive responses under saline-alkali stress circumstances are heavily dependent on the interplay between WRKY transcription factors and phytohormones. The salt excessively sensitive, protein kinase, and ABA signal transduction pathways make up the majority of the signaling pathways linked to the saline alkali stress. For osmotic signal transduction, protein kinase and ABA pathways are primarily involved, whereas the SOS route is activated in response to ionic stress (Zhu, 2016). In addition, ABA also affects how cells react to environmental cues (Li et al., 2023b). WRKY proteins have either an activating or repressing effect on transcription in *Arabidopsis*. The advantageous impacts of *AtWRKY18* and *AtWRKY60* on plants' ABA sensitivity have been established. More precisely, it inhibits the process of seed germination and root growth, while simultaneously increasing the plant's ability to withstand salt and osmotic stress. All three types of mutants-single, double, and triple-as well as lines that overexpressed WRKY genes were found to exhibit the effects that were discussed earlier. The induction of *AtWRKY40* and *AtWRKY18* occurs rapidly after being exposed to ABA, whereas the induction of *AtWRKY60* is time-delayed by ABA. In order to control the degree to which plants are sensitive to ABA and other abiotic stimuli, these three genes compete with one another (Chen et al., 2010; Wang et al., 2023a). The *AtWRKY40* mutant exhibits variable expression of ABA-regulated genes, for instance ABI1, ABI2, and ABF, indicating that *AtWRKY40* exerts direct control over these genes. It has been determined that *AtWRKY18, AtWRKY60*, and *AtWRKY40* exhibit binding affinity towards W-box sequences located in the promoters of ABI4 as well as ABI5 genes. The negative regulatory function of this binding interaction on these genes implies that plays detrimental function in ABA signaling (Grzechowiak et al., 2022). The absence of *AtWRKY60* expression in both mutant forms is attributed to the fact that both *AtWRKY18* and *AtWRKY40* induce the synthesis of *AtWRKY60* in protoplasts via identification of distinct W-box sequences located inside the promoter region of *AtWRKY60*. This implies that AtWRKY18 and AtWRKY40 have the potential to directly interact with *AtWRKY60* during ABA signaling (Chen et al., 2010).

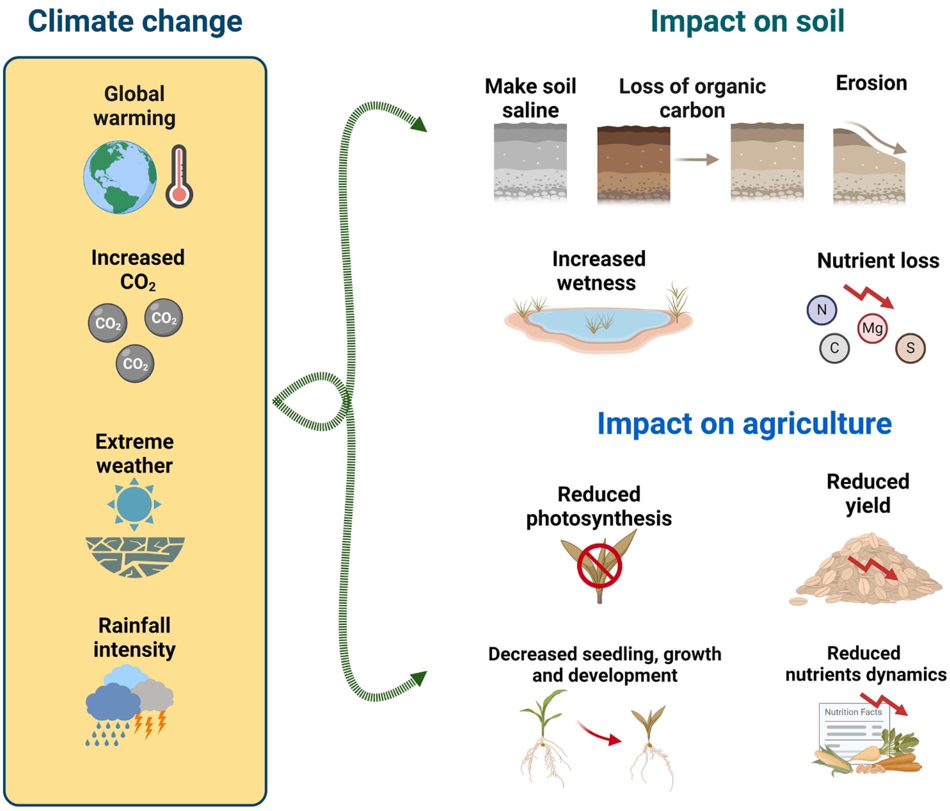

Fig 1. Impact of climate change on soil and its damages. The figure was created by bioreder.com.

