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Invited Review **Open Access**

Mechanisms of Environmental Stress Resistance in Kiwifruit: A Systematic Review

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Abstract This study aims to examine the physiological, biochemical, and molecular mechanisms underlying kiwifruit's resistance to both abiotic stresses-such as drought, cold, heat, and salinity-and biotic stresses, including pathogen and pest resistance. The study delves into mechanisms such as water use efficiency, antioxidant responses, secondary metabolite production, and gene regulation, which contribute to stress tolerance. Additionally, advances in molecular breeding, genomics, and proteomics are explored, with a specific focus on resistance to bacterial canker. Integrative approaches, including the potential application of CRISPR/Cas9 and other biotechnological innovations, are discussed as avenues to enhance kiwifruit resilience. The study identifies key research gaps and emphasizes the need for interdisciplinary collaborations to address the complexities of stress resistance. Future research should focus on developing comprehensive strategies to improve kiwifruit stress tolerance, thereby supporting sustainable production.

Keywords Kiwifruit; Environmental stress; Drought resistance; Molecular breeding; Antioxidant responses

1 Introduction

Kiwifruit, belonging to the genus *Actinidia*, is a perennial fruit tree known for its high nutritional and economic value. The most commonly cultivated species include *Actinidia chinensis* and *Actinidia deliciosa*, which are prized for their rich vitamin C content and unique flavor. However, the cultivation of kiwifruit is significantly challenged by various environmental stresses, including drought, salinity, cold, waterlogging, and pathogen attacks (Zhang et al., 2019; Abid et al., 2022). Environmental stressors can severely impact the growth, yield, and quality of kiwifruit. For instance, drought and salinity stress can lead to reduced photosynthetic activity and impaired metabolic functions, ultimately affecting fruit development and productivity. Cold stress, particularly freezing temperatures, poses a significant threat to kiwifruit, causing chilling injuries that degrade fruit quality during storage (Lin et al., 2021). Waterlogging, another critical stress factor, can lead to root hypoxia, affecting the plant's overall health and resilience (Hill et al., 2015; Li et al., 2022). Additionally, pathogen stress, such as infections by *Pseudomonas syringae* pv. *actinidia*e, can cause bacterial canker, leading to substantial economic losses in the kiwifruit industry (Wang et al., 2018).

Understanding the mechanisms of environmental stress resistance in kiwifruit is crucial for sustaining and improving production in the face of changing climate conditions. With rising instances of extreme weather events, including prolonged droughts, heat waves, and unpredictable frosts, it is imperative to develop kiwifruit varieties that can withstand such challenges (Baldi et al., 2024). Moreover, the increasing threat from pests and diseases, such as bacterial canker, further emphasizes the need for robust resistance mechanisms (Zhang et al., 2023). Studying the plant's response to these stresses at the physiological, biochemical, and molecular levels can provide insights into breeding strategies and biotechnological interventions aimed at enhancing resilience (Jin et al., 2021).

This study attempts to compile and analyze the current body of research on the mechanisms of stress resistance in kiwifruit, discuss the physiological, biochemical, and molecular responses of kiwifruit to abiotic and biotic stresses, and provide an overview of key resistance pathways, advances in breeding, and biotechnological approaches. Additionally, it seeks to identify research gaps and propose future directions to support the development of stress-resistant kiwifruit cultivars.

2 Environmental Stresses Affecting Kiwifruit

2.1 Abiotic stresses

Drought stress is a significant abiotic factor that affects kiwifruit growth and productivity. The R1R2R3-MYB transcription factor AcMYB3R has been identified as a key player in enhancing drought tolerance in kiwifruit. Overexpression of AcMYB3R in *Arabidopsis thaliana* has shown to upregulate stress-responsive genes such as RD29A, RD29B, COR15A, and RD22, leading to improved drought resistance (Zhang et al., 2019).

Cold stress, including chilling injury, poses a major challenge for kiwifruit storage and quality. The bZIP transcription factor AchnABF1 has been found to enhance cold tolerance by upregulating genes associated with ABA-dependent and ABA-independent pathways, as well as improving ROS-scavenging abilities (Jin et al., 2021). Additionally, the bZIP transcription factor AcePosF21 regulates ascorbic acid biosynthesis, which helps mitigate oxidative damage caused by cold stress (Liu et al., 2023).

Heat stress can adversely affect kiwifruit by disrupting cellular homeostasis and metabolic processes. Although specific studies on heat stress in kiwifruit are limited, the general stress-responsive mechanisms involving transcription factors like AcMYB3R, which also respond to heat stress, suggest potential pathways for enhancing heat tolerance (Zhang et al., 2019).

