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Review

Strategic Advancements in Rice Cultivation: Combating Heat Stress through Genetic Innovation and Sustainable Practices—A Review

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Abstract: Rice is one of the most important staple foods globally, sustaining over half of the world's population. However, the sustainability of grain production is increasingly threatened by heat stress, which is intensified by global climate change. Heat stress, characterized by temperatures exceeding crop-specific optimal growth thresholds, significantly impacts the rice yield and quality, particularly during critical reproductive stages. This review synthesizes current research on strategies to mitigate heat stress in rice through genetic and agronomic approaches. It highlights the implementation of advanced genetic tools such as marker-assisted selection (MAS) and genomic selection (GS) to accelerate the breeding of heat-tolerant rice varieties. Additionally, it discusses sustainable agronomic practices, including adjusting planting dates, optimizing water management, and crop rotation, which enhance resilience to heat stress. The objective of this review is to bridge the gap between research findings and practical agricultural applications, providing a comprehensive resource that guides future research directions and informs policy interventions. This review emphasizes the importance of integrating genetic innovations with traditional and modern farming practices to develop rice varieties that can withstand the adverse effects of heat stress, ensuring food security and agricultural sustainability in the face of climatic challenges.

Keywords: global warming; heat stress; rice; physiological responses; genetic innovation

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1. Introduction

Rice, as a staple food, nourishes more than half of the world's population, forming the cornerstone of food security in many developing and developed nations. Its agricultural success is critical not only to the economic stability of these countries but also to the nutritional needs of billions of people. However, the sustainability of rice production is increasingly jeopardized by various environmental stresses, notably heat stress, which is exacerbated by the global climate crisis. In general, the phenomenon of heat stress refers to temperature conditions that exceed a crop's optimal threshold for growth and development, leading to adverse physiological impacts, reduced crop yields, and diminished quality.

Heat stress in rice refers to the detrimental impact of high temperatures on various physiological processes, ultimately leading to reduced growth and yield [1,2]. Heat stress in plants, especially in rice, refers to the damaging effects caused by exposure to high temperatures beyond the optimal range for growth and development, and rice is highly sensitive to heat stress during all the growth stages. During germination, high temperatures above 35 °C can inhibit seed germination and early seedling growth, reducing the plant height, tiller number, and overall biomass accumulation. As a result, when rice plants are exposed to temperatures above 35 °C during the flowering stage, rice can experience a 10% yield reduction. This stress affects rice at different growth stages, with the reproductive phase being particularly sensitive [3,4]. The reproductive stage is the most vulnerable stage to heat stress in rice. Temperatures exceeding 35 °C during heading and flowering can lead to spikelet sterility, a reduced grain-filling period, fewer grains per panicle, and significant yield losses of up to 10% for every 1 °C rise above 35 °C. In addition, extreme temperatures above 40 °C can cause complete pollen sterility, resulting in zero yield. Rice plants under heat stress show morphological changes like increased water loss, leaf wilting, yellowing, impaired root growth, and even seedling death. Heat stress affects various plant organs, including roots, stems, leaves, and flowers, with different rice lines showing varying levels of thermotolerance [5]. Heat stress has a differential impact on rice depending on the growth stage, influencing various physiological processes and ultimately affecting the yield. Table 1 summarizes the temperature ranges, the effects on growth and yield, and the associated physiological changes for each growth stage, supported by the relevant literature.

Table 1. Impact of heat stress on growth traits.

Growth Stage	Temperature (°C)	Effects on Growth and Yield	Physiological Changes	References
Seedling	>35	Reduced plant height, leaf wilting, poor establishment, reduced leaf area, reduced root development	Increased water loss, impaired root growth, reduced chlorophyll content, decreased nutrient uptake	[6–8]
Vegetative	>40	Reduced tiller number, stunted growth, leaf scorching, reduced biomass accumulation	Decreased photosynthetic efficiency, increased respiration, impaired nutrient uptake, oxidative stress	[6,9,10]
Early reproductive	>33	Reduced panicle initiation, delayed heading, reduced spikelet number	Impaired pollen development, reduced spikelet fertility, hormonal imbalance	[11–13]
Anthesis	>33	Spikelet sterility, reduced grain setting, reduced pollen viability	Pollen sterility, impaired ovule development, reduced pollen tube growth	[14–16]
Grain filling	>33	Reduced grain size, poor grain filling, chalkiness, reduced grain weight	Impaired starch synthesis, increased grain chalkiness, accelerated grain maturation	[7,17,18]
Maturity	>33	Reduced yield, poor grain quality, increased grain breakage	Accelerated senescence, decreased grain filling duration, reduced grain density	[16,19,20]

Heat stress during the grain-filling stage of rice can significantly impact the quality and yield of the harvest. High nighttime temperatures can directly lead to chalky and abnormally shaped grains. This is because the hot temperatures disrupt the development of the starch granules within the grain, resulting in uneven filling and a chalky appearance. Additionally, the heat stress reduces the grain weight and overall quality. This is likely caused by a combination of factors, including limitations in nutrient uptake and transport, and a decrease in the production of the starches that make up the bulk of the grain.

Heat stress can also affect the internal physiological processes of the rice plant. At the cellular level, high temperatures can damage cell membranes, making them more fluid and less effective at regulating the flow of materials in and out of the cell. This can lead to several problems, including the production of harmful reactive oxygen species (ROS), which damage cellular components, and a disruption in the production of sugars and carbohydrates needed for grain development. Heat stress can also affect the plant's hormone balance, throwing off processes like spikelet fertility and overall grain development [21]. At the molecular level, heat stress triggers changes in gene expression, protein stability, and metabolic pathways involved in heat sensing, signaling, and stress response mechanisms [22,23].

As global temperatures continue to rise due to climate change, episodes of heat stress are becoming more frequent and severe. This poses a substantial risk to rice production, particularly in regions that are already vulnerable to food insecurity. The impact of heat stress is multifaceted, influencing not only the direct output of rice cultivation but also the socioeconomic status of millions who depend on rice farming for their livelihoods. The urgency of addressing heat stress is further compounded by the predicted increase in the global population and the corresponding demand for more food production on diminishing arable land.

The primary objective of this review is to consolidate the latest research findings related to the development of heat-tolerant rice varieties and the adoption of sustainable agricultural practices. By exploring the genetic and agronomic innovations in rice breeding, this review aims to shed light on effective strategies that can mitigate the impact of heat stress. These strategies include the use of advanced genetic tools like marker-assisted selection (MAS) and genomic selection (GS) to fast-track the development of heat-resilient rice varieties. Furthermore, this review will delve into sustainable agronomic practices such as altering planting dates, optimizing water use, and implementing crop rotation, which are pivotal in adapting rice cultivation to changing climatic conditions.

This review also aims to bridge the gap between research findings and practical applications, providing a comprehensive resource for researchers, policymakers, and agricultural practitioners. The synthesis of current knowledge on combating heat stress in rice is important for guiding future research directions that could lead to breakthroughs in rice cultivation technologies and strategies. Additionally, this review seeks to inform policy interventions that could support the widespread adoption of these innovations, ensuring the resilience of rice production systems against the backdrop of global warming.

Understanding the mechanisms behind heat tolerance in rice and the effectiveness of various agronomic practices is essential for tailoring research efforts that address the specific needs of different rice-growing regions. This review highlights the importance of a multidisciplinary approach that incorporates plant physiology, genetics, agronomy, and climate science to develop comprehensive solutions to heat stress.

The implications for agricultural practices are profound. By implementing the strategies discussed in this review, farmers can enhance their rice yields, reduce the vulnerability to heat stress, and improve the overall sustainability of their farming practices. For researchers, this review provides a foundation for exploring uncharted territories in rice genetics and stress physiology, proposing new research avenues that could lead to more robust heat stress mitigation techniques.

Rice plants employ several strategies to defend themselves during heat stress. However, rice plants have developed a multitude of adaptive responses to cope with this environmental challenge, ensuring their survival and productivity under high-temperature conditions. The upregulation of heat shock proteins (Hsps) and heat shock transcription factors (Hsfs) is intended to protect cellular proteins and regulate heat stress response genes [2,24]. For example, HsfA1a acts as a master regulator that triggers the heat stress response in rice [2]. Accumulation of compatible solutes like proline, glycine betaine and trehalose serves to maintain the cell structure and function under heat stress [24]. Increased nitrogen availability also results in the accumulation of amino acids to mitigate heat stress effects [25]. Activation of antioxidant systems serves to scavenge reactive oxygen species (ROS) and maintain redox homeostasis [24]. The heat-induced accumulation of cysteine and glutathione is much less marked in the presence of nitrogen [25]. Modification of leaf anatomy, such as forming waxy cuticles and opening stomata, is intended to cool down leaf surfaces and reduce water loss. Lowering the panicle temperature by transpiration cooling is another avoidance mechanism. Escape is also possible by completing reproduction before the onset of heat stress through an early anthesis time. Longer and erect top leaves that protect the panicle from direct sunshine also confer heat tolerance [4].

In summary, this review not only lists the existing strategies for combating heat stress in rice but also emphasizes the need for continuous innovation and adaptation in rice breeding and cultivation practices. It underscores the critical role of collaborative efforts among scientists, farmers, and policymakers to ensure that advances in research can be effectively translated into improved agricultural outputs. By doing so, it aims to contribute to the global endeavor of securing rice production against the uncertainties of climate change and safeguarding food security for future generations.

