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Review Article

Agronomic and genetic approaches for enhancing tolerance to heat stress in rice: a review

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Abstract

Rice is an important cereal crop worldwide that serves as a dietary component for half of the world's population. Climate change, especially global warming is a rising threat to crop production and food security. Therefore, enhancing rice growth and yield is a crucial challenge in stress-prone environments. Frequent episodes of heat stress threaten rice production all over the world. Breeders and agronomists undertake several techniques to ameliorate the adverse effects of heat stress to safeguard global rice production. The selection of suitable sowing time application of plant hormones, osmoprotectants and utilization of appropriate fertilizers and signaling molecules are essential agronomic practices to mitigate the adverse effects of heat stress on rice. Likewise, developing genotypes with improved morphological, biochemical, and genetic attributes is feasible and practical way to respond to this challenge. The creation of more genetic recombinants and the identification of traits responsible for heat tolerance could allow the selection of early-flowering cultivars with resistance to heat stress. This review details the integration of several agronomic, conventional breeding, and

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molecular approaches like hybridization, pure line selection, master-assisted-selection (MAS), transgenic breeding and CRRISPR/Cas9 that promise rapid and efficient development and selection of heat-tolerant rice genotypes. Such information's could be used to determine the future research directions for rice breeders and other researchers working to improve the heat tolerance in rice.

Keywords: agronomic approaches; breeding approaches; heat stress; plant hormones; rice

Introduction

Rice (*Oryza sativa* L.) is an important staple food crop for half of the world's population (Aslam *et al.*, 2015; Liang *et al.*, 2021; Badawy *et al.*, 2021). It fulfils the dietary needs of more than 3 billion people across the globe (Rasheed *et al.*, 2020a, 2020b; Rasheed *et al.*, 2020; Rasheed *et al.*, 2021b). Asian countries are the primary rice consumers, accounting for more than 80% of total rice consumption (Suh, 2015). Rice contains a significant amount of protein, nutrients, carbohydrates, fiber, and sugar (Kennedy and Burlingame, 2003; Badawy *et al.*, 2021). Rice is a model crop because of its small genome size (Bennetzen, 2002), and it is suitable for effective genetic transformation (Rodríguez *et al.*, 2005). The above mentioned characteristics suggested that the yield potential of rice could be increased by selecting genetic variants that can cope with changes in heat, drought, and salinity stresses (Jwa *et al.*, 2006). In 2019 rice was grown on an area of 162, 666.00 thousand hectares and global rice production was remained at 497.76 million metric tons (FAO, 2019).

Abiotic stresses are significant constraints (Rasheed *et al.*, 2021a; Badawy *et al.*, 2021) for rice growth and production (Hassan *et al.*, 2017; Hassan *et al.*, 2020). Heat stress (HS) refers to an increase in the temperature level beyond the threshold limit (Kumari *et al.*, 2020; Mukhtar *et al.*, 2020) for a definite period that permanently decreases growth and development (Govindaraj *et al.*, 2018). Cereal production has decreased by 9-10% over the last 50 years due to extreme heat and drought stress (Lesk *et al.*, 2016). A daytime temperature of over 35 °C during flowering decreases the fertility rate (Wang *et al.*, 2019b) and causes a substantial reduction in rice productivity (Khan *et al.*, 2019). Moreover, the occurrence of HS at the flowering stage induces pollination failure and results in a severe yield reduction (Abd El-Daim *et al.*, 2014; Song *et al.*, 2014) . Heat stress also reduces the production of assimilates and enzymatic activities and leads to a severe reduction of the final yield (Chaturvedi *et al.*, 2017; Mukhtar *et al.*, 2020). There is a negative relationship between the increment of temperature and the yield of rice, wheat, and maize. Heat stress affects plants by blocking the metabolic pathways and reducing the seed setting rate, plant growth, and development, and seed ripeness, which can cause a significant reduction in final grain yield. Long-term heat stress reduces plants photosynthetic activity, decreases water use efficiency, reduces seed weight and grain weight, and shortens the leaf area (Hassan *et al.*, 2020). The ability of plants to sustain their yield and maintain average growth under heat stress conditions is driven by various metabolic and morphological features referred to as heat tolerance traits (Wahid *et al.*, 2007; Mukhtar *et al.*, 2020). Heat tolerance traits are governed by many genetic factors and are linked to rice physiological and morphological adaptations (Impa *et al.*, 2021).

Heat tolerance mechanisms can be divided into three types: avoidance, escape, and tolerance. Escape mechanisms include the completion of the reproduction cycle before the heat stress period. A plant retains more water by decreasing the leaf area, stomatal closure, and dropping old leaves (Mohammed *et al.*, 2021). Some researchers have determined the adaptation approaches of rice against heat stress (Julia and Dingkuhn, 2013). Rice escapes heat stress by regulating the panicle emergence time and the opening of spikelets (Julia and Dingkuhn, 2012). Spikelet sterility has been generally investigated to improve rice tolerance to HS. Variations among the cultivars in terms of spikelet fertility under harsh conditions can be considered as essential for heat tolerance mechanisms in rice (Weerakoon *et al.*, 2008). Rice crop can decrease the HS via panicles up to 10 °C through transpiration, which determines the potency of spikelet's (Matsui *et al.*, 2001). Erect and long leaves safeguard the panicles from the direct impacts of heat stress and induce HS tolerance in rice (Julia and

Dingkuhn, 2013). Heat tolerance can be gained by altering several morphological, molecular, and biochemical traits. The heat-tolerant wild genotype (*Oryza meridionalis*) maintained a high photosynthesis rate under HS conditions owing to better maintenance of the enzyme Rubisco (Qu *et al.*, 2021). The chlorophyll content and electrolyte leakage from leaves and roots increased during HS and can be utilized as marker to investigate heat tolerance.

Different agronomic and breeding approaches could be used to enhance the heat tolerance in rice crops. Agronomic approaches involve early sowing, spraying of signalling molecules, and hormones and osmoprotectants to mitigate the adverse effects of heat stress. The early sowing ensures the plant's survival at high temperatures, increasing overall productivity and quality (Krishnan *et al.*, 2011). The application of plant hormones (auxins, salicylic acid, ascorbic acid, methyl jasmonate, alpha-tocopherol, and brassinosteroids) can also alleviate the adverse effect of heat stress and ensures better productivity (Khan *et al.*, 2019). Likewise, the application of signalling molecules reduced the heat-induced adverse effects in rice crop by increasing the PS II efficiency, water use efficiency, and activity of anti-oxidants (Chandrakala *et al.*, 2013). Additionally, the application of variable osmolytes (proline, glycine-betaine, and spermidine) is also considered a critical approach to improving the robust approach to improving rice crops heat tolerance (Khan *et al.*, 2019; Sakamoto and Murata, 2000).

Breeding techniques are considered a long-term solution to solve the heat stress problem in rice crop. Conventional breeding approaches, including the selection of heat-tolerant cultivars, can help to improve the heat tolerance of rice crops. Likewise, recently developed molecular approaches have adopted the omics technique to develop transgenic plants by manipulating targeted genes, which can also help to improve the heat tolerance of rice crops (Duque *et al.*, 2013; Kosová *et al.*, 2011). Additionally, the identification of heat-tolerant QTLs and the use of proteomics and transcriptomics approaches may help identify underlying molecular heat tolerance processes, providing development to the heat-tolerant crop genotypes. Therefore, the current review reports on the agronomic approaches, conventional, and molecular approaches that can improve heat stress tolerance in rice. We discuss the heat stress mechanisms, agronomic approaches, conventional approaches, molecular approaches, heat tolerance QTL and genes, and the future outlook for heat tolerance in rice.

