

Review Article

Effect of Heat Stress on Rice and its management

ABSTRACT

Rice is a major staple food, consumed by more than half of the world's population and providing 20% of calories consumed worldwide. However, rice production is under serious threat due to rapid increase in the earth's rising temperatures. Heat stress(HS) destroys the physiological processes like seed germination, photosynthesis, respiration and plant growth. HS also has detrimental effects on the plant root system that provides water uptake, nutrient uptake and supports other parts of the plant, leading to disruption of root growth and development, as well as decrease in shoot and root fresh, and dry weight. As a result there is a drastic reduction in the yield and quality of the grain. HS affects all the growth stages of rice. However, the reproductive phase of rice is more sensitive to HS than other stages. Most agronomic management approaches concentrate on early sowing, site-specific cropping and irrigation system changes, and adoption of a late or early maturing cultivar to avoid high temperatures during grain filling to combat HS. Growth regulators such as cytokines, salicylic acid, and ethylene precursors can also be used to treat rice plants suffering from HS related damage such as pollen abortion, decreased spikelet's per panicle and kernel weight, and low seed-setting rate. In numerous rice cultivars, exogenous treatment of spermidine boosted photosynthetic and antioxidant capability and partially reduced the yield penalty brought on by HS. Developing germplasm with higher tolerance to climate-induced stresses through breeding is a sound climate change or abiotic stresses adaptation strategy. Higher thermo-tolerance may be induced by choosing cultivars that flower in the early morning before the temperature rises and have larger anthers with long basal pores, higher basal dehiscence, and pollen viability. Breeding rice varieties tolerance to high temperature has so far received little attention as compared to other abiotic stresses like drought and salinity. Therefore, there is an urgent need to explore the breeding aspect for heat tolerance in rice varieties for better management of loss due to heat stress.

Please structure your abstract in the format below:

- Introduction. This is the first part of the abstract, must be clear and concise.
- Research significance/problem statement. It has been stated
 - Methodology: Please elaborate ?
- Results:
- Conclusions sometimes with recommendations:

KEYWORDS: *Thermo-tolerance, Heat shock proteins, Quantitative trait loci, Reactive oxygen species.*

ABBREVIATION:

Comment [R1]: The topic needs the different kinds of question words to formulate a theme in your research topic.

- Who?
- What?
- Why?
- Where?
- When?

It is too broad at this state, the topic needs to highlight the research case study area.

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HS - Heat Stress, e[CO₂] - Elevated carbon dioxide, FATI - Free Air Temperature Increment, TGT - Temperature Gradient Tunnel, HSPs - Heat shock proteins, ROS - Reactive oxygen species, QTLs - Quantitative trait loci, IWP - Improved White Ponni.

1. INTRODUCTION:

Rice is a major staple food, consumed by more than half of the world's population providing 20% of calories consumed worldwide, and up to 80% of caloric necessities in Asia [1]. With each 1°C rise in minimum temperature, there is a 10% loss in yields [2]. In addition to the detrimental effects of heat stress (HS), heat can also damage the quality of the grain, resulting in considerable economic losses. Due to environmental constraints, it is estimated that rice yield will decline by 41% by the end of this century [3]. Therefore, the global rice production growth rate must be increased 1.0–1.2% annually to fulfill the requirements of a rapid population growth [4].

Carbon dioxide and temperature are major drivers of climate change affecting global food production [5]. HS destroys rice crop physiological processes like photosynthesis, respiration, leaf temperature, and plant growth. Higher temperatures can be catastrophic to seed germination and result in death of rice plants at the seedling stage. HS also has detrimental effects on the plant root system that provides water uptake, nutrient uptake and supports other parts of the plant, leading to disruption of root growth and development, as well as decrease in shoot and root fresh, and dry weight [6]. The chlorophyll content is the primary key component for photosynthesis [7]. It is drastically affected by high temperature at the vegetative stage. Elevated temperature induces cell membrane injury [8], which can be determined by releasing damaged cells' electrolyte leakage [9]. Also, the electrolyte leakage production rate is directly correlated with the increment of high temperature and its duration [10].