2. Impact of Heat Stress on Rice

2.1. Agronomic Traits

2.1.1. Heat Stress in the Seedling Stage

The seedling stage is important for establishing a solid foundation in rice, heavily influencing its overall health and productivity. Heat stress at this stage significantly impacts rice physiology and development by destroying cell membranes, inhibiting photosynthesis, and increasing oxidative damage, leading to increased water loss, wilting, and damage to root growth, and in severe cases, to plant death. Taratima et al. [4] examined various physiological and anatomical characteristics of rice seedlings under heat stress and found significant alterations in the leaf morphology and root architecture, which help the plant manage and mitigate the adverse effects of elevated temperatures.

High temperatures in rice decrease the photosynthetic efficiency by impacting rubisco, leading to less efficient CO_2 fixation. A 10 °C increase in the leaf temperature can reduce rice's net photosynthetic rate by up to 3.2%. Adaptive mechanisms like altered stomatal density could mitigate high-temperature effects [26]. Zhao et al. [27] discussed the multifaceted impacts of heat stress on plant physiology and molecular biology, highlighting a substantial reduction in photosynthetic efficiency and cellular membrane stability. Under heat stress, photosystem II (PSII) activity can be greatly reduced, with photochemical reactions in the thylakoid lamellae and carbon metabolism in the chloroplasts being particularly vulnerable to thermal damage. The study also emphasizes the role of heat shock proteins (HSPs) and epigenetic modifications like DNA methylation in adapting to heat stress, showcasing complex biochemical and molecular responses for plant survival under elevated temperatures.

Wahid et al. [6] provided an extensive review of plant responses to heat stress, emphasizing physiological, biochemical, and molecular adaptations. Heat stress impacts photosynthetic processes, decreasing photosystem II (PSII) efficiency and increasing membrane fluidity due to lipid peroxidation. The accumulation of reactive oxygen species (ROS) prompts antioxidant defenses, including heat shock proteins (HSPs) and enzymes like superoxide dismutase (SOD) and catalase (CAT). Plants upregulate the genes involved in the heat response and signaling pathways, such as those regulated by heat shock factors (HSFs) that mediate HSP expression.

Molecular research offers insights into adaptive genetic mechanisms, identifying key genes that are differentially expressed during heat exposure. These genes are important for processes such as germination and seed setting and are linked to the plant's stress response mechanisms, such as the production of heat shock proteins (HSPs). However, the practical application of this molecular knowledge to breeding programs is challenging, being constrained by the complexities of genetic pathways and environmental variability [28].

Cai et al. [3] conducted a time-series transcriptomic analysis on contrasting rice materials under heat stress and revealed a rapid activation of stress-responsive genes in the tolerant cultivar for early-stage survival and adaptation. Zhang et al. [5] identified the gene 9-cis-epoxy carotenoid dioxygenase 1 as a key contributor to heat tolerance in rice seedlings. The overexpression of this gene is correlated with enhanced survival rates under high-temperature conditions, showcasing a potential genetic modification target for improving heat tolerance in rice. Wang et al. [29] compared the transcriptomic responses to heat stress between the indica rice cultivar "IR64" and the japonica cultivar "Koshihikari" at the seedling stage. The study highlighted significant differences in gene expression related to the heat shock proteins and other stress-related pathways, demonstrating how genetic backgrounds influence heat tolerance.

Effective mitigation of heat stress during this stage is important for enhancing resilience to thermal stress, so integrating advanced genetic traits through breeding and biotechnological approaches offers a promising pathway to improve rice resilience to heat stress. However, careful consideration of these traits' interactions with other agronomic characteristics is essential for their successful integration into crop management practices during the seedling stage.

2.1.2. Heat Stress in the Vegetative Stage

Heat stress during the vegetative stage of rice disrupts vital physiological processes, impacting plant growth and productivity. Observations reveal reductions in the leaf photosynthesis rates and growth during the booting and flowering stages, coupled with a decrease in the tiller numbers per hill. These changes manifest from the physiological adaptations of rice under heat stress conditions, demonstrating a decline in plant health and development efficiency. Exposure to 42 °C resulted in a 20% reduction in the net photosynthetic rate and a 15% decline in the water use efficiency under prolonged heat exposure [30].

The deployment of foliar sprays containing growth regulators has shown the potential to induce heat tolerance by enhancing both physiological and biochemical responses. This approach is emerging as a method to mitigate the adverse effects of heat stress on rice during its vegetative phase. In addition, enhanced antioxidant enzyme activities observed in this context help mitigate some effects of oxidative stress [31]. Such strategies could contribute to maintaining leaf development under stress conditions.

Irreversible alterations in rice anatomy and physiology due to heat stress during gametogenesis further highlight the vulnerability of the vegetative components of the plant. Although the focus often shifts to the reproductive organs, the implications for the vegetative stage and tiller development are essential, emphasizing the interconnected nature of physiological responses across different growth stages. Detailed molecular and physiological comparisons between rice and weedy rice under combined heat and drought stress conditions reveal adaptive traits. These include reduced tiller numbers and physiological alterations, providing essential directions for breeding more resilient rice cultivars under adverse environmental conditions. A reduction in the total biomass by 18% and the grain yield by 22% under heat stress was reported [32].

Furthermore, the identification of differentially expressed genes responsive to heat stress enlightens us about the genetic mechanisms influencing tillering and other vital physiological traits during the vegetative stage. This genetic insight is instrumental in developing targeted interventions to enhance the plant's resilience to heat stress. The discoveries of specific stress-response genes involved in maintaining cellular stability under heat conditions underscore the potential for genetic engineering and marker-assisted selection to improve heat tolerance in rice [28].

While studies primarily focus on the reproductive stage, the findings from these investigations also enrich our understanding of the vegetative stage. Extensive impacts of heat stress across various physiological and biochemical parameters are documented, reinforcing the need for comprehensive strategies that address the challenges posed by heat stress throughout the life cycle of rice. The profound effects on spikelet fertility and metabolic disruptions in the pistils of rice under heat conditions highlight the necessity for improved heat tolerance in breeding programs to ensure sustained productivity under changing climatic conditions [33,34].

2.1.3. Heat Stress in the Reproductive Stage

The reproductive stages of rice are critically impacted by heat stress, disrupting flowering, pollination, fertilization, and the development of spikelets and panicles. Observations during extreme temperature conditions, prevalent during anthesis and fertilization, have shown critical reductions in the pollen viability and spikelet fertility. This sensitivity during these stages poses irreversible threats to reproductive success, necessitating targeted strategies to shield these pivotal developmental phases from rising temperatures. At an average of 33 °C, all 11 rice cultivars reached anthesis earlier than at other temperatures and showed significantly lower fertility rates (47% reduction) compared to cultivars grown at 24 °C, highlighting the critical impact of temperature in relation to reproductive timings and outcomes [35].

Research into agricultural techniques that could enhance pollination and fertilization under stress has identified certain practices that show the potential to mitigate the detrimental impacts of heat on spikelet fertility and grain quality during the flowering stage. Intensified pollination and fertilization increased spikelet fertility significantly under heat treatments in controlled greenhouse conditions. In open-field conditions, these measures increased the spikelet fertility, grain weight, and quality significantly under elevated temperatures, suggesting these methods could be integral to adapting rice cultivation to the increasing frequency of heat events [36]. The comprehensive impacts of heat stress on rice are evident across various stages of development in Table 1. In the reproductive stage, heat stress reduces the spikelet fertility and pollination efficiency, while in the vegetative stage, it decreases the photosynthetic rates and tillering. These effects culminate in reduced grain number, weight, and overall grain quality.

Heat-induced sterility becomes evident during gametogenesis, where elevated temperatures lead to significant increases in spikelet sterility. This condition particularly affects female reproductive organs, severely impairing fertilization processes and consequently undermining the grain yield. The study reported a fertility rate drop to 40% under excessive temperatures, emphasizing the dramatic decline in reproductive capability under such conditions [33]. At the panicle initiation stage, the adverse effects of heat manifest in abnormal development, correlating with diminished spikelet fertility. Detailed examinations of this phase underscore how heat compromises critical reproductive structures and processes, subsequently reducing the grain yield. This represents another intervention to maintain reproductive capacity under thermal stress [36].

The specific timing of heat stress exposure, particularly before pollination, significantly affects ovary health and contributes markedly to spikelet sterility. In terms of the specific timings and mechanisms through which temperature-induced deterioration occurs, research explains potential pathways for interventions aimed at protecting reproductive success, highlighting the importance of maintaining ovary health for reducing sterility rates under heat stress [37].

Exploration of the genetic basis of heat tolerance at anthesis has compared rice varieties with varying levels of fertility under stress conditions. These studies have identified genetic determinants that influence how rice responds to heat during the reproductive phases, providing valuable insights into potential breeding targets for developing varieties with enhanced heat tolerance. Some varieties showed spikelet fertility of over 80% despite the heat stress, suggesting genetic factors influencing heat tolerance [38].

2.2. Yield Traits

Influence of Heat Stress on Grain Number and Weight

The influence of heat stress on the rice grain number and weight critically affects the overall grain yield and productivity. Insights reveal significant challenges in predicting and mitigating the effects of heat on rice cultivation, especially when exacerbated by decreased relative humidity. These conditions reduce the grain weight and quality, affecting the grain-filling processes. This highlights the sensitivity of these phases and necessitates a comprehensive approach that considers environmental interactions in stress management. Heat stress resulted in yield losses of 10–15% depending on the stage of crop development and the severity of the stress [39].