Salt stress is another critical abiotic factor that impacts kiwifruit. The AcMYB3R transcription factor has been shown to enhance salt tolerance by upregulating stress-responsive genes in transgenic *Arabidopsis thaliana*, indicating its potential role in improving salt stress resistance in kiwifruit (Figure 1) (Zhang et al., 2019).

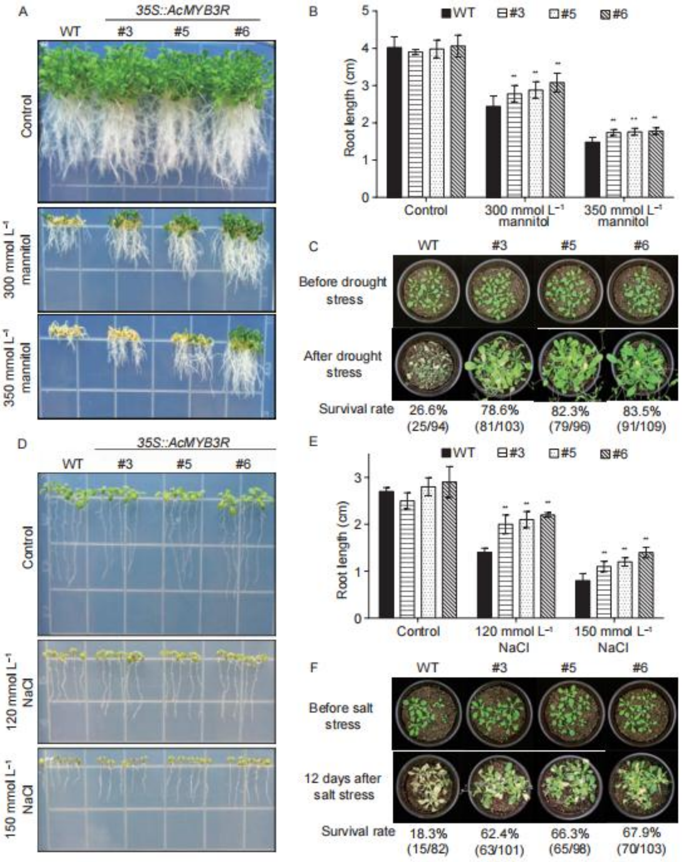

Figure 1 Overexpression of *AcMYB3R* results in enhanced drought or salt tolerance (Adopted from Zhang et al., 2019)

Image caption: A and B, phenotypes and the root length of wild type (WT) and *AcMYB3*R-overexpressing lines (#3, #5 and #6) under mimic drought stress on 0.5× MS medium. C, phenotype of WT and *AcMYB3R*-overexpressing lines (#3, #5 and #6) before and after drought stress treatments in pots. D and E, phenotypes and the root length of WT and *AcMYB3R*-overexpressing lines (#3, #5 and #6) under salt stress on 0.5× MS medium. F, phenotype of WT and *AcMYB3R*-overexpressing lines (#3, #5 and #6) before and after NaCl treatment in pots. Data in Fig. 4-B and E are mean±SD from three independent experiment. **, significant differences at $P<0.01$ by Student's *t*-test (Adopted from Zhang et al., 2019)

2.2 Biotic stresses

Bacterial canker caused by *Pseudomonas syringae* pv. *actinidia*e (Psa) is a severe threat to kiwifruit production. Several studies have identified mechanisms and genetic loci associated with Psa resistance. For instance, quantitative trait loci (QTLs) have been mapped to identify genetic markers for Psa resistance, providing insights into breeding resistant cultivars (Tahir et al., 2019). Additionally, salicylic acid (SA) has been found to enhance resistance by upregulating defense-related proteins and pathways (Qu et al., 2023). Sulfur treatments have also been shown to induce resistance by increasing phenolic components and modifying morphological structures in kiwifruit stems (Gu et al., 2021).

Pest resistance in kiwifruit involves complex interactions between the plant and various pests. While specific studies on pest resistance mechanisms in kiwifruit are limited, general plant defense responses, including the activation of stress-responsive genes and pathways, play a crucial role in mitigating pest damage. The role of transcription factors and signaling molecules in enhancing overall stress resistance can indirectly contribute to improved pest resistance (Tahir et al., 2019; Zhang et al., 2019; Qu et al., 2023). By understanding these mechanisms, researchers and breeders can develop strategies to enhance kiwifruit resistance to both abiotic and biotic stresses, ensuring sustainable production and quality.