The evaluation of stomata closure was performed with tobacco overexpressing lines, and the results demonstrated that ABA contributes to the closure of stomata generated by *GhWRKY41*. The experiment examined the stomatal motility, both with and without ABA treatment. The study findings indicated that the implementation of ABA resulted in a reduction in the quantity of stomatal apertures in both the wild-type and overexpression control groups (Chu et al., 2015; Wang et al., 2023a). The ABA-induced gene promoter was repressed by the genes *OsWRKY24* and *OsWRKY45* in rice aleurone cells, while the same promoter was activated through *OsWRKY72* as well as *OsWRKY7* (Zhou et al., 2020a). Through the inhibition of a gene promoter that is activated by ABA, it has been proven that the *OsWRKY24, OsWRKY53*, and *OsWRKY70* paralogs all operate in a manner that is almost identical (Zhang et al., 2015). The *SbWRKY55*, an essential element of the ABA-mediated signaling pathway, plays a role in controlling salt stress via suppressing the transcription of *SbBGLU22* (glucosidase 22), a gene responsible for ABA-GE hydrolysis, and reducing levels of endogenous ABA.

Additionally, *SbWRKY55* inhibits the ABA signaling pathway by interacting with *SbFYVE1*, a zinc finger protein of the FYVE family found in sorghum. The dual functions of *SbWRKY55* in ABA signaling have been examined, revealing its essential role in the ABA-mediated signaling cascade. This study also demonstrated that *SbWRKY55* could control how sensitive sorghum is to salt (Song et al., 2022). The combination of salt stress and ABA treatments resulted in a significant increase in the activation of the nuclear-localized transcription activator *AtWRKY66*. The plants that had their expression of *AtWRKY66* suppressed, which was generated by the CRISPR/Cas9 method, displayed decreased activities of SOD, POD, and CAT, as well as decreased seed germination rate and increased REL when they were subjected to treatments that included both salt stress and ABA. Based on these observations, it seems that the mutants exhibited a greater vulnerability to salt stress and ABA. Furthermore, the RNA-seq study demonstrated that the gene expressions linked with ABA signaling pathways and the stress response in the plants that had *AtWRKY66* knocked down exhibited patterns that were consistent across both experimental situations. The fact that a number of regulatory genes that are engaged in the ABA signal transduction pathway were shown to be subject to significant regulation is also noteworthy (Zhang et al., 2023b). ABA signaling regulates a significant proportion of stress response genes and is a crucial endogenous regulator in plants' responses to environmental stresses.

Association between the perception of stimuli and the responses of molecular cells is made by MAPKs, which regulate various plant signaling processes, comprising responses to stresses (De Zélicourt et al., 2016). According to a number of studies, MAPKs can target specific WRKY proteins and change their activity. For instance, two kinases that have been extensively investigated in relation to stress response are WIPK and SIPK. In context of pathogen infection, the phosphorylation of these entities occurs through the action of MAPK NtMEK2 in tobacco, as well as an unidentified MAPK upstream. According to Kim and Zhang (2004), *NtWRKY1* and *NtWRKY3* appear to be downstream of both WIPK and SIPK in the signaling cascade of Nicotiana's defense response. Additionally identified as being downstream in the MAPK signaling cascade are *AtWRKY22* and *AtWRKY29* (Kim and Zhang, 2004; Boro et al., 2022). The Camalxine is the primary phytoalexin in *Arabidopsis thaliana*, and the MAPK genes MPK3 as well as MPK6 are sensitive to pathogens as well as crucial in its induction. In addition, Camalxine synthesis caused by pathogens was impaired in *Arabidopsis* mutants of the WRKY33 gene with gain of MPK3 and MPK6 activity. Pathogens stimulate the transcription factor *AtWRKY33*, its expression is controlled via MPK3/MPK6 cascade.

Furthermore, immunoprecipitation studies have provided evidence that *AtWRKY33* interacts with its own promoter *in vivo*, suggesting the possibility of a feedback loop-mediated regulation (Doll et al., 2020; Zhou et al., 2020b). The MPK3/MPK6 enzymes phosphorylate the