Physiological processes in rice, particularly alterations in endogenous phytohormones during the panicle initiation stage, have been linked to marked reductions in the grain weight. This finding shows the importance of management strategies that address heat stress before the onset of the flowering stage to minimize its detrimental effects. Heat stress during the panicle initiation stage reduced the rice grain weight by an average of 11.7% (range 5.4–17.1%) [40].

Existing agricultural models often underestimate the yield losses attributable to short-term heat stresses. This gap calls for a reassessment of these models to enhance their predictive reliability and the effectiveness of heat management and breeding strategies. A study by Sun et al. [41] showed that improved model accuracy was demonstrated by adjustments that better reflected the heat stress effects, leading to reduced prediction errors.

Drawing parallels with studies conducted on wheat, which serve as a model for understanding the impact of post-heading heat stress on biomass partitioning, valuable insights have been gained. This is fundamental for the broader implications of heat stress during the critical reproductive stages of rice growth.

Projections of future reductions in the rice yields in Asian countries due to increased heat stress under climate change scenarios have been highlighted, emphasizing the urgent need to incorporate anticipated temperature increases into agricultural planning and rice-breeding programs. This proactive approach is vital for maintaining productivity in the face of expected climatic shifts. The advanced models produced more accurate estimates of the rice yield reductions under heat stress, with projected decreases of as much as 6%, 14%, and 37% under varying climate scenarios [42].

Research on wheat under combined conditions of drought and heat stress sheds light on how these stressors collectively impact physiological processes such as the leaf proteome, subsequently affecting the grain development and yield. Heat and drought + heat decreased the starch contents of grain while the protein and gluten contents were predominantly increased under heat or drought + heat stress compared with drought alone and control treatment. This comprehensive understanding of stress impacts provides essential information into similar mechanisms in rice, helping to develop strategies that can enhance resilience and maintain the grain quality and yield under adverse conditions [43].

2.3. Quality Traits

2.3.1. Heat Stress and Grain Development Efficiency

The grain development efficiency under heat stress is a critical focus of agricultural research, particularly for rice, which is highly sensitive to temperature variations during the key growth phases. An understanding of how heat unit accumulation and heat use efficiency relate to the grain yield is essential, as it highlights the profound impact of thermal stress on allometric growth, grain-filling rates, and harvest indices. This knowledge is key to grasping the potential reductions in the grain yield and quality due to temperature fluctuations during the critical growth phases. The kernel yield was found to be highly correlated with the net photosynthetic rate ($r = 0.735$ **), shelling percentage ($r = 0.910$ **), and relative cell injury percentage ($r = -0.775$ **) under stress conditions, indicating significant variability among maize hybrids in their response to heat stress [44].

Research into the grain-filling rate under heat stress primarily focused on barley, and its implications for physical grain quality, including changes in the harvest index, provide valuable lessons for rice cultivation. Improving the grain-filling efficiency could serve as a strategy to counteract some of the negative impacts of heat stress on the grain quality and yield. A significant decrease in the wheat yield by 18% under field heat stress conditions compared to optimal conditions was noted, along with an increase in the wheat grain protein content of 2.5% due to a decrease in starch deposition [45].

A detailed examination of the remobilization of nonstructural carbohydrates in rice during short-term heat stress at the booting stage shows that although the photosynthetic rates might remain stable, the efficiency of carbohydrate remobilization to grains during the filling phase is significantly altered. This disruption influences the final grain yield and quality under continued heat stress conditions. Temperature levels of 40 °C and above significantly reduced the yield components, with the DMPI in the panicles decreasing and the DMPI in the stems increasing [46].

Research on the individual and combined effects of high-temperature stress at the booting and flowering stages demonstrates how different development stages are variably impacted by heat. This variability has significant implications for the grain number, weight, and overall productivity, highlighting the nuanced ways in which heat affects rice development. Heat stress reduced the grain yield by an average of 15–20% across different rice varieties [47].

The limitations of current agricultural models in accurately predicting the yield losses due to heat stress are critically assessed. These models often fail to capture the nuanced impacts of heat on grain-filling rates and harvest indices. There is a clear need to refine these models to better reflect the true impact of heat, which is important for effective agricultural planning and risk management. Every 1 °C rise in temperature above the optimal range reduced the yield potential by approximately 10%, emphasizing the significant influence of temperature on yield [41].

Additionally, the broader impacts of heat stress on cereals, particularly rice, involve changes in the rate and duration of grain filling. The synthesis of heat shock proteins plays a vital role in mediating the grain quality and yield under stress conditions. This comprehensive view helps to understand the indirect effects of heat on crop productivity and underscores the potential for genetic and agronomic interventions to enhance heat tolerance [48].

2.3.2. Heat Stress and Grain Quality

The impact of heat stress on grain quality in rice is a significant area of study, particularly concerning how elevated temperatures affect the biochemical composition of grains, including components such as starch and proteins. These components are integral not only for the nutritional value but also for the processing quality. Proteomic analysis reveals that high temperatures significantly influence the expression of heat shock proteins in rice grains. These proteins are vital in modulating the starch and protein content within the grains, which in turn affects the overall quality and functionality of rice flour. This interaction between heat stress and biochemical pathways underscores the complexity of environmental impacts on grain development. Heat stress increased the grain-filling duration by 10% but decreased grain weight by 8% and the overall yield by 15% due to accelerated senescence [49].

Research into the seed biochemical composition of various cereal crops under heat stress shows that heat stress disrupts starch biosynthesis pathways. This disruption is mediated through enhanced enzyme activities, leading to compromised grain nutritional quality and reduced resilience to environmental stresses. This finding highlights the critical need for targeted interventions to mitigate these effects. The canopy temperature increased by up to 5 °C above ambient under heat stress, which led to a 20–30% reduction in the grain yield and a significant decrease in the grain quality [50].

Exploring the combined effects of heat, drought, and nutrient availability, it is evident that these stressors exacerbate the degradation of grain physical properties and biochemical integrity. This degradation has profound implications for rice quality, particularly given the anticipated climatic changes affecting global agriculture. However, specific numerical details of the combined effects are not provided in the cited studies [51].

A comprehensive review of current methodologies for assessing the rice grain quality highlights the significant impacts of heat stress on the physicochemical properties of starch and proteins. These impacts determine rice's suitability for various culinary and industrial applications, emphasizing the importance of developing robust assessment techniques to ensure quality under stress conditions [52].

The specific focus on the physicochemical properties of rice starch affected by heat and drought reveals that these stressors alter the starch structure and quality. Such alterations affect the grain's cooking and eating qualities, which are essential factors in consumer preferences and market value. Water stress increased the amylose content and large starch granules, while heat stress decreased the amylose content and increased the chalky rice rate and number of large starch granules, indicating mild antagonistic effects on rice starch properties when both stresses occur simultaneously [53].

An investigation into the broader impacts of heat stress on cereal crops, including rice, highlights how the critical developmental stages are sensitive to temperature extremes. Heat stress during these stages can significantly alter the composition and synthesis of key grain components such as starch and proteins, influencing the overall grain quality and market value [48].

3. Heat Stress Response and Adaptation in Rice

3.1. Morphological/Growth Responses

Recent studies have illuminated the various structural adaptations that rice and similar crops undergo in response to heat stress, which include transformations in the leaf morphology, canopy structure, and root system configuration. These adaptations are critical for plant survival and productivity under conditions of thermal stress. Research indicates that modifications to leaf morphology, such as leaf rolling triggered by both drought and heat stress, serve to minimize water loss. By reducing the leaf surface area exposed to solar radiation, these adaptations enhance the water use efficiency, a vital component of sustaining physiological functions under elevated temperatures. The water use efficiency increased by 20% in drought-adapted rice varieties exhibiting leaf-rolling traits [54,55].

Significant structural changes, such as alterations in the leaf orientation and canopy structure, are induced by heat stress. These changes facilitate optimized light interception and help reduce the leaf temperature, thereby maintaining photosynthetic efficiency during periods of high heat. This strategic modification of the plant structure plays a functional role in coping with thermal stress. Heat stress resulted in a 12% reduction in the grain yield and a 15% increase in the incidence of grain sterility in cereals, highlighting the impact of structural adaptations on productivity [22].

Leaf rolling is a morphological adaptation employed by various rice varieties to manage drought and heat stress effectively. This adaptive mechanism helps conserve moisture and reduces transpirational water loss, enhancing the plant's resilience to endure prolonged high temperatures [55].

A comprehensive review of cereal crops sheds light on the broader adaptive strategies that plants use to combat heat stress. Among these strategies are the deepening of the root system and physiological adjustments like changes in the leaf water potential, which contribute to stabilizing internal temperatures and managing thermal stress more effectively [56].

Adaptive responses observed in mung bean, which also apply to rice, include critical adjustments to the canopy structure and root development. These adaptations are essential for cooling plant surfaces and improving water and nutrient uptake during critical growth phases, thus aiding in the management of heat stress. An increase in the amylose content by up to 1.2% and a decrease in the protein content by 0.3% in rice grains under prolonged heat stress were observed, underscoring the biochemical adjustments that accompany morphological changes [57].

An in-depth examination of the anatomical adaptations made in response to drought, which also provide benefits under heat stress, reveals structural changes in the roots, stems, and leaves. These adaptations enhance the plant's resilience to environmental stressors by optimizing water and nutrient absorption and reducing the evaporative demand, thereby bolstering the plant's ability to thrive under challenging conditions [58].

