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Review

Improvements in Tolerance to Heat Stress in Rice via Molecular Mechanisms and Rice Varieties

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Abstract: Global warming affects crop growth and development, threatening food security. As one of the essential food crops, rice is severely affected by high temperature stress, which compromises both its yield and quality. Therefore, gaining a deep understanding of the molecular mechanisms by which rice responds to heat stress and breeding rice varieties that are tolerant to such stress is crucial for maintaining food security. This review summarizes the impacts of heat stress on yield and quality-related traits at different growth and development stages of rice, the molecular mechanisms of rice perception and response to heat stress, and the improvement in and breeding of heat-tolerant rice varieties using existing superior alleles/QTLs. We also discuss the opportunities and challenges in creating highly heat-tolerant rice germplasm, providing new ideas and insights for the future breeding of heat-tolerant rice varieties.

Keywords: rice; heat stress; molecular mechanism; breeding utilization

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1. Introduction

Rice is one of the major staple crops in the world and holds a significant position in agricultural production. Increasing food production is a crucial strategy for ensuring food security. The Intergovernmental Panel on Climate Change (IPCC) indicated in its Sixth Assessment Report that over the past century, the combustion of fossil fuels and unsustainable energy and irrational land use have led to a continuous increase in global temperatures, which are now 1.1 °C higher than pre-industrial levels [1]. The high temperatures caused by climate change greatly affected the growth and development of major food crops, severely restricting agricultural production. Studies indicate that for every 1 °C increase in global average temperature, the yields of several major food crops, particularly wheat, rice, maize, and soybeans, decrease by 6.0%, 3.2%, 7.4%, and 3.1%, respectively [2]. In the southern regions of China, the average temperature from 2009 to 2018 increased by 0.7 °C compared to the period from 1961 to 1970. Early rice is highly sensitive to high temperatures during the grain-filling stage, during the growing season, an increase of 1 °C in temperature results in an 8% reduction in early rice yield [3]. Over the past 35 years in China, from 1985 to 2020, the average rate of high-quality rice has declined from 65% to 60%. In Japan, the statistical period spans from 1979 to 2018, during which the rate of high-quality rice also showed a downward trend overall, this trend is expected to persist in the foreseeable future [4]. Temperature-induced heat stress is typically defined as a rapid increase in temperature exceeding a threshold level within a certain period, causing irreversible damage to plant growth and development [5]. Heat stress exerts a significant negative impact on the entire growth cycle of rice, severely restricting the enhancement of both rice yield and quality [6]. Rice accounts for 21% of the global caloric intake and sustains over half of the world population. Given this, there is an urgent need to develop rice varieties with enhanced heat tolerance.

Rice is highly sensitive to heat stress throughout its growth and development stages. During the seedling stage, the optimal growth temperature for rice is 28 °C during the day and 22 °C at night, when temperatures exceed 32 °C, the growth and development of rice are affected across all stages. For instance, the heading stage is advanced to avoid heat damage, and the elongation of the hypocotyl and petiole helps maintain an appropriate plant architecture; stomatal closure and increased trichome density aid in maintaining plant water content. These thermomorphogenic responses mitigate the adverse effects of warm temperatures on rice growth [7]. Temperatures above 35 °C can severely restrict grain filling and yield [2,8–10]. As a sessile organism, rice has evolved a sophisticated set of response mechanisms to heat stress over the course of its long-term evolution. Therefore, an in-depth investigation into the molecular mechanisms underlying the response to heat stress is conducive to the development of rice varieties with enhanced heat tolerance. Firstly, this review provides a comprehensive overview of the effects of high-temperature stress on yield and quality across different growth stages of rice, then delving into the impact of high-temperature stress on the physiological mechanisms of rice, outlines the response mechanisms and molecular regulatory networks of rice to high-temperature stress, and finally discusses the improvement in heat tolerance in rice varieties using the identified superior haplotypes/QTLs and gene editing technologies. It also proposes the idea of leveraging gene editing in conjunction with artificial intelligence to discover new heat tolerance genes and create heat-tolerant rice germplasm, thereby breeding heat-tolerant rice varieties.

2. For Rice Yield and Quality: Heat Stress Effect Vegetative and Reproductive Growth

The vegetative and reproductive growth stages are critical phases that delineate the complete life cycle of rice (Figure 1). Prolonged exposure to high-temperature environments induces heat stress, which adversely affects both of these stages, ultimately impacting rice yield and quality [11]. Specifically, during the vegetative growth stage, heat stress damages plant growth and inhibits effective tillering. In the reproductive stage, heat stress affects key processes of spikelet development, including stages such as spike formation, heading, and flowering, which determine critical yield traits such as the number of grains per spike and the seed setting rate. Additionally, processes crucial to the final grain quality, such as pollination, grain filling, and material accumulation, are also adversely affected by high temperatures [12].

2.1. For Rice Yield: Heat Stress Effect Tillering Number, Grain Number, and Setting Percentage

Nutrient growth is the critical period for the accumulation of basic biomass in rice, and the amount of basic biomass directly determines the level of final yield. The initial stage of nutrient growth begins with seed germination. Since a persistent high-temperature environment significantly restricts the seed germination process and inhibits the growth and development of seedlings, this means that heat stress almost spans the entire life cycle of rice [13]. During the seedling stage, high-temperature stress accelerates water loss and inhibits photosynthesis in plants, which leads to leaf chlorosis and root damage. These effects significantly undermine the viability of rice during the early vegetative growth phase, thereby jeopardizing the accumulation of basal biomass [14]. The tillering stage is a crucial phase that determines rice yield, as the stability of the number of effective tillers directly influences the overall plant architecture and the total number of grains formed in subsequent stages. Continuous exposure to high temperatures inhibits the initiation and growth of tiller buds, resulting in a reduction in both the total number of tillers and the number of effective tillers, thereby affecting the yield potential of rice [15].

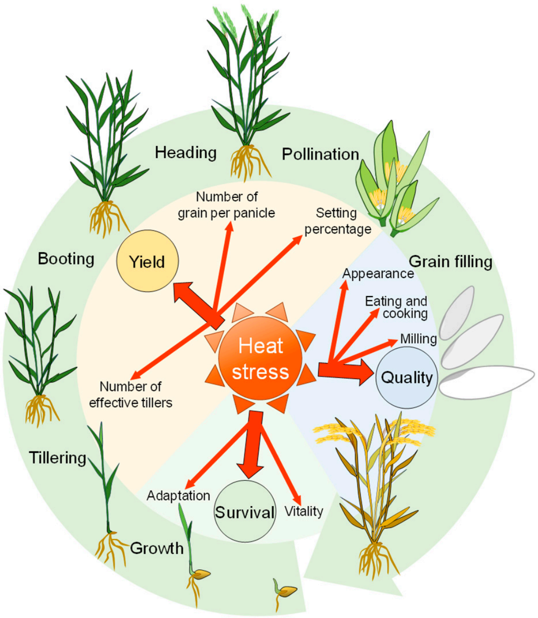

Figure 1. Continuous high temperature inhibits rice survival, yield, and quality by threatening all life stages of rice.