Elevated [CO₂] could enhance rice yield through increased photosynthesis, improved water use efficiency and lower photo-respiratory losses. However, competing energy requirement of carbon and nitrogen assimilation in plants leads to a higher tissue C: N ratio under e[CO₂], decreasing the protein content of grains and other associated quality parameters in rice [11]. e[CO₂] leads to photosynthetic carbon gain and enhanced carbohydrate metabolism enzymatic activity within the source (leaf) tissue under non-stress conditions leading to higher non-structural carbohydrate (NSC) accumulation in sink (seeds) among crop plants [12]. Interestingly, photosynthesis and net primary production under e[CO₂] is directly associated with sink efficiency in utilizing or storing the additional NSC, which could otherwise result in photosynthetic acclimation in the source tissue [13]. Hence, cultivars with enhanced sink size and strength to store or utilize photo-assimilate could benefit under e[CO₂] by minimizing photosynthetic acclimation and maintaining higher leaf level.

Conversely, HS during reproductive and grain filling stage is documented to reduce rice yield by reducing the proportion of fertile spikelets [14], shorter grain filling period [15] and loss of sink activity [16]. Additionally, leaf senescence, resulting in net photosynthesis reduction and lower sucrose-starch conversion enzymatic activity under heat stress reduces final grain weight in rice [15].

2. EFFECTS OF HEAT STRESS ON DIFFERENT GROWTH STAGES OF RICE

The optimum temperature for normal development of rice ranges from 27 to 32 °C. High temperature affects majority of the growth stages of rice, i.e. from vegetative to grain filling stage (Figure 1). The developmental stage at which the plant is exposed to HS determines the severity of the possible damage to the crop.

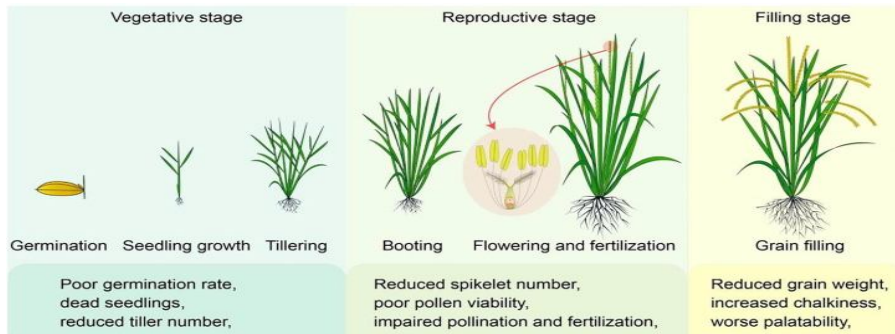


Figure 1: Effect of heat stress in different stages of Rice [17]

2.1. VEGETATIVE STAGE

The primary determinants of seedling vigour are germination capacity and early seedling growth. Prolonged elevated temperature reduces seed germination potential, leading to poor germination rate and seedling vigor [18]. The optimum growth temperature of rice at the seedling stage is 25-28°C. Rice can withstand temperatures as high as 35/25°C during the vegetative stage (day/night temperature regime). Temperature beyond this critical limit could reduce plant height, number of tillers and total dry matter accumulation. At the tillering stage, plants exposed to HS exhibit a variety of morphological symptoms, including wilting, leaf curling and yellowing, and decreased tiller number and biomass [19].

In a study, rice was exposed to 3.6 and 7.0°C higher temperatures than ambient in a temperature gradient chamber. It was observed that photosynthesis was reduced by 11.2-35.6%, respectively from heading to middle ripening stage [20]. The decline in photosynthesis is due to the structural changes in the organization of thylakoid and more particularly due to loss of stacking of grana in the chloroplast [21]. Significant reduction in growth duration, leaf area index, biomass, yield, and harvest indices were observed in rice plants exposed to HS in the free air temperature increment (FATI) chamber and temperature gradient tunnel (TGT). In contrast, significant increases in spikelet sterility and stability indices were observed [22]. HS has a more significant impact on tiller and panicle number in *japonica* than in *indica* rice. Tiller number under HS is often used as a marker for the selection of thermo-tolerant rice cultivars.

Comment [R2]: This is important as described in the topic, you need to narrow your study to a specific geographical area. This broad topic is not applicable to all environments. Please state your study area. If it is a literature review, you can also state the geographical area of the literature.

2.2. REPRODUCTIVE STAGE

The reproductive phase of rice is more sensitive to HS than the vegetative stage [23]. The effects of HS include stunted panicle start and spikelet development, distorted floral organs, and decreased spikelet size and quantity. Spikelet reduction is caused due to degeneration of spikelets at the tops of panicles [24]. HS during anther development, particularly during the pollen mother cell meiosis stage, causes the tapetal cells to prematurely degrade and disintegrate, impairing the microspores' ability to obtain nutrients and the development of the pollen wall, and ultimately leading to pollen grain abortion [25].