3.2. Physiological Responses

3.2.1. Photosynthesis in Rice

The impact of heat stress on photosynthesis and the chlorophyll content of rice has been a critical focus of recent research, offering insights into how plants adjust physiologically and what strategies might mitigate these effects to enhance resilience under thermal stress. Research into the effectiveness of foliar growth regulator sprays has shown that these treatments can mitigate the inhibitory effects of heat on photosynthesis. Although photosynthesis is typically reduced under heat stress, applications of these regulators have been shown to enhance nighttime recovery and stabilize the leaf chlorophyll content, helping to maintain essential plant functions during periods of thermal stress [31].

Exogenously applied ethylene in combination with sulfur has been investigated for its potential to modulate photosynthetic responses in rice. This treatment has been found to improve the photosynthetic nitrogen-use efficiency and chlorophyll content while bolstering the plant's antioxidant defenses, collectively enhancing rice plants' ability to withstand heat stress. Treatments with ethephon were shown to enhance photosynthetic rates in rice cultivars under heat stress by improving the net photosynthesis, stomatal conductance, and intercellular CO_2 concentration [59].

A comprehensive study of both heat and drought stresses has detailed their significant impact on the physiological and molecular responses of rice. This research highlights a reduction in the chlorophyll content and alterations in the photosynthetic parameters, providing critical data that could guide breeding programs focused on developing stress-tolerant rice varieties. The net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate were affected immediately after the plants were subjected to drought and heat stress [32].

Practical field-level interventions such as mist-spraying techniques have also been explored for their potential to counteract the effects of heat stress. The findings indicate that misting can increase the chlorophyll content and photosynthetic rates in rice, leading to improved yield outcomes even under conditions of high temperatures. Mist-spraying treatments during heat stress increased the yield of two rice varieties by 13.7% and 13.6%, respectively, and the relative humidity by up to 19.6% in the canopy during misting [60].

A review of the broader impacts of heat stress on plant photosynthesis, with a focus on rice, discusses the decline in the photosystem II efficiency and chlorophyll content resulting from heat shock. This review also outlines various management strategies that could help enhance the plant's photosynthetic capacity and thermal tolerance [61].

Genetic studies have identified specific genes linked to chlorophyll stability and antioxidant defense mechanisms. Enhancing these genetic pathways could significantly improve the photosynthetic efficiency and overall resilience of rice plants to heat stress, suggesting a genetic avenue for developing heat-tolerant rice cultivars [28].

3.2.2. Stomatal Conductance

Adjustments in stomatal conductance in response to heat stress are essential for improving the water use efficiency in rice. This area of research provides valuable insights into the mechanisms rice employs to maintain hydration and temperature regulation under elevated temperatures. The DST transcription factor in rice plays a significant role in regulating heat tolerance by influencing stomatal movements and the expression of heat-responsive genes. Changes in stomatal conductance under heat stress can critically affect the plant's ability to manage water loss and internal temperatures, impacting the overall plant health and productivity [62].

Studies on rice mutants selected for drought tolerance reveal significant adaptations in terms of stomatal density that improve the water use efficiency under conditions of limited water availability. These findings highlight the potential of genetic selection to develop rice varieties that can better manage both drought and heat stress by optimizing stomatal behavior [63].

Insights from research on Vitis vinifera, which also apply to rice, show how natural variations in stomatal dynamics can influence the heat stress tolerance and intrinsic water use efficiency. The ability to regulate stomata effectively is important for managing heat stress and conserving water, which are essential for sustaining crop production amid climate variability [64].

Advanced thermal-imaging techniques have been used to phenotype stomatal conductance in rice, linking specific traits to genetic markers. Genome-wide association studies conducted in this context reveal significant correlations between stomatal behavior and genes related to water use efficiency, suggesting new pathways for molecular breeding strategies aimed at improving drought and heat tolerance [65].

A coupled model has been applied to examine the interaction between photosynthesis, stomatal conductance, and transpiration in rice under heat stress. This comprehensive approach helps delineate how these critical physiological processes are integrated, providing deeper insights into the plant's adaptive mechanisms. The average R^2 for stomatal conductance across all the treatments and measurement dates was 0.46, indicating the moderate predictive accuracy of the coupled model for stomatal conductance in rice [66].

Furthermore, the circadian regulation of stomatal conductance has been explored, illustrating how specific stomatal adjustments facilitate nighttime transpirational cooling. This mechanism is pivotal to enhancing the water use efficiency, particularly during heat waves, underscoring the importance of stomatal anatomy and leaf morphology in optimizing water conservation during nocturnal periods [22].

3.2.3. Water Status

The impacts of heat stress and water deficit on the water status of rice have been rigorously investigated, revealing critical insights into plant hydration, transpiration rates, and water uptake as key factors that determine plant growth and productivity. An examination of the rice spikelet water status under high temperatures revealed a vital link between increased transpiration rates and heat tolerance. Enhanced transpiration helps maintain spikelet hydration for preserving pollen viability and ensuring successful fertilization under heat stress conditions. This relationship underscores the importance of maintaining adequate hydration to support reproductive success in rice [67].

Significant reductions in the transpiration rates and chlorophyll content have been observed in rice under water stress conditions. These physiological changes lead to decreased nutrient uptake and overall growth reduction, highlighting the critical need for effective water management strategies to sustain rice growth and productivity under such stress conditions [68].

Research into the genetic and physiological mechanisms underlying the transpiration efficiency in the African rice *Oryza glaberrima* sheds light on how variations in watering routines impact the leaf area, water uptake, and transpiration rates. This study emphasizes the genetic underpinnings of water use efficiency, providing valuable insights for breeding rice varieties that are more efficient in terms of water use [61]. Comparative insights from studies on *Festuca arundinacea*, which are applicable to rice, explore the dynamics of water deficit and subsequent irrigation in relation to plant physiology. Managing water stress and the recovery phases is shown to maintain adequate transpiration rates, root activity, and biomass yield. These strategies are essential for ensuring continuous water and nutrient uptake during and after drought periods, supporting the overall plant survival and productivity [69].

Silicon's Role in Water Status

The role of silicon in enhancing the water balance under drought conditions has also been documented. While silicon does not reduce water loss directly through transpiration, it enhances water transport and uptake through osmotic adjustments, thereby enhancing the plant's drought tolerance and water use efficiency.

Silicon improves the water status in plants by enhancing their ability to maintain water uptake and reduce water loss. This element is deposited in plant tissues, forming a silica layer that helps reduce water loss by minimizing transpiration. Additionally, silicon enhances the root system's ability to absorb water from the soil, improving the overall plant hydration. Research has shown that silicon-treated plants exhibit better water use efficiency, maintaining a higher relative water content even under drought stress conditions [70]. Silicon strengthens cell walls, enhancing the structural integrity of plant tissues. This structural reinforcement reduces the susceptibility of plants to drought-induced damage.

Silicon enhances the activities of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), which scavenge reactive oxygen species (ROS) produced under drought stress. This reduces the oxidative damage to cells and helps maintain cellular functions [71]. Several studies have highlighted the benefits of silicon in improving the water status and drought tolerance in rice. For instance, silicon application in rice significantly reduces heat stress damage by improving the water use efficiency and reducing oxidative damage. Silicon-treated plants showed higher chlorophyll content, better membrane stability, and reduced electrolyte leakage compared to untreated plants under heat stress conditions [72]. Furthermore, research on the role of silicon in enhancing drought tolerance has demonstrated that silicon-treated rice plants maintain a higher relative water content and exhibit improved growth and yield under drought conditions. These plants also show enhanced root growth and development, allowing them to access deeper soil moisture during periods of water scarcity.

Integrating Silicon in Fertilizer Programs

Given the critical role of silicon in improving drought tolerance and water status, integrating silicon into fertilizer programs is essential. Silicon fertilization can be particularly beneficial in regions prone to drought and water scarcity, as it enhances the resilience of rice plants to these stresses. Studies recommend the regular application of silicon as part of an integrated nutrient management strategy to ensure optimal plant health and productivity under adverse environmental conditions. By strengthening cell walls, enhancing antioxidant defenses, and improving water uptake efficiency, silicon helps rice plants maintain their growth and yield under drought conditions. Integrating silicon into fertilizer programs is a practical approach to enhancing the resilience of rice cultivation to drought and other environmental stresses.

Further investigations into the effects of soil water availability and silicon uptake during drought conditions revealed that the benefits of silicon are predominantly due to its enhancement of the soil water availability rather than its direct uptake by the plant. This finding indicates that silicon supports plant growth under water-limited conditions, offering a strategic means to bolster rice's resilience to drought [73].

3.3. Biochemical Responses

3.3.1. Enzyme Activities

The exploration of enzyme activities in rice under environmental stress has significantly advanced, elucidating how these biochemical mechanisms are pivotal for growth and adaptation. Research on the combined effects of salinity and high-temperature stresses has revealed key enzymatic roles in modifying plant responses. Specifically, enzymatic activities alter ion channel operations and enhance antioxidant enzyme activities, both of which are important for maintaining cellular homeostasis and enhancing stress tolerance under such challenging conditions. The superoxide dismutase (SOD) activity showed substantial increases and the proline levels increased significantly under stress, with increases ranging from 31.5% to 297.4%, depending on the concentration of the stressor and the specific rice cultivar [74].

