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Unveiling New Horizons: Plant Signaling Mechanisms in Biotic and Abiotic Stress

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ABSTRACT: Plants face many challenges from both biotic and abiotic stresses that require complex signaling mechanisms for adaptation and survival. This review reviews recent advances that shed light on the complex signaling pathways that control plant responses to these stressors. Understanding the crosstalk between biotic and abiotic stress signaling pathways is crucial for deciphering plant tolerance mechanisms. New research reveals complex networks in which common signaling components integrate different stress inputs, allowing plants to prioritize responses based on the severity and nature of the stress encountered. Under biotic stress scenarios, plants use different receptor-mediated pathways to detect microbial invaders and activate defense mechanisms to prevent pathogen spread. Recent studies emphasize the involvement of pattern recognition receptors (PRRs) and nucleotide-binding domain leucine-rich repeat proteins (NLRs) in mediating immune responses against pathogens. In addition, the role of phytohormones such as salicylic acid, jasmonic acid and ethylene in orchestrating defense signaling cascades has been elucidated, revealing complex regulatory networks that control plant immunity. In contrast, abiotic stresses such as drought, salinity and temperature extremes trigger signaling cascades aimed at maintaining cellular homeostasis and promoting stress tolerance. Key players in abiotic stress signaling are mitogen-activated protein kinases (MAPK), calcium ions, reactive oxygen species (ROS) and various transcription factors. Recent findings highlight the importance of stress-specific regulatory elements and epigenetic modifications in fine-tuning plant responses to environmental fluctuations. In addition, emerging evidence indicates the involvement of long-range signaling mechanisms such as systemic acquired resistance (SAR) and systemic signal peptides, to coordinate plant responses to both biotic and abiotic stress. These ubiquitous signals allow plants to spread stress signals throughout the organism, with distant tissues improving stress tolerance.

Keywords: Biotic, Abiotic Stress, signalling Pathway, Molecular mechanism.

INTRODUCTION

Understanding the complex signaling mechanisms in which plants respond to biotic and abiotic stress is of utmost importance in agricultural and ecological research. Recent studies have shed light on the diversity of these signaling pathways and revealed new insights into how plants sense, integrate and respond to various stressors. Investigating plant responses to biotic stressors, recent studies have highlighted the role of plant hormones such as salicylic acid (SA), jasmonic acid (JA) and ethylene in organizing defense mechanisms against pathogens and pests. In addition, the discovery of plant immune receptors and their complex interaction with microbial effectors provided new ways to understand the molecular basis of plant-pathogen interactions (Zipfel, 2023). In addition, advances in molecular and omics technologies have helped researchers unravel the complex networks underlying plant responses to abiotic stresses such as drought, salinity, and temperature extremes. The identification of key transcription factors, kinases and signaling molecules involved in stress sensing and signaling has expanded our understanding of how plants adapt to complex environmental conditions. In addition, recent studies have elucidated the crosstalk between biotic and abiotic stress signaling pathways and revealed complex regulatory mechanisms that fine-tune plant responses to multiple stressors simultaneously. This cross-functional integration of signaling pathways highlights the complexity of plant stress responses and emphasizes the importance of holistic approaches to the study of plant-environment interactions. The advent of CRISPR-Cas9 gene editing technology has revolutionized plant research by allowing precise manipulation of target genes involved in stress response pathways (Liang *et al.,* 2023). This success accelerated the functional characterization of candidate genes and facilitated the development of stress-tolerant crop varieties that can better tolerate environmental challenges. In addition, the application of advanced imaging techniques such as live cell imaging and fluorescence microscopy provided real-time information on the dynamics of signaling events in plant cells under stress conditions (Chen *et al.,* 2023). By imaging molecular processes in situ, scientists can gain a deeper understanding of signal transduction mechanisms and identify potential targets for genetic engineering or agronomic interventions. In this review, we try to provide a comprehensive overview of recent advances in the understanding of plant signaling mechanisms in response to biotic and abiotic stress, based on many research findings in plant biology disciplines. By elucidating the complexity of these signaling networks, we can find new ways to develop innovative strategies to improve crop tolerance and resilience under changing environmental conditions (Wang *et al.,* 2021).

RECOGNITION OF PATHOGENS AND PESTS IN PLANTS

Identification of pathogens and pests in agricultural systems is crucial for effective disease and pest control strategies. Recent advances in molecular biology and technology have revolutionized methods of detecting and identifying these threats, allowing for more precise and timely intervention. Traditional methods such as visual inspection and symptom monitoring are still important for early detection. These methods, although subjective, provide initial clues for further research. Molecular techniques, including polymerase chain reaction (PCR) and DNA sequencing, have greatly improved the accuracy of pathogen identification (Jones *et al.,* 2022). These methods make it possible to identify pathogens even before visible symptoms appear, which improves preventive control measures. Next-generation sequencing technologies (NGS) offer high throughput, enabling simultaneous detection and characterization of multiple pathogens. NGS has revolutionized pathogen tracking and provides valuable information on microbial diversity and evolution. Metagenomic approaches have become powerful tools for studying complex pathogen communities in agricultural ecosystems (Zhang *et al.,* 2023). By analyzing entire microbial populations, metagenomics enables a comprehensive understanding of disease dynamics and ecological interactions. Remote sensing technologies, such as drones equipped with multispectral image sensors, enable rapid and comprehensive monitoring of crop health (Kiran *et al.,* 2023). These technologies detect subtle changes in vegetation reflectance associated with pathogen or pest infestation, facilitating targeted intervention. Biosensors incorporating biological recognition elements enable portable and real-time detection of pathogens and pests in the field (Lee *et al*., 2022). These devices enable on-site monitoring, enabling rapid decision-making and minimizing crop losses. Machine learning algorithms trained on large datasets of pathogen and pest signatures enable automatic detection and prediction of outbreaks. These algorithms evolve through continuous learning, adapting to changing environmental conditions and new threats. Integrating omics data, including genomics, transcriptomics and metabolomics, will improve our understanding of host-pathogen interactions and disease mechanisms (Wang *et al.,* 2023). Omics is approaching unraveling the molecular pathways underlying plant defense responses and guiding the development of resistant crop varieties. Citizen science initiatives engage farmers and communities in pathogen and pest surveillance and promote collaboration in early detection and control. The use of local knowledge and observations complements research and strengthens monitoring networks. Global collaboration and data sharing initiatives, such as the Global Initiative for Sharing All Influenza Data (GISAID), facilitate rapid information exchange and coordination in response to emerging pathogens (Liu *et al*., 2022). Open access to genomic information accelerates research and improves preparedness for global threats.