Effects of heat stress on rice

In the future, rice production may face massive challenges due to an increase in extreme climatic events (Sun *et al.*, 2021). Heat stress can cause permanent injury to plants (Wahid *et al.*, 2007) by impairing growth, metabolic processes, and seed setting rate as well as causing pollen infertility (Hassan *et al.*, 2017), therefore leads to severe yield reduction (Hasanuzzaman *et al.*, 2013; Zafar *et al.*, 2017). Extreme heat stress rapidly decreases plants photosynthesis rate, grain weight (Table 1), leaf area, and water use efficiency (WUE) (Shah and Paulsen, 2003). High levels of heat stress may hinder vegetative and reproductive growth (Katiyar-Agarwal *et al.*, 2003). The booting and flowering stages are the most crucial stages of the rice life cycle, and exposure to HS at these stages can cause complete infertility in rice crop (Shah *et al.*, 2011).

Effects of heat stress on photosynthesis, growth, and yield

Heat stress (HS) significantly decreases rice growth during the initial stages (Figure 1) and, seedling mortality is considered as a common effect of HS (Abd El-Daim *et al.*, 2014; Xiao *et al.*, 2011). Depending on the genotype, heat stress reduces rice growth and final production by decreasing relative water content (RWC), photosynthetic pigment concentration, and assimilating production (Fahad *et al.*, 2016a; Ihsan *et al.*, 2016). The process of photosynthesis is vulnerable to HS, and it is adversely affected by high-temperature stress. Heat stress (30 °C and 35 °C) decreased photosynthesis, stomatal conductance, and transpiration, substantially reducing the final yield and quality (Fahad *et al.*, 2016b). Other impacts of HS are reductions in carbon dioxide pathways, electron transport chain and rubisco activity. Heat stress remarkably reduces photosynthetic processes and causes membrane instability and damage (Zheng *et al.*, 2016). However, the consequences of this stress might be different among plant species (Alghabari *et al.*, 2016). Heat stress decreases the concentrations of proteins and lipids; however, reducing lipids is relatively more significant (Johnston *et al.*, 2007). The presence of HS at the flowering stage has been shown to spikelet sterility (Figure 1) by stopping another dehiscence and germination of pollen on the stigma (Coast *et al.*, 2016). Heat stress also leads to a poor seed filling rate and poor seed development (Sehgal *et al.*, 2018). High temperatures cause low root vigor, and the selection of root base traits becomes tedious (Fahad *et al.*, 2017). In conclusion, HS reduces the chlorophyll content, rubisco activity, water use efficiency and induces oxidative damage and stomata closure, therefore causing significant reductions in the growth and yield of rice plants. The influences of heat stress on rice are given in Table 1.

Table 1. Influences of heat stress on rice growth, photosynthesis, yield and quality

Heat stress temperature	Effects	References
45 °C	Heat stress reduced the seed setting and seed yield	(Akman, 2009)
35/25, 40/30, 45/35, and 50/40 °C	Heat stress reduced the length of pollen tube, and decreased pollen protein and sugar contents	(Das *et al.*, 2014)
38 °C	Heat stress decreased 1000 grain weight, and rice yield	(Aghamolki *et al.*, 2014)
35°C	Heat stress reduced yield traits, grain size, and rice yield	(Wu *et al.*, 2016)
29 °C	Heat stress reduced growth and increased kernel chalkiness	(Shi *et al.*, 2016)
34 °C	Reduced Pollen fertility	(Wada *et al.*, 2020)
33, 35, or 37 °C	Reduced grain weight	(Yan *et al.*, 2021b)
42 °C	Reduced 1000 grain weight	(Chaudhary *et al.*, 2021)
28 °, 42 °C	Reduced photosynthesis	(Qu et al., 2021)
33 °C	Photosynthesis	(Huang *et al.*, 2021)
32 °C	Reduce grain yield	(Nakano *et al.*, 2021)
33 °C	Reduced spikelets fertility	(Chidambaranathan *et al.*, 2021)

Effect of heat stress on water usage efficiency and nutrient uptake

Heat stress reduces the water use efficiency in rice (Zou *et al.*, 2011) by increasing transpiration rate (Topbjerg *et al.*, 2015). Rice plant showed reduction in WUE under extreme heat stress and it leads to lower photosynthesis (Piveta *et al.*, 2021). HS also disrupts plant minerals and their translocation. Likewise, Cabral *et al.* (2016) noted that higher nitrogen (N) concentration was allocated to grains than tillers under HS, and the phosphorus (P) concentration was also decreased in wheat plants subjected to the HS. High temperature (>2 °C above the average level) was shown to enhance the C: N (Figure 1) ratio and decreased the concentration of nutrients in maize plants (Zhang *et al.*, 2013a). In another study the effects of heat stress on nutrients uptake were studied. The heat stress significantly reduced the nitrogen application rate in Boro rice variety (Hossain *et al.*, 2021). In general, few studies have investigated the impacts of HS on the mineral status of plants. More extensive investigation could help to establish nutrient absorption pathways for heat-stressed plants.

Effects of heat stress on the production of reactive oxygen species and antioxidant enzymes

Oxidative stress is also accompanied by heat stress (Figure 1) and occurs due to the accumulation of ROS in plants (Pucciariello *et al.*, 2012), which cause substantial damage to the significant molecules, including the DNA, proteins, sugars, and carbohydrates, and can induce cell death (Gill and Tuteja, 2010). In crops, reactive oxygen species exist in molecular forms. Their ionic form is superoxide anions, and their molecular state is singlet oxygen (Mittler *et al.*, 2004). Numerous enzymes, such as NADPH oxidases, polyamine, and a large family of class III peroxidases present on the cell surface, create ROS (Cosio and Dunand, 2009). The overproduction of ROS during the HS is highly toxic to lipids, proteins, and nucleic acids, eventually, damaging cells and leading to cell death (Gill and Tuteja, 2010). Plants use different types of antioxidant enzymes, like catalase (CAT), superoxide dismutase (SOD), and glutathione reductase (GR), to scavenge ROS. The antioxidant molecules are positioned in plant cells and work in groups to detoxify ROS (You and Chan, 2015). In conclusion, HS induces the production of ROS, which cause damage to significant molecules and eventually leads to cell death. Therefore, proper measures should be adopted to reduce ROS production under HS conditions to ensure better rice production.

