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Review and Perspectives **Open Access**

Breeding Kiwifruit for Enhanced Stress Tolerance: Advances and Challenges

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Abstract Kiwifruit (*Actinidia* spp.) is a valuable fruit crop that faces significant challenges due to various environmental stresses, including drought, salinity, heat, cold, and waterlogging. Recent advances in molecular breeding and functional genomics have identified several key genes and regulatory mechanisms that enhance stress tolerance in kiwifruit. For instance, the R1R2R3-MYB transcription factor AcMYB3R has been shown to improve drought and salinity tolerance in transgenic Arabidopsis plants by upregulating stress-responsive genes. Similarly, the heat shock transcription factor (Hsf) gene family has been implicated in high-temperature tolerance, with specific Hsf genes like *AcHsfA2a* playing crucial roles. Salt stress tolerance has been linked to various physiological and biochemical adaptations, including increased proline content and enhanced antioxidant enzyme activities. Waterlogging tolerance mechanisms involve complex metabolic and transcriptional responses, as demonstrated by the superior performance of certain kiwifruit genotypes and rootstocks under waterlogged conditions. Additionally, melatonin application has been found to mitigate heat stress by promoting antioxidant pathways. These findings provide a comprehensive understanding of the genetic and molecular bases of stress tolerance in kiwifruit, offering valuable insights for breeding programs aimed at developing more resilient cultivars.

Keywords Kiwifruit; Stress tolerance; Molecular breeding; Transcription factors; Antioxidant enzymes

1 Introduction

Kiwifruit (*Actinidia* spp.) is a globally significant horticultural crop known for its high nutritional value, including rich contents of vitamin C, potassium, and various phytochemicals (Kim et al., 2023). Its popularity has surged due to its unique flavor and health benefits, making it a staple in many diets worldwide. The economic importance of kiwifruit is underscored by its extensive cultivation and the development of various cultivars to meet market demands (Wu et al., 2019). The fruit's quality is primarily determined by key metabolites such as sugars, flavonoids, and vitamins, which are crucial for consumer acceptance and marketability (Shu et al., 2023).

Kiwifruit production is highly susceptible to a range of environmental stresses, including drought, salinity, heat, cold, and waterlogging, as well as biotic stresses like phytopathogens (Zhang et al., 2019). These stress factors can significantly impact fruit quality and yield, leading to substantial economic losses. For instance, cold stress can cause chilling injury, reducing fruit quality and increasing nutrient loss during storage (Jin et al., 2021). Similarly, heat stress can induce oxidative damage, affecting the overall health and productivity of the plants (Liang et al., 2018). The plant microbiota also plays a crucial role in promoting stress resilience, but the precise interactions between kiwifruit and its associated microorganisms remain to be fully understood (Kim et al., 2023).

Given the vulnerability of kiwifruit to various abiotic and biotic stresses, there is a pressing need to develop stress-tolerant varieties to ensure stable production and high fruit quality. Advances in molecular breeding and functional genomics have identified several key genes and transcription factors that enhance stress tolerance in kiwifruit. For example, the R1R2R3-MYB transcription factor AcMYB3R has been shown to enhance drought and salinity tolerance in transgenic Arabidopsis plants (Zhang et al., 2019). Similarly, the bZIP transcription factor AchnABF1 has been implicated in improving cold tolerance by regulating reactive oxygen species (ROS) metabolism and osmotic stress responses (Jin et al., 2021). These findings highlight the potential of genetic interventions to mitigate the adverse effects of environmental stresses on kiwifruit production.

2 Kiwifruit Stress Factors and Their Impact

2.1 Abiotic stresses

Kiwifruit is highly sensitive to various abiotic stresses, including drought, salinity, and temperature extremes. Drought and salinity are particularly detrimental, as they can severely affect plant growth and productivity. The R1R2R3-MYB transcription factor AcMYB3R has been identified as a key player in enhancing drought and salinity tolerance in kiwifruit. Overexpression of AcMYB3R in *Arabidopsis thaliana* has shown to upregulate stress-responsive genes, thereby improving drought and salt stress tolerance (Zhang et al., 2019). Similarly, the bZIP transcription factor AchnABF1 has been found to enhance cold tolerance by regulating reactive oxygen species (ROS) metabolism and osmotic stress responses (Jin et al., 2021). High temperatures also pose a significant threat, with heat shock transcription factors (HSFs) playing a crucial role in heat stress tolerance. The Hsf gene family in kiwifruit has been extensively studied, revealing that genes like *AcHsfA2a* are highly expressed under high-temperature conditions, contributing to heat stress resistance (Tu et al., 2023). Additionally, melatonin has been shown to improve heat tolerance by promoting antioxidant enzymatic activity and glutathione S-transferase transcription (Liang et al., 2018; Farooqi et al., 2022).