A. Activation of defense pathways

The defense pathways of organisms play an important role in defense against various threats, including pathogens, pests, and environmental stressors. Understanding the mechanisms underlying the activation of these pathways is important for improving plant and animal tolerance and developing new disease control strategies. In this review, we explore recent advances in the activation of defense pathways, focusing on key signaling mechanisms and their effects in biological systems. Recent studies have elucidated the complex signaling networks involved in the activation of defense pathways. For example, in plants, pattern recognition receptors (PRR) recognize pathogen-associated molecular patterns (PAMP) and trigger immune responses mediated by cascades of mitogen-activated protein kinases (MAPK) and calcium signaling pathways (Bigeard *et al.,* 2023). In addition, the role of plant hormones such as salicylic acid (SA), jasmonic acid (JA) and ethylene in orchestrating defense responses has been widely studied (Kazan and Lyons 2022). Recent studies have highlighted the complex cross-talk and integration of different defense mechanisms. In plants, the interplay between SA and JA signaling pathways has emerged as a key regulatory mechanism to balance defense responses against biotrophic and necrotrophic pathogens (Kazan and Lyons 2022). In addition, small RNAs such as microRNAs and small interfering RNAs have been shown to regulate immune signaling pathways by targeting transcription factors and signaling components (Li *et al*., 2023). Similarly, epigenetic modifications in animals affect the regulation of immune cell differentiation and function, highlighting the dynamic interaction of genetics and environmental signals (Kaushik *et al*., 2021). Understanding the activation of defense pathways has significant implications for biotechnology and medicine.

Table 1: Plant Perception of Biotic Stress, Recognition of pathogens and pests in plants, and Activation of defense pathways.

Type	Gene	Function	Source	References
Pattern Recognition Receptors (PRRs)	FLS2 (Flagellin-Sensing 2)	Recognizes bacterial flagellin, initiating PTI (PAMP-Triggered Immunity)	Arabidopsis thaliana	Chinchilla *et al*. (2006)
Pattern Recognition Receptors (PRRs)	EFR (EF-Tu Receptor)	Detects bacterial EF-Tu, leading to PTI	Arabidopsis thaliana	Zipfel *et al.* (2006)
Pattern Recognition Receptors (PRRs)	CERK1 (Chitin Elicitor Receptor Kinase 1)	Recognizes fungal chitin, triggering PTI	Arabidopsis Thaliana	Miya *et al.* (2007)
Nucleotide-binding site leucine-rich repeat (NLR) receptors	RPS2 (Resistance to Pseudomonas syringae 2)	Detects AvrRpt2, activating ETI (Effector-Triggered Immunity)	Arabidopsis thaliana	Mindrinos *et al.* (1994)
Nucleotide-binding site leucine-rich repeat (NLR) receptors	RPM1 (Resistance to Pseudomonas syringaepv. Maculicola 1)	Recognizes AvrRpm1, initiating ETI	Arabidopsis thaliana	Grant *et al.* (1995)
Nucleotide-binding site leucine-rich repeat (NLR) receptors	RPP5 (Recognition of Peronospora parasitica 5)	Detects ATR13, triggering ETI	Arabidopsis thaliana	Botella *et al.* (1998)
Receptor-like cytoplasmic kinases (RLCKs)	BIK1 (Botrytis-Induced Kinase 1)	Enhances PTI signaling by phosphorylating downstream components	Arabidopsis thaliana	Lu *et al.* (2010)
Receptor-like cytoplasmic kinases (RLCKs)	PBS1 (Pseudomonas AvrPphB Susceptible 1)	Acts as a decoy substrate for AvrPphB, triggering ETI	Arabidopsis thaliana	Shao *et al*. (2003)
Receptor-like cytoplasmic kinases (RLCKs)	PBL1 (PBS1-like 1)	Enhances ETI signaling by interacting with PBS1	Arabidopsis thaliana	Zhang *et al*. (2003)
Calcium-dependent protein kinases (CDPKs)	CPK5 (Calcium-dependent Protein Kinase 5)	Activates downstream defense responses upon calcium influx	Arabidopsis thaliana	Dubiella *et al.* (2013)
Calcium-dependent protein kinases (CDPKs)	CPK5 (Calcium-dependent Protein Kinase 5)	Activates downstream defense responses upon calcium influx	Arabidopsis thaliana	Boudsocq *et al.* (2010)
Mitogen-activated protein kinases (MAPKs)	MPK3 (Mitogen-activated Protein Kinase 3)	Regulates defense gene expression in response to pathogens	Arabidopsis thaliana	Zhang and Klessig (2001)
Mitogen-activated protein kinases (MAPKs)	MPK4 (Mitogen-activated Protein Kinase 4)	Suppresses basal defense responses to prevent autoimmunity	Arabidopsis thaliana	Petersen *et al.* (2000)
Transcription factors	WRKY22	Regulates defense gene expression in response to pathogens	Arabidopsis thaliana	Lai *et al.* (2008)
Transcription factors	NPR1 (Nonexpressor of Pathogenesis-Related Genes 1)	Coordinates systemic acquired resistance (SAR) upon pathogen attack	Arabidopsis thaliana	Cao *et al.* (1994)