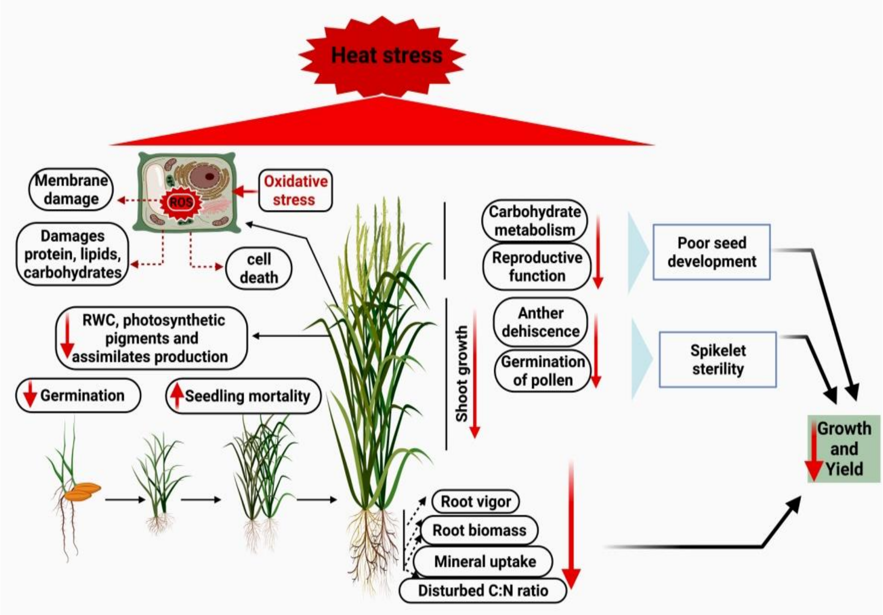

Figure 1. Effects of heat stress on various growth, physiological, biochemical, and yield traits of rice crops

Heat tolerance mechanisms in rice

Plants have different mechanisms, including escape, avoidance, and survival, to cope with HS. Plants undergo several types of modifications to avoid heat stress. Rice varieties have covered panicles to reduce HS by decreasing the evaporation rate (Shah *et al.*, 2011). Early flowering varieties have a better capability to tolerate heat stress by using a heat avoidance mechanism (Bheemanahalli *et al.*, 2017; Ishimaru *et al.*, 2012) . Genetic variations in rice plants can be exploited to screen the germplasm for HS tolerance (Ishimaru *et al.*, 2012).

Size of anther and basal pore

The length of anther varies among genotypes. Genotypes associated with longer anthers are considered more heat tolerant than those associated with short anthers (Matsui and Omasa, 2002). Under heat stress conditions, floret sterility is a direct cause of reduced pollen grain germination on the stigma owing to poor anther dehiscence (Ishimaru *et al.*, 2012) . Anther size has a positive association with the number of pollen grains per anther. It is considered that cultivars with more prominent anthers have more pollen grains, allowing them to compensate for temperature-induced effects (Matsui and Omasa, 2002). Likewise, the size of basal pores varies among cultivars. The large anther size can minimize the effects of heat stress and could be use as tolerance criteria in rice under extreme heat stress (Santiago *et al.*, 2021). Large basal pores induce the release of pollen grains to the stigmata during another dehiscence; thus, the number of pollen grains in the plant sigma depends on the basal pore size (Matsui, 2005). Conversely, pollen grains remain inside the anther in plants with tiny basal pores until the floret opens. Then, the anther bends and spreads pollen. Thus, genotypes with tiny basal pores undergo self-pollination and are more likely to cross-pollinate (Matsui and Kagata, 2003). Large basal pores facilitate the release of pollen from the anther and increase the chance of pollination. Basal pore can also be used as tolerance criteria under condition of extreme heat stress and pollination rate can be enhanced (Wang *et al.*, 2021). In conclusion, cultivars with large anthers and basal pores should be cultivated to reduce the effects of heat stress.

Photosynthesis and the carbohydrate content

The selection of genotypes that can accumulate a high concentration of nonstructural carbohydrates produce more biomass, and maintain a higher photosynthesis rate under extreme heat stress could be used to develop the heat-tolerant cultivars to minimize yield loss induced by heat stress. Genotypes tolerant to heat stress at the anthesis and reproductive stages can maintain a higher rate of photosynthesis for a long time and thus produce more grains (Egeh, 1991). To attain heat tolerance and maximum growth, retention of a high photosynthetic rate is critical. The response of photosynthetic parameters to HS was observed in two rice cultivars (IR46 and IR53) under high heat stress conditions during the day-time. It was noted that photosynthetic traits like the chlorophyll content were more prominent in cultivar N22 than another cultivar. It was found that all photosynthetic traits of N22 were more prominent than in the other genotypes at elevated temperatures, showing the greater tolerance of N22. The rate of photosynthesis was first improved with temperature up to an optimal temperature of 32 °C, which then reduced when the temperature continued to increase to 42 °C (Gesch *et al.*, 2003). Thus, we should develop rice cultivars with improved photosynthesis and carbohydrate synthesis capacities to achieve the maximum yield potential under HS conditions.

Heat shock protein content

Heat shock proteins (HSPs) are considered significant molecular chaperons that help in folding protein assembly and the maintenance of homeostasis under both ideal and adverse conditions (Lin *et al.*, 2014). In a previous study, Jagadish *et al.* (2010) observed the changes in protein expression under HS conditions and showed that the tolerant genotype N22 expressed more HSPs. Hence, it was proven that HSPs enhance HS tolerance. The gene expression analysis showed a variation in the expression levels of genes encoding HSPs in rice leaves. Higher expression of HSPs was found in the heat-tolerant rice cultivars R-1389 and N22 (Chandel *et al.*, 2013). The HSPs (*OsHsfA7* and *OsHsfA2a*) were strongly upregulated in plants with the N22 genotype under HS conditions (42 °C) at the flower opening phase. The functions of Hsfs, *OsHsfA2e* and *OsHsfA7* were also upregulated in the Vandana variety, but the increase in function was lower than in N22 (Sailaja *et al.*, 2015). In another experiment, Lin *et al.* (2014) tested the heat tolerance of the japonica and indica N22 varieties of rice. Both studies analyzed the heat-stress tolerance of different rice varieties to allow a clear comparison between varieties to be made. These cultivars exhibited conflicting levels of heat tolerance. N22 showed a rapid decline in HSP101 compared with japonica, which might have been due to environmental alterations. The Nipponbare genotype attained HS tolerance over the long term, while N22 showed greater basal HS tolerance (Katiyar-Agarwal *et al.*, 2003). The high expression of genes related to the heat shock transcription factor (Hspf) is one of the important factors in the reaction of plants to heat waves (Liu *et al.*, 2009). Consequently, HSPs are associated with higher heat-stress tolerance in rice crops as they reduce the permanent accumulation and degradation of mis-folded proteins and maintain cellular homeostasis.

Thermostability of the cell membrane and chlorophyll fluorescence

Genetic variations have been identified in rice cultivars regarding chlorophyll fluorescence traits under HS (Sailaja *et al.*, 2015). The rice genotype N22, tolerant to heat-stress, demonstrated a high Fv/Fm ratio when exposed to HS (42 °C) (Bahuguna *et al.*, 2015). Heat stress declined the chlorophyll contents, and the decline was more prominent in heat-sensitive cultivars (Sailaja *et al.*, 2015; Zhou *et al.*, 2007). Moreover, membrane thermostability (MTS) is a trustworthy feature that could be exploited to select tolerant genotypes. It has been shown to have a, more significant association with yield under HS conditions (Sailaja *et al.*, 2015). Heat stress was shown to increase electrolyte leakage, leading to a significant reduction in the final yield (Mohammed and Tarpley, 2009). Zhang *et al.* (2005) examined the influence of HS on the physiological and biochemical features of rice at the flowering and heading stages. They noted that the sensitive variety (4628) had lower membrane permeability than the heat-tolerant (line-96) under HS conditions. In another study, membrane thermostability was found to have a significant association with the grain yield/plant. Earlier studies showed that early-morning flowering could minimize the effects of HS on rice and be used as a selection criteria. In this study, a set of diverse rice genotypes were exposed to HS and the flowering time was observed (Bheemanahalli *et al.*, 2017). Membrane and chlorophyll fluorescence must be increased in rice cultivars under changing HS scenarios to ensure better rice production.