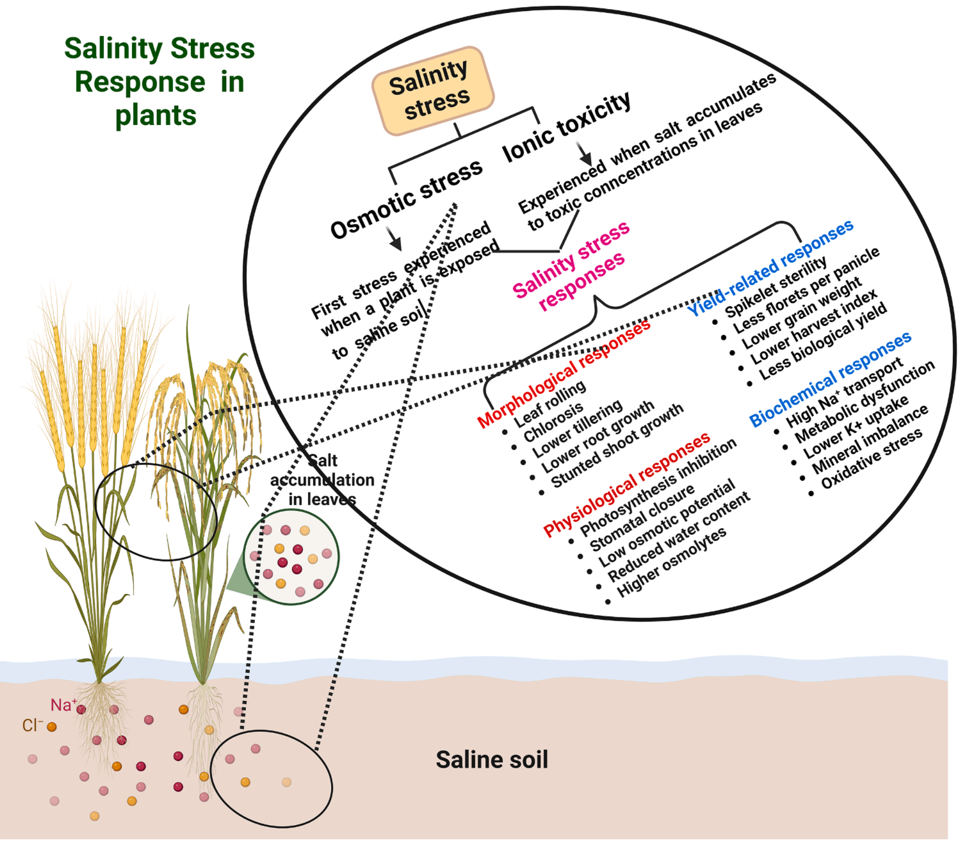

Fig 2. Effects of salinity-alkali stress in plants. The figure was created by bioreder.com.

AtWRKY33 protein, which makes MPK3/MPK6 less effective at complementing the induction of camalexin in *AtWRKY33* mutants. Phosphoprotein mobility assays additionally revealed that MPK3/MPK6 phosphorylates *AtWRKY33 in vivo* in response to infection with *Botrytis cinerea*. When pathogens are present, *AtWRKY33* boosts metabolic flux toward the production of *Arabidopsis camalexin* by acting downstream of MPK3/MPK6 to reprogrammed the genes involved in *camalexin* biosynthesis. Similarly, a different study indicates how *AtWRKY33* and a MAPK are related (Zhou et al., 2020b; Jiang et al., 2022). The link between *AtWRKY33* and a MAPK is also shown in another paper. PAD3 (Phytoalexin Deficient3) mRNA was found to be reduced in the Atwrky33 mutant, and this was also seen in an mpk4-WRKY33 double

Table 1
List of WRKY TF involved in plants response to salt and alkalinity stress.

Name of WRKYTF	Origin of species	Regulatory mechanisms	Type of stress tolerance	Refs.
MsWRKY11	Alfalfa *(Medicago sativa)*	Concentrations of soluble sugar, proline, SOD, and CAT should be increased, while those of MDA and ROS should be lowered and relative electrical conductivity should be elevated. Increase plant weight per 100 seeds, plant pods per plant, and plant density.	NaCl and $Na_2CO_2^+$ $NaHCO_3$	Wang et al. (2018a)
MDWRKY100	Apple (*Malus domestica*)	Boost chlorophyll concentration while lowering MDA and H_2O_2 levels.	NaCl	Ma et al. (2021)
SlWRKY28	*Populus davidiana x P. bolleana*	Transgenic lines may increase talkaline salt tolerance by regulating the ROS-scavenging enzyme gene.	NaCl and $Na_2CO_2^+$ $NaHCO_3$	Wang et al. (2020)
IlWRKY1	*I. lactea* var. *chinensis*	Role in sodium salt tolerance and develop novel germplasm of highly salt-tolerant plants that are employed in the future to remediate saline soil.	NaCl and $Na_2CO_2^+$ $NaHCO_3$	Tang et al. (2018)
PsnWRKY70	*Populussimonii* × *Populusnigra*	Responds to salt or pathogen stress by acting as an activator or repressor.	NaCl	Zhao et al. (2017)
PcWRKY11	*Polygonum cuspidatum*	Reduced ROS levels and increased production of osmosis substances have a beneficial effect in plants adaptation to salinity environments.	NaCl and $Na_2CO_2^+$ $NaHCO_3$	Wang et al. (2022)
MxWRKY55	*M. xiaojinensis*	Positively affects the process by which plants become resistant to salt, low-Fe, and high-Fe stress.	NaCl	Han et al. (2020)
HcWRKY44	Kenaf *(Hibiscus cannabinus* L.*)*	ABA signaling and salt tolerance are both influenced by this factor.	NaCl	Chen et al. (2022)
PbWRKY40	*Arabidopsis Thaliana*	Regulates *PbVHA-B1*, salt tolerance, and organic acid buildup.	NaCl	Lin et al., 2022)
MxWRKY55	*Arabidopsis Thaliana*	The gene *MxWRKY53* has a significant role in enhancing plant resilience to salt, low iron, and high iron stressors.	NaCl	Han et al. (2021b)
ZmWRKY20 *ZmWRKY115*	Maize	*ZmWRKY20* and *ZmWRKY115* TFs directly decrease *ZmbZIP111* expression in the nucleus, making maize seedlings more salt-sensitive.	NaCl	Bo et al. (2022)
AhWRKY75	Peanut	Increasing the ability to withstand salt stress	NaCl	Zhu et al. (2021)