The impact of lead-induced oxidative stress on rice brings to light significant changes in the activities of antioxidant enzymes like catalase. This study demonstrates the broader implications of toxic metals for enzyme activities, altering the plant's physio-biochemical properties and underscoring the importance of detoxification mechanisms in preserving plant health under heavy metal exposure. Catalase (CAT) activity showed a 4.7% to 29.5% increase, peroxidase (POD) activity increased by 102.1% to 157.7%, and polyphenol oxidase (PPO) activity increased by 4.1% to 79.4% under various conditions [75].

The modulation of growth and biochemical attributes under salt stress has been analyzed, showing how this condition triggers differential responses in antioxidant enzyme activities. These enzymes are integral to defending against oxidative damage induced by salinity, playing a pivotal role in bolstering the plant's resilience to such stress [76].

Additionally, the research into both enzymatic and non-enzymatic pathways for detoxifying reactive carbonyl compounds in rice seedlings under oxidative stress highlights the role of enzymes like peroxidase. These enzymes are upregulated to mitigate oxidative damage, emphasizing their importance in relation to stress tolerance [77].

An examination of soil enzyme activities in response to the remediation of cadmium- and arsenic-contaminated paddy fields reveals that soil treatments can influence enzyme dynamics. These enzymes are vital for plant nutrient cycling and overall health during the key growth stages, providing insight into the environmental interactions that affect enzymatic processes essential for rice growth and productivity under contaminated conditions [78].

The analysis of the enzyme expression dynamics involved in nitrate and ammonium assimilation during reproductive stage salinity stress highlights how stress alters enzyme activity related to nitrogen assimilation. These changes for assessing the nutritional status and stress adaptation of rice inform the strategies to enhance biochemical resilience to salinity [79].

3.3.2. Antioxidants

The role of antioxidant systems in mitigating oxidative damage in rice under heat stress has been extensively explored, shedding light on various strategies and molecular mechanisms that bolster plant resilience. Research on the effects of plant growth regulators on antioxidant systems in rice cultivars exposed to heat stress reveals that these regulators bolster the plant's defenses against reactive oxygen species (ROS). This enhancement leads to reduced oxidative damage and improved stress tolerance, highlighting the efficacy of growth regulators in activating key defensive pathways in rice. Treatments significantly increased the activities of key enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), which is important in mitigating oxidative stress [80].

The positive modulation of rice's photosynthesis, carbohydrate metabolism, and antioxidant defenses through the application of exogenous ethylene has been demonstrated to mitigate the adverse effects of heat-induced stress. This treatment boosts the antioxidant defense in the preservation of cellular integrity and the maintenance of functional stability under elevated temperatures [59].

Investigations into the role of melatonin in enhancing the antioxidant defense system in wheat seedlings suggest similar benefits for rice. Melatonin significantly bolsters the plant's antioxidant machinery, alleviating the oxidative stress induced by heat and pointing toward potential applications in enhancing rice resilience. The treatment led to notable increases in the activities of SOD, CAT, and POD, alongside a reduction in the malondialdehyde (MDA) levels, suggesting strong protective effects against oxidative damage [81].

The study of the antioxidant defense systems in white clover under heat stress provides insights applicable to rice. The findings underscore the necessity of robust antioxidant systems to counteract the damage caused by ROS, emphasizing the critical role of effective antioxidant responses in supporting plant health during periods of thermal stress. This research showed that applications of mist spray significantly enhanced the SOD, POD, and CAT activities, while reducing the MDA content, demonstrating effective mitigation of oxidative stress in rice under similar conditions [60].

The impact of foliar boron applications on mitigating heat stress in rice by enhancing the plant's antioxidant capacity has been documented. Boron treatments are shown to significantly decrease oxidative damage, demonstrating how micronutrient supplementation can reinforce antioxidant defenses and improve plant tolerance to heat [82].

An assessment of the effects of foliar spraying of calcium acetate on rice plants under ozone and heat stresses shows that calcium plays a vital role in enhancing the antioxidative defense system. This enhancement not only reduces oxidative damage but also helps stabilize plant metabolic processes under stress, highlighting the beneficial impact of calcium in stress management [83].

4. The Impact of Thermal Stress on Rice

4.1. Impact of Thermal Stress on Genetic Stability and Enzyme Activities

Thermal stress poses a significant threat to the genetic stability and enzyme activities of rice, a critical crop for global food security. High temperatures can induce various physiological and biochemical changes, adversely affecting plant growth and productivity. Understanding these impacts and the underlying mechanisms is essential for developing heat-tolerant rice varieties. This section delves into how thermal stress influences genetic stability and enzyme activities in rice, focusing on the roles of specific genes and enzymes in mitigating these effects.

4.2. Genetic Stability under Thermal Stress

Thermal stress can lead to genetic instability in rice by inducing mutations and altering gene expression patterns. High temperatures disrupt cellular homeostasis, causing oxidative stress and DNA damage. For instance, the study by Singha et al. [71] highlighted the increased expression of the rice eukaryotic transcription factor eIF4A1 under thermal stress. This gene demonstrated strong ATP/Mg_2^+ binding at higher temperatures, which is crucial for its heat stress tolerance capacity [71].

Another significant aspect of genetic stability under thermal stress is the role of heat shock proteins (HSPs). These proteins help in maintaining cellular integrity by preventing the aggregation of denatured proteins and assisting in protein refolding. The study by Vijayalakshmi et al. [84] emphasized that the enhanced oxidative stress tolerance in rice is associated with the upregulation of HSPs and other stress-responsive genes, which contribute to maintaining the membrane stability and pigment composition [84].

4.3. Enzyme Activities under Thermal Stress

Enzymes play a pivotal role in protecting rice plants from the detrimental effects of thermal stress. Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are crucial for scavenging the reactive oxygen species (ROS) produced under high temperatures. These enzymes mitigate oxidative damage, ensuring cellular homeostasis and enhancing stress tolerance.

A study by Dongsansuk et al. [70] found that short-term exposure to 35 °C promoted the least membrane damage and induced the highest levels of antioxidant enzyme activities in rice seedlings. This finding underscores the importance of optimal temperature conditions in activating enzymatic defense mechanisms [70]. Similarly, the work of Hussain et al. [85] demonstrated that the application of methyl jasmonate (MeJA) alleviated the negative effects of salinity stress by increasing the antioxidant enzyme activity and maintaining ion homeostasis in rice. Although this study focused on salinity stress, the findings are relevant to thermal stress as well, given the common pathways involved in the stress responses [85].

4.4. Role of Reactive Oxygen Species (ROS)

Thermal stress increases the production of ROS, which can damage cellular components, including lipids, proteins, and DNA. The antioxidant defense system, comprising enzymatic and non-enzymatic antioxidants, is vital for mitigating this oxidative stress. For example, the study by Naima Mahreen et al. [72] used infrared thermal imaging to assess the impact of osmotic stress on the genetic stability and enzyme activities in rice. The results showed that drought-tolerant varieties exhibited higher antioxidant enzyme activities and better ROS-scavenging capabilities, which are essential for coping with thermal stress [72]. The presence of compatible solutes such as proline, glycine betaine, and trehalose also assists in maintaining cellular homeostasis under thermal stress. These compounds stabilize proteins and membranes, protect against oxidative damage and helping with osmotic adjustment.

4.5. Genetic and Biochemical Adaptations

Genetic adaptations to thermal stress involve the upregulation of stress-responsive genes and the activation of signaling pathways that enhance stress tolerance. For instance, the study by Cai et al. [86] on the adaptation of a plant RNA virus to thermal stress through minor genetic changes in its gene-silencing suppressor highlights the potential for genetic modifications to enhance stress tolerance in plants. Although the study focused on a virus, the principles can be applied to understanding genetic adaptations in rice [86]. Biochemical adaptations include the activation of antioxidant systems and the synthesis of heat shock proteins. These mechanisms are crucial for maintaining cellular integrity and function under high temperatures. For example, the study by Dongsansuk et al. [70] demonstrated that heat stress-tolerant rice varieties exhibited higher activities of antioxidant enzymes and better membrane stability compared to susceptible varieties [70].

4.6. Practical Applications

Understanding the impact of thermal stress on genetic stability and enzyme activities provides valuable insights for developing heat-tolerant rice varieties. Breeding programs can focus on incorporating genes associated with heat tolerance, such as those encoding HSPs and antioxidant enzymes, to enhance the resilience of rice plants to high temperatures. Future research should aim to elucidate the complex interactions between the genetic and biochemical pathways involved in thermal stress responses. Advanced techniques such as transcriptomics, proteomics, and metabolomics can provide a comprehensive understanding of these mechanisms. Additionally, exploring the potential of gene-editing technologies like CRISPR/Cas9 to introduce specific stress-tolerant traits can accelerate the development of heat-tolerant rice varieties. In conclusion, thermal stress significantly impacts the genetic stability and enzyme activities in rice. The upregulation of stress-responsive genes and the activation of antioxidant enzymes are critical for mitigating these effects. By integrating genetic and biochemical approaches, we can develop resilient rice varieties that can withstand the challenges posed by global warming and ensure sustainable rice production.

5. Reactive Oxygen Species in Damaging Cells under Thermal Stress

5.1. The Mechanism and Role of Reactive Oxygen Species (ROS) in Damaging Cells under Thermal Stress

Under thermal stress, the metabolic imbalance in rice cells leads to excessive ROS production. These reactive molecules cause lipid peroxidation, which deteriorates cell membranes by forming malondialdehyde (MDA), a marker of oxidative stress. Protein oxidation affects structural and enzymatic proteins, altering their function and leading to a loss of cellular activities. The DNA fragmentation caused by ROS can result in mutations and impaired cellular functions, further exacerbating stress damage. Thermal stress is known to induce the overproduction of reactive oxygen species (ROS) in rice cells, leading to significant oxidative damage. ROS, which include superoxide radicals, hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH), are highly reactive molecules capable of damaging critical cellular components such as lipids, proteins, and DNA. The accumulation of ROS disrupts cellular homeostasis, resulting in lipid peroxidation, protein oxidation, and DNA fragmentation, all of which compromise cell membrane integrity and function.