The tillering stage is a crucial phase that determines rice yield, as the stability of the number of effective tillers directly influences the overall plant architecture and the total number of grains formed in subsequent stages. Continuous exposure to high temperatures inhibits the initiation and growth of tiller buds, resulting in a reduction in both the total number of tillers and the number of effective tillers, thereby affecting the yield potential of rice [16]. The morphological integrity and normal development of spikelets are not only directly related to grain formation but also have a profound impact on the final quality of rice. Regarding the total number of grains per panicle, continuous high-temperature stress damages the differentiation process of spikelets, leading to a decrease in panicle size and density, which significantly reduces the total number of grains per panicle. Under the negative effect of reduced total grain number, heat stress severely inhibits spikelet fertility by hindering normal meiosis, resulting in a substantial decrease in seed setting rate. During the heading and flowering stages, the impact of heat stress on floral organs is particularly significant and severe. In high-temperature environments, rice anthers are prone to inactivation, leading to a marked decline in pollen viability, which, in turn, causes spikelet sterility [2,17]. These effects are specifically manifested as impaired anther dehiscence, inhibited pollen grain swelling, and restricted pollen tube elongation. Collectively, these factors impede the normal processes of pollination and fertilization [18–20]. Ultimately, heat stress affects the reproductive growth stage of rice, leading to a reduction in the number of grains per panicle and the seed setting rate, which significantly decreases rice yield.

2.2. For Rice Yield: Heat Stress Efect Contents of Sucrose, Chalkiness Degree, and Starch Content

During the grain filling stage, high environmental temperatures have a significant impact on rice quality. This is because the grain filling stage determines the final yield and the accumulation process of storage substances in the grains; ultimately, this affects the appearance, milling quality, nutritional value, and cooking and eating qualities of the rice [21]. Insufficient grain filling and grain shriveling are affected by elevated grain filling rates and shortened grain filling periods, respectively. The plumpness of the grains is primarily determined by the accumulation of photosynthetic products and the transport between source and sink [22]. Sucrose is the predominant form of carbohydrate synthesized in photosynthetic source tissues such as leaves. It is initially loaded into the phloem and subsequently transported via long-distance vascular pathways to sink tissues [23]. During the grain filling period, high temperatures lead to increased chalkiness and reduced grain size in rice, thereby deteriorating the appearance quality. Elevated temperatures promote the accumulation of reactive oxygen species (ROS) in rice grains, and the increase in ROS during this period significantly enhances both chalkiness and chalky grain rate [24]. After experiencing short-term extreme high-temperature stress during the flowering stage, the grain filling is inhibited. The stems are activated as the main absorption organ, leading to increased accumulation of nutrients, resulting in a decline in grain quality [25]. Since the starch content and structural composition determine appearance and cooking–eating quality, insufficient grain filling under high-temperature condition, which leads to abnormal starch content and structure, is one of the primary factors contributing to the alteration in rice quality [26]. The content and molecular size of amylose and amylopectin, as well as the chain length distribution, collectively determine starch quality. This is attributed to the downregulation of gene expression related to starch synthesis and the decreased activity of corresponding synthase enzymes under heat stress. For instance, scanning electron microscopy reveals that the endosperm cells of the *flo24* mutant produce loosely arranged starch granules, and the grain filling rate of *flo24* is consistently lower than that of the wild-type line, a situation that becomes more pronounced under heat stress. Additionally, studies have shown that the FLO24 protein interacts strongly with key enzymes involved in starch synthesis, including AGPL1, AGPL3, and PHO1 [27]. The expression of genes and enzyme activities involved in starch hydrolysis pathways are significantly induced by high temperatures, ultimately leading to reduced starch synthesis and accelerated starch degradation. Additionally, grain protein content is also affected by high temperatures, which, in turn, influences the appearance, nutritional value, and texture of the grains.

3. Molecular Mechanisms of Rice Perception and Response to Heat Stress

3.1. Heat Stress Signal Sensing Drives Calcium Ion Conduction Mechanism in Rice

The cell membrane is highly sensitive to high temperatures. Heat stress promotes the influx of calcium ions (Ca^{2+}), and the increase in intracellular Ca^{2+} concentration forms a Ca^{2+} signal that plays a crucial role in the perception and response pathway of heat stress in rice [28]. The generation of intracellular Ca^{2+} signals is closely related to the perception of temperature by the cell membrane. Heat stress induces changes in membrane fluidity, structure, and stability, which, in turn, trigger cellular stress and the occurrence of intracellular heat stress response signals. The influx of Ca^{2+} under high temperatures is mediated by membrane-localized channels that may perceive and respond to thermal signals. Cyclic nucleotide-gated ion channels (CNGCs) represent a class of relatively conserved Ca^{2+} channels in plants (Figure 2). In rice, the membrane-localized members of the *CNGC* family that have been identified include *OsCNGC1*, *OsCNGC2*, *OsCNGC4*, *OsCNGC5*, *OsCNGC6*, *OsCNGC9*, *OsCNGC10*, *OsCNGC12*, *OsCNGC13*, *OsCNGC14*, *OsCNGC15*, and *OsCNGC16*, and these are likely to be closely associated with temperature responses [29–31]. Under heat stress conditions, *OsCNGC14*, *OsCNGC15*, and *OsCNGC16* promote the influx of Ca^{2+} (Table 1). However, the mutant lines *cngc14*, *cngc15*, and *cngc16* exhibit weakened abilities to respond to heat stress and induce cytosolic Ca^{2+} signals, rendering them more susceptible to damage from heat stress [30,31]. A recent study has demonstrated that *OsCNGC14*, *OsCNGC15*, and *OsCNGC16* form heteromers to collectively mediate stress responses [31]. The overexpression of *OsCNGC16* enhances Ca^{2+} influx and confers increased tolerance to high temperatures and other stresses, primarily due to its ability to rapidly control stomatal closure in response to stress [31]. In addition, Ca^{2+} permeable annexins also regulate Ca^{2+} influx. *OsANN1*, a rice annexin with Ca^{2+} binding and ATPase activities, modulates reactive oxygen species (ROS) scavenging and manipulates Ca^{2+} influx and Ca^{2+} channel transport under heat stress [32,33]. *OsANN1*-overexpressing plants exhibit enhanced growth under heat stress and other abiotic stress conditions, whereas RNA interference (RNAi) lines of *OsANN1* are more sensitive to heat and drought stresses [32]. However, the specific effects of Ca^{2+} signaling on rice thermotolerance are highly complex and cannot be simply classified as either positive or negative regulation under different signaling pathways. Research has shown that the G protein γ subunit TT2 promotes the binding of calmodulin (CaM) to the Ca^{2+}-modulated protein binding transcription factors SCT1 and SCT2 through Ca^{2+} signaling, thereby inhibiting the expression of the wax biosynthesis regulatory gene *OsWR2*, and consequently negatively regulates rice thermotolerance by reducing wax content [34]. Thus, heat stress induces sensitivity to high temperatures in rice through the G protein Ca^{2+} signaling wax biosynthesis pathway. In summary, Ca^{2+} play a pivotal role in the heat stress response pathway of rice. Maintaining the post-stress abundance and influx rate of Ca^{2+} in the cytoplasm is crucial for the function of key downstream proteins that resist heat stress.