Anthesis is the most sensitive to high temperature during reproductive stage followed by microgametogenesis [22]. High spikelet sterility in rice can result from temperatures more than 35°C during anthesis and continuing for longer than an hour. There was a significant decrease in diameter and length of pollen tube with

an increase in temperature, resulting in poor pollen grain germination. Therefore, the male reproductive system has been targeted to increase tolerance to warmer climates because it is mostly responsible for spikelet sterility under HS. HS during anthesis leads to an irreversible effect with a reduction in panicle dry weight even with subsequent environmental improvement.

Reduction in pollen viability by 78.8% and seed-setting rate by 48.5% were observed when rice plants were subjected to HS (40°C day/30°C night) at the pollen mother cell meiosis stage for 10 days in comparison with the values under normal conditions (30°C day/24°C night) [26].

2.3. RIPENING STAGE

According to Sreenivasulu *et al.* (2015) [27], the grain filling stage marks the end of crop plant growth and development as well as the beginning of the transport and synthesis of lipids, proteins, and carbohydrates in seeds. HS at grain filling stage reduces grain yield and quality due to the adverse effect of high temperature on cellular and developmental process during ripening stage. When rice is exposed to high temperatures during the grain filling stage, common impacts include decreased grain weight, reduced grain filling, a larger percentage of white chalky rice, and milky white rice [28]. Additionally, rising temperatures significantly reduce grain size and amylase content [29]. The test weight, dry matter accumulation and grain filling percentage are dramatically reduced by the post anthesis high temperature stress resulting in lower yield [30].

3. APPROACHES TO IMPROVE HEAT TOLERANCE IN RICE

3.1. AGRONOMIC MANAGEMENT

Agronomic management techniques provide favorable condition for the crop plants by minimizing the damages caused by warm temperatures. Most agronomic management approaches concentrate on early rice sowing, site-specific cropping and irrigation system changes, and adoption of a late or early maturing cultivar to avoid high temperatures during grain filling to combat HS. The time of the sowing has a significant impact on how the rice plant responds to different temperature regimes [31]. A simulation model study was conducted by Setiyono *et al.* (2018) [32] in rice fields in two districts of Andhra Pradesh where the late-planted rice field suffered high yield losses due to the occurrence of heat stress at the reproductive stage and heat-induced spikelet sterility. They therefore proposed that early planting of rice could help to mitigate the output losses in these places.

According to some reports, delaying planting to prevent heat stress could reduce the detrimental effects of heat stress caused by global warming and the degradation of rice grain quality. According to Zhu *et al.* (2013) [33], adjusting the sowing time is an effective management tactic for preventing heat stress. They studied the impact of high temperatures under various sowing times on the grain quality of different rice genotypes. However, the adjustment of sowing time is difficult, as it also affects the preceding crop and farmers have to plan about the cropping pattern of the whole year [34].

3.2. CROP CANOPY AND ORIENTATION

Tolerance to extreme temperature stress can be significantly influenced by plant architecture. Compared to traditional varieties, varieties that have panicles surrounded by plant leaf canopy are greatly benefited

by combined transpiration cooling during the sensitive anthesis period. Thus, the improvement and introduction of semi-dwarf types with better canopy architecture will aid in coping with the rise in temperature. The reduced height may also enhance resistance to lodging, thus giving more resilience to the crop against indirect stresses such as floods, which will become more frequent due to global warming [3].

Rice genotypes can either escape or avoid high temperatures during anthesis, by heading during the cooler periods of the season, altered flowering pattern or by increase in transpiration cooling of the canopy [35]. When rice plants are exposed to high temperatures during critical stages, they can avoid heat by maintaining their microclimate temperature below critical levels by efficient transpiration cooling.

3.3. USE OF GROWTH REGULATORS, PROTECTANTS AND CHEMICALS

Growth regulators such cytokines, salicylic acid, and ethylene precursors can be used to treat rice plants suffering from HS related damage such as pollen abortion, decreased spikelet's per panicle and kernel weight, and low seed-setting rate. Auxin plays a role in maintaining spikelet fertility and a reduced level of active IAA could cause pollen abortion, which is a common reason for male sterility [34]. Under high temperature, the level of auxin reduced, and IAA and GAs reduced more in heat susceptible cultivar than tolerant genotype. The effect of spraying auxin on the elongation of pollen tubes of heat-tolerant and sensitive genotypes was investigated by Tang *et al.* (2008) [36]. They reported that spraying naphthalene acetic acid reduced and reversed the spikelet sterility of both the heat susceptible and tolerant genotypes of rice by inhibiting the reduction of pollen tube growth.