2.2 Biotic stresses

Biotic stresses, such as pests and diseases, also significantly impact kiwifruit cultivation. One of the most notorious pathogens affecting kiwifruit is Pseudomonas syringae pv. *Actinidia*e (PSA), which causes bacterial canker. This disease can lead to severe yield losses and even plant death. The management of PSA and other biotic stresses requires a comprehensive understanding of the plant's defense mechanisms. Research has shown that transcription factors like AcePosF21, which are involved in ascorbic acid biosynthesis, play a role in enhancing the plant's defense responses against cold stress, which can indirectly affect its resistance to pathogens (Liu et al., 2023). Moreover, the identification of stress-responsive genes and their regulatory networks is crucial for developing disease-resistant kiwifruit varieties.

2.3 Physiological and yield impacts of these stresses on kiwifruit

Abiotic and biotic stresses have profound physiological impacts on kiwifruit, affecting growth, yield, and overall plant health. Under salinity stress, kiwifruit plants exhibit reduced growth parameters such as relative lateral branch length, plant fresh weight, and plant dry weight. Salinity also leads to increased sodium and chloride ion accumulation, which disrupts cellular homeostasis and reduces the potassium ion ratio, further impairing plant function (Figure 1) (Abid et al., 2020). Waterlogging stress, another abiotic factor, affects root activity and energy supply, leading to reduced photosynthetic efficiency and increased ROS damage. Grafting kiwifruit onto waterlogging-tolerant rootstocks like KR5 has been shown to mitigate these effects, enhancing the plant's physiological responses and stress tolerance (Huang et al., 2013; Bai et al., 2022). Cold stress, on the other hand, triggers the biosynthesis of ascorbic acid, which helps in scavenging ROS and reducing oxidative damage. The transcription factor AcePosF21 has been identified as a key regulator in this process, enhancing cold stress tolerance and potentially improving yield under adverse conditions. Overall, understanding the molecular and physiological responses of kiwifruit to various stresses is essential for developing resilient cultivars and ensuring sustainable production.

3 Advances in Breeding for Stress Tolerance

3.1 Conventional breeding approaches

Conventional breeding approaches in kiwifruit have primarily focused on selecting and cross-breeding varieties that exhibit natural tolerance to various environmental stresses. For instance, grafting sensitive cultivars onto tolerant rootstocks has been a successful strategy. The use of KR5 (*Actinidia valvata*) as a rootstock has shown significant improvements in waterlogging tolerance, enhancing photosynthetic efficiency and reducing reactive oxygen species (ROS) damage in grafted plants (Bai et al., 2022). Similarly, micrografting techniques have been employed to evaluate and enhance drought tolerance in kiwifruit cultivars, demonstrating significant differences in physiological and biochemical responses under stress conditions (Bao et al., 2019).