mutant. This finding provides evidence that the formation of nuclear complexes between MPK4 and *AtWRKY33* is reliant on MKS1, which serves as a substrate for MPK4. The *Pseudomonas syringae* infection stimulates MPK4 and phosphorylates MKS1, subsequently, MKS1 binds to AtWRKY33. The PAD3 promoter encodes an enzyme responsible for the synthesis of camalexin, which serves as the binding site for this complex (Wani et al., 2021; Liu et al., 2023b).

According to a recent study, MPK3 and MPK6 work together to target the phosphorylation of about 48 *Arabidopsis* WRKY TFs *in vitro*. In the majority of the WRKYs that were investigated, MPK targets were found. When the phosphorylation of *AtWRKY46* in living species was investigated, it was shown that the *flg22* peptide, which is a pathogen-associated molecular pattern (PAMP), was responsible for the responses that were observed in living organisms in response to *AtWRKY46 activation.* The MAPK-dependent pathway was observed to enhance basal plant defense, as evidenced by the observed increase in *NHL10* promoter activity (a PAMP-responsive gene). It was proposed that *AtWRKY46* controls a MAPK-mediated plant defense mechanism (Sheikh et al., 2016; Ghorbel et al., 2023). ABA plays various functions in plant growth, such as controlling bud and seed dormancy, promoting germination, facilitating cell migration and division, and regulating leaf senescence and abscission Fig. 1.

WRKY TFs associated with salinity and alkalinity stress

Plants responses to salt and alkalinity stress are mediated by a number of WRKY TF discovered (Table 1). Through the involvement of *SlWRKY28*, transgenic lines have the ability to improve their resistance to alkaline salt by controlling the enzyme gene that is involved in the ROS scavenging pathway. In *Populus davidiana x P. bolleana*. It has been shown that many TFs related with SlWRKY28 play a role in the regulation of alkaline salt tolerance. In addition to their theoretical significance, the conclusions of this study have practical implications (Wang et al., 2020). The *IlWRKY1* gene is a WRKY transcription factor obtained by cloning from *I. lactea* var. *chinensis*. The length of the ORF of the *IlWRKY1* cDNA (sequence) is 1083 base pairs (bp), and it is responsible for encoding a protease (Tang et al., 2018). In this work, 46 WRKY transcription factor genes were found inside the kenaf genome, and their characteristics were analyzed. In the *HcWRKY* genes, the natural variety may have been caused by tandem and segment duplication, according to the findings of phylogenetic research and the structure of the genes themselves. The examination of the expression patterns revealed that *HcWRKY2/14/25* exhibit pivotal roles in the phloem of kenaf. The root systems of *HcWRKY*, namely *HcWRKY7, HcWRKY14 and HcWRKY44*, exhibited heightened expression and demonstrated positive responses to the environmental conditions of salt and drought. Further investigation into the functional characteristics of the *HcWRKY44* gene in *Arabidopsis* has shown that *HcWRKY44* overexpression improves salt tolerance via ABA and stress-related gene modulation. The fact that the improvement was caused by the upregulation of *HcWRKY44* served as evidence for this (Chen et al., 2022). The role of the *GmWRKY16* gene, which responds to a variety of stressors including drought, salt, alkali, PEG, and ABA, in determining *Arabidopsis* stress tolerance has been studied. Compared to wild type plants, the transgenic *Arabidopsis* plants of *GmWRKY16* showed improved resistance to drought and salt. Additionally, a study was carried out in *Arabidopsis* to investigate the possible pathways, such as an ABA-mediated pathway, for the regulation of genes that respond to stress (Ma et al., 2019).