Spikelet fertility and yield traits

There are genetic differences in the sensitivity of spikelets to HS (Buu *et al.*, 2021). Spikelet's from heat-tolerant genotypes show better results than sensitive ones under HS (Jagadish *et al.*, 2010; Prasad *et al.*, 2006). Two traits, spikelet fertility and yield/plant could be selected to attain HS tolerance. For instance, N22, a highly heat-tolerant rice cultivar, maintains spikelet fertility of 71%. In contrast, cultivars with moderate or poor heat tolerance (IR 64 and Moroberekan) retained 48% and 18% spikelet fertility levels, respectively. Nevertheless, Prasanth *et al.* (2016) stated that spikelet fertility is not a significant criteria for determining heat tolerance after excluding the yield/plant.

Agronomic approaches to enhancing heat tolerance in rice

Early planting

Determining an appropriate sowing time is an imperative agronomic strategy for reducing the damaging effects of heat stress. Most agronomic practices focus on the early sowing of rice crop, the adjustment of irrigation systems, and the adaptation of early and late maturing cultivars to mitigate the adverse effects of heat stress (Krishnan *et al.*, 2011) . Early sowing of rice has significant role in avoiding stress in rice. Ding *et al.* (2020) adjusted the sowing date of rice under adverse climatic conditions and concluded that shifting of sowing date showed promising results in terms of rice yield. In this way yield loss can be compensated. Jagadish *et al.* (2015) also presented a detailed review in which they showed that management of sowing date in rice could protect rice from extreme heat stress. Appropriately timed sowing of rice is crucial to reduce the effects of heat stress at critical growth stages. Setiyono *et al.* (2018) found significant reductions in the rice yield with heat stress at the plant reproductive stage due to a high rate of spikelet sterility. They also suggested that yield losses in rice crops can be reduced substantially by early sowing. The use of optimum sowing dates also reduces the unfavorable adverse effects of heat stress on the grain yield and quality. Zhu *et al.* (2013) studied the impacts of various sowing dates on the rice yield and quality. They found that adjusting the sowing time can reduce the effects of heat stress on the rice yield and quality. However, they also suggested that adjusting the sowing time is very difficult because it affects the proceeding crops. In a flooded anaerobic system, methane and nitrous oxide emissions are the main factors responsible for global warming. Therefore, adjusting the irrigation system, for example, using alternate wetting and drying periods, can help to decrease the effects of heat stress by reducing greenhouse gas emissions (Yu *et al.*, 2004; Aamer *et al.*, 2021). Additionally, covering the soil surface with crop residue and modifying the microclimate by shading can reduce the effects of heat stress in rice crops (Krishnan *et al.*, 2011) . In conclusion, optimizing the sowing time can help reduce the harmful effects of heat stress in rice crops.

Employing plant hormones to increase heat tolerance in rice

It is well known that the five classical phytohormones have drawn the interest of many scientists and have been investigated for decades (Chattha *et al.*, 2017). Plant hormones may be targeted to enhance abiotic stress tolerance and the growth and yield of rice (Ciura and Kruk, 2018). Increasing the auxin level during panicle formation increases heat tolerance in rice (Sarwar, 2019). The gaseous hormone ethylene is developed in response to heat stress (Wu and Yang, 2019), and ethylene-mediated signaling induces heat tolerance in rice seedlings. In a previous experiment, ethylene-responsive mutants were identified and characterized in rice. It was concluded that ethylene significantly increases heat tolerance in rice seedlings (Wu and Yang, 2019) by maintaining the seed ripening rate during extreme heat waves.

Abscisic acid is an important plant hormone that contributes to the response to diverse stress conditions including HS, drought, and cold stress (Zou *et al.*, 2017). Many studies have revealed that ABA improves thermos-tolerance in various plant species (Claeys *et al.*, 2014). Amino acids also play key roles in HS tolerance in rice crops. Amino acids are involved in metal binding, cell signaling, and the antioxidant defense system. Therefore, they play essential roles in plant defenses when exposed to different stresses (Sharma and Dietz, 2006). Proline is vital amino acid that protects the plants from stressful conditions (Verbruggen and Hermans, 2008). It plays a significant role in different mechanisms, including antioxidant defense, turgor production, N, and carbon assimilation (Verbruggen and Hermans, 2008), and protein stabilization (Maggio *et al.*, 2002). Proline minimizes the negative impacts of HS by lowering the ROS concentration and increasing the activity of antioxidants and the accumulation of different metabolites, including proline, ascorbic acid, and glutathione (Ali *et al.*, 2020). Spermidine is a natural polyamine that is involved in the adaptation of plants to various abiotic stresses, such as heat (Tian *et al.*, 2012), cold (Yamamoto *et al.*, 2012), heavy metals (Xu *et al.*, 2011), and drought (Fu *et al.*, 2019). Spermidine was shown to increase, therefore, antioxidants activity, therefore increasing plant survival under stressful conditions (Tian *et al.*, 2012).

Ethylene and cytokinin also play a significant role under heat stress in plants as well as rice. In response to extreme heat stress in rice, the gaseous hormone like, ethylene is produced in plants and its manipulation under heat stress brings promising results (Poór *et al.*, 2021). Likewise, cytokinin (CK) a plant growth promoting hormone also protects plants under heat stress. In rice, CK governs several biological features like, growth of shoot and increase spikelets number under heat stress (Wu *et al.*, 2017).

Foliar spraying of spermidine has been shown to improve the tolerance of rice to HS by reducing oxidative damage and increasing photosynthetic and antioxidant activity under HS conditions (42 °C) (Mostofa *et al.*, 2014). Moreover, spermidine was found to increase plant growth and the chlorophyll content under HS conditions (Murkowski, 2001; Zain *et al.*, 2017). Salicylic acid is a type of phytohormones with an abundant distribution in plants. It governs the response of a large number of physiological features to abiotic stresses. The exogenous application of SA to rice seedlings was found to minimize the adverse effects of high heat waves at a up to 32 °C and enhance dry matter portioning at up to 16% (Mohammed and Tarpley, 2009). The induction of a class 11 HSP, *Oshsp18.0*, by SA in rice demonstrated the role of SA in response to heat waves (Chang *et al.*, 2007). Methyl jasmonates play a crucial role in alleviating heat stress, and their application increased early flowering under heat stress conditions (Kobayasi and Atsuta, 2010). Zhang *et al.* (2018) revealed the consequences of spraying auxin on the elongation of pollen tubes of heat-tolerant and susceptible plant varieties. They stated that spraying naphthalene acetic acid reduced and upturned the spikelet sterility in heat susceptible and tolerant rice plant genotypes by obstructing the reduction of pollen tube growth. These findings suggest that plant hormones could increase growth and improve HS tolerance in rice crops.