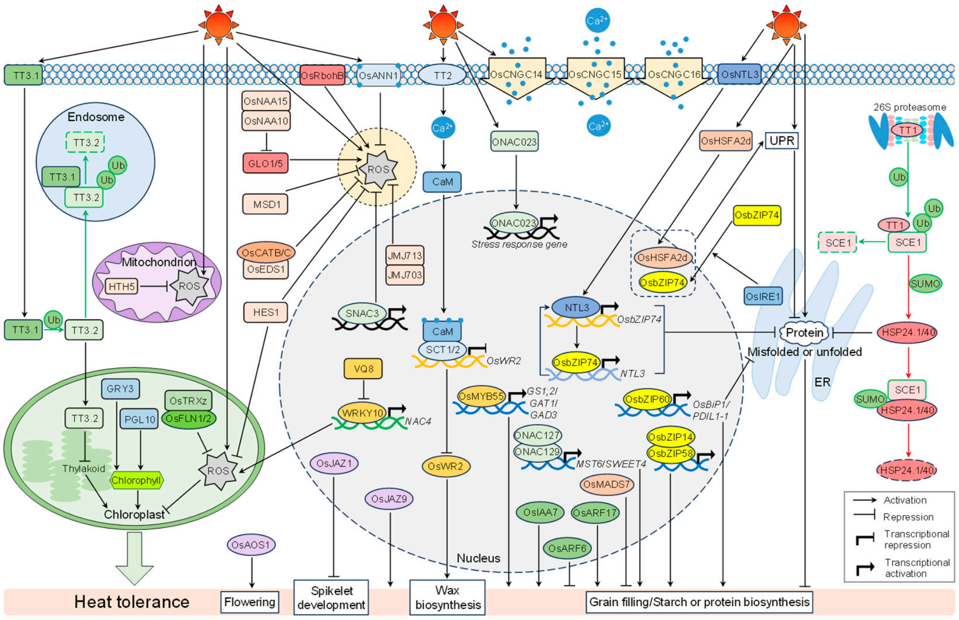

Figure 2. Regulatory network of rice heat stress response and resistance. When plants are subjected to heat stress, the fluidity of the cell membrane changes, promoting the entry of extracellular Ca2^{+} into the cytoplasm. Heat stress stimulates ROS accumulation in chloroplasts, mitochondria and other organelles. TT3.1 ubiquitinates and degrades TT3.2 under heat stress, which inhibits the damage of TT3.2 to PSII. The 26S proteasome subunit A series of reactive oxygen related enzymes can inhibit the production of intracellular ROS. A series of chloroplast proteins protect chloroplasts from heat stress. Heat stress can stimulate ER stress and form a large number of unfolded or misfolded proteins. ER stress activating the unfolded protein response (UPR), which relieves the inhibitory effect of IRE1. IRE1 regulates the alternative splicing of bZIP60 mRNA, activating it, and the active form of bZIP60 is involved in regulating the degradation pathway of misfolded proteins. TT1 degrades SCE1 through ubiquitination and inactivates SUMO modification of downstream sHSPs. In addition, high-temperature stress modulates the heat stress response by modulating the activity of a range of transcription factors.

3.2. Regulation of ROS Homeostasis in Rice Under Heat Stress

Exposure of plants to high-temperature stress results in the substantial accumulation of reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-). Maintaining ROS at moderate levels is essential for the healthy growth of plants [35]. Generally, the ROS scavenging mechanisms play a crucial role in protecting plants from damage caused by high-temperature stress, which, in turn, results in a significant positive correlation between the antioxidant capacity and thermotolerance of rice. *HTH5* encodes a pyridoxal phosphate homeostasis protein, which promotes ROS scavenging. *HTH5*-overexpression rice lines enhance tolerance to high-temperature stress by reducing oxidative damage caused by the accumulation of ROS under heat stress conditions [36]. Superoxide dismutase (SOD) functions as the primary defense against reactive oxygen species (ROS) by catalyzing the conversion of superoxide radicals (O_2^-) to molecular oxygen (O_2) and hydrogen peroxide (H_2O_2), which is subsequently reduced to H_2O by ascorbate peroxidase (APX) [37]. Shiraya et al. identified a thermotolerant manganese superoxide dismutase 1 (MSD1) in rice [38]. Transgenic plants with the constitutive expression of *MSD1* exhibit significantly superior grain quality under high-temperature conditions (33 °C) compared to wild-type plants. This is accompanied by higher expression levels of ROS scavenging-related genes, including copper/zinc superoxide dismutase, antioxidant proteins, thioredoxins, and ascorbate peroxidase, compared to wild-type plants [38]. *SNAC3* encodes a stress-responsive NAC transcription factor that regulates the expression of ROS-related genes to modulate the dynamic balance of H_2O_2, thereby enhancing thermotolerance [39]. In rice, loss-of-function mutants of the H_2O_2 regulating gene *OsEDS1* exhibit increased sensitivity to heat stress. Further analysis revealed that *OsEDS1* forms complexes with catalases *OsCATB* and *OsCATC* to scavenge H_2O_2 under heat stress conditions [40]. The successful colonization of endophytes within rice plants serves as an eco-friendly approach to enhance rice thermotolerance. Pseudomonas linzhiensis RS16, which produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase, effectively reduce the elevated levels of ethylene triggered by high temperatures when inoculated into rice. Since ethylene-responsive genes are often correlated with the production of reactive oxygen species (ROS), this results in a significant reduction in ROS content [41]. *OsRbohB* is a respiratory burst oxidase gene in rice. Under high-temperature conditions, the mutant lines with impaired function of *OsRbohB* exhibit varying degrees of reduced ROS accumulation in different parts of the plant compared to wild-type plants. Meanwhile, the expression of heat shock related genes, including *OsHSP23.7*, *OsHSP17.7*, *OsHSF7*, and *OsHsfA2a*, is significantly induced [12]. In rice, a heat stress response regulatory model primarily involving methylation modifications exists. The demethylase JMJ713 interacts with JMJ708 to enhance the demethylation level of H3K36me2, thereby promoting ROS scavenging and enhancing rice thermotolerance [42]. The expression levels of several ROS scavenging-related genes, including *OsCATC*, *OsCSD3*, and *OsAPX*, are significantly induced in transgenic plants overexpressing JMJ713 under heat stress conditions [42]. A recent study has revealed that the N-terminal acetyltransferase A (NatA) auxiliary subunit *OsNAA15* undergoes temperature-dependent alternative splicing, giving rise to two protein variants: *OsNAA15.1* and *OsNAA15.2*. The *OsNAA15.1* isoform is beneficial for normal rice growth under high-temperature stress, whereas *OsNAA15.2* exerts the opposite effect [43]. This differential effect is attributed to the ability of *OsNAA15.1* to form a stable NatA complex with the catalytic subunit OsNAA10, which promotes the acetylation of glycolate oxidase (GLO1/5) and targets it for degradation by the 26S proteasome. This process effectively reduces the accumulation of H_2O_2 produced by GLO1/5, particularly under high-temperature stress conditions [43]. In summary, the homeostasis of peroxide levels in rice under high-temperature conditions is achieved through the regulation of a series of ROS scavenging enzymes and ROS-generating related genes.