In a recent research, the high expression of *AcWRKY28* resulted in an increase in the pineapple's tolerance to salt. The genes that were upregulated were much more prevalent in the "plant pathogen-interaction" pathway, as shown by the findings of a comparative transcriptome analysis between *AcWRKY28-OE* lines and WT pineapple, which was studied using KEGG. The ChIP and Y1H approaches were used in the research project in order to verify the existence of five *AcWRKY28* downstream CPK genes. It was proven that *AcCPK12* plays a crucial role in the response to salt, drought, ABA, and disease resistance by the demonstration of its overexpression (Zhou et al., 2023). In addition, another study indicated that the WRKY transcription factor *CbWRKY27* was present inside the nucleus, where it displayed action in both the activation of transcription and the binding of W-box DNA structures. The overexpression of *CbWRKY27* in *C. bungei* bacteria was observed to result in a significant increase in the susceptibility of transgenic plants to salt stress. Subsequent investigation revealed that transgenic plants exhibited higher ABA sensitivity when subjected to salt stress. Under addition, compared to wild-type plants, the transgenic plants showed higher MDA levels and lower POD and SOD enzyme activity under salt stress conditions. Based on the findings, it seems that the manipulation of ABA response and ROS homeostasis by *CbWRKY27* may have a detrimental effect on the capacity of plants to adjust to salt environments (Gu et al., 2023). It has been shown that the *MsWRKY11* TF is a stress-inducible factor that demonstrates sensitivity to a extensive range of environmental variables, for instance alkalinity, cold, drought, ABA, and salt stress. The increase of soybeans' salt tolerance by the overexpression of *MsWRKY11* provided more evidence that the WRKY gene family plays a significant role in the salt stress response and has the potential to be used in the development of soybean lines that are resistant to salty soil. It is necessary to do more research in order to get a full understanding of the unique regulation processes and functions of the *MsWRKY11* gene in response to diverse stresses (Wang et al., 2018b).

Plant expression induction of WRKY TFs

Plants respond to salt and alkaline stress through a variety of pathways, particularly the WRKY gene family, which is made up of TFs unique to plants, plays a significant role in many of these processes. A considerable number of WRKYs in plants have been functionally characterized. Specifically, 79 *IbWRKY* TFs were identified in sweet potato. Furthermore, expression of 35 *IbWRKY* genes exhibited substantial alterations upon exposure to NaCl (Qin et al., 2020; Abdul Aziz and Masmoudi, 2023). There is a total of 58 possible *BvWRKY* genes that can be found in the genome of sugar beetroot. The application of alkaline stress led to a substantial rise the expression levels of the genes *BvWRKY10* and *BvWRKY16* in both the shoots and the roots of the plant (Wu et al., 2019). Due to the fact that *IlWRKY1* expression was considerably increased in response to NaCl stress in this species, it is conceivable that *IlWRKY1* is involved in the response of *Iris lactea* var. *chinensis* to sodium salts (Tang et al., 2018).

When salt is present in soybeans, there is a possibility that the expression of *GmWRKY16* will be increased. Through the overexpression of key genes involved in the ABA system, the transgenic Arabidopsis plants that overexpressed *GmWRKY16* displayed increased salt tolerance. These genes included *AtWRKY8, KIN1*, and *RD29A* (Ma et al., 2019; Wang et al., 2023e). In alfalfa plants that were subjected to salt and alkalinity stressors, it was discovered that the expression of *MsWRKY11* was significantly elevated. By increasing the quantities of soluble protein and proline, as well as decreasing the amounts of ROS, the *MsWRKY11* gene was overexpressed in soybeans, which led to an increase in the plant's ability to tolerate salt. It is not yet known what the exact regulatory mechanisms were that were primarily responsible for this impact (Wang et al., 2018b). Additionally, the *miR156/SPL* regulatory module increased *MdWRKY100,* which resulted in an increase in *M. domestica's* tolerance to salt (Ma et al., 2021). A newly discovered WRKY gene that was taken from *Malus xiaojinensis* was shown to be triggered in seedlings by the application of salt stress. This gene was designated as *MxWRKY64*. It was shown that the overexpression of *MxWRKY64* in modified *A. thaliana* led to the emergence of both physical and biological markers, which indicated the relevance of this gene in the stress response to salt (Han et al., 2021a). The inhibitory effect of the sweet sorghum transcription factor *SbWRKY50* on the salt response and salt tolerance in *A. thaliana* is achieved by direct interaction with the upstream promoters of *SOS1* and *HKT1* (Song et al., 2020).

Table 2
List of key WRKY TFs contributing to a variety of stress tolerances.