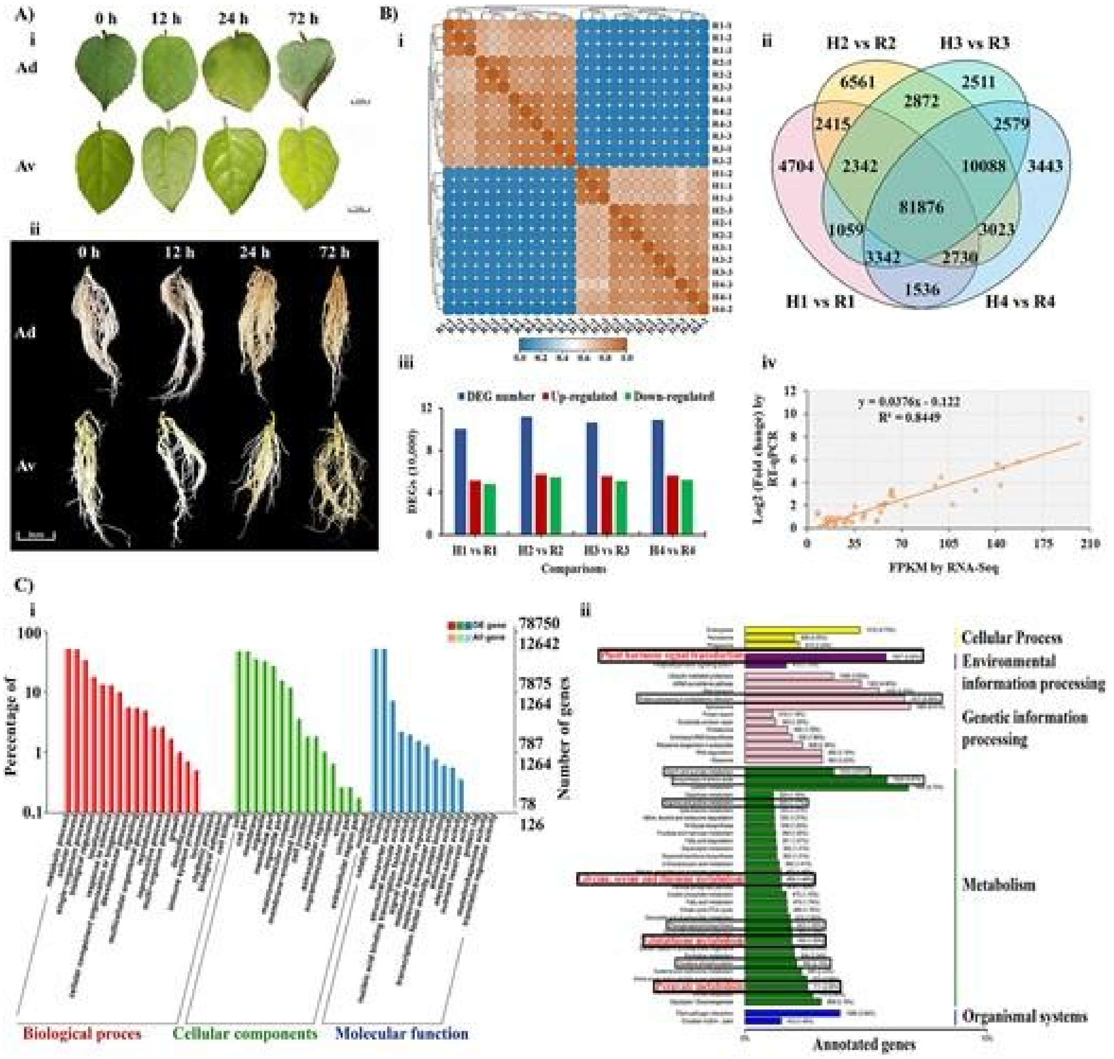

Figure 1 Morphological changes of R and H, an overview of RNA-seq data, and validation of DEGs expression pattern in R and H under 0.4% NaCl stress (Adopted from Abid et al., 2020)

Image caption: (A) Morphological changes of R and H in (i) leaves and (ii) roots. (B) Overview of RNA-seq data (i) expression-dependent heatmap of samples obtained from R and H by using data from spearman correlation coefficient analysis. The x-axis and y-axis represents samples taken from Av and H under salt stress, (ii) statistics of commonly up-regulated genes in R and H, (iii) statistics of up-regulated and down-regulated DEGs in roots, and (iv) validation of RNA-seq data by RT-qPCR analysis. (C) GO terms and KEGG enrichment analysis of up-regulated genes in R4 vs H4. (i) GO terms enrichment analysis. The x-axis represents enriched GO terms and y-axis represents the number of up-regulated genes in a particular GO term. The red columns are for GO terms under biological process, the Green color represents GO terms under cellular components and the blue color stands for GO terms in molecular function. (ii) KEGG enrichment analysis. Vertical columns represent enriched pathways and horizontal columns are for annotated genes. R, *Actinidia valvata*; H, *A. deliciosa*; h, hours (Adopted from Abid et al., 2020)

Through these conventional methods, several stress-tolerant kiwifruit varieties have been developed. For example, the ZM-H genotype from *Actinidia* valvata has shown strong tolerance to salt stress, making it a valuable resource for breeding salt-tolerant rootstocks (Abid et al., 2020). Additionally, the use of drought-tolerant rootstocks like MX1 has improved the drought resistance of grafted kiwifruit cultivars, aiding in sustainable production (Bao et al., 2019).