3.3. Chloroplast Function Maintained Stable Rice Production Under Heat Stress

Chloroplasts are essential organelles for maintaining photosynthesis and supporting plant growth under heat stress. Numerous proteins within chloroplasts play a critical role in protecting against heat stress-induced damage. Regarding the transcriptional processes within chloroplasts, *OsFLN1* and *OsFLN2* in rice function as part of the plastid-encoded RNA polymerase (PEP) complex to protect the normal occurrence and development of chloroplasts under heat stress [44,45]. *OsTRXz* regulates chloroplast RNA editing under heat stress through interactions with multiple organellar RNA editing factors 2 (*OsMORF2*), *OsMORF8*, and *OsMORF9* [46]. Both OsFLN1 and OsFLN2 interact with thioredoxin OsTRXz to form the TRX-FLN module, which maintains chloroplast redox balance under heat stress [44,47]. The impairment of the OsTRXz-OsFLN1/2 module disrupts the stability of transcriptionally active chromatin complexes and PEP (plastid-encoded RNA polymerase) activity, leading to the suppression of PEP-dependent gene expression within chloroplasts [44,47]. The photosystem II (PSII) located on the thylakoid membrane of chloroplasts is highly sensitive to high-temperature stress, which more readily disrupts the photosynthetic electron transport chain by damaging PSII [48]. Upon exposure to heat stress, the chloroplast precursor protein TT3.2 in rice is recruited into the vacuolar pathway for ubiquitination and degradation, its translocation from chloroplasts to endosomes reduces the thermal stress damage to thylakoids, thereby maintaining chloroplast functionality under heat stress [49]. Chlorophyll, a key pigment for chloroplast photosynthesis, is synthesized via the tetrapyrrole biosynthetic pathway, in which NADPH (protochlorophyllide oxidoreductase B) catalyzes the reduction of protochlorophyllide to chlorophyllide [50]. Research has shown that PGL10 maintains photosynthetic activity under high-temperature stress by preserving normal chloroplast function [50]. In addition, within the chlorophyll biosynthesis pathway known as the methylerythritol 4-phosphate (MEP) pathway, the enzyme 4-hydroxy-3-methylbut-2-enyl diphosphate reductase (GRY3) is involved in the synthesis of geranylgeranyl diphosphate in chloroplasts. This process is crucial for maintaining normal chlorophyll production and chloroplast development while also sustaining the response to high-temperature and high-light stress [51]. Abnormal function of PGL10 or GRY3 both lead to decreased chlorophyll content and abnormal chloroplast development, making plants more susceptible to ROS over-accumulation induced by heat stress, which ultimately impairs rice growth [50,51]. Heat stress also affects chloroplast stability by stimulating ROS accumulation within chloroplasts. Under moderate high-temperature stress, HES1 (UDP-N-acetylglucosamine pyrophosphorylase), which has certain ROS scavenging capabilities, once loses its function, will cause ROS burst in chloroplasts and heat-induced nuclear DNA damage, resulting in premature leaf senescence, a significant reduction in photosynthetic products, and severe yield loss [52]. In addition to the aforementioned mechanisms, high temperatures also inhibit the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), a key enzyme in photosynthesis that determines the rates of carbon assimilation and photorespiration [53,54]. A recent study demonstrates that transgenic plants overexpressing both Rubisco and Rubisco activase (oxRCA-RBCS) maintained higher photosynthetic rates and exhibited better growth under high-temperature conditions (40 °C) compared to wild-type plants. This suggests that enhancing Rubisco activase content without reducing Rubisco content could improve yield and sustainability in rice under high-temperature stress, potentially contributing to future strategies for increasing rice productivity and ensuring sustainable production in a warming climate [54]. Therefore, maintaining the integrity of chloroplast function has positive implications for coping with heat stress, scavenging reactive oxygen species (ROS), and stabilizing yield.

3.4. Ubiquitination Modification and Degradation of Misfolded Proteins in Rice Under Heat Stress

Heat stress induces an endoplasmic reticulum (ER) stress response in plant cells, which leads to the production and accumulation of unfolded or misfolded proteins within the cell. The accumulation of these aberrant proteins interferes with the function of other normal proteins, particularly during the grain filling stage, where ER stress severely damages final yield and rice quality [55,56]. In plant cells, the unfolded-protein response (UPR) pathway is activated under heat stress to enhance protein folding and accelerate protein degradation, thereby reducing translation and clearing the accumulation of misfolded proteins in the ER [57,58]. Heat shock proteins (HSPs), acting as molecular chaperones, prevent the irreversible aggregation of partially unfolded proteins [59]. The membrane-bound transcription factor *OsNTL3* from the NAC family in rice transduce signals from the plasma membrane to the nucleus under heat stress and regulate ER proteins folding under heat stress by binding to the promoter of *OsbZIP74* (also known as *OsbZIP50*; this article collectively refers to it as *OsbZIP74*) [60]. Interestingly, the upregulation of *OsNTL3* expression under heat stress is regulated by *OsbZIP74*, which enables the OsNTL3-OsbZIP74 transcriptional regulatory module to mediate signaling between the endoplasmic reticulum (ER), plasma membrane, and nucleus through mutual transcriptional regulation, thereby collectively contributing to the alleviation of heat stress damage [60]. Under ER stress, the rice ER sensor inositol-requiring enzyme 1 (OsIRE1) splices *OsbZIP74* mRNA into a form lacking the membrane-bound domain, allowing the activated *OsbZIP74* to more efficiently enter the nucleus to exert its transcriptional regulatory function in response to high temperature and other stresses [58,61]. During endosperm development after grain filling, *OsbZIP60* (also known as *OPAQUE3*) directly binds and activates the ER chaperone genes *OsBiP1* and *PDIL1-1*, thereby maintaining ER homeostasis under high-temperature conditions [56]. Studies have shown that *OsbZIP60* mutants exhibit ER stress, which is exacerbated by high temperature, leading to the abnormal synthesis of grain storage proteins and starch [56]. To counteract heat stress under impaired *OsbZIP60* function, *OsbZIP74* and other ER transcription factors are partially activated in the nucleus through feedback regulation to induce the expression of unfolded protein response (UPR) genes, thereby reducing ER stress [56].

To counteract the accumulation of misfolded or functionally lost proteins caused by heat stress, the ubiquitin-proteasome pathway degrades these proteins, thereby protecting cells from the toxic effects of protein accumulation [62]. Under heat stress, the 26S proteasome $\alpha 2$ subunit TT1, a key component of the ubiquitin-proteasome pathway, enhances the degradation rate of ubiquitinated substrates, reducing the variety and quantity of toxic denatured proteins accumulated within the cell, and thus protecting plant cells from heat damage [62]. A recent study demonstrates that TT1 negatively regulates the SUMO E2 ligase SCE1, which is involved in rice thermotolerance, by ubiquitination and targeting it for degradation by the 26S proteasome [63]. SUMOylation proteins are increased in rice cells under heat stress, including the small heat shock protein (sHSP) Hsp24.1, which is a key positive regulator of thermotolerance [63]. In the sce1 mutant, the abundance of SUMOylated proteins is reduced, while the accumulation of Hsp24.1 is increased, leading to enhanced thermotolerance and higher yield under heat stress [63]. *TT3.1* encodes a plasma membrane-localized E3 ubiquitin ligase that responds to heat stress signals. Under heat stress, TT3.1 translocates from the plasma membrane to endosomes and ubiquitinates the chloroplast precursor protein TT3.2, which negatively regulates rice thermotolerance, targeting it for degradation and thereby maintaining chloroplast stability and enhancing thermotolerance [49]. In addition, the E3 ubiquitin ligase OsHIRP1 and the Golgi-localized RING-type E3 ligase OsHCI1 also contribute to rice thermotolerance [64,65]. Therefore, whether they are unfolded, misfolded, or proteins that have a negative impact on rice thermotolerance, these proteins are typically maintained through a series of positive regulatory mechanisms, such as the ubiquitination-degradation pathway and the unfolded protein response, to ensure cellular protein stability in response to continuous heat stress.

3.5. Hormone Regulation Mechanism of Rice Under Heat Stress

Jasmonic acid (JA) is a class of hormones that regulate plant stress resistance. Recent studies have found that JA is involved in the regulation of rice thermotolerance. The JA signaling pathway gene *OsJAZ9* positively regulates rice thermotolerance, and its expression is positively regulated by the heat stress response gene *HTG3a* [66]. Under heat stress conditions, *OsJAZ9*-overexpression lines significantly increase green leaf area and stabilize the seed setting rate compared to wild-type plants [66]. In the presence of JA, the JA signaling pathway inhibitor *OsJAZ1* is methylated by the arginine methyltransferase *OsPRMT6a*. The methylated form of *OsJAZ1* can be ubiquitinated and degraded by the E3 ubiquitin ligase OsCOI1a/OsCOI1b, thereby releasing the inhibition of the jasmonic acid signaling pathway and promoting the normal growth of rice spikelets under high-temperature conditions [67]; meanwhile, the transcription factor OsMYC2 is released, which is inhibited by OsJAZ1, and OsMYC2, in turn, inhibits OsPRMT6a, acting as a negative feedback mechanism for jasmonic acid signaling [67]. Thus, the existence of the OsPRMT6a-OsJAZ1-OsMYC2 module links JA signaling with the normal development of spikelets under heat stress and functions as a switch to respond to heat stress while coordinating the homeostasis of the JA signaling pathway within the rice plant. Daytime flowering time (DFOT) is an important indicator for studying rice growth and development. Overexpression of the JA biosynthesis-related gene *OsAOS1* in rice significantly promotes JA accumulation and advances DFOT to avoid flowering under high-temperature conditions [68]. In addition, genes related to DFOT, such as OsAOS1, OsSWEET4, OsPIP2;2, and OsXTH9, are directly targeted and regulated by *OsMYC2* [68]. *OsFBN1* encodes a plastid lipid-associated protein, fibrillin. OsFBN1 inhibits the expression of the jasmonic acid biosynthesis gene *OsAOS2*. Under heat stress conditions, compared to wild-type plants, transgenic rice lines overexpressing OsFBN1 exhibit significantly reduced JA content, as well as significantly decreased thermotolerance during the seedling and reproductive stages [69]. These results indicate that JA primarily regulates rice adaptation to high-temperature stress by participating in processes such as spikelet growth and flowering.