WRKY Gene	Plant species	Influencing via factors	Function in stresses	Refs.
GhWRKY25	Cotton	Drought	Overexpression decreases drought tolerance	Liu et al. (2016b)
TaWRKY1–2D	Arabidopsis	Drought	Overexpression enhanced drought tolerance	Yu et al. (2023)
GmWRKY46	soybean	Phosphorus	Enhance low P tolerance using gene editing techniques	Liu et al. (2022b)
MdWRKY56	Apple	Drought	An essential positive regulator of drought stress tolerance	Duan et al. (2023)
ZjWRKY18	Jujube	Triterpenoid biosynthesis,	Boost triterpenoid production and resistance to salt stress	Wen et al. (2023)
CbWRKY27	*Catalpa bungei*	Salt	Inversely affects salt tolerance	Gu et al. (2023)
GmWRKY81	Soybean	Aluminum	Enhancing aluminum tolerance	Shu et al. (2022)
CSWRKY	Sweet orange	*P. digitatum infection*	*Penicillium digitatum*-induced expression in response to infection	Xi et al. (2023)
CasWRKY	*Cannabis sativa L*	GA3	Respond to GA3 stress, which has an impact on fiber development and exerts a significant influence on the growth and development of stems.	Wei et al. (2022)
VvWRKY28	Grape	Cold and salt	Contribute to the enhancement of plant resistance to cold and salinity stress.	Liu et al. (2022a)
PyWRKY75	Poplar	Cadmium	Controlling plant responses to Cd stress.	Wu et al. (2022b)
CoWRKY78	*Camellia oleifera*	Anthracnose	Resistance mechanisms to antracnose.	Chang et al. (2022)
GhWRKY70	*Gossypium hirsutum*	Verticillium wilt	Regulate the expression of *GhAOS1* to positively boost the production of JA.	Zhang et al. (2023a)
TtWRKY256	Wheat	Salt	Increasing tolerance to salt.	Li et al. (2022)
IgWRKY32/50	Arabidopsis	Drought	The enhancement of drought tolerance can be achieved through the regulation of the ABA signal transduction system.	Zhang et al. (2022a)
MfWRKY40	*Myrothamnus flabellifolia*	Drought and salt	Facilitate the enhancement tolerance towards drought and salinity stressors.	Huang et al. (2022b)
AcWRKY31	Rice & Arabidopsis	Drought and salt	Lower tolerance for salt & drought	Huang et al. (2022a)
PheWRKY86	*Moso bamboo*	Drought	Positively impacts drought tolerance via controlling the expression of *NCED1*	Wu et al. (2022a)
McWRKY71	Malus crabapple	Anthocyanins and Proanthocyanidins	Control the synthesis of secondary metabolites that react to ozone stress.	Zhang et al. (2022b)
CsWRKY29 /37	Tea	Cold	playing a part in cold tolerance	Zhao et al. (2022)

Moreover, the *ZmWRKY114* gene in maize has inhibitory properties on ABA signaling, hence reducing the transgenic rice's ability to endure salt stress (Bo et al., 2020).

WRKY TFs are necessary for several other stress tolerances

A significant part of the regulation of saline-alkaline stress is played by the WRKY TFs. However, they also have a significant impact on various biotic and abiotic stressors, such as heat stress, temperature inversion, oxidative stress, drought, and nutritional insufficiency. These stressors have a harmful effect on plant physiological and biochemical processes (Joshi et al., 2016). Consequently, of encountering a number of biotic stressors, such as pathogen attacks during their life cycle, plants have evolved methods to respond (Table 2). The up-regulation of the WRKY gene in medicinal dandelion is considerably more pronounced given the contrast between high-temperature stress circumstances and low-temperature stress situations, according to results from recent studies. Elevated temperatures induce an upregulation of *AtWRKY25* and *AtWRKY26* expression in *A. thaliana*. Conversely, a decrease in *AtWRKY33* expression is observed upon exposure to high temperatures. Consequently, alterations to any of the three genes implicated in this phenomenon render *A. thaliana* plants more susceptible to high-temperature stress. At increased temperatures, there is a significant increase in the expression level of *TaWRKY70* during the initial stages of wheat streak rust infection. The presented data provides evidence of a positive association between the expression of *TaWRKY70* and the heat stress tolerance of wheat seedlings. Furthermore, it signifies the likelihood that SA as well as ET signaling pathways were triggered through the early stages of infection (Cheng et al., 2021).

Drought is a substantial environmental challenge, leading to a substantial decline in world food output. The expression levels of *PmWRKY6, PmWRKY10,* and *PmWRKY30* have been seen to increase in various plants and tissues during conditions of drought. In contrast, the expression of *PmWRKY22* is decreased in these conditions. When comparing wild-type tobacco to transgenic tobacco plants that express *PmWRKY31*, it is shown that the latter demonstrate a decrease in malondialdehyde levels, accompanied by an elevation in proline content. Transgenic tobacco plants that have been genetically modified to produce *PmWRKY31* have shown a notable upregulation in the expression of associated genes, resulting in an enhanced capacity to endure arid environmental conditions (Sun et al., 2022). Further research was carried out with the purpose of elucidating the mechanisms that *McWRKY57* used in order to exercise control over plant growth, osmolyte accumulation, antioxidant enzyme activities, and the regulation of stress-related genes in transgenic Arabidopsis, therefore imparting drought resistance. According to the findings, *McWRKY57* plays a part in the plant's capacity to adjust to circumstances of drought (Bai et al., 2023). Current study indicates that the WRKY gene family, together with the downregulation of *GhWRKY25* and *GhWRKY33,* is associated with cotton's ability to withstand whiteflies and drought stress (Ehsan et al., 2023). Another research has shown that *SbWRKY45* may have a vital function in enhancing the sorghum's response to drought stress and abiotic stress (Baillo et al., 2023).