3.2 Molecular breeding techniques

Molecular breeding techniques such as marker-assisted selection (MAS) have been instrumental in accelerating the breeding process for stress tolerance. By identifying and utilizing specific genetic markers associated with stress tolerance traits, breeders can more efficiently select and propagate desirable traits. For example, the development of a RAD-based linkage map has facilitated the identification of markers linked to important traits, including stress tolerance, thereby enhancing the efficiency of breeding programs (Scaglione et al., 2015).

QTL mapping has been crucial in understanding the genetic basis of stress tolerance in kiwifruit. By mapping QTLs associated with traits like drought and salt tolerance, researchers can pinpoint specific genomic regions that contribute to these traits. This information is vital for developing new varieties with enhanced stress tolerance through targeted breeding strategies (Scaglione et al., 2015).

3.3 Genomic and transcriptomic approaches

Genomic and transcriptomic approaches have provided deeper insights into the molecular mechanisms underlying stress tolerance in kiwifruit. Genome-wide association studies (GWAS) and transcriptome analyses have identified key genes and pathways involved in stress responses. For instance, transcriptome analysis of waterlogging-tolerant kiwifruit roots revealed significant changes in carbohydrate and amino acid metabolism, as well as ROS scavenging pathways, under stress conditions (Li et al., 2022).

Several key genes have been identified that play crucial roles in stress tolerance. For example, the R1R2R3-MYB transcription factor AcMYB3R has been shown to enhance drought and salinity tolerance by upregulating stress-responsive genes in transgenic plants (Zhang et al., 2019). Similarly, the bZIP transcription factor AchnABF1 has been implicated in cold and osmotic stress tolerance through its role in ROS metabolism and ABA-dependent pathways (Jin et al., 2021).

3.4 Biotechnological interventions

Biotechnological interventions, including genetic engineering and CRISPR/Cas9, offer promising avenues for developing stress-tolerant kiwifruit. For instance, overexpression of the NAC domain transcription factor AvNAC030 in transgenic plants has been shown to enhance salt stress tolerance by improving osmotic adjustment and antioxidant defense mechanisms. Additionally, CRISPR/Cas9-mediated editing of key genes involved in stress responses, such as AcePosF21, has demonstrated potential in enhancing cold tolerance by regulating ascorbic acid biosynthesis and reducing oxidative damage (Liu et al., 2023).

While these biotechnological approaches hold great promise, they also raise potential ethical and regulatory considerations. The use of genetic engineering and genome editing technologies must be carefully evaluated for their long-term impacts on the environment and biodiversity. Moreover, public acceptance and regulatory frameworks will play crucial roles in the adoption of these technologies in commercial kiwifruit breeding programs.

4 Key Challenges in Breeding Stress-Tolerant Kiwifruit

4.1 Genetic diversity and breeding constraints

Breeding stress-tolerant kiwifruit is significantly hampered by the limited genetic diversity within the species. The high heterozygosity and polyploidy of kiwifruit complicate the breeding process, making it challenging to select and stabilize desirable traits. For instance, the application of genome selection (GS) in kiwifruit breeding has shown promise but still faces hurdles due to the complexity of the genome and the need for improved genotyping approaches. Additionally, the dioecious nature of kiwifruit, where male and female plants are separate, further complicates breeding efforts as it necessitates the selection of appropriate male parents, which is both time-consuming and costly.