3 Physiological Mechanisms of Stress Resistance

3.1 Water use efficiency and drought resistance

Kiwifruit plants exhibit various physiological adaptations to enhance water use efficiency and drought resistance. The R1R2R3-MYB transcription factor AcMYB3R has been identified as a key player in improving drought tolerance. Overexpression of AcMYB3R in *Arabidopsis thaliana* resulted in upregulation of stress-responsive genes such as RD29A, RD29B, COR15A, and RD22, which are crucial for drought resistance (Zhang et al., 2019). Additionally, the abscisic acid (ABA) pathway plays a significant role in drought response, with ABA levels increasing significantly under drought conditions, leading to the upregulation of ABA-responsive genes (Wurms et al., 2023).

3.2 Temperature tolerance mechanisms

Temperature tolerance in kiwifruit involves complex regulatory networks. The bZIP transcription factor AchnABF1 has been shown to enhance cold tolerance by upregulating key genes associated with ABA-dependent and ABA-independent pathways. This transcription factor also improves reactive oxygen species (ROS) scavenging ability, reducing oxidative damage under cold stress (Jin et al., 2021). Another bZIP transcription factor, AcePosF21, regulates ascorbic acid (AsA) biosynthesis, which is crucial for neutralizing ROS induced by cold stress. Overexpression of AcePosF21 leads to increased AsA levels and reduced oxidative damage (Figure 2) (Liu et al., 2023).

3.3 Salt exclusion and osmotic adjustment

Salt stress tolerance in kiwifruit involves mechanisms such as salt exclusion and osmotic adjustment. The NAC domain transcription factor AvNAC030 enhances salt tolerance by improving osmotic adjustment ability and antioxidant defense mechanisms (Li et al., 2021). Additionally, the *HSF* gene *AeHSFA2b* has been shown to improve salt tolerance by increasing the expression of genes involved in osmotic adjustment and ROS scavenging (Ling et al., 2023). Comparative studies of different kiwifruit genotypes under salt stress revealed that genotypes with higher proline and total soluble sugar levels exhibited better osmotic adjustment and salt tolerance (Abid et al., 2020).

3.4 Antioxidant responses to biotic and abiotic stress

Antioxidant responses are critical for kiwifruit's resistance to both biotic and abiotic stresses. The bZIP transcription factor AchnABF1 enhances ROS-scavenging ability by increasing the activity of catalase (CAT) and peroxidase (POD), thereby reducing oxidative damage under various stresses (Jin et al., 2021). Similarly, the expression of genes encoding antioxidant enzymes such as APX, GST, and GR is upregulated under salt stress, contributing to enhanced stress tolerance (Abid et al., 2020). The role of antioxidants in mitigating oxidative damage is further supported by the increased activity of peroxidase (POD) and catalase (CAT) under waterlogging stress (Li et al., 2022). By understanding these physiological mechanisms, researchers can develop strategies to improve the stress resistance of kiwifruit, ensuring better crop yield and quality under adverse environmental conditions.