The significance of WRKY TFs in enabling plants to effectively mount defenses against various pathogens has been proven. The *CaWRKY27* protein, derived from the *Capsicum annum*, modulates the signaling pathways mediated by SA, JA, and ET in *Nicotiana tabacum*. This modulation subsequently leads to a favorable regulation of the stress

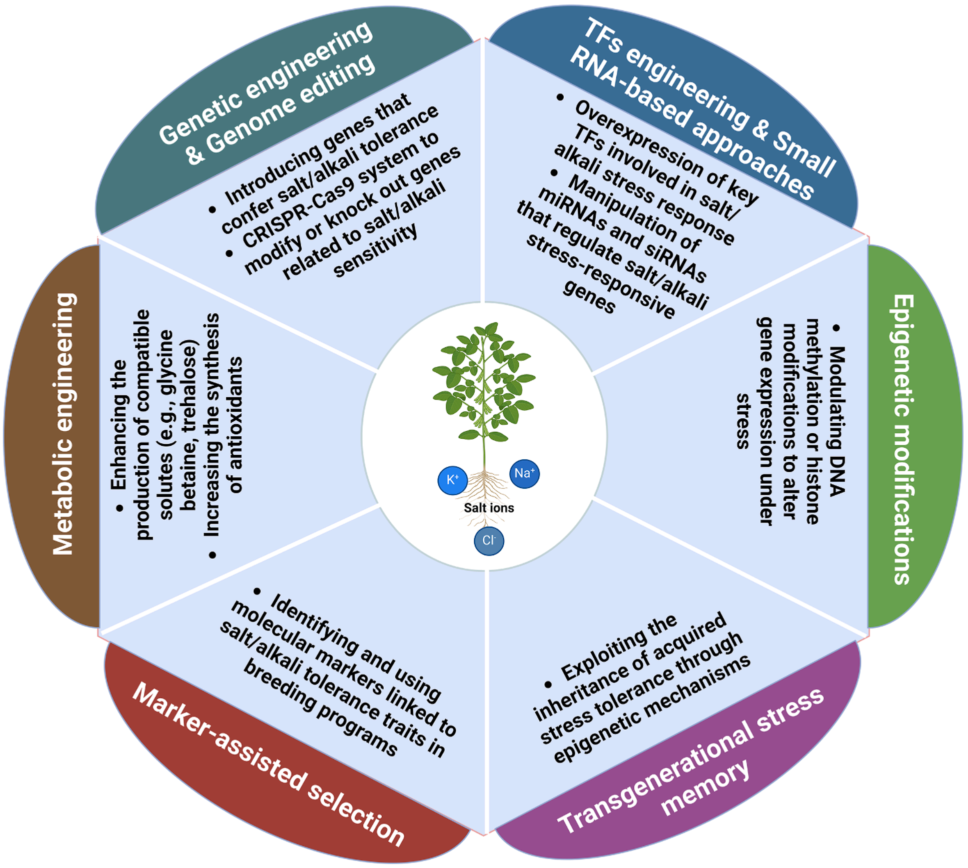

Fig 3. Molecular tools to improve saline-alkali and salt stress in plants. The figure was created by bioreder.com.

resistance response to infection caused by *R. solanacearum* (Dang et al., 2014). Recent research has demonstrated that Rice *WRKY80* and *WRKY4* have been identified as factors that make a valuable contribution towards the improvement of resistance against sheath blight disease in rice. The results of this study provide evidence that WRKY TFs have important functions in controlling the immune responses to the invasion of pathogens. The WRKY4 W-box promoter region serves as the site of attachment for *WRKY80*, thus, creating a beneficial regulatory loop that improves rice's ability to resist *Rhizoctonia solani*. The genes WRKY7, WRKY58, WRKY62, WRKY64, as well was WRKY76 exhibited significant levels of expression in rice blast disease, as determined through expression analysis. A study conducted shown that the upregulation of the rice gene WRKY67 led to an increased level of resistance against commonly occurring rice diseases, blast and bacterial blight, hence establishing WRKY67 as a promising candidate for the enhancement of rice crops (Liu et al., 2016a; Peng et al., 2016; Delicado et al., 2019).