Utilizing fertilizers and signaling molecules to increase heat tolerance in rice

The application of signaling molecules and fertilizers can significantly reduce the negative impacts of heat stress in rice. Likewise, the application of CaCl2 (10 mM) was shown to mitigate the adverse effects of heat stress in rice by improving the PS-II efficiency and water use efficiency and increasing the chlorophyll content and spikelet fertility (Chandrakala et al., 2013). Similarly, nitric oxide regulated different processes in plants and was shown to improve flowering, fertilization, and high-stress tolerance (Hasanuzzaman *et al.*, 2013). Rice seedlings treated with hydrogen peroxide showed significant improvements in PS-II efficiency, antioxidant activity, and gene expression, which increased rice heat tolerance. The basal application of boron mitigated the adverse effects of heat stress in rice by improving the membrane stability and spikelet fertility (Shahid *et al.*, 2018). The soil application of potassium fertilizers remarkably reduced the effects of drought stress by increasing the photosynthetic efficiency and antioxidant activity and decreasing the MDA content. Thus, the application of fertilizers and signaling molecules can reduce the adverse impacts of heat stress by increasing the photosynthetic efficiency, membrane stability, and activity antioxidants.

Using osmoprotectants to increase heat tolerance in rice

The accumulation of various osmoprotectants in response to different abiotic stresses can alleviate the adverse impacts of stressful conditions (Hassan *et al.*, 2020). Osmoprotectants protect plant metabolic processes by stabilizing cellular membranes and increasing different antioxidants' photosynthetic efficiency and activity. Glycine betaine (GB) is an essential osmolyte that accumulates in plants under heat stress conditions (Hassan *et al.*, 2020). It induces heat tolerance by protecting different enzymes (Rubisco and citrate synthase) from heat degradation (Quan *et al.*, 2004). Many plant species such as maize and sugarcane accumulate higher concentrations of GB under heat stress conditions, whereas rice, *Arabidopsis*, and mustard do not accumulate GB (Annunziata *et al.*, 2019). Thus, the exogenous application of GB increases the rice yield under heat stress conditions by promoting the activity of antioxidants which, in turn, protects the membrane, enzymes, and major molecules from the damaging effects of heat stress (Mohammed and Tarpley, 2009). The application of GB prevents the degradation of rubisco due to heat stress which, in turn, improves the photosynthetic efficiency and, consequently, the rice yield (Dionisio-Sese *et al.*, 2000).

Proline also accumulates in plants in response to heat stress and protects the plants from the damaging effects of heat stress. Proline protects the rubisco enzyme from degradation due to heat stress which, in turn, increases the overall photosynthetic efficiency and rice yield (Dionisio-Sese et al., 2000). Spermidine is also a critical osmoprotectant that plays a vital role in increasing the tolerance to different stresses, including heat stress (Liu *et al.*, 2015). Spermidine-induced tolerance to heat stress in rice is attributed to an increase in antioxidant, starch, and polyamine metabolism. Spermidine increases the expression of the starch synthesis enzyme, favouring an increase in starch accumulation (Tang *et al.*, 2018).

Moreover, spermidine reduces the hydrogen peroxide content in japonica rice by modulating the glutathione and glyoxalase systems (Mostofa *et al.*, 2014; Tang *et al.*, 2018). The application of spermidine also increase the grain yield and grain filling rate in rice by increasing antioxidant activity, photosynthetic activity, the efficiency of PS-II, and the sugar content and modulating starch and polyamine metabolism (Fu *et al.*, 2019). It is concluded that osmoprotectants are important contributing factor in heat stress tolerance in rice. These osmoprotectants can be used in different modified forms and significant heat tolerance can be achieved in rice. Their role can be studied by exposing rice under different heat stress conditions.

Breeding approaches for enhancing heat tolerance in rice

Phenotypic selection of tolerant cultivars

Developing breeding methods that promote HS tolerance in rice crops requires a proper understanding of HS tolerance mechanisms (Karwa *et al.*, 2020). Considerable and significant genotypic variation is present in rice cultivars subjected to HS, and the selection of heat-tolerant genotypes will ensure sustainable production under HS conditions (Prasad *et al.*, 2006; Shah *et al.*, 2011). Rice genotypes show varying responses to heat stress, and this increases the possibility of identifying heat-tolerant genotypes. With the changing climate, the selection of tolerant genotypes will become a greater focus. In a previous experiment, 1217 rice genotypes collected from different areas were tested for heat tolerance, and it was observed that only 2% of cultivars were heat tolerant under changing environments (Masuduzzaman *et al.*, 2016). Heat-tolerant genotypes should be investigated to identify the heat stress tolerance mechanism present in rice crop. A schematic display of increasing heat tolerance in rice using several factors and development of heat tolerant cultivars using breeding methods is provided in Figure 2 and Figure 3.

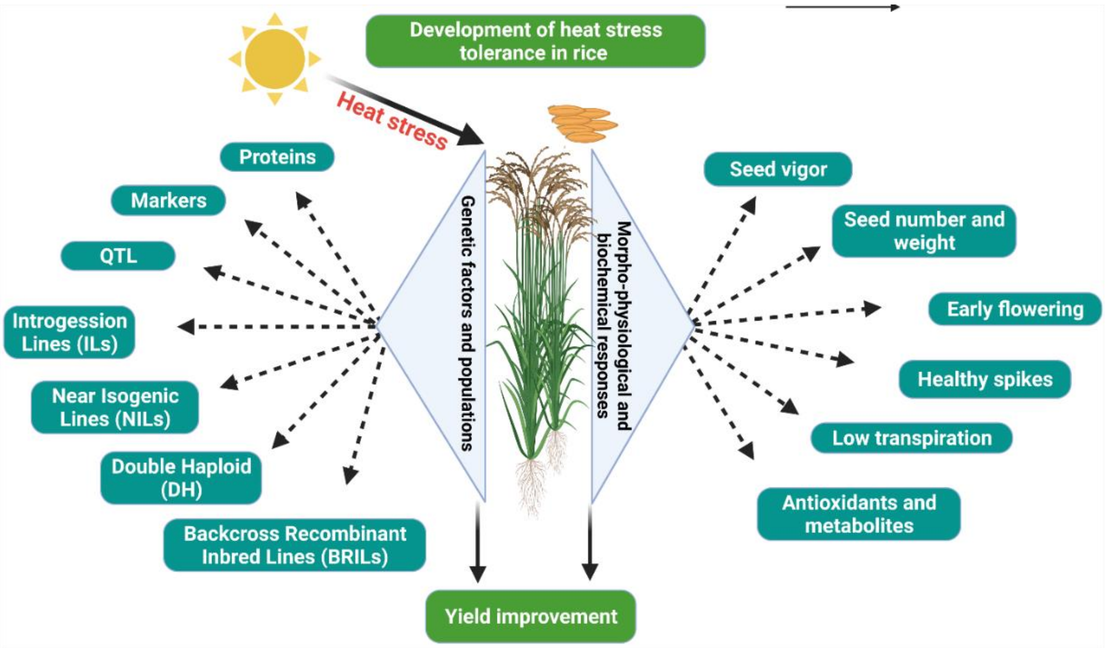

Figure 2. Development of heat-tolerant rice genotypes. The use of different genetic, phenotypic, physiological, and biochemical factors to enhance heat tolerance in rice. A complete graphical overview