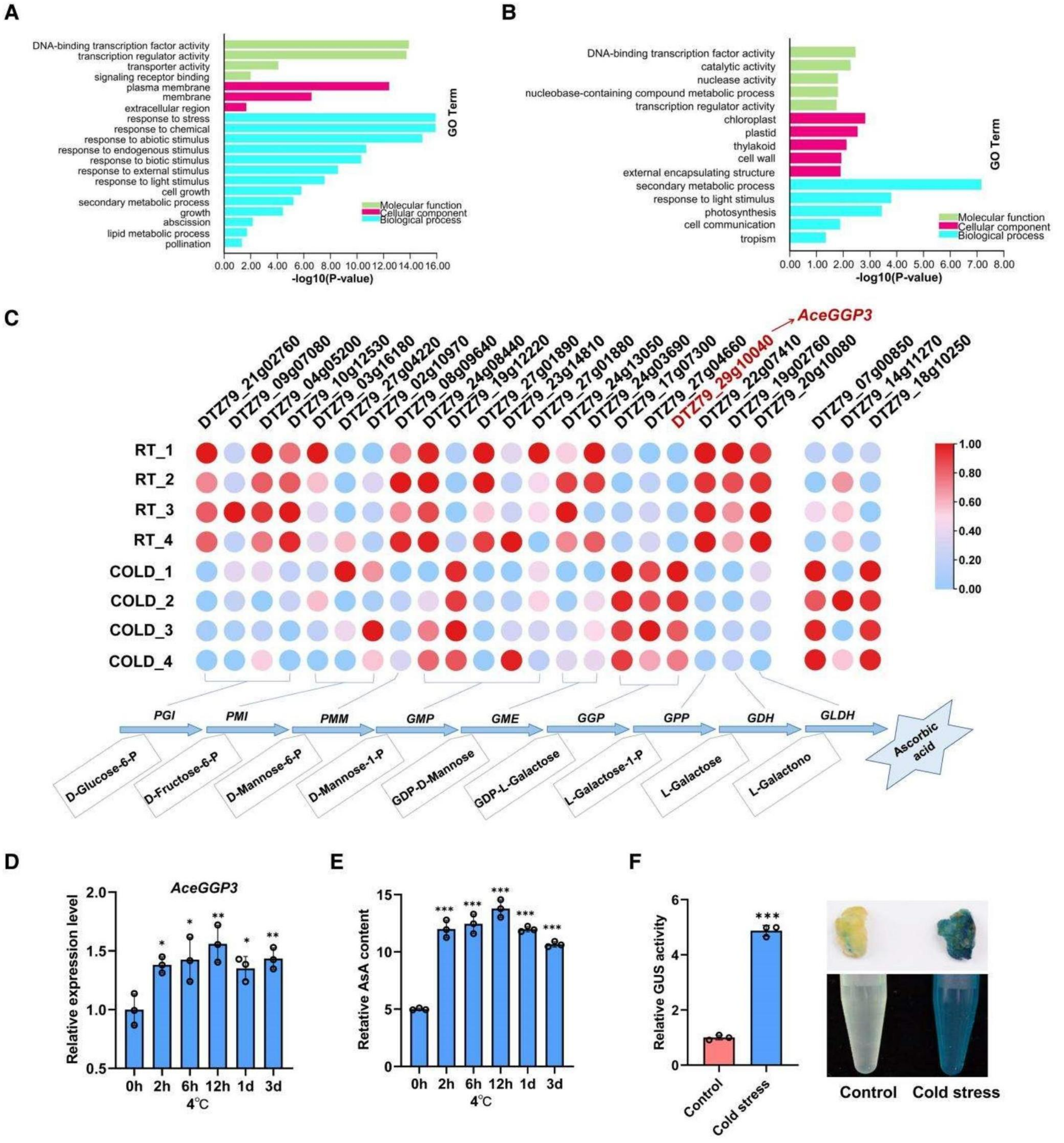

Figure 2 The *AceGGP3* expression is induced by cold stress (Adopted from Liu et al., 2023)

Image caption: (A-B) Gene ontology (GO) analysis of significantly up-regulated (A) and down-regulated (B) genes in kiwifruit calli at RT (room temperature) and COLD (4 °C) for 6 h. (C) Expression profiles of 21 genes of L-galactose pathway and 3 transcription factors in kiwifruit under RT and COLD. Log-transformed expression values range from 0 to 1. (D) RT-qPCR analysis of *AceGGP3* expression of kiwifruit (*A. eriantha*) calli treated at 4 °C for 0 h, 2 h, 6 h, 12 h, 1 d, and 3 d. E) Relative AsA content of kiwifruit calli in (D). AsA content of calli in 0 h was taken as 5 for normalization. F) Relative GUS activity and histochemical staining of the *AceGGP3* promoter expression construct *AceGGP3:: GUS* in transgenic kiwifruit calli at 25 °C (control) and 4 °C (cold stress) for 9 h. Error bars denote the standard deviation (± SD), *n* = 3. Significant differences were detected by *t*-test (**P* < 0.05; ***P* < 0.01; ****P* < 0.001) (Adopted from Liu et al., 2023)

4 Biochemical Mechanisms of Stress Resistance

4.1 Secondary metabolites in stress response

Secondary metabolites play a crucial role in the stress response of kiwifruit. These compounds, including phenylpropanoids, flavonoids, and terpenoids, are often upregulated in response to various stressors. For instance, the phenylpropanoid pathway, which is involved in the biosynthesis of lignin and flavonoids, is activated in kiwifruit in response to biotic stress such as *Botrytis cinerea* infection. This activation enhances the plant's resistance by strengthening cell walls and producing antimicrobial compounds (Li et al., 2023). Additionally, secondary metabolites are implicated in the response to abiotic stresses like salinity, where pathways related to glycine, serine, and threonine metabolism are enriched, contributing to enhanced salt tolerance (Abid et al., 2022).

4.2 Enzymatic antioxidants and reactive oxygen species (ROS) scavenging

Enzymatic antioxidants are vital for scavenging reactive oxygen species (ROS) generated under stress conditions. In kiwifruit, enzymes such as catalase (CAT) and peroxidase (POD) play significant roles in mitigating oxidative damage. For example, the overexpression of the bZIP transcription factor AchnABF1 in kiwifruit enhances the activity of CAT and POD, leading to reduced ROS accumulation and improved cold tolerance (Jin et al., 2021). Similarly, the transcription factor AcePosF21 regulates ascorbic acid (AsA) biosynthesis, which neutralizes excess ROS during cold stress, thereby reducing oxidative damage (Liu et al., 2023). The priming of plants with hydrogen peroxide (H_2O_2) has also been shown to modulate ROS detoxification pathways, enhancing tolerance to various abiotic stresses (Figure 3) (Hossain et al., 2015).