The phytohormone indole-3-acetic acid (IAA) and its signaling pathway have been extensively studied in rice growth processes, including root development, above-ground growth, and photosynthesis. However, reports on their involvement in thermotolerance regulation are relatively limited. Under heat stress conditions, the *OsIAA7*, encoding an auxin response factor family protein, is significantly induced. The overexpression of *OsIAA7* significantly increases the survival rate of seedlings under high-temperature conditions. Several heat stress-related genes, such as *OsFKBP20*, *OsTOGR1*, *OsTT1*, and *OsTT3.1*, are significantly upregulated by OsIAA7 under high-temperature conditions, while OsARF6 (an IAA-responsive factor) downregulates these genes. Additionally, OsIAA7 inhibits OsARF6 to integrate the IAA signaling pathway and enhance rice thermotolerance [70]. Similarly, OsIAA29 competes with OsIAA21 to bind and activate the transcriptional activation activity of *OsARF17*, thereby promoting grain filling under high-temperature conditions [71]. Both thermotolerant and heat-sensitive rice varieties suffer reduced spikelet fertility and pollen viability under heat stress, while the exogenous application of IAA effectively alleviates the damage caused by heat stress [72]. Under heat stress, endogenous IAA levels significantly decrease and are positively correlated with pollen viability, grains per panicle, panicle weight, and single plant yield [72].

Under high-temperature stress, the contents of ABA and ROS in anthers significantly increase, pollen viability is inhibited, and programmed cell death (PCD) in tapetal cells is accelerated [73]. Additionally, the ABA biosynthesis rate-limiting genes *OsNCED3* and *OsNCED5* are significantly induced by high temperatures. The exogenous application of high concentrations of ABA leads to a significant increase in ROS content in anthers, reduced microspore viability, pollen viability, and poorer fertility [73,74]. The loss of function of the ABA signaling kinase SAPK2 impedes ABA signaling and results in blocked PCD in the tapetum, but it does not affect the production of ABA-mediated ROS under heat stress [74]. Under heat stress conditions, the exogenous application of ABA helps to inhibit the excessive accumulation of ROS in grains and improves grain yield, milling quality, and appearance quality [75]. *OsRbohH* is a respiratory burst oxidase gene in rice. In *OsRbohH*-overexpressing transgenic lines under heat stress, the ABA biosynthesis-related genes *OsNCED3* and *OsNCED4* are significantly upregulated, while the ABA metabolism pathway gene *OsABA8ox3* is significantly downregulated. These lines are highly sensitive to exogenous ABA, with improved seedling survival rate and chlorophyll levels under heat stress [76]. Additionally, in *OsRbohH*-overexpressing transgenic lines, ABA signaling-related genes *OsDREB2A*, *OsLEA3*, *OsbZIP66*, and *OsbZIP72* are significantly downregulated, but their expression levels show an opposite trend under drought stress, indicating the complex regulatory mechanisms of ABA in rice in response to different abiotic stresses [76].

Salicylic acid (SA), a small phenolic molecule, has been shown to be involved not only in plant defense responses but also in responses to abiotic stresses. For example, in Arabidopsis thaliana, after 10 days of low-temperature treatment, the endogenous SA level significantly increases, but plant growth rate is reduced due to the trade-off between growth and stress resistance [77]. During the grain-filling period in maize, high-temperature exposure significantly decreases the duration and maximum rate of grain filling, but this heat damage is alleviated by the exogenous application of SA [78]. Consistently, in rice, the exogenous application of 1 mM and 10 mM SA significantly increases the number of spikelets per panicle and seed setting rate under high-temperature stress compared to untreated plants [79,80]. Moreover, after SA application, the contents of osmoprotectants in spikelets, such as soluble sugars, proline, other plant hormones, and antioxidant enzymes, are significantly induced [79,80].

Brassinosteroids (BRs) are highly efficient and environmentally friendly plant hormones that can regulate ion channel transport and enhance crop yield by modulating the expression of stress-resistant genes. Under high-temperature stress, the spikelet degeneration rate of the heat-sensitive rice variety IR36 increased by 62%, whereas the heat-tolerant variety HHZ exhibited a relatively lower spikelet degeneration rate. However, the application of 2,4-epibrassinolide significantly reduced the spikelet degeneration rate in both varieties, with a more pronounced reduction in IR63, thereby alleviating the spikelet damage caused by high-temperature stress [81]. Heat stress and exogenous EBR (a synthetic brassinosteroid) jointly induce the expression of BR synthesis-related genes *D11*, *BRD2*, and *D2*, and heat stress alone also induce the expression of BR metabolism genes *OsCYP734A2*, *OsCYP734A4*, and *OsCYP734A6*. In contrast, the expression levels of these BR metabolism-related genes are significantly downregulated upon EBR application [81]. Another study demonstrated that under high-temperature stress, moderate irrigation helps to increase the BR content in rice spikelets and roots. Additionally, the stomatal conductance, transpiration rate, and photosynthetic rate of leaves in rice irrigated with this method are significantly higher than those of rice irrigated with well water under high-temperature stress [82]. BRs induce the production of heat shock proteins under high-temperature stress to maintain proper protein folding. Moreover, BRs enhance the activity of enzymes related to the ascorbate-glutathione (AsA-GSH) cycle, thereby increasing the cellular antioxidant level, which is beneficial for promoting plant growth homeostasis under high-temperature stress [83,84].

3.6. Transcriptional Regulation Mechanism of Rice Under Heat Stress

Transcription factors play a crucial role in plant thermotolerance. After rice perceives heat stress and transduces the signal into the cell, transcription factors from families such as NAC, MYB, WRKY, and bZIP in the nucleus activate corresponding transcriptional regulation and initiate the expression of heat stress resistance genes. Generally, heat shock transcription factors (HSFs) can bind to specific regions known as heat shock elements in the promoters of heat shock protein (HSP) genes to regulate their expression and counteract heat stress [85]. Under high-temperature stress, *OsHSFA2d* is selectively spliced into a transcriptionally active form that is localized only in the nucleus and may respond to heat stress through the unfolded protein response pathway [85]. The rice WRKY transcription factor OsWRKY10 negatively regulates thermotolerance. The overexpression of *OsWRKY10* promotes ROS accumulation in chloroplasts, making plants more sensitive to heat stress and prone to death under high-temperature conditions [86]. It has been found that the protein *VQ8*, containing a valine-glutamine (VQ) motif, inhibiting the DNA-binding activity of OsWRKY10 to prevent its transcriptional activation of target genes such as *NAC4*, thereby repressing heat sensitivity caused by OsWRKY10-mediated ROS balance and hypersensitive response [86]. A fusion expression construct of the *OsHSP101* promoter and *OsWRKY11* cDNA, when overexpressed, significantly enhances thermotolerance and drought tolerance in transgenic plants [66].