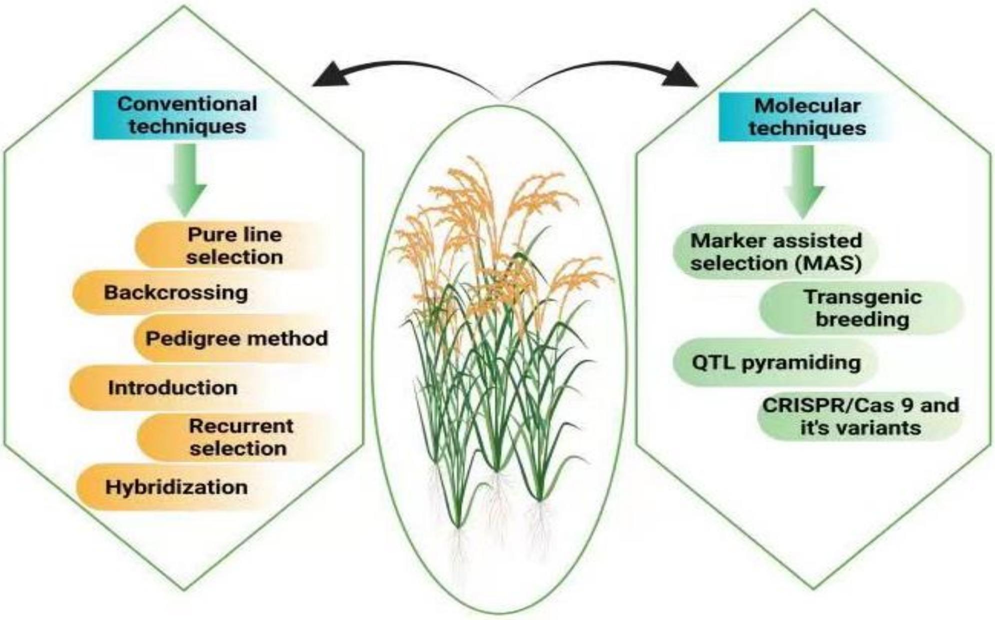

Figure 3. Diagrammatic representation of novel strategies used to improve the heat tolerance of rice crops. The development of heat-tolerant cultivars by traditional breeding practices and advanced molecular techniques can help to improve heat tolerance in rice crops

Loci with a putative quantitative trait confer heat tolerance in rice

QTL mapping is an effective technique that can be used to locate genomic regions controlling several traits (Rasheed *et al.*, 2020a, 2020b; Rasheed *et al.*, 2020; Rasheed *et al.*, 2021b). Multiple QTLs have been mapped for HS tolerance (Xu *et al.*, 2021), especially for rice flowerings (Ye *et al.*, 2012; Ye *et al.*, 2015a). Such markers can be used to initiate MAS for a pyramid of genes to promote the breeding of plants with greater HS tolerance (Cheng *et al.*, 2012; Ye *et al.*, 2015b). Nonetheless, before the use of these QTLs in MAS, the potential of subsequent populations to be used in large germplasm must be determined after initial mapping (Ye *et al.*, 2015a).

Nowadays, rice breeders use double haploid (DH), backcross inbred lines (BIL), and RIL to unfold the genetic backgrounds of HS-tolerant rice plants (Qingquan *et al.*, 2008; Tao *et al.*, 2008). A previous study used a set of introgression lines (ILs) developed from a cross of *Oryza officinalis* and Koshihikari. The lines showed earlier flowering and improvement in the spikelet fertility and yield/plant compared with late-flowering genotypes (Ishimaru *et al.*, 2010). Heat-stress tolerance is a polygenic feature governed by multiple genes that varies by stage and between plants species (Ashraf and Harris, 2005; Bohnert *et al.*, 2006). Due to the advancement of marker technology, identifying QTLs associated with heat tolerance is an important approach. QTL identification assists in unfolding genetic mechanisms and the cloning of QTL. Many QTLs have been identified in previous studies (Wang *et al.*, 2011; Xiao *et al.*, 2011). The majority of these QTL were identified in rice genotypes at the flowering stage. QTLs governing spikelet fertility and the yield/plant were mainly mapped on chromosomes, 1, 4, 10, and all 12 linkage groups (Qingquan *et al.*, 2008; Tao *et al.*, 2008). In a previous study, Zhao *et al.* (2016) evaluated chromosome segment substitution lines (CSSL) from Habataki (heat-tolerant) and Sasanishiki (heat-sensitive) cultivars. Two QTLs (*qSFht2* and *qSFht4.2*) correlated with spikelet fertility, and two (*qDFT3* and *qDFT10.1*) correlated with flowering time were mapped. *SL412* presented a considerably higher spikelet fertility level in Habakati than Sasanishiki, and 6 CSSL exhibited a high pollen detachment level.

Zhang *et al.* (2009) identified two SSR markers (RM3586 and RM3735) accountable for 3% and 17% of the difference in HS tolerance among plants. They recommended the exploitation of genetic loci using MAS to develop HS-tolerant cultivars. Jagadish *et al.* (2010) used the F_6 progeny of RIL and documented eight QTLs related to spikelet fertility in HS on dissimilar chromosomes. A QTL accountable for 18% of the phenotypic deviation in tolerance to heat stress was identified on chromosome 1. Xiao *et al.* (2011) used pollen sterility to indicate HS tolerance and recognized two QTLs (*qPF4* and *qPF6*) that improved pollen fertility. Ye *et al.* (2015a) identified several QTLs with a deviation in spikelet fertility in HS. In another investigation, Shanmugavadivel *et al.* (2017) crossed the heat-tolerant genotype (Nagina 22) with the heat-susceptible genotype (IR64) to investigate the QTL responsible for heat tolerance. Huang *et al.* (2012) recognized 32 novel loci linked to the flowering time. Lafarge *et al.* (2017) used the GWAS technique to identify the QTL associated with preserving spikelet fertility under high HS conditions. They selected 167 indica lines with 13,162 single nucleotide polymorphisms (SNPs). A total of 14 loci were linked with spikelet sterility, and 8 of these were consistent with previously identified QTLs. Genes at loci related to the fertility of spikelets were linked with the response of plants to HS conditions. N22 and some Indian and Taiwanese genotypes are active contributors of HS tolerance in rice (Lafarge *et al.*, 2017). Kushwah *et al.* (2021) identified a QTL *Qdg-01* for days to germination under heat stress using recombinant inbred lines population (RIL). A list of QTLs related to heat-stress tolerance is given in Table 2.

Table 2. QTLs associated with heat-stress tolerance in rice crops

Source	Trait	QTL	Chromosome	Reference
Rice	Pollen sterility	*qPF6*	6	(XIAO *et al.*, 2011)
Rice	Flowering stage	*qHTSF4*	4	(Ye *et al.*, 2012)
NILs	Flowering time	*qEMF3*	3	(Hirabayashi *et al.*, 2015)
Giza 178	Flowering stage	*qHTSF4*	4	(Ye et al., 2015a)
Habataki, Sasanishiki	Spikelet fertility	*qSFht2*	2	(Zhao *et al.*, 2016)
Habataki, Sasanishiki	Spikelet fertility	*qSFht4.2*	4	(Zhao *et al.*, 2016)
N22 and IR64	Root length	*rlht5.1*	5	(Kilasi *et al.*, 2018)
Rice	Heat tolerance	*rMQTL9.1*	9	(Raza *et al.*, 2020)
127 RILs	Spikelet's fertility	*qSF1*	1	(Ravikiran *et al.*, 2020)
Oryza rufipogon	Booting stage	*qHTB1-1*	1	(Cao *et al.*, 2020)
Takanari and IR64	Spikelet fertility	*qHTSF4.1*	4	(Takai *et al.*, 2020)
IR64/N22	Heat tolerance	*qSSPF10* and *qHT6*	10,6	(Withanawasam *et al.*, 2021)
F2:3 Population	Heat tolerance	*TT1-2*	1	(Yan *et al.*, 2021a)
SSSLs	Grain chalkiness	*qPGC9*	9	(Yang *et al.*, 2021)
Uma, N22	Spikelet fertility	*qSF3*	3	(Waghmare *et al.*, 2021)
HHZ, 9311	Flowering stage	*qHTT8*	8	(Chen *et al.*, 2021)
Rice	Heat stress	*qSSR6-1*	1	(Nguyen *et al.*, 2021)
Rice	Spikelet's fertility	*qHTSF4*	4	(Jin *et al.*, 2021)
RILs	Days to germination	*Qdg-01*	1	(Kushwah *et al.*, 2021)