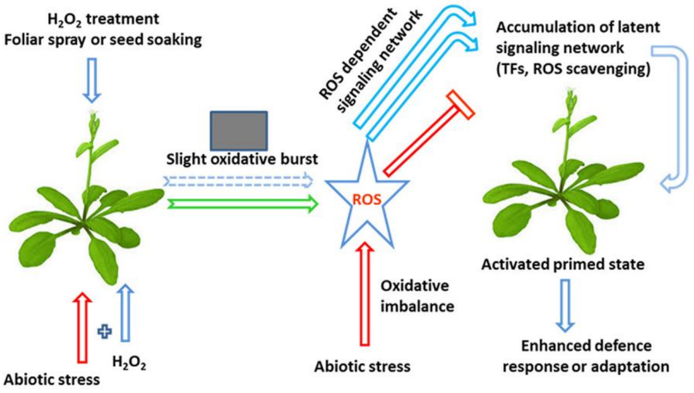

Figure 3 A hypothetical model of the influence of H_2O_2 on plant defense mechanisms associated with abiotic stresses (Adopted from Hossain et al., 2015)

Image caption: H_2O_2 treatment is capable of inducing abiotic stress tolerance through the development of a small oxidative burst. This burst subsequently activates a ROS-dependent signaling network, thereby enhancing the accumulation of latent defense proteins, such as ROS-scavenging enzymes and transcription factors (TFs), resulting in a primed state and an enhanced stress response (Adopted from Hossain et al., 2015)

4.3 Signal transduction pathways involved in stress response

Signal transduction pathways are integral to the stress response in kiwifruit, involving a complex network of signaling molecules and transcription factors. ROS act as signaling molecules that trigger various stress-responsive pathways. For instance, the respiratory burst oxidase homologues (RBOHs) are involved in ROS production, which in turn activates systemic acquired resistance (SAR) and systemic acquired acclimation (SAA) (Baxter et al., 2014). Additionally, the mitogen-activated protein kinase (MAPK) signaling pathway is significantly affected by cold stress, playing a role in the regulation of genes involved in starch and sucrose metabolism, which are crucial for freezing tolerance (Sun et al., 2021). The involvement of transcription factors such as AP2/ERF, bHLH, and MYB in these pathways further underscores the complexity of the signal transduction mechanisms in kiwifruit (Yoon et al., 2020; Wang et al., 2021).

In summary, the biochemical mechanisms of stress resistance in kiwifruit involve a multifaceted approach, including the production of secondary metabolites, the activity of enzymatic antioxidants, and the intricate network of signal transduction pathways. These mechanisms collectively enhance the plant's ability to withstand various environmental stresses.

5 Molecular Mechanisms of Stress Resistance

5.1 Gene regulation under stress conditions

Gene regulation plays a pivotal role in the stress resistance of kiwifruit. Various genes are differentially expressed in response to environmental stresses such as drought, salinity, and cold. For instance, the R1R2R3-MYB transcription factor AcMYB3R has been shown to enhance drought and salinity tolerance in *Arabidopsis thaliana* by upregulating stress-responsive genes like RD29A, RD29B, COR15A, and RD22 (Zhang et al., 2019). Similarly, the expression of genes involved in carbohydrate and amino acid metabolism, as well as reactive oxygen species (ROS) scavenging, is significantly altered under waterlogging stress in *Actinidia valvata* (Li et al., 2022). These findings highlight the complex regulatory networks that enable kiwifruit to adapt to various abiotic stresses.

5.2 Role of transcription factors in stress tolerance

Transcription factors (TFs) are crucial in modulating the expression of stress-responsive genes. The heat shock transcription factors (HSFs) in kiwifruit, particularly AeHSFA2b, have been identified to play a significant role in salt tolerance by binding to the promoter of stress-responsive genes and enhancing their expression (Ling et al., 2023). Additionally, the bZIP transcription factor AchnABF1 has been shown to improve cold tolerance by upregulating genes associated with ABA-dependent and ABA-independent pathways, thereby enhancing ROS-scavenging abilities (Jin et al., 2021). Another bZIP TF, AcePosF21, interacts with the R2R3-MYB TF AceMYB102 to regulate ascorbic acid biosynthesis, which is crucial for mitigating oxidative damage under cold stress (Liu et al., 2023). These TFs orchestrate a coordinated response to environmental stresses, thereby enhancing the resilience of kiwifruit.