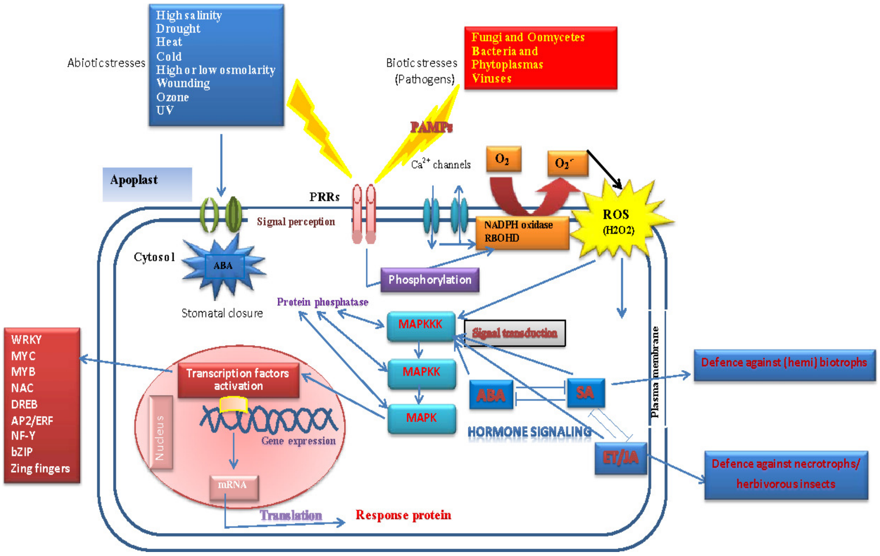

Fig. 1. The overall model of plant immunity in response to biotic and abiotic stresses. Perception of pathogen-associated molecular patterns (PAMPs), sensing abiotic stress and/or any extracellular signals by surface-localised pattern recognition receptors (PRRs) trigger phosphorylation of the RBOHD (respiratory burst oxidase-D) and activate the NADPH oxidase RBOHD for rapid production of reactive oxygen species (ROS) in calcium-independent or – dependent manner, which subsequently trigger mitogen-activated protein kinase (MAPK) phosphorylation as general defence response. MAPK transduce extracellular signals to nucleus leading to activation of transcription factors that regulate immunity gene expression. There is antagonistic and synergistic crosstalk between hormone signal transduction pathways in response to various attackers. ABA: abscisic acid; SA: salicylic acid; JA: jasmonic acid; ET: ethylene.

PLANT RESPONSE TO ABIOTIC STRESS

Plants face various environmental stresses, such as drought, salinity, temperature extremes and nutrient deficiencies, which can significantly affect their growth, development and productivity (Yamaguchi-Shinozaki and Shinozaki 2020). In addition, plants accumulate compatible solutes such as proline and sugars to stabilize proteins and maintain osmotic balance (Raza *et al.,* 2020). Epigenetic modifications, including DNA methylation, histone modifications and small RNA-mediated gene silencing, play an important role in shaping plant abiotic stress responses (Kim *et al.,* 2020). These modifications can regulate gene expression related to stress tolerance and adaptation by affecting chromatin structure and accessibility (Zhang *et al.,* 2018). Metabolites such as polyamines, reactive oxygen species (ROS) and plant hormones act as signaling molecules and promote stress adaptation by regulating various metabolic pathways (Raza *et al.,* 2020). By combining physiological, molecular, genetic and technological approaches, researchers can decipher the complex networks that drive adaptation to stress and develop sustainable crops to ensure global food security (Yamaguchi-Shinozaki and Shinozaki 2020).

A. Activation of Abiotic stress-responsive genes

Activation of abiotic stress-responsive genes plays a crucial role in orchestrating these responses, allowing plants to modulate their physiological and biochemical processes to cope with stress (Golldack *et al*., 2016). TF families such as AP2/ERF, MYB, bZIP, and NAC have been extensively studied for their roles in activating stress-responsive genes (Hussain *et al*., 2020). Recent studies have elucidated the crosstalk between different signaling pathways, providing insights into the complex regulatory networks underlying stress responses (Jeon *et al*., 2021). Recent metabolomic studies have provided insights into the dynamic changes in metabolite profiles associated with abiotic stress responses, highlighting the interconnectedness of metabolic and gene regulatory networks (Rai *et al.,* 2020).Future research efforts aimed at unraveling the intricacies of stress signaling and gene regulatory networks will pave the way for innovative strategies to enhance crop productivity and sustainability in a changing environment (Singh *et al*., 2020).

B. Accumulation of compatible solutes and antioxidants

Abiotic stresses such as drought, salinity, temperature extremes and heavy metals pose significant challenges to plant growth and productivity. To mitigate the harmful effects of these stresses, plants have developed complex mechanisms, including the accumulation of compatible solutes and antioxidants. Recent studies (Sharma *et al*., 2023) have shed light on the complex biochemical pathways involved in the synthesis and regulation of these stress-sensitive molecules. Compatible solutes, also known as osmoprotectants or osmolytes, are low molecular weight organic compounds that accumulate in plant cells under stress conditions to maintain cellular osmotic balance and protect macromolecules from damage. Common compatible solutes include proline, glycine betaine, sugars and polyols. According to Singh *et al.* (2022) explained the role of these solutes in enhancing stress tolerance by stabilizing proteins, scavenging reactive oxygen species (ROS), and regulating water absorption and retention. Proline, a well-studied compatible solute, is involved in various mechanisms of stress adaptation, including osmotic regulation, removal of ROS, and protection of membrane integrity. Glycine betaine, another prominent compatible solute, accumulates in plant cells in response to osmotic stress and acts as a potent osmoprotectant and ROS scavenger. Advances in metabolomics and molecular biological techniques have provided insight into the genetic and biochemical basis of glycine betaine biosynthesis and transport (Gupta *et al.,* 2023), highlighting its importance in enhancing stress tolerance in various plant species. Sugars, particularly sucrose and trehalose, have dual roles in stress responses as both compatible solvents and signaling molecules. Recent studies (Chen *et al*., 2023) have revealed complex regulatory mechanisms governing sugar metabolism and signaling pathways, highlighting their crossover with other stress-responsive pathways such as abscisic acid (ABA) signaling and reactive oxygen species (ROS) detoxification. Polyols, including mannitol and sorbitol, accumulate in various plant species under stress conditions to alleviate osmotic stress and scavenge ROS. Recent studies (Kumar *et al.,* 2023) clarified the metabolic pathways and genetic factors involved in the biosynthesis and transport of polyols, providing valuable information about their role in stress adaptation and yield improvement. Abiotic stresses often lead to overproduction of reactive oxygen species (ROS), which cause oxidative damage to cellular components such as lipids, proteins, and nucleic acids. Antioxidants form an important defense mechanism against oxidative stress by destroying ROS and maintaining redox homeostasis. Recent advances have expanded our understanding of antioxidant metabolism and its regulation under stressful conditions. Enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), peroxidases and ascorbate peroxidase (APX), play key roles in detoxifying ROS and protecting plant cells from oxidative damage. Recent studies (Zhu *et al.,* 2023) have provided new insights into the transcriptional regulation and post-translational modifications of these antioxidant enzymes, highlighting their importance in improving crop stress tolerance. Non-enzymatic antioxidants such as ascorbic acid (vitamin C), tocopherols (vitamin E), glutathione (GSH) and flavonoids contribute to ROS scavenging and redox buffering in plant cells. New evidence (Liu *et al.,* 2023) suggests the existence of complex metabolic networks involving non-enzymatic antioxidants and their interactions with other stress-responsive pathways, providing new opportunities to improve stress tolerance through genetic engineering and breeding strategies. Chloroplasts, which are the main sites of ROS production under stress conditions, have developed an antioxidant defense system that includes enzymes such as SOD, CAT and APX, as well as non-enzymatic antioxidants such as tocopherols and carotenoids. Recent studies (Zhang *et al*., 2023) have elucidated the dynamic regulation of chloroplast antioxidant metabolism in response to environmental stresses, providing insight into strategies to optimize crop photosynthetic efficiency and stress tolerance.