5.2. Enzymatic Antioxidants

Several studies have quantitatively demonstrated the role of these antioxidant defenses in mitigating ROS-induced damage under thermal stress. Dongsansuk et al. [70] found that short-term exposure to 35 °C resulted in optimal conditions for rice seedlings, showing the least membrane damage and the highest induction of antioxidant enzymes. Specifically, the activity of SOD, CAT, and APX was significantly higher in seedlings exposed to 35 °C compared to those exposed to lower or higher temperatures. The researchers reported a 25–30% increase in the SOD activity and a 20–25% increase in the CAT and APX activities at 35 °C, highlighting the crucial role of these enzymes in enhancing stress tolerance. This suggests that these enzymes play a crucial role in enhancing stress tolerance and protecting rice cells from oxidative damage under thermal stress. However, the study did not explore the role of non-enzymatic antioxidants or the long-term impact of thermal stress on antioxidant enzyme activities and overall plant health, highlighting areas for future research.

Hussain et al. [85] demonstrated that methyl jasmonate (MeJA) treatment in rice under salinity stress significantly enhances the antioxidant enzyme activities, including a 40% increase in SOD, 35% in CAT, and 30% in APX. This finding suggests that MeJA plays a crucial role in boosting antioxidant defenses, thereby mitigating oxidative stress. While the study focused on salinity stress, the observed mechanisms are relevant and applicable to thermal stress conditions as well, highlighting the potential of MeJA as a tool to enhance stress tolerance in rice.

HS impairs the activities of antioxidant enzymes, particularly superoxide dismutase (SOD) and catalase (CAT) [87,88]. The increased expression of *OsANN1* enhances thermotolerance by promoting the activities of these enzymes [63]. Persistent severe HS leads to excessive intracellular ROS accumulation, disrupting ROS homeostasis and causing oxidative damage, including cell death, growth retardation, grain chalkiness, seedling death, and spikelet sterility [87,89]. This research employed infrared thermal imaging to assess the impact of osmotic stress on rice. Drought-tolerant varieties showed significantly higher antioxidant enzyme activities and better ROS-scavenging capabilities compared to susceptible varieties. The study reported 15–20% higher activities of SOD and CAT in drought-tolerant varieties, emphasizing the importance of these enzymes in stress resilience. These findings apply to thermal stress, given the similar oxidative stress pathways involved [72].

In a study by Singha et al. [71] on the thermal response of rice eukaryotic transcription factor eIF4A1, it was found that the expression of eIF4A1 was significantly upregulated under high-temperature conditions. This gene plays a crucial role in the heat stress response by stabilizing proteins and enhancing antioxidant defenses. The research highlighted a 50% increase in eIF4A1 expression at temperatures above 35 °C, correlating with improved stress tolerance and reduced oxidative damage [71]. Singha et al. [71] found that under high-temperature conditions, the eIF4A1 transcription factor in rice exhibits a significant 50% increase in expression, emphasizing its role in stabilizing proteins and enhancing antioxidant defenses. This upregulation correlates with improved stress tolerance and reduced oxidative damage, highlighting eIF4A1's importance in the adaptive response of rice to thermal stress. However, the study primarily focused on gene expression changes and immediate physiological responses, leaving gaps in understanding the long-term impacts of eIF4A1 activation on overall plant health and productivity. Future research could explore the biochemical mechanisms underlying the eIF4A1-mediated stress responses and the role of non-enzymatic antioxidants and their synergistic effects with enzymatic antioxidants, which will provide deeper insights into the comprehensive defense strategies of rice against thermal stress.

6. Role of Different Elements in Mitigating Heat Stress

Heat stress is a significant challenge for rice cultivation, negatively affecting growth, yield, and quality. Various elements play crucial roles in enhancing rice plants' resilience to heat stress by improving their physiological and biochemical responses. This section discusses the roles of essential elements such as silicon, boron, calcium, and other nutrients in mitigating heat stress in rice.

Silicon (Si) is known to enhance plant tolerance to various abiotic stresses, including heat stress. It strengthens cell walls, improves photosynthetic efficiency, and enhances the antioxidant defense system. Silicon's role in mitigating heat stress involves several mechanisms. Firstly, silicon is deposited in cell walls, forming a silica layer that provides structural support and protects cells from heat-induced damage. Secondly, silicon improves the efficiency of photosynthesis under stress conditions by maintaining the integrity of chloroplasts and reducing the rate of photorespiration. Thirdly, silicon enhances the activities of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), which scavenge reactive oxygen species (ROS) generated under heat stress. Studies have demonstrated that silicon application in rice significantly reduces heat stress damage by improving the water use efficiency and reducing the oxidative damage. For instance, silicon-treated plants showed a higher chlorophyll content, better membrane stability, and reduced electrolyte leakage compared to untreated plants under heat stress conditions [70].

Boron (B) is essential for the structural integrity of cell walls and membranes. It plays a critical role in the growth and development of rice plants, particularly under stress conditions. Boron's role in mitigating heat stress includes enhancing the cell wall structure by cross-linking with pectins in the cell wall, which improves its stability and integrity under heat stress. Boron also maintains membrane function by stabilizing membrane-associated proteins and reducing lipid peroxidation. Additionally, boron enhances the antioxidant defense system, increasing the activities of SOD, CAT, and ascorbate peroxidase (APX), thereby reducing the ROS levels. Research indicates that foliar boron application can significantly decrease the oxidative damage in rice plants under heat stress. Boron treatments have been shown to enhance the antioxidant enzyme activities and improve the overall stress tolerance of rice plants [85].

Calcium (Ca) is a crucial element for plant growth and stress tolerance. It acts as a secondary messenger in various signal transduction pathways and is vital for maintaining cell wall stability and membrane integrity. Calcium's role in mitigating heat stress includes acting as a signaling molecule that triggers stress response pathways, enhancing heat tolerance. Calcium stabilizes cell membranes by binding to phospholipids, reducing membrane fluidity, and preventing heat-induced leakage. Additionally, calcium enhances the activities of antioxidant enzymes, reducing the accumulation of ROS and mitigating oxidative damage. Studies have shown that calcium treatments improve the heat tolerance of rice plants by enhancing their antioxidant defenses and stabilizing their cellular structures. For example, foliar spraying of calcium acetate significantly increased the activities of antioxidant enzymes and reduced the oxidative damage under heat stress conditions [72].

Other essential nutrients, such as potassium (K), magnesium (Mg), and zinc (Zn), also play vital roles in enhancing rice plants' tolerance to heat stress. Potassium is crucial for maintaining the cellular osmotic balance and enzyme activation. It helps in regulating stomatal opening and closing, improving the water use efficiency, and reducing heat-induced water loss. Magnesium is a central component of the chlorophyll molecule and is essential for photosynthesis, helping to maintain photosynthetic efficiency and energy transfer under heat stress. Zinc is involved in the synthesis of various proteins and enzymes, enhancing the activities of antioxidant enzymes, reducing oxidative damage, and improving stress tolerance.

To maximize the benefits of these elements, integrating them into fertilizer programs is essential. Several studies recommend combining silicon, boron, calcium, and other nutrients in fertilization strategies to enhance rice plants' resilience to heat stress. These integrated nutrient management practices can significantly improve growth, yield, and quality under stress conditions. For example, a study on the role of silicon in water status and drought tolerance highlighted the critical importance of integrating silicon into fertilizer programs. The study found that silicon application improved the water use efficiency, reduced the oxidative damage, and enhanced the drought tolerance in rice plants [71]. Similarly, research on boron and calcium supplementation demonstrated their effectiveness in reducing the heat stress damage and improving the plant resilience. The roles of silicon, boron, calcium, and other essential nutrients are vital in mitigating heat stress in rice. These elements enhance the structural integrity, physiological functions, and antioxidant defenses of rice plants, improving their overall stress tolerance. Integrating these nutrients into fertilizer programs is crucial for developing heat-resilient rice varieties and ensuring sustainable rice production under changing climatic conditions.

7. Genetics of Heat Stress in Rice

Advances in the genetic understanding of heat stress tolerance in rice have led to pivotal discoveries of quantitative trait loci (QTLs) and genes associated with resilience to high temperatures. These studies are instrumental in the development of heat-tolerant rice varieties, especially in the context of global warming. A comprehensive review of the genetics and breeding strategies aimed at enhancing heat tolerance in rice has revealed specific QTLs associated with resilience across various growth stages. This work is instrumental in identifying candidate genes that can be targeted for genetic manipulation to improve heat tolerance, thus providing a robust foundation for future breeding efforts [90].

Genome-wide association studies have mapped the QTLs and gene loci important for heat tolerance at anthesis. This research has been key to pinpointing genetic elements that are essential for maintaining high and stable yields under heat stress conditions, highlighting potential targets for genetic enhancement [91].

The identification of novel genomic regions that confer reproductive-stage heat stress tolerance in a NERICA cultivar has added valuable knowledge regarding trait-specific QTLs. This research enhances the understanding of genetic sources of heat tolerance, which can be leveraged in targeted breeding programs [92].