Under heat stress, the transport of nutrients between the source and sink in rice is also manipulated by transcriptional regulation. The rice transcription factors OsMADS7 and OsbZIP58 are involved in regulating the heat stability of grain starch synthesis [21,87]. The suppression of *OsMADS7* results in more stable endosperm starch synthesis under heat stress [87]. In contrast, high temperature induces the selective splicing of *OsbZIP58* into a truncated form with lower activity, leading to the suppression of transcription of the major gene for amylose synthesis, Wx [21]. A recent study showed that *OsbZIP14* and *OsbZIP58* may maintain stable rice grain filling under heat stress through synergistic regulation, and transgenic plants overexpressing *OsbZIP14* exhibit enhanced thermotolerance [88]. The MYB transcription factor OsMYB55 can bind to and activate the expression of genes such as *OsGS1;2* (glutamine synthetase), *GAT1* (glutamine amidotransferase), and *GAD3* (glutamate decarboxylase). The overexpression of *OsMYB55* promotes the accumulation of l-glutamate, GABA, arginine, and total amino acids, thereby enhancing rice thermotolerance [89]. The NAC transcription factors ONAC127 and ONAC129 form a heterodimer to maintain normal grain filling and starch accumulation in rice under heat stress [90]. It has been found that under heat stress, ONAC127 and ONAC129 regulate nutrient transport-related genes, such as *OsMST6* (monosaccharide transporter) and *OsSWEET4* (sugar transporter), that affect sugar transport [90]. The latest research indicates that there may be a conserved mechanism between thermomorphogenesis and nutrient levels under high-temperature stress in plants such as rice, with transcriptional regulation playing a major role. Under heat stress, when nitrogen and phosphorus nutrients are sufficient in the environment, the transcription factor HY5 inhibits the expression of the nitrogen and phosphorus absorption pathway integrator gene *NRT1.1* in Arabidopsis thaliana, promoting rapid root growth and thereby controlling the input of the source [91]. When nitrogen and phosphorus are deficient in the environment and plants are subjected to heat stress, the inhibitory effect of HY5 on

NRT1.1 is significantly reduced, which is beneficial for the plant to enhance nutrient uptake. Meanwhile, root growth is slowed, which is advantageous for plant survival under adverse conditions [91].

Under continuous heat stress, drought stress often occurs concurrently. The NAC transcription factor SNAC3 positively regulates rice tolerance to high temperature and drought stresses by activating the expression of ROS scavenging genes [39]. Additionally, a recent study has shown that ONAC023 is a key NAC transcription factor involved in the regulation of drought and heat stress responses in rice during most of its growth stages [92]. Heat stress and drought can activate the expression and nuclear translocation of ONAC023, thereby promoting the expression of stress-responsive genes such as *OsPIP2;7*, *PGL3*, *OsFKBP20-1b*, and *OsSF3B* [92].

These transcription factors play a crucial role in rice heat tolerance, enhancing plant adaptability to high-temperature stress by regulating specific gene expression. Further research and application of these transcription factors can provide important genetic resources for improving heat tolerance in rice and other crops.

4. Breeding of and Improvement in Heat-Resistant Rice Varieties

The exploration of excellent genetic resources is of great significance for the breeding of high-quality rice varieties and the sustainable development of agricultural production. Up to now, we have utilized a number of superior alleles and QTLs to improve rice varieties, enabling rice to maintain good growth and stable yield under heat stress conditions (Figure 3).

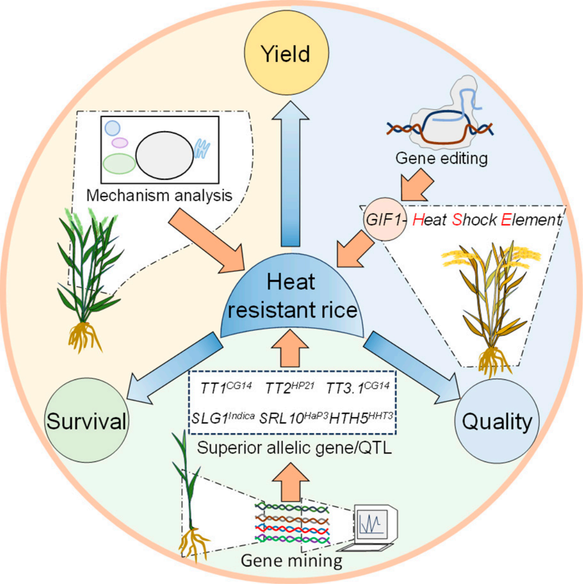

Figure 3. Through in-depth analysis of heat-resistant regulation mechanism, exploration of heat-resistant genes/QTLS, and rational use of gene editing technology, rice varieties with heat-resistant, stable yield, and stable quality were cultivated.

In the course of evolution, *SLG1* has been selectively disseminated in Asian cultivated rice. Sequence alignment analysis reveals that the promoter and coding regions of *SLG1* exhibit distinct differences between indica and japonica rice varieties [93]. The superior allele of *SLG1* in indica varieties enhances the level of thiolated tRNA, a highly conserved tRNA modification in living organisms, which is beneficial for increasing tolerance to abiotic stresses such as heat stress [94]. The introgression of the *SLG1* allele from the indica variety ZF802 into the japonica variety KY131 resulted in the near-isogenic line (NIL) NIL-

SLG1 ^{Ind}, which significantly improved survival rates under high-temperature stress [94]. Similarly, introducing *TT1* from the *O. glaberrima* variety CG14 into the japonica variety WYJ produced NIL-*TT1* ^{SG42}, which exhibited significant tolerance to high-temperature stress during both the seedling and mature stages. Lines carrying *TT1* ^{SG42} showed higher thousand-grain weight, seed-setting rate, and grains per panicle under high-temperature stress during the flowering and grain-filling stages [62]. The introgression of the *TT2* gene from the African cultivated rice variety HP21 as the donor parent into the recipient parent HJX resulted in the highly thermotolerant NIL-*TT2* ^{HPS32}. This was attributed to the maintenance of stable cuticular wax layers and reduced Ca^{2+} influx under high-temperature stress compared to NIL-*TT2* ^{HJX} [34]. A single-segment substitution line was constructed using the African rice variety CG14 and the japonica variety WYJ, and the introgression of *TT3* ^{CG14} into WYJ resulted in NIL-*TT3* ^{CG14}, which exhibited thermotolerance during the reproductive growth stage under high-temperature stress [49]. Genomic sequencing analysis revealed that the *TT3* gene contains two temperature-responsive loci, *TT3.1* and *TT3.2*, with opposite regulatory functions in heat stress adaptation. Overexpression of *TT3.1* ^{CG14} conferred stronger high-temperature tolerance in rice, while the *tt3.2* mutant exhibited high resistance to heat stress [49]. Additionally, the overexpression of the major transcript *HTG3a* of *HTG3* significantly enhanced tolerance to high-temperature stress. MITE (a B-like superfamily of miniature inverted-repeat transposable elements) deletion in the promoter of the *HTG3* gene in the japonica variety NIP significantly increased *HTG3* expression. Conversely, the insertion of MITE into the promoter of the *HTG3* gene in the indica variety ZH97 via gene editing technology significantly reduced *HTG3* expression [93]. The introgression of the *HTH5* gene from the indica variety HHT3 into Shuhui527 and the japonica variety Sasanishiki resulted in near-isogenic lines that significantly improved the seed-setting rate and final yield under high-temperature stress during the heading stage, with a more pronounced increase in the Sasanishiki variety [36]. Most japonica varieties carrying *PWL1* ^{Hap1} avoid premature senescence under heat stress [95].