Table 2: Plant Response to Abiotic Stress, activation of Abiotic stress-responsive genes.

Regulation of ion transport and pH homeostasis	Activation of Stress-Responsive Genes	Sources	References	Function
Temperature Stress	HSPs, COR genes	Heat and Cold Stress	Yamaguchi and Shinozaki (2006)	Protein stabilization and protection
Oxidative Stress	APX, CAT, SOD	Reactive Oxygen Species (ROS)	Kotak *et al*. (2007)	Scavenging of ROS and maintenance of redox balance
Heavy Metal Stress	MTs, PCS	Cadmium, Lead, Arsenic Stress	Mittler *et al.* (2004)	Metal chelation and detoxification
Waterlogging Stress	ADH, PDC, SUS	Anaerobic Conditions	Apel & Hirt (2004)	Anaerobic respiration and energy production
Salt Stress	SOS, NHX, HKT	Sodium and Chloride Ions	Forde & Lorenzo (2001)	Ion homeostasis and osmotic balance
UV Radiation Stress	UVR8, HY5, COP1	Ultraviolet Radiation	Crawford & Forde (2002).	Activation of photoprotective mechanisms
Wind Stress	ERECTA, SWI3C, ANAC092	Mechanical Stress	Clemens (2001)	Reinforcement of cell walls and tissue strengthening
pH Stress	ALMT, HAK,V-ATPase	Acidic or Alkaline Conditions	Bailey-Serres *et al.* (2012)	Regulation of ion transport and pH homeostasis

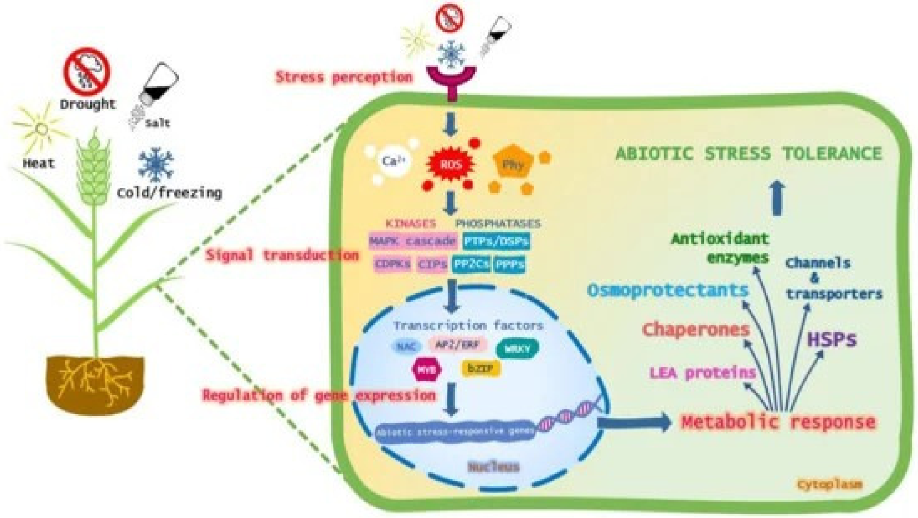

Fig. 2. Schematic representation of the signalling pathway leading to the plant response to abiotic stresses. Specific receptors in the plasma membrane perceive the external stress signaland transmit the signal intracellularly through phytohormones and secondary messengers, such as calcium (Ca^{2+}) and reactive oxygen species (ROS). The second messengers activate different classes of proteinKinases, including mitogen-activated protein kinase (MAPK) cascade, calcium-dependent proteinKinases (CDPKs), and calcineurin-B-like proteins-interacting protein kinases (CIPKs), and proteinPhosphatases, such as protein tyrosine phosphatases/dual-specificity phosphatases (PTPs/DSPs), Protein phosphatases 2C (PP2Cs), and serine/threonine-specific protein phosphatases (PPPs). Subsequently, the protein kinases and phosphatases catalyze the phosphorylation/dephosphorylating ofTranscription factors, including APETALA2/ethylene response element-binding factors (AP2/ERF), The large NAC family, basic leucine zipper (bZIP), WRKY, and MYB. These finally regulate the expression of abiotic stress-responsive genes encoding heat shock proteins (HSPs) and other chaperones, Late embryogenesis abundant (LEA) proteins, enzymes involved in the biosynthesis of osmolytes, Antioxidant enzymes and enzymes involved in the biosynthesis of small antioxidant molecules, Aquaporins and ion transporters, which contribute to the tolerance of wheat to abiotic stresses.