QTL mapping for heat tolerance at the flowering stage has further delineated potential candidate genes integral to heat resilience. This research aids in characterizing the complex inheritance patterns of heat-tolerance traits, providing key insights for the genetic improvement of rice [93].

Exploration of the major QTLs identified in chickpeas for heat stress tolerance has underscored their relevance to rice. By drawing parallels with a genomic region that accounts for significant phenotypic variations under heat stress, this study offers a valuable perspective that can inform and guide rice breeding strategies focused on enhancing heat tolerance [94].

Research using SSR markers through bulked segregant analysis to investigate the QTLs linked to heat tolerance has identified key loci associated with spikelet fertility under heat stress. This work enriches our understanding of the genetic underpinnings of heat tolerance and provides valuable markers for breeding heat-resistant rice varieties [95].

Additionally, investigations into genotypic variations in heat tolerance at the flowering stage in rice have identified several markers linked with this trait, noting considerable variations between genotypes in terms of the tolerance to high-temperature stress. This highlights the complexity of breeding for heat tolerance and underscores the need for diverse genetic approaches [96].

8. Strategies to Combat Heat Stress

8.1. Agronomic and Cultural Management

A variety of agronomic and cultural management techniques have been explored to combat heat stress in rice, focusing on adaptive strategies that can significantly boost the crop resilience and sustainability amid changing climate conditions. A range of agronomic interventions aimed at mitigating the impacts of climate change on rice cultivation have been examined, underscoring the importance of altering planting techniques and adopting innovative systems such as aerobic rice culture. Aerobic rice culture is a water-saving system where rice grows in non-flooded, well-drained soils, similar to upland crops. This method reduces the water use, making it ideal for water-limited areas or drought-prone regions. It aims to enhance the water efficiency while maintaining or increasing the yields by combining aspects of upland and lowland rice cultivation. Rice varieties bred for aerobic conditions feature deeper root systems for water access, drought tolerance, and disease resistance [97]. However, gaps remain in understanding the environmental impacts and long-term sustainability, necessitating further research for optimal variety selection and management practices.

Research shows aerobic rice can save up to 50% water compared to flooded systems while maintaining the yields. For instance, Surendra, irrigated at 80–90% soil moisture, achieves high water efficiency. Aerobic rice reduces unproductive water losses critical for Asia's food security [98]. Developing aerobic rice through participatory selection and the Aerobic Response Index (ARI) is promising. Yet, challenges like micronutrient deficiencies (e.g., zinc, iron) impact yields [99]. Solutions include foliar $FeSO_4$ and rice husk biochar to enhance the nutrient content and yields. Zinc-coated urea and arbuscular mycorrhiza improve growth and nutrient uptake. Further research is needed to understand and mitigate the challenges. Validation of qRCA4 and novel KASP markers facilitates integrating traits, fertilizer, and biochar application, boosting the water efficiency and rice resilience in aerobic conditions [100–104].

These adaptations are designed to cope with increased frequencies of heat and drought stress, ensuring more sustainable rice production practices that align with evolving environmental conditions [105].

In Bangladesh, comprehensive management strategies that encourage farmers to adopt climate-resilient practices have been investigated. These strategies include crop rotation, selecting appropriate crop varieties, and adjusting planting dates to optimize resource utilization and enhance crop yields under climate stress, fostering a proactive approach to agricultural sustainability. Proper water management techniques, such as alternate wetting and drying, not only reduced water use by 30% but also minimized the heat stress impact, leading to a 15% increase in the yield [106].

The impact of rice establishment techniques on the soil properties, global warming potential, and crop yields has been discussed, highlighting the critical role of strategic timing in wheat planting following rice. This practice optimizes the water usage and mitigates the climate impacts, illustrating how targeted agronomic decisions can influence environmental sustainability and enhance crop productivity. Mulching reduced the soil temperature by up to 2 °C and conserved the soil moisture by 20%, which helped mitigate heat stress during the critical growth phases of rice [107].

Insights into improved farming practices to counteract climate change effects focus on the proper crop rotation, fertilization, and cultural practices. These strategies are pivotal for achieving high yields in lowland rice and coping with complex defense mechanisms against heat stress, thus ensuring effective adaptation to adverse climatic conditions [108].

Alternative and non-conventional soil and crop management strategies aimed at increasing the water use efficiency have been reviewed, emphasizing the effectiveness of crop rotation and other agronomic methods in boosting yield and water efficiency. Soil amendments led to a significant decrease in soil surface temperature (up to 4 °C lower) and an increase in soil moisture content by approximately 18–25% under heat stress conditions [109].

Strategies to alleviate the effects of climate change on crop production have been discussed, focusing on the integration of native and forgotten species in crop rotations. This approach is a key strategy for managing heat stress and enhancing the overall resilience of agricultural systems, offering a diversified strategy to ensure food security under the pressures of global warming [110].

8.2. Marker-Assisted Selection

The use of marker-assisted selection (MAS) in rice breeding for heat tolerance has marked significant progress in integrating specific genetic traits associated with resistance to heat stress, thereby enhancing the breeding of heat-tolerant rice varieties suitable for addressing global climate changes. The effectiveness of marker-assisted backcross breeding (MABB) in wheat, which is equally applicable to rice, illustrates the potential of MAS in improving heat tolerance. This method involves the introgression of heat tolerance traits from tolerant donors into susceptible commercial varieties, highlighting MAS as a powerful tool for enriching rice breeding programs with desirable genetic traits for heat resistance [111].

Research that combines biotic and abiotic stress resistance in rice using MAS emphasizes the strategic integration of traits for multiple stress tolerances, including heat. This approach not only bolsters heat resilience but also enhances the overall stability and productivity of rice cultivars, demonstrating the versatility and effectiveness of MAS in comprehensive breeding programs [112].

A study on the pyramiding of multiple heat tolerance quantitative trait loci (QTLs) to enhance rice resilience under heat stress utilized MAS to combine several beneficial genetic traits. This method developed rice varieties better equipped to withstand high temperatures, offering a holistic strategy for breeding in challenging climates [90].

Investigations into improving the grain yield under heat and moisture stress through marker-assisted pedigree breeding underscore the potential of MAS to select rice varieties that maintain high productivity in adverse environmental conditions. This highlights the role of genetic selection in adapting rice to a wide range of growing conditions [113].

Research into the utilization of MAS for identifying and incorporating high-temperature tolerance traits in rice sheds light on critical markers that facilitate the selection of heat tolerance during the breeding process. This underscores the practical application of MAS in crafting thermally resilient rice varieties, demonstrating the efficacy of targeted genetic interventions [114].

Hornai et al. [96] investigated genetic strategies to combat heat stress, focusing on the efficacy of using specific genetic markers to improve rice's heat tolerance.

Furthermore, the identification of QTLs linked to heat tolerance using SSR markers through bulked segregant analysis illustrates the direct application of MAS in pinpointing specific genetic markers. This method enhances the precision of breeding heat-resistant rice by utilizing these markers to guide the selection process, thus optimizing the breeding outcomes. The significant association between marker RM5749 on chromosome 4 and spikelet fertility under heat stress, with a LOD value of 6.86, indicates a strong genetic linkage [95].

8.3. Genomic Selection for Crop Improvement

The use of marker-assisted selection (MAS) in rice breeding for heat tolerance has enhanced the efficiency and precision of developing heat-resistant rice varieties, contributing to improved yield stability and resilience in high-temperature environments. Recent advancements in genomic selection have significantly propelled the development of heat-tolerant rice varieties, showcasing innovative approaches to enhancing crop resilience against climate-induced stresses. The integration of genomic selection with shuttle breeding and speed breeding techniques has been effectively demonstrated to rapidly produce rice varieties that are early maturing and more tolerant to heat stress. This multidisciplinary approach underscores the potential of genomic tools to streamline breeding cycles, thereby adapting rice cultivation to rapidly changing climatic conditions [115].

Genomic selection has been utilized to rapidly improve crop varieties without the need for extensive phenotype-based selections, as discussed in a study focusing on wheat but offering valuable insights for rice. This research highlights the potential for developing heat-tolerant varieties through accelerated breeding programs, showcasing a faster route to enhancing crop resilience. The predictive abilities of GS models ranged from 0.35 to 0.79 for traits related to heat stress tolerance in rice [115].

The genetic improvement of heat stress tolerance in cereals, including rice, using genomic selection tools and cropping simulations has been explored. This approach emphasizes the development of crop genotypes with traits specifically tailored to withstand high temperatures. This approach demonstrates how molecular breeding can significantly enhance crop resilience, offering a robust strategy for combating climate challenges [91].

A review of the use of genomic resources, including genomic selection and genome editing, to facilitate the development of climate-resilient crops notes significant progress in breeding heat-tolerant rice varieties. The study shows how these advanced genomic tools contribute to creating sustainable agricultural systems that can withstand environmental stresses. GS increased the genetic gain by approximately 1.2-fold compared to conventional breeding methods [116].

The combination of phenomics with genomic selection to optimize the timing of anthesis in rice has been examined, highlighting how this approach can enhance the development of heat-tolerant cultivars. The phenotypic traits for breeding programs aim at increasing heat tolerance, and this method offers a precise way to improve crop resilience [117].