Development of transgenic rice tolerant cultivars

Heat shock proteins are synthesized by many genetic factors (Buu *et al.*, 2021) that switch on when exposed to HS and play critical roles in the recovery of plants after HS (Liu *et al.*, 2006; Nakamoto and Hiyama, 1999). Alterations in transgenic rice associated with HSPs have the potential to increase HS tolerance in rice (Zou *et al.*, 2011). The genetic enhancement of rice cultivars is a reliable approach to sustain rice production under a changing environment (Zou *et al.*, 2011). Heat tolerance in rice using the transgenic approach has rarely been reported. The overexpression of HSPs in rice has been associated with heat tolerance (Katiyar-Agarwal *et al.*, 2003). HSPs improve HS tolerance in mutant and transgenic rice species (Katiyar-Agarwal *et al.*, 2003). Earlier, Katiyar-Agarwal *et al.* (2003) used *Arabidopsis thaliana* and transformed HSP (*AtHSP101* cDNA) into the indica variety of rice (Pusa basmati 1). Compared with typical plants, the existence and development of T2 lines were enriched with proteinaceous material under HS.

In a previous study, a transgenic rice variety (Hoshinoyume) showed overexpression of HSP (*sHSP17.7*), which was confirmed to be associated with greater tolerance to HS (Murakami *et al.*, 2004). Qi *et al.* (2011) described that, in transgenic rice cultivars, the overexpression of mitochondrial genetic factors associated with *mtHsp70* enhanced HS by decreasing programmed cell death, improving the stability of the mitochondrial membrane, and inhibiting ROS production. *WRKY* genetic factors are recognized as the encoding for many transcription factors, contributing to numerous abiotic factors. Wu *et al.* (2009) merged cDNA from *OsWRKY11* with the *HSP101* promoter and transferred it to rice d plants grown under HS conditions. The *WRKY* genes e overexpressed in rice were associated with improved HS tolerance and growth and growth traits under HS. Proteomic investigations can help us to understand the molecular foundations of HS tolerance in rice plants. Lee *et al.* (2007) examined the proteomes of rice leaves grown under HS conditions and identified nearly 73 low molecular mass proteins, and these were mostly linked to HSPs. In conclusion transgenic cultivars can play significant roles in increasing HS tolerance in rice crops. However, future studies must be conducted to develop cultivars and tested these cultivars in a wide range of field conditions to ensure their availability across the globe. List of genes related to heat tolerance in transgenic rice and normal rice is given in Tables 3 and 4.

Table 3. Candidate genes identified in transgenic rice associated with heat tolerance

Gene	Crop	Source plant	Mechanism of action	Reference
sHSP17.7	Hoshinoyume	Rice	CaMV 35S promoter, improved heat stress	(Sato and Yokoya, 2008)
OsWRKY11	Sasanishiki	Rice	The promoter of *HSP101*, improved dehydration tolerance	(Wu *et al.*, 2009)
PHT3	Rice	Rice	Improved heat tolerance	(Jia *et al.*, 2015)
DPB3-1	Rice	Arabidopsis	Overexpression of DPB3, upregulation of stress-related genes	(Sato *et al.*, 2016)
rcbs	Rice	*Oryza australiensis*	Due to overexpression of the yield	(Scafaro *et al.*, 2018)
UGT73B3	Rice	Rice	Improved heat tolerance	(Lee and Bailey-Serres, 2019)
OsBiP2	Rice	Rice	Improved dehydration tolerance	(Raza *et al.*, 2020)
OsNTL3	Rice	Rice	NAC transcription factor improved thermal tolerance in rice	(Liu *et al.*, 2020b)
AtPLC9	Rice	Rice	Expression of transcription factors	(Liu *et al.*, 2020b)
OsWRKY	Rice	Rice	Improved thermal tolerance	(Jeyasri *et al.*, 2021)
OsIAA13, Os IAA20	Rice	Rice	Improved heat tolerance	(Sharma *et al.*, 2021)
LOC_Os08g 07010	Rice	Rice	Decreased extreme heat stress	(Chen *et al.*, 2021)

Table 4. Important genes associated with heat tolerance in rice crops

Gene	Function	Protein	Reference
SBPase	Confers heat tolerance by overexpression of *SBPase* and increases photosynthesis	*SBPase*	(Feng *et al.*, 2007)
mtHsp70	Overexpression of *mthsp70* overwhelmed cell death and ROS production	*HSP70*	(Qi *et al.*, 2011)
ZFP	Enhances HS tolerance during the seedling stage	Protein	(Wei *et al.*, 2013)
OsLea14-A	Confers stress tolerance		(Hu *et al.*, 2019)
MTH1745 (MtPDI)	Increase heat stress tolerance	Isomerase-like protein	(Wang *et al.*, 2019a)
OsPAL	Increases heat stress tolerance	*OsProDH*	(Akhter *et al.*, 2019)
HsfA2a	Controls heat tolerance	Heat shock transcription factor	(Malumpong *et al.*, 2019)
OsGSK1	Improves heat tolerance		(Wahab *et al.*, 2020)
TT1	Improves heat tolerance		(Wahab *et al.*, 2020)
OsHSP20	Improve heat stress tolerance		(Guo *et al.*, 2020a)
eIF4A1	Enhances temperature stress		(Singha *et al.*, 2020)
OsProDH	Proline overproduction	*OsProDH*	(Guo *et al.*, 2020b)
PSL50	Promotes heat tolerance	*OsProDH*	(He *et al.*, 2020)
OsNTL3	Enhances heat tolerance	*NAC transcription factor*	(Liu *et al.*, 2020b)

OsBiP2, OsMed37_1	Controls heat tolerance	=	(Raza *et al.*, 2020)
OsHTAS	Controls heat tolerance		(Jan *et al.*, 2021)

Proteomics and transcriptomics approaches for increasing heat tolerance in rice

Comprehensive proteomic surveys of metabolic enzymes, storage and structural proteins, and different allergens found in rice grains have been done using two-dimensional polyacrylamide gel electrophoresis (2D-PAGE) and gel-free-based shotgun technologies (Koller *et al.*, 2002; Lee and Koh, 2011; Lin *et al.*, 2005). Lee and Koh (2011) identified 4172 non-redundant proteins with a range of pI (pH 2.9-12.6) and molecular weights (5.2-611 kDa) in developing and maturing grains of rice. The analysis of the expression of different protein groups linked with diverse functional categories showed dynamic changes in metabolism during rice grain development. A switch from carbon metabolism to alcohol fermentation is imperative for the synthesis and accumulation of starch during the development process (Xu *et al.*, 2008). It was also noticed that proteins involved in the citric acid cycle, lipid metabolism, glycolysis, and proteolysis were accumulated more in mature grains than developing grains (Lee and Koh, 2011). Proteomic studies also revealed that all classes of storage proteins increased considerably at the early ripening stages, whereas the polyamine concentration decreased considerably at the maturation and desiccation stages (Lin *et al.*, 2010). Moreover, Li *et al.* (2011) noted that pullulanase (PUL) was downregulated, whereas pyruvate phosphate dikinase (PPDK) was upregulated in a grain filling study. Thus, the proteomic approach can help us improve protein expression in rice to increase heat tolerance.