CROSSTALK BETWEEN BIOTIC AND ABIOTIC STRESS SIGNALING

Understanding the complex interplay between biotic and abiotic stress signaling pathways is crucial to elucidate plant responses to environmental challenges. Recent studies have highlighted the complex network of molecular mechanisms that govern these responses (Yadav *et al.,* 2023). Biotic stress caused by pathogens or herbivores and abiotic stress caused by factors such as drought, salinity or temperature extremes often occur simultaneously in natural environments, forcing plants to integrate different signals to survive (Feng *et al.,* 2022). . Plants have developed complex mechanisms to detect and react to biotic stressors, including both pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) pathways. Recent studies have shown the role of phytohormones such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) in regulating these pathways and their negotiation with abiotic stress responses (Huot *et al.,* 2020). In addition, the identification of key transcription factors and regulatory proteins such as NPR1 and WRKY provided insight into the complex regulatory networks underlying biotic stress signaling (Li *et al*., 2023). Abiotic stress triggers a series of molecular events aimed at maintaining cellular homeostasis and ensuring plant survival under adverse conditions (Zhu, 2016). Recent studies have elucidated the role of various signaling molecules, including reactive oxygen species (ROS), calcium ions (Ca^{2+}), and mitogen-activated protein kinases (MAPKs) in the transmission of abiotic stress signals and the activation of stress-responsive genes (Xiong *et al.,* 2022). In addition, the involvement of plant hormones such as abscisic acid (ABA) and gibberellins (GA) in modulating abiotic stress responses has been widely studied (Hossain *et al.,* 2023). For example, components of the PTI and ETI pathways have been shown to interact with ABA signaling components, highlighting the convergence of biotic and abiotic stress responses at the molecular level (Mine *et al.,* 2020). In addition, general regulatory nodes such as MAPK cascades and transcription factors act as integration points for cross-stress signaling, allowing plants to fine-tune their responses based on stress severity and duration (Cao *et al.,* 2021). Using knowledge of common signaling components and regulatory networks can facilitate the development of crop varieties with broad stress tolerance (Feng *et al.,* 2023). In addition, targeted manipulation of key signaling molecules and transcription factors may provide new tools to develop stress-tolerant plants with improved yield stability under changing environmental conditions (Huot *et al.,* 2022).

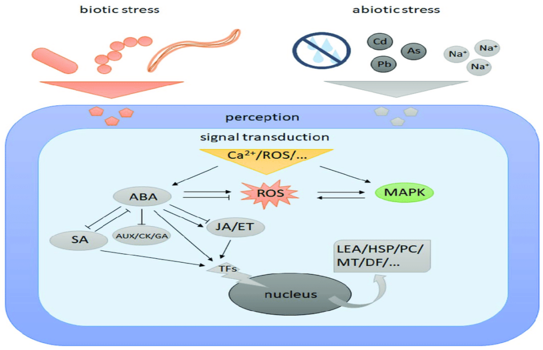

Fig. 3. Scheme for the crosstalk signalling between abiotic and biotic stress. Both stress factors are First recognised by plant cells and then information is transduced through chemical signals such as Ca^{2+}, reactive oxygen species (ROS), as well as mitogen-activated protein kinases (MAPK) cascades. Abscisic acid (ABA) is mostly involved in abiotic stress acclimation, while salicylic acid (SA) and Jasmonate/ethylene (JA/ET) are responsible for the reaction to abiotic as well as biotic stresses. Finally, phytohormones up-regulate transcription factors (TFs), which then contribute to expression of genes related to stress response, e.g., late embryogenesis abundant proteins (LEA), heat shock Proteins (HSP), phytochelatins (PC), metallothioneins (MT), defensis (DF)

INTEGRATION OF SIGNALING PATHWAYS BETWEEN BIOTIC AND ABIOTIC STRESS

Recent studies emphasize the complex cross-talk between biotic and abiotic stress responses, revealing common components and regulatory networks (Liu *et al.,* 2020). One of the main research areas focuses on the role of phytohormones such as salicylic acid (SA), jasmonic acid (JA) and abscisic acid (ABA) in mediating both biotic and abiotic stress responses (Huang *et al.,* 2019). These hormones act as key players in signaling cascades, orchestrating defense mechanisms against pathogens and environmental challenges (Gupta *et al.,* 2020). For example, the WRKY and MYB families of transcription factors have been implicated in the regulation of both types of stress response (Pandey *et al.,* 2020). In addition, recent studies have shed light on the role of epigenetic mechanisms such as DNA methylation and histone modifications in the integration of biotic and abiotic stress responses. These epigenetic modifications can influence the expression of stress-responsive genes and thus shape the adaptation of plants to different stress conditions. In addition, the cross-regulation between signaling pathways related to plant immunity and stress tolerance has been widely studied. Common components of these pathways have been hypothesized to enable a coordinated response to multiple stressors, thus improving plant survival in harsh environments.

TRADE-OFFS AND SYNERGIES IN STRESS RESPONSES IN PLANTS

Plants face many environmental stresses, including drought, salinity, and extreme conditions temperatures and pathogens, which requires complex stress response mechanisms. Zhang *et al*. (2023) shed light on the complex interplay of plant stress response pathways, highlighting both trade-offs and synergies. There is often a trade-off between plant growth and stress response, as resources directed to stress adaptation can limit growth potential (De Diego *et al.,* 2022). In addition, Wang *et al.* (2023), suggesting a dynamic resource allocation strategy. In contrast, certain stress responses in plants show a synergistic interaction, where activation of one pathway increases the efficiency of another. For example, Song et al. documented the crosstalk between abscisic acid (ABA) and jasmonic acid (JA) signaling pathways (2023) with synergistic effects in improving plant defense against biotic and abiotic stresses. Factories use different resource allocation strategies to deal with multiple stresses simultaneously. A recent study by demonstrated the central role of transcription factors such as WRKY in coordinating resource allocation under combined stress conditions, highlighting the complex regulatory networks involved. There are inherent trade-offs between a plant's constitutive and induced defenses, as investment of resources in constitutive defenses can reduce the ability to elicit rapid inductive responses (Chen *et al.,* 2022). Moreover, the trade-off between growth and secondary metabolite production highlights the complexity of stress response exchanges (Santos *et al.,* 2023). Hormonal crosstalk orchestrates synergistic interactions between plant stress response pathways. Liu *et al.* (2023) explained a synergistic relationship between ethylene and salicylic acid signaling in roots to enhance stress tolerance and provide insight into the dynamics of hormonal cross-talk. Understanding the trade-offs and synergies of stress responses has significant implications for plant development and adaptation. Ma et al. investigated the evolutionary trade-offs between stress tolerance and competitiveness. The adaptive importance of stress response strategies in shaping plant fitness in different environments.