5.3 Molecular breeding for enhanced stress resistance

Molecular breeding techniques have been employed to enhance stress resistance in kiwifruit. Overexpression of specific genes, such as AcMYB3R and AeHSFA2b, in model plants like *Arabidopsis thaliana* has demonstrated significant improvements in drought, salinity, and cold tolerance (Zhang et al., 2019; Ling et al., 2023). Furthermore, the functional validation of candidate genes like betaine aldehyde dehydrogenase (AvBADH) from *Actinidia valvata* has shown improved salt tolerance in transgenic kiwifruit and Arabidopsis plants (Abid et al., 2022). These molecular breeding strategies provide valuable insights and tools for developing kiwifruit cultivars with enhanced stress resistance.

5.4 Advances in genomic and proteomic studies

Recent advances in genomic and proteomic studies have provided deeper insights into the stress response mechanisms in kiwifruit. Genome-wide identification and analysis of gene families, such as the HSF and bZIP families, have revealed their roles in stress tolerance (Jin et al., 2021; Ling et al., 2023; Tu et al., 2023). Transcriptome and metabolome analyses have identified key regulatory networks and differentially expressed genes involved in stress responses, such as those related to glycine betaine, pyruvate metabolism, and ROS scavenging (Abid et al., 2022; Li et al., 2022). Additionally, the identification of cold-responsive gene modules, such as the AaCBF4-AaBAM3.1 module, has elucidated the molecular basis of freezing tolerance in kiwifruit (Sun et al., 2021). These studies provide a comprehensive understanding of the molecular mechanisms underlying stress resistance and pave the way for targeted breeding and genetic engineering approaches.

By integrating findings from various studies, we can better understand the complex molecular mechanisms that enable kiwifruit to withstand environmental stresses, ultimately contributing to the development of more resilient cultivars.

6 Case Study: Resistance to Bacterial Canker in Kiwifruit

6.1 Overview of bacterial canker disease

Bacterial canker, caused by *Pseudomonas syringae* pv. *actinidia*e (Psa), is a significant threat to the kiwifruit industry, leading to substantial economic losses globally. The disease was first identified in Japan in 1984 and has since spread to major kiwifruit-growing regions, including Korea, Italy, and New Zealand. The pathogen is genetically diverse, with strains grouped into four biovars based on molecular and pathogenic characteristics. The recent outbreaks, particularly those caused by biovar 3, have been highly virulent, affecting over 60% of the kiwifruit plantations in New Zealand within two years (Reglinski et al., 2013).

6.2 Molecular and genetic basis of resistance

The molecular mechanisms underlying kiwifruit resistance to Psa involve complex interactions between the plant's defense pathways and the pathogen. Salicylic acid (SA) has been identified as a key regulator in enhancing kiwifruit's resistance to Psa. SA treatment induces significant changes in the proteomic patterns of kiwifruit, activating resistance pathways such as the MAPK cascade, phenylpropanoid biosynthesis, and hormone signaling transduction (Qu et al., 2023). Additionally, sulfur treatments have been shown to increase the activities of defense-related enzymes like phenylalanine ammonia-lyase (PAL), peroxidase (POD), and polyphenol oxidase (PPO), and promote lignin accumulation, which strengthens the plant's structural defenses (Gu et al., 2021).

6.3 Breeding approaches and biotechnological interventions

Breeding for resistance to bacterial canker in kiwifruit involves both traditional and biotechnological approaches. One effective strategy has been the use of acibenzolar-S-methyl (ASM), a commercial elicitor of host resistance, which has shown promising results in enhancing resistance in both *Actinidia chinensis* and *A.deliciosa* (Reglinski et al., 2013). Furthermore, sulfur treatments have demonstrated high protection efficiency, reducing disease severity and improving the morphological defenses of kiwifruit stems (Gu et al., 2021). These findings suggest that integrating chemical elicitors and sulfur treatments into breeding programs could enhance the development of resistant kiwifruit varieties.

6.4 Future directions and challenges

Future research should focus on elucidating the detailed molecular mechanisms by which SA and sulfur induce resistance in kiwifruit. Understanding the specific genes and pathways involved could lead to the development of more targeted and effective breeding strategies. Additionally, there is a need to explore the potential of combining multiple resistance-inducing treatments to achieve synergistic effects. The challenge remains in translating these findings into practical, sustainable solutions that can be widely adopted by the kiwifruit industry. Continuous monitoring and management of pathogen diversity and virulence are also crucial to stay ahead of evolving threats. By integrating molecular insights with practical breeding and biotechnological interventions, the kiwifruit industry can develop robust strategies to combat bacterial canker and ensure sustainable production (Li et al., 2023).