Transcriptomics has been widely used to study the molecular mechanisms associated with heat tolerance in wheat, tomato, and potato (Bita *et al.*, 2011; Ginzberg *et al.*, 2009; Qin *et al.*, 2008) and different pathways and genes have been identified as being heat-responsive. In rice crops, few transcriptomic analyses have been conducted to determine the heat response at the flowering stage (Endo *et al.*, 2009; Zhang *et al.*, 2013b). Most of these studies were conducted on spikelets and flag leaves, with limited studies conducted on anthers or pistils (González-Schain *et al.*, 2016; Li *et al.*, 2015). Liu *et al.* (2020a) found a stable anther structure in rice line SDWG005 under heat stress conditions. Their transcriptomic analysis found 3559 differentially expressed genes in anthers of SDWG005 plants under heat stress at the anthesis stage. They also stated that the agmatine-coumarin-acyltransferase gene is involved in heat tolerance in SDWG005 plants (Liu *et al.*, 2020a).

Mutation for improving heat tolerance in rice

A mutation is an essential tool that can create genetic variability (Mba *et al.*, 2010). Over the last century, physical mutagens, including ultraviolet rays, X-ray and chemical rays, and chemical mutagens such as N-methyl-N-nitrosourea (MNU), sodium azide, hydrogen fluoride (HF), methyl methanesulfonate (MMS), and ethyl methanesulfonate (EMS), have been used to create mutations in plants (Krishnan *et al.*, 2009).

The EMS-induced mutation is considered very effective, and it is commonly used in a diverse range of breeding programs to develop improved crop genotypes. The application of EMS improves agronomic traits and the rate of photosynthesis in rice leaves while reduces the concentration of mesophyll interveinal cells (Feldman *et al.*, 2017; Feldman *et al.*, 2014). Moreover, MNU is another important mutagen that is mainly used to create mutations in rice. The application of MNU is a more efficient way to create mutations in developing rice cells than in seeds (Satoh *et al.*, 2010). MNU-induced mutagenesis affects various physiological processes and leads to discovering gene functions and increased genetic variability in rice (Satoh *et al.*, 2010). Therefore, mutagens can be used to change the genetic makeup of rice to develop genotypes with desired traits.

Role of CRISPR/Cas9 in improving the heat tolerance in rice

Conventional breeding techniques also bring undesirable genes along with desirable genes (Rasheed *et al.*, 2021c). These techniques are time-consuming and hence they are not suitable to increase the rice production for rapidly growing world population. In addition, hybridization is possible among two plants of the same species, limiting new traits and genes (Jiang *et al.*, 2012). Therefore, in these scenarios, the novel genome editing techniques (GET) can tackle the limitations of conventional breeding by improving the desirable traits in any species in a short time (Jiang *et al.*, 2012). Nonetheless, information related to gene sequencing, genes function, and QTL responsible for traits of interest is vital for GET application. The application of GET modifies the particular gene of the desired trait by DNA cutting via target-specific nucleases. Different site-specific endonucleases (SSE), i.e., zinc finger nucleases, transcription activator-like effector nucleases introduced in the last decade, have been widely used in gene editing tools (Chen and Gao, 2014). Different studies were conducted in which several genes were knock out using CRISPR/Cas9 technique to improve heat stress tolerance in rice. The CRISPR/Cas based editing tool to edit genes responsible for heat tolerance has been widely used in rice (Wang *et al.*, 2020). CRISPR/Cas9 application can help to develop the heat-tolerant cultivars of rice by changing plant and panicle architecture, leaf morphology, and ABA signalling pathway by modifying desired genes (Jiang *et al.*, 2012). The knockout of *OsNAC006* gene significantly increased heat stress tolerance in rice (Wang *et al.*, 2020). Likewise in another study, *OsProDH* gene was mutated using CRISPR/Cas9 technique and it was concluded that this gene negatively regulates the heat tolerance in rice by scavenging of ROS. Recent advances in GET involve developing a clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein (Cas) system. Multiple Cas proteins, such as Cas8, Cas9, Cas12a, or Cpf1 are identified, used in genome editing by CRISPR technology to improve the diverse traits in plants (Cebrian-Serrano and Davies, 2017; Naeem *et al.*, 2020). CRISPR/Cas9 is considered as an easier, reliable, and efficient system used for improving stress resistance, grain yield, herbicide resistance, and product quality in many crops such as sativa, barley, maize, cucumber, soybean, wheat, and rice (Komor *et al.*, 2016).

Conclusions

As a complex polygenic trait, heat stress tolerance is difficult to improve by using conventional breeding methods. Genetic factors which are governing the heat stress tolerance in rice and least influenced by the environment can be explored to improve heat stress tolerance in rice. Cultivars with strong and stable genetic makeups can maintain a higher rate of spikelet fertility, early flowering, and a higher yield under frequent heat episodes. The complex genetic architecture of this polygenic characteristic has still not been fully explored. Investigations are underway to detect the roles of morphological, physiological and biochemical features in sustainable rice production under exposure to heatwaves. Integrating several molecular techniques, including genomics, proteomics, and transcriptomics, is critical to develop highly heat-tolerant genotypes in rice. The high yielding genotypes are specially used because they can maintain high yield under heat stress. Hormonal applications significantly increased heat stress tolerance in rice. QTL pyramiding technique is very effective to transfer multiple heat tolerant QTL in genotypes and we can bring durable tolerance in rice genotypes. Hence, we have concluded that there are several factors needed to study to improve heat stress tolerance in rice. The novel breeding techniques like improved hybridization and molecular breeding methods can be effectively used to enhance heat stress tolerance in rice. The CRISPR/Cas9 and its variants need to use to edit targeted gene in rice responsible for heat stress tolerance in rice.

A recent period of extreme heat stress had damaging effects on crop production, and it is expected that this situation will continue to occur in the near future. This will threaten the global food supply chain. To overcome this and sustain rice production, effective management strategies must be implemented, and tolerant rice cultivars must be produced. We must improve the tolerance of rice to heat stress at the physiological, molecular, and biochemical levels through the development of tolerant cultivars to maintain the quality and quantity of rice across changing environments. Heat stress affects grain filling and pollen fertility, disturb plant water relation, lead to lipid peroxidation, and cause oxidative stress in rice. Plant hormones and inorganic osmolytes can induce an acclimation response in plants. The use of these hormones and osmolytes is an excellent solution to reduce the consequences of heat stress. Few studies have described the roles of these regulators in plant responses to heat stress, and further studies are needed. In the era of modernized genetics, high throughput phenotypic, and genotyping approaches like GWAS to identify phenotypic diversity can contribute to the development of heat-tolerant genotypes. For unique trait such as heat tolerance, the recent development of advanced gene-editing technique, like CRISPR-Cas9 will further speed up crop improvement.

Authors' Contributions

AR conceptualized and prepared the draft; MFS, MN, AM, MRA, MAA, MA, MAE, EHE, and MA, and MUH reviewed the manuscript; MB improved the scientific figures; ZU and HL supervised the study. All authors read and approved the manuscript. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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