AtPLC9 is a heat-shock signal-related gene in Arabidopsis thaliana. The heterologous expression of *AtPLC9* in the Asian rice variety Changyou No. 1 significantly increased chlorophyll content and seedling survival rate under high-temperature stress, demonstrating the great potential value of heterologous expression in breeding improvement [96]. Given the highly conserved cell wall invertase gene *LIN5* in tomato, the optimization of carbon allocation under heat stress was achieved in different tomato varieties, M82 and a modern tomato inbred line variety Yuanwei-1 (YW1). Using gene editing technology, the heat stress response element ‘ATTCTAGAAT’ was inserted into the promoter of the cell wall invertase gene *GIF1* in Wuyoudao-4 (WYD-4). The resulting line *wyd-gif1-de* exhibited higher single plant yield and harvest index under heat stress, achieving more rational source-sink allocation under heat stress [97].

Using the indica variety Huajingxian74 as the recurrent parent and the American japonica variety Lemont as the donor parent, a near-isogenic line (NIL) NIL-gs10 was obtained through the construction of a substitution line. This line exhibited smaller grains and reduced thousand-grain weight. Correspondingly, we defined the allele of Huajingxian74 as *GS10*, also known as *MADS56* [98,99]. Genomic inversion is a complex type of genomic structural variation. The inversion site eQTL *OsINV10* located in the promoter region of *MADS56* significantly enhanced the expression of *MADS56* and strongly increased its tolerance to heat stress [98,99]. During evolution, the *SRL10* ^{HaP3} haplotype gene was highly selected in aus-type rice. This haplotype exhibited significantly higher expression levels than other haplotypes and achieved significantly improved seed-setting rates under 42 °C heat stress [100]. microRNAs (miRNAs) also have great potential in rice thermotolerance. The transfer of miR169r-5p from the thermotolerant rice variety Gan-Xiang-Nuo (GXN) into the heat-sensitive variety Hua-Jing-Xian-74 (HJX) significantly optimized heat stress adaptation at the flowering stage [101].

The single-segment substitution line IL01-15, formed by introducing the single fragment containing *qHTB1-1* ^{HHT4} from Hehuatang No. 4 into the R53 variety, exhibited extremely high spikelet fertility under high-temperature stress, with significant increases in seed-setting rate and spikelet number [102]. By constructing recombinant inbred lines, QTL segments *DTH8*, *qHD3*, *qHD5*, and *qHD7* from the rice variety Dan 71 were introduced into the variety Zhonghui 161, delaying the heading stage and effectively avoiding heading during high-temperature periods, thereby reducing the damage of high temperature to yield. The QTLs *qSF1*, *qSF2*, *qSF3.2*, and *qSF8* in Zhonghui 161, as well as *qSF3.1* in Dan 71, effectively improved spikelet fertility under high-temperature conditions [103]. The heat-sensitive variety IR64 contains a heat-tolerant QTL segment *qHTSF1.1*, introducing it into the heat-tolerant rice variety N22 slightly improved its fertility under high temperature. *qHTSF4.1* is a heat-tolerant QTL segment located in the N22 variety, introducing *qHTSF4.1* ^{N22} into IR64 significantly enhanced its fertility during the panicle initiation stage under heat stress. Moreover, analysis of panicle initiation fertility in the progeny of the cross between N22 and IR64 indicated an interaction between the two QTLs *qHTSF1.1* and *qHTSF4.1* [104]. The indica variety IR64 contains an early-flowering QTL *qEMF3*. By constructing near-isogenic lines and introducing them into the recurrent parent Nanjing 11, the flowering time of Nanjing 11 was significantly advanced, which helped to avoid flowering under the highest temperature conditions and prevented high-temperature damage [105]. Gene pyramiding is conducive to more efficient breeding of superior varieties. Similarly, by constructing near-isogenic line hybrids NIL-*qHTSF4.1* ^{N22} and NIL-*qEMF3* ^{IR64}, the resulting gene pyramiding line NIL-*qHTSF4.1* ^{N22} *qEMF3* ^{IR64}, with IR64 as the background, significantly enhanced spikelet fertility and seed-setting rate under high-temperature stress and advanced flowering time to avoid the harm of high temperatures, fully demonstrating the superiority of gene pyramiding in gene aggregation [106]. The heat-tolerant rice variety Liaoyan241 contains QTL segments *qHTS3*, *qHTS1b*, and *qHTS4*. Similarly, by constructing recombinant inbred lines and introducing these three QTL segments into the heat-sensitive upland rice variety IAPAR-9, tolerance to high temperature during the heading and flowering stages was improved. The superior haplotype *qHTS1a* $^{IAPAR-9}$ exhibited strong tolerance to heat stress, while *qHTS3* $^{IAPAR-9}$ only slightly improved tolerance to heat stress [107,108].

Despite the fact that the utilization of superior heat-tolerant genetic resources has already yielded some favorable outcomes, our understanding of this field remains limited. Future research should focus on vigorously exploring excellent heat-tolerant genetic resources, with the aim of pyramiding heat-tolerance genes to develop high-quality, heat-tolerant rice varieties.

5. Conclusions and Prospects

With global climate change and the increasing frequency of extreme high-temperature events, heat stress has already had a widespread impact on crop production. To meet the ever-growing demand for food, the breeding of highly heat-tolerant varieties is the primary task in coping with heat stress at present. Up to now, although many genes related to rice heat stress tolerance have been identified, their application is still very limited, and there are many deficiencies in the understanding of rice heat stress responses [109,110]. So far, our understanding of the main resistance genes, including heat stress and the superposition of multiple abiotic stresses, is still very lacking, which indicates that it may be a problem worthy of in-depth exploration. In addition, at present, the understanding of the sensors in rice cells that directly perceive heat stress signals is still very limited. Due to the possible redundancy of some sensor-encoding genes and the lethality of mutations in these genes, the lack of appropriate research techniques makes the identification of these temperature stress-related sensors very challenging [111]. The experimental results obtained under laboratory conditions often differ greatly from those obtained under real field conditions. For example, under single heat stress conditions, plant leaf stomata will open to cool down through transpiration. However, the reality is that drought stress often occurs concurrently with heat stress, and drought stress will inhibit the opening of stomata to reduce water loss in plants [112]. The co-occurrence of multiple stresses will severely damage plant growth and development, which is also the focus of future researchers. For a long time, research on heat sensors under high-temperature stress has mainly focused on the cell membrane. However, the cell nucleus, as the core organelle for heat stress transcriptional regulation, may also contain primary signal sensors. Scientists are developing nanothermometers. These tiny thermometers can reveal temperature differences between different cells and within the same cell to study the direct response of the cell nucleus to temperature changes [113]. In the future, this technology is expected to be applied to plants to identify more nuclear heat stress signal sensors. In addition, with the gradual maturation of supporting technologies, the rational use of GWAS and other technical means to mine excellent natural alleles, the use of CRISPR/Cas9 and other gene editing technologies to precisely create excellent alleles, and the use of AI and big data analysis to predict combinations of alleles with excellent traits and new genes with heat resistance functions, these methods have positive significance for improving heat resistance of rice. Combining traditional breeding methods with modern molecular breeding technologies can more quickly and accurately achieve the breeding of and improvement in heat-tolerant rice varieties, which requires in-depth analysis of heat tolerance gene functions to assist in determining the specific pathways of rice heat tolerance and thus obtain the most suitable strategies for improving heat-tolerant rice varieties. In summary, the application of new technologies has brought great changes to breeding methods, improved breeding efficiency and accuracy, and provided the possibility for the rapid and efficient breeding of high-yielding and heat-tolerant rice varieties, which is helpful in meeting the growing demand for food and coping with environmental challenges.

Table 1. Key genes involved in rice heat adaptation.