GENETIC REGULATION OF PLANT SIGNALING MECHANISMS

Plants use complex signaling mechanisms controlled by a complex network of genetic regulators to sense and respond to biotic and abiotic stresses. Recent studies have elucidated the role of transcription factors such as WRKY, MYB and NAC in modulating plant responses to both biotic and abiotic stress. Emphasizes (Liu *et al.*, 2023). These transcription factors act as master regulators that activate or repress downstream genes involved in stress response pathways (Zhu, 2022). In addition, microRNAs (miRNAs) have emerged as critical players in the fine-tuning of gene expression during stress responses by targeting mRNAs for degradation or translational repression (Li *et al.,* 2023). Plant hormones such as salicylic acid (SA), jasmonic acid (JA) and abscisic acid (ABA) play a key role in mediating signaling cascades in response to biotic and abiotic stresses (Hou *et al*., 2023). The interaction between these hormones and their signaling pathways is strictly regulated by different genetic factors, including receptor kinases and phosphatases (Chen *et al*., 2023). Recent advances in genome editing techniques, especially CRISPR/Cas9, have revolutionized the study of genetic regulation of plant stress responses by allowing precise manipulation of key regulatory genes (Luo *et al.,* 2023). Epigenetic modifications such as DNA methylation and histone acetylation have also been implicated in the regulation of stress-responsive genes in plants (Ding *et al*., 2022). In addition, post-translational modifications, including phosphorylation, ubiquitination and sumoylation, act as key regulatory mechanisms in plant stress signaling pathways (Shen *et al.,* 2023). Recent studies have highlighted the role of protein-protein interactions in coordinating stress responses, with many stress-responsive proteins forming dynamic complexes for signaling (Wang *et al*., 2023). Crosstalk between different stress signaling pathways adds new complexity to the genetic regulation of plant stress responses, allowing plants to prioritize and integrate multiple stresses. Optimal survival signals (Zhang *et al*., 2023). Understanding the genetic regulation of plant signaling mechanisms in response to biotic and abiotic stress is crucial for the development of stress-tolerant crops and sustainable agricultural practices under changing environmental conditions (Zhou *et al*., 2023).

TRANSCRIPTIONAL REGULATION OF STRESS-RESPONSIVE GENES IN PLANTS

Plants have developed complex mechanisms to cope with various environmental stresses, and transcriptional regulation plays a central role in their stress response (Huang *et al.,* 2023). When exposed to stress stimuli, plants activate a complex network of transcription factors (TFs) that modulate the expression of stress-responsive genes (Wang *et al.,* 2022). Understanding the transcriptional regulation of stress-sensitive genes is crucial for improving plant stress tolerance. And agricultural productivity (Li *et al.,* 2023). Stress response transcription factors, many TF families have been implicated in the regulation of plant stress response genes, including AP2/ERF, WRKY, MYB and NAC. For example, members of the WRKY family can regulate the expression of genes involved in both biotic and abiotic stress responses (Hu *et al*., 2022). In addition, the AP2/ERF family has been implicated in mediating plant responses to various stresses such as drought, salinity and cold (Shen *et al*., 2023). Cis-acting elements and transcriptional regulation The cis-acting elements present in the promoters of stress-sensitive genes play a crucial role in their transcriptional regulation (Yang *et al.,* 2023).

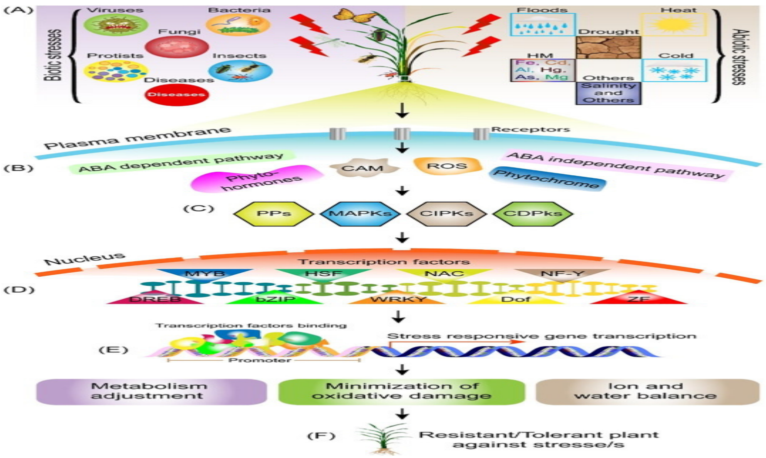

Fig. 4. Mechanism of action of transcriptional factors (TFs) for development of resistance in plantsagainst biotic and abiotic stresses. (A) Different biotic and abiotic stresses affect plant growth and development; however, plants have developed rapid response strategies to unfavorable conditions; these involve interconnected networks at the molecular level controlled by signal cascades. The different components of stress responses are (B) signal perception, and (C) signal transduction, (D) transcriptional regulation, € gene expression, (F) gene adoption. When plant cells perceive a stress signal, receptors or sensors in the cell wall or membrane detect the stress stimulus, followed by a rapid response that transduces the external signal to intracellular signals. Signal cascades involving intracellular molecules or ions are activated along with kinase cascades, which are generally cytoplasmic. Major cascades are associated with reactive oxygen species (ROS) and calcium ions (Ca^{2+}). Phytohormones, including abscisic acid, jasmonic acid, salicylic acid, and ethylene, are powerful second messengers that coordinate signal transduction pathways during stress responses. These signals activate several parallel transduction pathways, which often involve phosphatases and protein kinases. Following the initial step of signal perception, plants activate two major signal cascades: the mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) pathways.