7 Integrative Approaches to Enhancing Kiwifruit Stress Resistance

7.1 Combined physiological, biochemical, and molecular strategies

Kiwifruit's resistance to environmental stress can be significantly enhanced through a combination of physiological, biochemical, and molecular strategies. For instance, the bZIP transcription factor AcePosF21 has been identified as a key player in the biosynthesis of ascorbic acid (AsA) during cold stress. This factor interacts with the R2R3-MYB transcription factor AceMYB102 to upregulate the expression of GDP-L-galactose phosphorylase 3 (AceGGP3), thereby increasing AsA production and reducing oxidative damage caused by reactive oxygen species (ROS) (Liu et al., 2023). Additionally, the R1R2R3-MYB transcription factor AcMYB3R has been shown to enhance drought and salinity tolerance in *Arabidopsis thaliana* by upregulating stress-responsive genes such as RD29A, RD29B, COR15A, and RD22 (Zhang et al., 2019). These findings underscore the importance of transcription factors in modulating stress responses at the molecular level.

7.2 Role of biotechnology and genetic engineering

Biotechnology and genetic engineering offer promising avenues for enhancing kiwifruit's resistance to various stresses. The use of virus-induced gene silencing (VIGS) and overexpression techniques has revealed that miR160d positively regulates kiwifruit resistance to *Botrytis cinerea* by increasing antioxidant enzyme activities and the content of phytohormones like indole-3-acetic acid (IAA) and salicylic acid (SA) (Li et al., 2023). Furthermore, grafting kiwifruit onto waterlogging-tolerant rootstocks such as KR5 has been shown to improve waterlogging tolerance by enhancing photosynthetic efficiency and reducing ROS damage (Bai et al., 2022). These biotechnological approaches provide valuable tools for developing stress-resistant kiwifruit cultivars.

7.3 Potential for CRISPR/Cas9 and other modern techniques

Modern genome editing techniques, particularly CRISPR/Cas9, hold significant potential for improving kiwifruit stress resistance. The CRISPR/Cas9 system has been successfully used to edit genes involved in stress responses, such as the phytoene desaturase gene (AcPDS), achieving high-efficiency multiplex genome editing (Wang et al., 2018). This system allows for the precise modification of stress-related genes without introducing foreign DNA, thereby addressing biosafety concerns associated with traditional genetic engineering methods (Sardar et al., 2023). Additionally, the development of optimized paired-sgRNA/Cas9 vectors has further enhanced the efficiency of genome editing in kiwifruit, making it a powerful tool for functional genomic studies and molecular breeding.

In summary, the integration of physiological, biochemical, and molecular strategies, coupled with advanced biotechnological and genome editing techniques, offers a comprehensive approach to enhancing kiwifruit's resistance to environmental stresses. These methods not only improve the plant's ability to withstand adverse conditions but also pave the way for the development of more resilient kiwifruit cultivars.

8 Future Perspectives and Research Gaps

8.1 Identified research gaps in current literature

Despite significant advancements in understanding the mechanisms of environmental stress resistance in kiwifruit, several research gaps remain. Firstly, while individual stress responses such as drought, salinity, and cold have been studied, there is a lack of comprehensive studies that integrate multiple stress factors to understand their combined effects on kiwifruit (Zhang et al., 2019; Liu et al., 2023; Wurms et al., 2023). Additionally, the role of specific transcription factors and their interactions in stress responses is not fully elucidated. For instance, while the role of AcMYB3R in drought and salinity tolerance has been identified, its interaction with other stress-responsive genes and pathways remains unclear. Furthermore, the molecular mechanisms underlying the regulation of phytohormones like abscisic acid (ABA) in response to water stress need further exploration. Another gap is the limited understanding of the genetic and molecular basis of heat stress tolerance, despite the identification of heat shock transcription factors (Hsfs) (Tu et al., 2023). Lastly, the role of RNA editing in pathogen stress and its impact on kiwifruit resistance is still not fully understood (Zhang et al., 2023).

8.2 Future research directions and innovative approaches

Future research should focus on a holistic approach to studying environmental stress resistance in kiwifruit by integrating multiple stress factors. This can be achieved through advanced omics technologies such as transcriptomics, proteomics, and metabolomics to provide a comprehensive understanding of the stress response mechanisms (Abid et al., 2022). Additionally, exploring the interactions between different transcription factors and their target genes can provide insights into the regulatory networks involved in stress tolerance. For example, the interaction between AcePosF21 and AceMYB102 in cold stress response could be further investigated to understand their combined effect on ascorbic acid biosynthesis and ROS metabolism (Liu et al., 2023). Moreover, the use of CRISPR-Cas9 technology to edit specific genes involved in stress responses, such as those identified in the ABA pathway, can help in developing stress-resistant kiwifruit cultivars (Jin et al., 2021; Wurms et al., 2023). Another promising direction is the study of epigenetic modifications and their role in stress tolerance, which can provide new targets for breeding programs (Zhang et al., 2023).