The expression of Pi in *Arabidopsis* is modulated by the TFs *AtWRKY75, AtWRKY6*, and *AtWRKY42*. In the context of Pi insufficiency, the activation of *AtWRKY75* is significantly heightened in the plant. On the other hand, the downregulation of WRKY75 expression leads to heightened vulnerability to Pi stress and reduced Pi uptake in plants with genetic mutations (Tang et al., 2023). A rice *OsWRKY74* was also engaged in the ability of rice to withstand cold stress and variation of Pi homeostasis and probable crosstalk between P and Fe deprivation. The *OsWRKY74* overexpression dramatically improved tolerance to Pi starvation. In a hydroponic solution deficient in Pi, rice plants that overexpressed the *OsWRKY74* gene exhibited elevated levels of root as well as shoot biomass, and increased phosphorus content, in comparison to their wild-type counterparts. Rice plants that expressed *OsWRKY74* in soil pot tests exhibited higher amount, grain weight, and P concentration when grown in P-deficient media (Dai et al., 2016). In numerous plant species, a multitude of WRKY TFs have been associated in control of the both positive and negative senescence. Wax deposition on leaf surfaces increased in transgenic rice plants overexpressing *OSWRKY89*, and they were also more resistant to UV-B exposure (Kanwal et al., 2022).

Future prospective and conclusion

Further investigation into the role of WRKY TFs in plant resistance to alkaline salt stress shows great potential. The subsequent are some potential avenues for future study on genetically modifying WRKY TFs to increase plant resistance to alkaline salt stress. This could involve exploring the overexpression or knockdown of specific WRKY TFs to assess their impact on plant response and resilience to alkaline salt stress. Investigating the processes in more detail how particular WRKY TFs control signal transduction pathways and gene expression in response to alkaline salt stress. This might entail pinpointing downstream target genes and clarifying the precise biochemical mechanisms by which WRKY TFs function. Researchers have made significant strides in enhancing salt tolerance in plants through the manipulation of WRKY TFs genes. WRKY genes are a large family of TFs that play crucial roles in plant stress responses, including tolerance to high salinity. One of the key approaches researchers have explored is the overexpression of WRKY genes in various plant species. By increasing the expression of specific WRKY genes, scientists have been able to enhance the plants' ability to withstand high levels of salt in their environment. For example, the investigation has revealed that *CeqWRKYs* may control the response to NaCl and $NaHCO_3$ stress in *C. equisetifolia*, with the expression of *CeqWRKY11* being associated with enhanced stress tolerance (Zhao et al., 2024). Similarly, the resilience of *N. tabacum* to treatments with NaCl and drought was markedly enhanced by the exogenous overexpression of *IlWRKY70* (Shi et al., 2023).

Additionally, scientists have investigated the role of various signaling pathways and transcriptional networks that control the expression of WRKY genes in response to salt stress. By targeting these regulatory mechanisms, scientists can fine-tune the plants' salt tolerance responses. For instance, studies have revealed that the ABA signaling pathway plays a crucial role in the regulation of WRKY genes during salt stress. By modulating the components of the ABA signaling cascade, researchers have been able to enhance salt tolerance in plants. The future implications of these advancements in WRKY-mediated salt tolerance are far-reaching. As climate change continues to exacerbate soil salinization worldwide, the ability to engineer salt-tolerant crops becomes increasingly important for ensuring food security and sustainable agriculture. By incorporating these WRKY-based strategies into crop breeding and genetic engineering programs, researchers can develop new varieties of crops that can thrive in saline environments, reducing the impact of salt stress on agricultural productivity. Moreover, the insights gained from the study of WRKY genes and their roles in salt tolerance can also be applied to other abiotic stress responses, such as drought, temperature extremes, and heavy metal toxicity. The fundamental understanding of the molecular mechanisms underlying stress tolerance can be leveraged to develop more resilient and adaptable plant varieties that can withstand a range of environmental challenges.

In conclusion, there is ongoing investigation into the role of WRKY TFs in plant resistance to alkaline salt stress. Deciphering the molecular processes and regulatory mechanisms underpinning plant responses to alkaline salt stress may yield important insights into the function of WRKY TFs (Fig. 3). Researchers can create strategies to improve plant productivity and resilience in areas affected by alkaline salt by comprehending these systems. In-depth research into the above-discussed future prospects will contribute to our understanding of the complex regulatory networks governing plant tolerance to saline-alkaline as well as salt stress, open the door to the creation of novel crop improvement strategies in difficult settings.

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CRediT authorship contribution statement

Sindho Wagan: Writing – review & editing, Writing – original draft, Visualization, Validation, Funding acquisition, Conceptualization. **Maqsood Ali:** Visualization, Validation, Formal analysis. **Muneer Ahmed Khoso:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Intikhab Alam:** Visualization, Validation, Investigation. **Khuzin Dinislam:** Formal analysis. **Amjad Hussain:** Visualization, Validation, Formal analysis. **Nazir Ahmed Brohi:** Formal analysis, Validation. **Hakim Manghwar:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Conceptualization. **Fen Liu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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