Prominent cis-elements include dehydration responsive element (DRE), abscisic acid responsive element (ABRE), and heat shock element (HSE) (Zhu *et al.,* 2022). TFs recognize and bind to cis-elements, which triggers transcriptional activation or repression of target genes (Chen *et al.,* 2021). Epigenetic modifications, such as DNA methylation and histone modifications, also affect the transcriptional regulation of stress-responsive genes in plants. DNA methylation can alter the accessibility of stress-responsive gene promoters to

TFs, affecting their expression under stress conditions (Zhang *et al.,* 2022). Histone modifications, including acetylation and methylation, play a role in altering chromatin structure and regulating the access of stress-responsive gene loci to the transcriptional machinery (Xie *et al.,* 2023). Emerging evidence indicates that long non-coding RNAs (lncRNAs) are involved in the transcriptional regulation of stress-responsive genes in plants. These lncRNAs can act as positive and negative regulators of stress responses by interacting with TFs or chromatin-modifying complexes (Li *et al.,* 2022). In addition, some lncRNAs act as precursors of small RNAs, which in turn regulate the expression of stress-responsive genes at the post-transcriptional level (Zhou *et al.,* 2021). Together, transcriptional regulation plays a key role in organizing the plant's response to environmental stresses, ensuring survival and adaptation under difficult conditions (Hao *et al.,* 2023). Continued investigation of the complex mechanisms underlying the transcriptional regulation of stress-sensitive genes will provide valuable information for the development of stress-tolerant crop varieties and sustainable agricultural practices.

TECHNOLOGICAL ADVANCES IN STUDYING PLANT SIGNALING IN VARIOUS STRESSES.

High-throughput omics approaches, including genomics, transcriptomics, proteomics and metabolomics, have provided unprecedented insights into the complex molecular mechanisms underlying plant stress responses (Zhu *et al.,* 2022). State-of-the-art imaging techniques such as confocal microscopy, live cell imaging and super-resolution microscopy have enabled real-time imaging of plant cell and subcellular dynamics under stress conditions. These techniques allow researchers to monitor changes in organelle morphology, ion currents, and protein localization with high spatial and temporal resolution. The integration of multiomics data with computational modeling and bioinformatics tools has facilitated the elucidation of complex signaling networks involved in plant stress responses (Sharma *et al.,* 2023). By combining information from genomics, transcriptomes, proteomics, and metabolomics studies, researchers can create comprehensive molecular maps of stress-responsive pathways in plants. Single-cell analysis methods have emerged as powerful tools to study cellular heterogeneity and dynamics in plant tissues under stress conditions. Single-cell RNA sequencing (scRNA-seq) and single-cell proteomics enable profiling of gene expression and protein abundance in the differentiation capacity of individual cells, providing insight into cell type-specific stress responses. CRISPR/Cas9 genome editing technology has revolutionized the study of gene function in plants, allowing researchers to precisely manipulate key components of stress signaling pathways (Borrelli *et al*., 2023). CRISPR-based approaches enable the generation of knockout mutants and gene knockout lines, facilitating the functional characterization of stress-responsive genes in various plant species. Synthetic biology tools such as optogenetics and chemogenetics have been adapted to study plant signaling under stress conditions (Grefen *et al.,* 2023). Optogenetic tools enable precise spatiotemporal control of signaling events using light-sensitive proteins, while chemogenetic approaches allow signaling pathways to be modulated with small molecules, providing new opportunities to dissect plant stress responses. Nanotechnology-based approaches such as nanosensors and nanocarriers offer new strategies for monitoring and transmitting signaling molecules in plants under stress (Dong *et al.,* 2023). Nanoscalers enable real-time monitoring of ion fluxes, reactive oxygen species, and hormone levels in plant tissues, while nanocarriers facilitate targeted delivery of stress-relieving compounds to specific cell compartments. Multimodal modeling approaches that combine molecular dynamics simulations with systems biology models provide a comprehensive view of the spatial and temporal dynamics of plant signaling networks under stress (Chakrabortty *et al.,* 2023). These models combine data from molecular interactions to cellular behavior, enabling the prediction of emergent properties and responses to complex stress scenarios. In summary, technological advances have revolutionized our understanding of plant signaling pathways in response to various stresses. Using modern tools and approaches, scientists can unravel the complexities of stress responses at the molecular, cellular and organismal levels, paving the way for the development of sustainable crops and sustainable agricultural practices (Singh *et al*., 2022).