Gene Name	MSU Locus	Encoded Protein	Heat Adaptation Effects Positive (+)/Negative (−)	References
FLO24	*LOC_Os03g31300*	Starch granule development protein	(+)	[27]
OsCNGC14	*LOC_Os03g55100*	Cyclic nucleotide-gated ion channel protein	(+)	[31]
OsCNGC15	*LOC_Os01g57370*	Cyclic nucleotide-gated ion channel protein	(+)	[31]
OsCNGC16	*LOC_Os05g42250*	Cyclic nucleotide-gated ion channel protein	(+)	[31]
OsANN1	*LOC_Os02g51750*	Calcium-binding protein; rice annexin	(+)	[32]
SCT1	*LOC_Os03g09100*	Sensing Ca^{2+} transcription factor 1	(+)	[34]
SCT2	*LOC_Os10g22950*	Sensing Ca^{2+} transcription factor 1	(+)	[34]
OsWR2	*LOC_Os06g40150*	Ethylene response factor	(−)	[34]

Table 1. *Cont.*

Gene Name	MSU Locus	Encoded Protein	Heat Adaptation Effects Positive (+)/Negative (−)	References
HTH5	*LOC_Os05g05740*	Pyridoxal phosphate homeostasis protein	(+)	[36]
MSD1		Manganese superoxide dismutase	(+)	[38]
SNAC3	*LOC_Os01g09550*	Stress-responsive NAC transcription factor	(+)	[39]
OsEDS1	*LOC_Os09g22450*	Enhanced disease susceptibility 1	(+)	[40]
OsCATB	*LOC_Os06g51150*	Catalase	(+)	[40]
OsCATC	*LOC_Os03g03910*	Catalase	(+)	[40]
JMJ713		Histone demethylase	(+)	[40]
JMJ708		Histone demethylase	(+)	[40]
OsRbohB	*LOC_Os01g25820*	Respiratory burst oxidase homolog	(−)	[12]
OsNAA15	*LOC_Os01g43030*	N-terminal acetyltransferase auxiliary subunit	(+)	[43]
OsNAA10	*LOC_Os04g54330*	N-terminal acetyltransferase auxiliary subunit	(+)	[43]
OsFLN1	*LOC_Os01g63220*	White leaf and panicle 2	(+)	[44]
OsFLN2	*LOC_Os03g40550*	Heat-stress sensitive albino 1 gene	(+)	[44]
OsTRXz	*LOC_Os08g29110*	Thioredoxin z	(+)	[46]
TT3.2	*LOC_Os03g49940*	Thermo-tolerance 3.2	(−)	[50]
PGL10	*LOC_Os10g35370*	Protochlorophyllide oxidoreductase B	(+)	[50]
GRY3	*LOC_Os09g36250*	4-hydroxy-3-methylbutyl-2-enyldiphosphate reductase	(+)	[51]
HES1	*LOC_Os08g10600*	UDP-N-acetylglucosamine pyrophosphorylase	(+)	[52]
OsNTL3	*LOC_Os01g15640*	NAC domain transcription factor	(+)	[60]
OsbZIP74	*LOC_Os06g41770*	Basic leucine zipper transcription factor	(+)	[60]
OsbZIP60	*LOC_Os07g44950*	Basic leucine zipper transcription factor; opaque3	(+)	[56]
OsBiP1	*LOC_Os02g02410*	Endoplasmic reticulum chaperone	(+)	[56]
PDIL1-1	*LOC_Os11g09280*	Protein disulphide isomerase-like enzyme	(+)	[56]
TT1	*LOC_Os03g26970*	Thermo-tolerance 1	(+)	[62]
TT2	*Os03g0407400*	G protein gamma subunit	(+)	[34]
SCE1	*LOC_Os10g39120*	SUMO-conjugating enzyme E2	(+)	[63]
TT3.1	*LOC_Os03g49900*	Thermo-tolerance 3.1	(+)	[49]
OsHCI1	*LOC_Os10g30850*	RING finger E3 ligase	(+)	[65]
OsJAZ1	*LOC_Os04g55920*	Jasmonate ZIM-domain protein	(−)	[67]
OsJAZ9	*LOC_Os03g08310*	Jasmonate ZIM-domain protein	(+)	[66]

Table 1. *Cont.*

Gene Name	MSU Locus	Encoded Protein	Heat Adaptation Effects Positive (+)/Negative (−)	References
OsPRMT6a	*LOC_Os10g34740*	Protein arginine methyltransferase	(+)	[67]
OsMYC2	*LOC_Os10g42430*	JA-inducible basic helix–loop–helix transcriptional factor	(+)	[67]
OsFBN1	*LOC_Os09g04790*	Fibrillin	(−)	[69]
OsAOS1	*LOC_Os03g55800*	Allene oxide synthase gene	(+)	[68]
OsAOS2	*LOC_Os03g12500*	Allene oxide synthase gene	(+)	[69]
HTG3	*LOC_Os03g06630*	Heat shock transcription factor	(−)	[66]
OsIAA7	*LOC_Os02g13520*	Auxin responsive Aux/IAA family protein	(+)	[70]
OsIAA21	*LOC_Os06g22870*	Auxin-responsive Aux/IAA family protein	(+)	[71]
OsIAA29	*LOC_Os11g11430*	Auxin-responsive Aux/IAA family protein	(+)	[71]
OsARF6	*LOC_Os02g06910*	Auxin response factor	(−)	[70]
OsNCED3	*LOC_Os03g44380*	9-cis-epoxycarotenoid dioxygenase	(+)	[73]
OsRbohH	*LOC_Os12g35610*	Respiratory burst oxidase homolog	(+)	[76]
OsNCED4	*LOC_Os07g05940*	9-cis-epoxycarotenoid dioxygenase	(+)	[76]
OsNCED5	*LOC_Os12g42280*	9-cis-epoxycarotenoid dioxygenase	(+)	[73]
SAPK2	*LOC_Os07g42940*	Stress-activated protein kinase	(+)	[74]
D11	*LOC_Os04g39430*	Cytochrome P450	(+)	[81]
BRD2	*LOC_Os10g25780*	FAD-linked oxidoreductase protein	(+)	[81]
OsHSFA2d	*LOC_Os03g06630*	Heat shock transcription factor	(+)	[85]
OsWRKY10	*LOC_Os01g09100*	WRKY transcription factor	(−)	[86]
OsWRKY11	*LOC_Os01g43650*	WRKY transcription factor	(+)	[66]
VQ8	*LOC_Os02g33600*	Valine-glutamine (VQ) motif-containing protein	(+)	[86]
OsHSP101	*LOC_Os07g05600*	Heat shock protein 101	(+)	[66]
OsMADS7	*LOC_Os08g41950*	SEPALLATA-like MADSbox gene	(+)	[87]
OsbZIP58	*LOC_Os07g08420*	bZIP transcription factor	(+)	[21]
OsbZIP14	*LOC_Os02g03960*	bZIP transcription factor	(+)	[88]
OsMYB55	*LOC_Os05g48010*	R2R3-MYB transcription factor	(+)	[89]
ONAC127	*LOC_Os11g31340*	Heat-stress-responsive NAC transcription factor	(+)	[90]
ONAC129	*LOC_Os11g31380*	Heat-stress-responsive NAC transcription factor	(+)	[90]
ONAC023	*LOC_Os02g12310*	NAC (NAM, ATAF, and CUC) transcription factor	(+)	[92]
SLG1	*LOC_Os12g39840*	Cytosolic tRNA 2-thiolation protein 2	(+)	[94]

Table 1. *Cont.*

Gene Name	MSU Locus	Encoded Protein	Heat Adaptation Effects Positive (+)/Negative (−)	References
GIF1	*LOC_Os11g40100*	Growth regulating factor-interacting factor 1	(+)	[97]
MADS56	*LOC_Os10g39130*	MADS-box protein gene; grain length 10	(+)	[98]
SRL10	*LOC_Os10g38540*	Double-stranded RNA-binding protein	(+)	[100]

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