4.2 Complexity of stress tolerance traits

Stress tolerance in kiwifruit involves a complex interplay of multiple physiological and biochemical pathways. For example, the response to cold stress in kiwifruit involves various metabolic pathways such as starch and sucrose metabolism, MAPK signaling, and plant hormone signal transduction (Sun et al., 2021). Similarly, salt stress tolerance is mediated through intricate networks involving glycine betaine, pyruvate metabolism, and glutathione biosynthesis (Abid et al., 2022). The multifaceted nature of these stress responses makes it difficult to pinpoint and breed for specific tolerance traits. Moreover, the expression of stress-responsive genes and transcription factors, such as those from the MYB and bZIP families, adds another layer of complexity to breeding programs aimed at enhancing stress tolerance (Zhang et al., 2019; Jin et al., 2023).

4.3 Environmental and regulatory challenges

Environmental factors and regulatory constraints pose additional challenges to breeding stress-tolerant kiwifruit. The impact of climate change, with increasing instances of extreme weather conditions, necessitates the development of cultivars that can withstand a range of stresses, including drought, salinity, and high temperatures (Zhang et al., 2019; Tu et al., 2023). Furthermore, regulatory hurdles related to the use of genetic modification and genome editing technologies, such as CRISPR/Cas9, can slow down the development and commercialization of new stress-tolerant varieties (Varkonyi-Gasic et al., 2021). The need for extensive field trials and compliance with biosafety regulations adds to the time and cost involved in bringing new cultivars to market.

4.4 Consumer acceptance and market dynamics

Consumer acceptance and market dynamics also play a crucial role in the success of breeding programs. While developing stress-tolerant kiwifruit is essential for ensuring crop resilience and productivity, it is equally important to consider consumer preferences for fruit quality, taste, and nutritional value. For instance, the introduction of new cultivars with enhanced stress tolerance must not compromise the desirable traits that consumers expect, such as sweetness, texture, and shelf life (Commisso et al., 2019; Abid et al., 2020). Additionally, market dynamics, including competition from other fruit crops and changing consumer trends, can influence the adoption and success of new kiwifruit varieties. Breeding programs must therefore strike a balance between improving stress tolerance and maintaining or enhancing fruit quality to meet market demands.

5 Case Studies

5.1 Successful breeding programs or studies that have developed stress-tolerant kiwifruit varieties

Several breeding programs and studies have successfully developed stress-tolerant kiwifruit varieties by focusing on different types of environmental stresses such as drought, salinity, heat, cold, and waterlogging. One notable study identified the R1R2R3-MYB transcription factor AcMYB3R in kiwifruit, which enhances drought and salinity tolerance when overexpressed in *Arabidopsis thalian*a. This gene upregulates stress-responsive genes, providing a valuable resource for improving stress tolerance in kiwifruit through molecular breeding (Figure 2) (Zhang et al., 2019).

Another study focused on the heat shock transcription factor (*Hsf*) gene family in two kiwifruit species, *Actinidia chinensis* and *Actinidia eriantha*. The study identified 36 Hsf genes in *A. chinensis* and 41 in *A. eriantha*, which were found to be crucial for high-temperature tolerance. The findings offer a theoretical foundation for developing heat-stress-resistant kiwifruit varieties (Tu et al., 2023).

Salt stress tolerance has also been a significant focus. A study on four different kiwifruit genotypes under varying salt concentrations revealed that the ZM-H genotype from *A. valvata* exhibited the highest salt tolerance. This genotype could serve as an important germplasm resource for breeding salt-tolerant kiwifruit rootstocks (Abid et al., 2020).

Cold stress tolerance was addressed by identifying the bZIP transcription factor AchnABF1 in kiwifruit, which enhances cold tolerance by upregulating key genes associated with ABA-dependent and ABA-independent pathways. This gene also improves ROS-scavenging ability, making it a valuable target for breeding cold-tolerant kiwifruit varieties.

Waterlogging tolerance was studied in *Actinidia valvata*, where transcriptome analysis revealed that the roots of the KR5 genotype responded to waterlogging stress through carbohydrate and free amino acids metabolism and ROS scavenging pathways. This study provides insights into the factors contributing to waterlogging tolerance, which can be used for breeding waterlogging-tolerant kiwifruit varieties.