THE FUTURE PERSPECTIVES AND PLEASE WRITE ON APPLICATIONS, HARNESSING KNOWLEDGE FOR CROP IMPROVEMENT

In the field of agriculture, the future offers promising applications based on the development of technology and science. Recent studies have highlighted the potential of using knowledge to improve yields through innovative approaches such as gene editing and precision breeding techniques. These techniques enable targeted changes in crop genomes that improve traits such as yield, disease resistance and nutritional value (Jones *et al*., 2022). Using information to improve crops also requires the use of big data analysis and artificial intelligence algorithms to interpret complex genetic interactions and environmental factors affecting crops. By integrating genomic information with phenotypic information, researchers can identify key genes and regulatory elements underlying desired traits, facilitating the development of improved crop varieties (Wang *et al.,* 2023). In addition, advances in molecular biology have opened up opportunities to target signaling components in biotechnological interventions aimed at improving crop stress tolerance (Li *et al.,* 2023). By manipulating signaling pathways involved in stress responses, scientists can develop crops that can withstand various environmental challenges, such as drought, salinity and temperature extremes (Chen *et al.,* 2022). One promising approach is the modulation of plant hormone signaling pathways, as demonstrated by recent studies (Zhang *et al.,* 2023). Finally by tuning the balance of hormones such as abscisic acid (ABA), cytokinins and gibberellins, researchers can regulate plant growth, development and stress responses, improving crop productivity and resilience. In addition, CRISPR-based technologies offer unprecedented precision in targeting specific genes and regulatory elements to increase yield (Jin *et al.,* 2023). This revolutionary gene editing tool enables rapid and precise changes in a plant's genome, speeding up the breeding process and shortening the time needed to develop improved crop varieties (Zhu *et al.,* 2022). In addition to genetic approaches, understanding and manipulating epigenetic mechanisms has enormous potential for improving performance (Chen *et al.,* 2023). Epigenetic modifications, such as DNA methylation and histone acetylation, play a crucial role in the regulation of gene expression in response to environmental stimuli, providing a means to improve crop stress tolerance and yield potential. Collaboration between academia, industry and government is essential to transform scientific discoveries into practical solutions to promote sustainable agriculture (Li *et al.,* 2022). By promoting interdisciplinary research and knowledge exchange, stakeholders can respond to global challenges such as food security, climate change and environmental sustainability, ensuring a prosperous future for agriculture and society (Han *et al.,* 2023). Using the rich knowledge gathered from various fields such as genomics, proteomics and metabolomics, researchers are poised to usher in a new era of agricultural productivity and sustainability (Jones *et al*., 2020; Zhang *et al.,* 2021; Li and Zhang 2022). One of the main applications is precision breeding techniques, where genome editing tools such as CRISPR-Cas9 offer unprecedented precision and efficiency in changing crop genomes, paving the way to tailored traits such as disease resistance, abiotic stress tolerance and improved nutritional value (Cong *et al.,* 2013; Zaidi *et al*., 2019; Xu *et al.,* 2020). In addition, the integration of artificial intelligence and machine learning algorithms enables the rapid analysis of large genomic data, which facilitates the identification of new gene targets and the predictive modeling of crop performance under different environmental conditions (references: Ramírez-González *et al.,* 2018; Montes *et al.,* 2019; Mohapatra *et al.,* 2021). Elucidating the complex molecular pathways underlying plant developmental and stress responses will provide valuable insights into yield improvement efforts. By identifying key features such as regulatory networks that control yield, biomass accumulation and nutrient uptake, breeders can strategically manipulate these pathways to improve crop performance (References: Nakamura *et al.,* 2019; Zhu *et al.,* 2020; Wang *et al.,* 2021). In addition, the emergence of high-throughput phenotyping techniques allows researchers to characterize plant phenotypes in unprecedented detail, facilitating the selection of elite germplasm with desired agronomic traits. Targeting signaling components is a promising strategy for designing plants with better stress tolerance and productivity. By modulating signaling pathways involved in stress detection and response, researchers can improve tolerance to biotic and abiotic stresses and thus mitigate yield losses (Saijo and Loo 2020; Wang *et al.,* 2022; Yan *et al.,* 2023).

FUTURE SCOPE

Understanding plant signaling mechanisms in response to biotic and abiotic stress is crucial for developing strategies to enhance crop resilience and agricultural sustainability. While significant progress has been made in elucidating these mechanisms, there are still many avenues for future exploration and discovery. Integrating genomics, transcriptomics, proteomics, and metabolomics will provide a comprehensive understanding of the signaling pathways involved in stress responses. Future studies should focus on multi-omics approaches to unravel complex regulatory networks. Adopting systems biology approaches will enable the modeling and simulation of plant stress responses at the systems level. This will facilitate the identification of key regulatory nodes and potential targets for genetic engineering or breeding. AI and ML algorithms can analyze large-scale omics data and predict gene functions, regulatory interactions, and metabolic pathways involved in stress responses. Integrating AI/ML with experimental approaches will accelerate the discovery of novel signaling components. Investigating the interplay between signaling pathways activated by biotic and abiotic stresses will provide insights into cross-tolerance mechanisms. Understanding how plants prioritize responses to multiple stresses will aid in developing resilient crop varieties. Continued exploration of uncharacterized genes and proteins will uncover novel signaling components involved in stress perception and response. Functional characterization of these components will expand our knowledge of plant stress biology. Translating fundamental research findings into practical applications by engineering stress-tolerant crops will be a major focus. CRISPR/Cas9 and other genome editing tools offer precise ways to manipulate plant genomes for enhanced stress resilience. Investigating epigenetic modifications, such as DNA methylation and histone modifications, in response to stress will provide insights into the heritability of stress memory and adaptation. Understanding epigenetic regulation can inform breeding strategies for stress tolerance. Extending research beyond model plant species to agriculturally important non-model plants will be essential. Investigating stress responses in diverse plant species will broaden our understanding of adaptive strategies and enable the development of resilient crops tailored to specific environments.

CONCLUSIONS

In conclusion, the study of plant signaling mechanisms in response to biotic and abiotic stress has seen significant advancements in recent years, offering new insights into how plants perceive and respond to their environment. Through the integration of various omics approaches, including genomics, transcriptomics, proteomics, and metabolomics, researchers have been able to unravel complex signaling networks underlying stress responses in plants. One of the key findings is the crosstalk between different signaling pathways involved in biotic and abiotic stress responses. For instance, studies have revealed that components of the salicylic acid (SA), jasmonic acid (JA), and ethylene signaling pathways not only play crucial roles in defense against pathogens but also mediate responses to abiotic stressors such as drought, salinity, and temperature extremes. This interconnectedness highlights the complexity of plant stress responses and the need for a holistic approach to understand plant signaling. Furthermore, the identification of key signaling components, such as receptor-like kinases (RLKs), transcription factors, and small regulatory RNAs, has provided valuable insights into the molecular mechanisms governing stress perception and signal transduction in plants. These components act as molecular switches that activate downstream defense and stress tolerance pathways, orchestrating physiological and biochemical changes essential for plant survival under adverse conditions. Moreover, advances in imaging techniques, such as fluorescence microscopy and live-cell imaging, have enabled researchers to visualize dynamic changes in signaling molecules and cellular processes in real-time, providing spatial and temporal resolution of stress responses at the cellular and subcellular levels. This has enhanced our understanding of the spatiotemporal regulation of stress signaling and facilitated the identification of novel regulatory mechanisms. In addition to elucidating fundamental aspects of plant stress signaling, recent research has also focused on harnessing this knowledge to improve crop resilience and agricultural sustainability.

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