8.3 Importance of interdisciplinary research and collaboration

Interdisciplinary research and collaboration are crucial for advancing our understanding of environmental stress resistance in kiwifruit. Collaboration between plant physiologists, molecular biologists, geneticists, and bioinformaticians can lead to the development of integrated models that predict plant responses to various environmental stresses. For instance, combining molecular biology techniques with computational modeling can help in identifying key regulatory genes and pathways involved in stress tolerance (Tu et al., 2023; Li et al., 2023). Additionally, partnerships with agricultural scientists and breeders can facilitate the translation of laboratory findings into practical applications, such as the development of stress-resistant kiwifruit varieties (Jin et al., 2021; Abid et al., 2022). International collaborations can also provide access to diverse germplasm resources and facilitate the exchange of knowledge and technologies, thereby accelerating the progress in this field (Xing et al., 2023; Zhang et al., 2023). By addressing these research gaps and fostering interdisciplinary collaborations, we can enhance the resilience of kiwifruit to environmental stresses, ensuring sustainable production and improved crop yields in the face of climate change.

9 Concluding Remarks

This study has highlighted several key mechanisms by which kiwifruit (*Actinidia* spp.) exhibit resistance to various environmental stresses. The studies reviewed have identified specific genes and molecular pathways that contribute to stress tolerance. Drought and salinity tolerance is enhanced by the R1R2R3-MYB transcription factor AcMYB3R, which upregulates stress-responsive genes such as *RD29A*, *RD29B*, *COR15A*, and *RD22*. In terms of disease resistance, miR160d and *AcPGIP* play significant roles in enhancing resistance to *Botrytis cinerea* by regulating antioxidant enzyme activities and hormone levels. Heat stress tolerance is mediated by heat shock transcription factors (Hsfs) such as *AcHsfA2a*, which are crucial for high-temperature tolerance, with their expression being induced under heat stress conditions. Cold stress responses are regulated by the bZIP transcription factors *AchnABF1* and *AcePosF21*, which enhance cold tolerance through the regulation of ROS metabolism and ascorbic acid biosynthesis. Waterlogging tolerance has been linked to carbohydrate and amino acid metabolism, along with ROS scavenging pathways, as revealed by transcriptome analysis of *A. valvata*. Insect resistance in the cultivar "LC-04285" is attributed to a thicker cuticle and higher expression of genes related to jasmonic acid and salicylic acid pathways, which contribute to its higher resistance to *Pseudaulacaspis pentagona*.

The findings from these studies have significant implications for the breeding and cultivation of kiwifruit. Molecular breeding involves the identification of key genes such as *AcMYB3R*, *Ac-miR160d*, and *AcPGIP*, which provide valuable targets for molecular breeding programs aimed at enhancing stress resistance in kiwifruit. Transgenic approaches, such as the overexpression of stress-responsive genes in transgenic plants, can be a viable strategy to improve drought, salinity, and cold tolerance, as demonstrated by the enhanced tolerance in *Arabidopsis* models. Cultivar selection focuses on selecting and cultivating kiwifruit cultivars with naturally higher resistance to specific stresses, such as "LC-04285" for insect resistance and *A. valvata* for waterlogging tolerance, which can improve yield and fruit quality. Pre-harvest treatments, including the application of substances like oxalic acid, can enhance postharvest quality and disease resistance, providing a practical approach to managing stress during storage.

Future research on stress resistance in kiwifruit should focus on several key areas. Functional genomics involves the further functional characterization of identified genes and their regulatory networks, which will provide deeper insights into the molecular mechanisms of stress resistance. Gene editing, using advanced technologies such as CRISPR-Cas9, can be employed to precisely modify stress-responsive genes, enhancing the development of stress-resistant kiwifruit varieties. Integrated stress management combines genetic approaches with agronomic practices, such as optimized irrigation and nutrient management, which will be crucial for developing comprehensive strategies to mitigate environmental stresses. Climate change adaptation is increasingly important as global temperatures rise. Understanding and enhancing heat and drought tolerance in kiwifruit should be a priority, with research focusing on the identification of heat-tolerant genes and the development of heat-resistant cultivars. In conclusion, the integration of molecular breeding, transgenic approaches, and practical cultivation strategies holds great promise for improving the resilience of kiwifruit to environmental stresses, ensuring sustainable production and high-quality fruit in the face of changing climatic conditions.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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