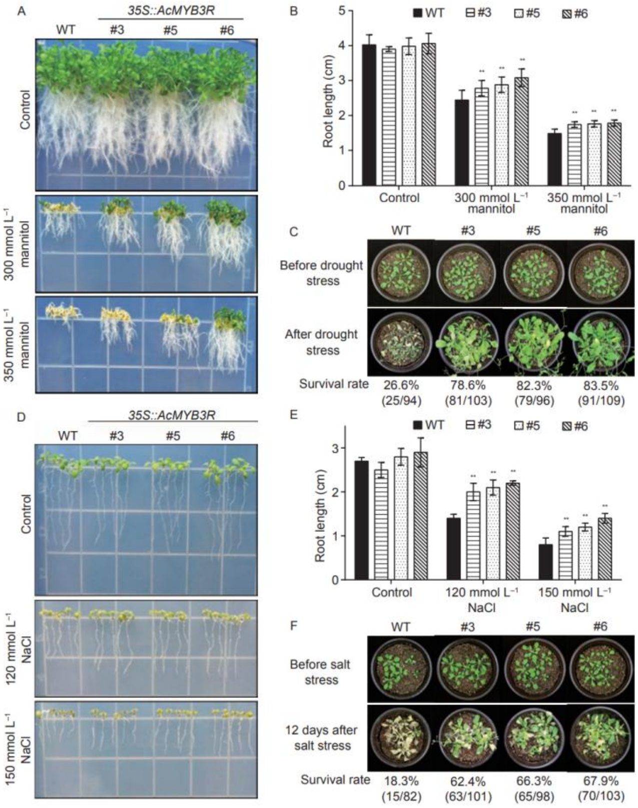

Figure 2 Overexpression of AcMYB3R results in enhanced drought or salt tolerance (Adopted from Zhang et al., 2019)

Image caption: A and B, phenotypes and the root length of wild type (WT) and AcMYB3R-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 (Adopted from Zhang et al., 2019)

5.2 Lessons learned from these case studies and their implications for future breeding efforts

The case studies highlight several key lessons that can inform future breeding efforts for stress-tolerant kiwifruit varieties. Firstly, the identification and functional characterization of specific transcription factors, such as AcMYB3R and AchnABF1, demonstrate the importance of targeted genetic modifications to enhance stress tolerance. These findings suggest that future breeding programs should focus on identifying and manipulating key regulatory genes involved in stress responses (Zhang et al., 2019).

Secondly, the studies underscore the value of using diverse germplasm resources, such as the ZM-H genotype from *A. valvata*, which exhibited strong salt tolerance. This indicates that exploring and utilizing genetic diversity within and across kiwifruit species can lead to the development of more resilient varieties (Abid et al., 2020).

The integration of advanced molecular techniques, such as transcriptome and metabolome analyses, has proven effective in uncovering the complex regulatory networks involved in stress tolerance. These approaches should be incorporated into future breeding programs to gain a comprehensive understanding of the molecular mechanisms underlying stress responses (Li et al., 2021; Abid et al., 2022).

Additionally, the successful use of heterologous expression systems, as seen in the overexpression of AcMYB3R and AchnABF1 in Arabidopsis, highlights the potential of cross-species gene transfer to validate the function of candidate genes. This strategy can accelerate the identification of valuable genes for stress tolerance and their subsequent application in kiwifruit breeding (Zhang et al., 2019; Jin et al., 2021).

The studies emphasize the importance of a multidisciplinary approach, combining physiological, biochemical, and molecular analyses to develop a holistic understanding of stress tolerance. Future breeding efforts should adopt this integrated approach to identify and select for multiple stress-tolerant traits, thereby enhancing the overall resilience of kiwifruit varieties to various environmental challenges (Abid et al., 2020; Tu et al., 2023).

6 Future Directions and Opportunities

6.1 Integrating omics technologies and bioinformatics for precision breeding

The integration of omics technologies, such as genomics, transcriptomics, proteomics, and metabolomics, has revolutionized the field of plant breeding by providing comprehensive insights into the molecular mechanisms underlying stress tolerance. High-throughput sequencing tools and bioinformatics pipelines enable the characterization of plant traits and the identification of stress-responsive genes, transcripts, proteins, and metabolites (Roychowdhury et al., 2023). For instance, the use of multi-omics approaches has been shown to enhance our understanding of abiotic stress responses in plants, facilitating the development of climate-smart crops (Roychowdhury et al., 2023; Wang et al., 2023). By combining these technologies with genome-assisted breeding, it is possible to develop kiwifruit cultivars with improved stress tolerance and agronomic traits.