Molecular breeding strategies for improving heat stress tolerance in rice have been detailed, emphasizing the discovery of heat-tolerant genes and how genomic selection has accelerated the development of new, robust rice varieties. This research highlights the ongoing progress and future perspectives in using genomic selection to enhance heat stress tolerance in rice, illustrating the transformative potential of these technologies in modern agriculture [90].

8.4. Role of Induced Mutations in Mitigating Heat Stress

The induced mutations in plant breeding have focused on enhancing crop varieties' tolerance to stresses like heat, significantly impacting rice production. The beneficial traits in space rice and other mutation-induced varieties are often linked to several physiological and molecular mechanisms. One such mechanism is the enhanced antioxidant defense. Mutation-induced varieties may show the increased activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). These enzymes play a crucial role in scavenging reactive oxygen species (ROS) generated under heat stress, thereby protecting cellular components from oxidative damage. For instance, studies have reported significant increases in the SOD and CAT activities in space rice compared to non-mutated controls, indicating a robust antioxidant defense system [85].

Mutations can lead to the production of proteins that help maintain cellular homeostasis under stress conditions. Heat shock proteins (HSPs), for instance, assist in protein folding and prevent the aggregation of denatured proteins under high temperatures. Research has shown that mutation-induced rice varieties express higher levels of HSPs, which correlate with better tolerance to heat stress [86]. Improved photosynthetic efficiency is another trait observed in some mutation-induced rice varieties. This is achieved through the maintenance of chloroplast integrity and function under high-temperature conditions, ensuring sustained photosynthesis and growth. Research has demonstrated that space rice varieties maintain a higher chlorophyll content and photosynthetic rates compared to conventional varieties under heat stress conditions. For example, studies have reported a 20–30% increase in the photosynthetic rates in space rice compared to non-mutated controls under heat stress [70]. The induced mutations offer significant potential for enhancing heat tolerance in rice varieties, crucial in regions facing high temperatures and environmental stresses. Techniques like space-induced mutagenesis show promise in developing resilient rice varieties for challenging environments. Integrating these methods with traditional breeding and biotechnological tools will be essential for sustainable rice production amidst global climate challenges.

9. Global Policy on Breeding for Stress Tolerance

9.1. International Research Programs

Recent scholarly contributions have significantly enhanced the understanding and development of stress-tolerant rice varieties through international research programs and collaborative efforts. These initiatives aim to address the challenges posed by various environmental stresses, including heat, salinity, and submergence, which are critical under the current scenario of global climate change. An extensive overview of the progress in breeding rice resilient to submergence, heat stress, salinity, drought, and cold emphasizes collaborative efforts within national agricultural research systems. These efforts have been used in disseminating new varieties and breeding technologies worldwide, thus improving global food security [118].

Ongoing initiatives to develop stress-tolerant rice varieties (STRVs) underscore the necessity for strategic international collaborations. These partnerships are pivotal in pooling resources and knowledge to enhance the sustainability of rice production in stress-prone regions, ensuring the resilience of this staple crop [119].

A focus on the global collaborative research program dedicated to breeding salt-tolerant rice varieties also contributes indirectly to improving heat tolerance. This program, by gathering and evaluating rice accessions from around the world, showcases the interconnected nature of the stress responses in rice [120].

The elaboration of genetic and genomic technologies revolutionizing rice breeding describes international collaborative efforts utilizing these advanced tools to tailor rice varieties capable of thriving under stressful environmental conditions. This work addresses future challenges in rice cultivation, demonstrating the potential of modern breeding technologies. This international collaboration has led to the development of rice varieties that can better manage the saline–alkaline soils prevalent in many parts of Asia, increasing the overall production while mitigating the effects of soil salinity on the crop yield [24].

The role of international cooperation, particularly with institutions like the International Rice Research Institute (IRRI), in enhancing rice breeding in Vietnam highlights the development of improved varieties that are better suited to withstand various stress factors. This illustrates the benefits of global scientific partnerships in developing robust agricultural solutions. The study shows a yield improvement of 15–20% in heat-stressed environments due to the adoption of advanced breeding strategies [75].

Speculations on the future trajectories of rice research point to initiatives like the C4 Rice Project. This project is a significant collaborative effort to enhance the photosynthesis efficiency in rice, a trait that could dramatically improve the stress tolerance and yield, particularly in the face of escalating global temperatures [121].

9.2. Research and Development

Recent scholarly contributions have significantly enhanced the understanding and development of stress-tolerant rice varieties through international research programs and collaborative efforts.

The focus of current research on rice breeding is increasingly centered on integrating heat tolerance traits into high-yielding varieties, a pivotal work given the rising global temperatures and their impact on agricultural productivity. This effort involves significant advancements and collaborative efforts aimed at enhancing rice resilience to heat stress through innovative breeding strategies (Table S1). A comprehensive review discusses the genetics and breeding practices involved in developing heat tolerance in rice. It emphasizes the importance of identifying and integrating heat-tolerant traits from donor varieties, such as N22, into high-yielding commercial varieties. This strategic approach not only enhances heat resilience but also maintains the yield potentials necessary for global food security, thus aligning breeding efforts with future climatic challenges [90].

A detailed study estimates the yield stability of heat-tolerant rice genotypes under various climatic conditions. It underscores the necessity of developing genotypes capable of withstanding diverse heat stress scenarios, particularly at the reproductive stages, to ensure the sustained productivity and yield stability under changing climatic conditions. This research is critical in guiding future breeding programs to focus on robustness as well [21]. Specifically, the study provides outcomes for several cultivars under combined heat and drought stress. For example, Cultivar Nagina22 experienced significant reductions in the yield and seed-setting rates across various stages, notably at the panicle initiation stage, where the grain yield decreased by 49.2%, the seed-setting rate by 30.9%, and the spikelet number by 14.3%. Similarly, Cultivar Shanyou63 and Cultivar Liangyoupeijiu also showed declines in the grain yield and fertility parameters during critical growth phases, underlining the severity of heat impacts on rice production.

Research on the pathways to sustainable rice production incorporates submergence and other stress tolerances into high-yielding varieties. This is important for developing potent rice varieties capable of thriving in unfavorable growing ecologies, integrating multiple stress resistance traits to meet the diverse challenges posed by climate change [119].

Furthermore, an exploration of the combined effects of drought and heat stress advocates for the development of cultivars that exhibit strong tolerance to both stressors. By integrating specific QTLs/genes known for enhancing stress tolerance, this approach aims to create versatile rice varieties that can effectively manage multiple environmental stresses simultaneously, thus improving the overall plant resilience [96,122].

A review of breeding strategies for enhancing heat tolerance within the broader context of climate change emphasizes the importance of incorporating well-defined heat tolerance traits in selected varieties. It is vital that breeding efforts are aligned with the evolving climatic challenges to optimize both the yield and stress tolerance, ensuring that new varieties can meet the demands of both productivity and environmental adaptability [123].

Future trends in rice research, particularly efforts to develop varieties with enhanced photosynthesis capacity by incorporating C4 pathways, are discussed as a forward-thinking approach. This aims to address one of the most pressing challenges in rice production by improving the heat tolerance while also enhancing the photosynthetic efficiency and yield under high-temperature conditions. Such initiatives are pivotal for pushing the boundaries of what is genetically and agronomically feasible in rice breeding [121].

9.3. Adoption of Sustainable Farming Practices

Recent research underscores the importance of sustainable farming practices in rice cultivation as an essential strategy to mitigate the impacts of climate change on agriculture. These studies provide a comprehensive view of how sustainable practices can be integrated into rice production systems globally, exploring various dimensions from technological adoptions to policy implications. Research in Central Java, Indonesia, has examined how innovative technologies and agricultural methods facilitate adaptation to climate change. Such initiatives emphasize the necessity of ongoing innovation and the dissemination of sustainable practices tailored to the local environmental and socio-economic conditions to ensure their adoption and effectiveness in combating climate change impacts [124].

An exploration of various mitigation options available to farmers in South Asia, such as improved management of soil, water, and nutrients, highlights the significant role these sustainable practices play in reducing greenhouse gas emissions and enhancing the resilience of rice production systems against climate change challenges. These practices are pivotal in promoting sustainability within intensive agricultural systems [125].

The strategies for rice production under the changing climate have been discussed, advocating for adaptive and mitigative approaches that incorporate sustainable agricultural practices. Aligning agricultural activities with environmental sustainability is vital for reducing the climate impact of rice production [126].

Research addressing the perceptions of climate change among rice farmers in the Yangtze River Basin and their adoption of low-carbon agricultural technologies indicates a noticeable gap between awareness and action. This finding suggests that more robust educational and policy-driven initiatives are needed to foster the adoption of sustainable practices that can effectively mitigate the environmental impacts of agriculture [67].

Farmers' perceptions and attitudes toward adopting more sustainable practices in Mauritius have been explored, highlighting the psychological and social barriers to such adoption. Addressing these barriers through targeted educational and community engagement programs is essential for encouraging a shift toward more sustainable farming practices, which are necessary for a more resilient agricultural future [127].

10. Conclusions

The research underscores significant advancements in rice production under climate change and stress conditions like heat. Integrating genetic techniques, sustainable practices, and international collaborations enhances resilience. Genetic modifications and sustainable practices like optimized water management improve crop resilience. International collaborations facilitate resource sharing and enhance global food security by developing stress-tolerant rice varieties. Future research should prioritize integrating stress-tolerance traits into high-yielding varieties and advancing genomic tools. Policy support, including subsidies and educational programs, is crucial for promoting sustainable practices and resilient agricultural systems.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/stresses4030030/s1, Table S1. Functional literature summary.

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