6.2 Exploring wild germplasm and underutilized kiwifruit species for new genetic resources

Wild germplasm and underutilized kiwifruit species represent a valuable reservoir of genetic diversity that can be harnessed for breeding programs aimed at enhancing stress tolerance. Studies have shown that different kiwifruit species exhibit varying levels of tolerance to abiotic stresses such as drought, salinity, and waterlogging (Zhang et al., 2019). For example, *Actinidia valvata* has been identified as a waterlogging-tolerant species, with specific metabolic and transcriptional responses that contribute to its resilience. By exploring and incorporating these genetic resources into breeding programs, it is possible to develop new kiwifruit cultivars with enhanced stress tolerance and adaptability to changing environmental conditions.

6.3 Collaborations between research institutions, government, and industry stakeholders

Effective collaboration between research institutions, government agencies, and industry stakeholders is crucial for the successful development and deployment of stress-tolerant kiwifruit cultivars. Such collaborations can facilitate the sharing of knowledge, resources, and technologies, thereby accelerating the breeding process and ensuring the practical application of research findings (Roychowdhury et al., 2023). For instance, partnerships between academic researchers and industry can help translate scientific discoveries into commercial products, while government support can provide funding and regulatory frameworks to promote sustainable agricultural practices. By fostering a collaborative environment, it is possible to address the challenges of climate change and ensure the long-term sustainability of kiwifruit production.

6.4 Sustainable and climate-resilient kiwifruit production systems

Developing sustainable and climate-resilient kiwifruit production systems is essential to mitigate the impacts of climate change and ensure food security. This involves adopting practices that enhance the resilience of kiwifruit plants to abiotic stresses, such as optimizing irrigation, improving soil health, and implementing integrated pest management strategies (Jin et al., 2021). Additionally, the use of advanced breeding techniques, such as CRISPR-Cas9, can facilitate the development of kiwifruit cultivars with specific stress-tolerant traits (Razzaq et al., 2021). By integrating these approaches, it is possible to create production systems that are not only more resilient to environmental stresses but also more sustainable in the long term.

7 Concluding Remarks

Recent advancements in kiwifruit breeding have significantly enhanced our understanding of the genetic and molecular mechanisms underlying stress tolerance. Key transcription factors such as AcMYB3R, which enhances drought and salinity tolerance, have been identified and characterized. Similarly, the heat shock transcription factor gene family has been explored, revealing their role in high-temperature tolerance. The bZIP transcription factors, including AchnABF1 and AcePosF21, have been shown to play crucial roles in osmotic and freezing stress adaptations. Additionally, comparative transcriptome and metabolome analyses have uncovered key regulatory networks involved in salt tolerance. Despite these advances, challenges remain, particularly in translating these findings into practical breeding programs and addressing the complex interactions between different stress factors.

The breeding of stress-tolerant kiwifruit necessitates a multidisciplinary approach that integrates genomics, transcriptomics, metabolomics, and advanced breeding techniques. The identification of stress-responsive genes and their regulatory networks requires comprehensive molecular studies, as demonstrated by the genome-wide analyses of various transcription facto families. Moreover, physiological and biochemical assessments are essential to understand the practical implications of these genetic modifications, as seen in studies on salt and waterlogging tolerance. Collaborative efforts across disciplines, including plant physiology, molecular biology, and bioinformatics, are crucial to develop robust kiwifruit cultivars capable of withstanding multiple environmental stresses.

The future of kiwifruit breeding lies in the continued integration of advanced molecular techniques with traditional breeding practices. The insights gained from recent studies provide a solid foundation for developing stress-tolerant kiwifruit varieties. However, the complexity of stress responses and the need for multi-stress tolerance pose significant challenges. Future research should focus on the holistic understanding of stress tolerance mechanisms and the development of multi-stress-resistant cultivars. Enhancing global fruit crop resilience will require not only scientific innovation but also practical implementation strategies that consider the diverse environmental conditions faced by growers worldwide. By fostering interdisciplinary collaborations and leveraging cutting-edge technologies, the kiwifruit industry can achieve sustainable production and contribute to global food security.

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Conflict of Interest Disclosure

The authors affirm 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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