The accumulation of osmoprotectants is an essential adaptive response of plants to many abiotic stressors, such as high temperatures. Glycine betaine is a significant compatible solute that accumulates in plants at high temperatures and promotes heat tolerance by preventing the heat-induced degradation of other enzymes including citrate synthase and rubisco [34]. The addition of glycine betaine reduces the thermal degradation of the rubisco enzyme in the leaves of rice seedlings under temperature stress of 35 to 45°C. The percentage of pollen germination and spikelet fertility in rice are both increased by glycine betaine. Under high-temperature stress, proline prevents the thermal degradation of the rubisco enzyme in rice seedlings.

In numerous rice cultivars, exogenous treatment of spermidine boosted photosynthetic and antioxidant capability and partially reduced the yield penalty brought on by HS [37]. The key mechanisms of spermidine induced heat tolerance include the induction of antioxidative enzyme activity and starch and polyamine metabolism. Starch synthesis enzymes expression was increased in rice seeds after the exogenous application of spermidine [34]. Spermidine treated plants had reduced concentrations of propionaldehyde and hydrogen peroxide. The exogenous application of spermidine also modulates glutathione and glyoxalase system levels. A mist spray treatment applied during the flowering season drastically lowers the temperature in the rice field, delays leaf senescence, and boosts the activity of antioxidant enzymes, reducing yield loss due to HS [38].

3.4. GENETIC IMPROVEMENT FOR HEAT TOLERANCE

Plants' ability to adapt to and survive heat stress can be greatly influenced by the rapid accumulation of Heat shock proteins (HSPs) in their sense organs. These HSPs can safeguard the cell's metabolic machinery and assist in coping with HS by enhancing photosynthesis, assimilation partitioning, nutrient and water use efficiency,

and membrane thermal stability. HSPs and overall plant heat tolerance have been shown to be positively correlated in several plant species. Also, a relationship between HSPs and reactive oxygen species (ROS) has been proposed which corroborates the hypothesis that during the course of evolution plants were able to suppress ROS and now plants are using these ROS as signaling molecules to induce HSPs [3].

Multiple genes are involved in the synthesis of HSP, which switched on under exposure of high temperature and have an essential role in recovery from heat stress. Manipulations of HSPs in transgenic plants have the potential to improve heat stress tolerance and they have a significant impact on the exploitation of the inherent genetic potential of rice. Katiyar-Agarwal *et al.* (2003) [39] introduced HSP101 in the *indica* rice variety Pusa Basmati1 from *Arabidopsis thaliana* cDNA, creating transgenic rice. Overall, this transgenic rice demonstrated typical growth and development, and greatly outperformed untransformed rice in terms of recovering from heat stress. Similarly, the over-expression of rice OsHSF7 gene in *A. thaliana* has very recently been reported to increase the thermo-tolerance by increasing the proportion of plants surviving 42°C for 16 hrs, from 0.22 to 0.52 [40]. Qi *et al.* (2011) [41] reported that transgenic rice overexpressing mitochondrial gene for mtHsp70 showed higher heat tolerance, as indicated by less program cell death by recovering mitochondrial membrane potential and preventing ROS.

3.5. BREEDING APPROACH FOR HEAT TOLERANCE

Developing germplasm with higher tolerance to climate-induced stresses through breeding is a sound climate change or abiotic stresses adaptation strategy. Breeding rice varieties tolerance to high temperature has so far received little attention as compared to other abiotic stresses like drought and salinity. High temperature tolerance of rice has only been treated within region specific breeding programmes with limited success. Cultivars that can withstand environmental shocks while maintaining economic output should be prioritized in order to successfully increase agricultural productivity in a stressful environment [21]. Therefore, genes or quantitative trait loci (QTL) underlying heat tolerance or avoidance need to be identified and then combined with traits such as high yield, resistance to multiple stresses acceptable grain quality and many others [35].

Heat tolerance is controlled by one major gene and several genes. The identification of quantitative trait loci (QTLs) is a promising approach to dissect the genetic basis of heat tolerance [42]. By using genetic resources with heat tolerance at flowering, QTL mapping studies for heat tolerance (spikelet fertility) have been conducted on various rice populations at booting and flowering stages [14]. Many QTL responsible for thermo-tolerance at various developmental stages of seedling, booting, flowering, and grain filling have been identified and validated. Numerous QTL have been found and confirmed to be involved in thermo-tolerance at many developmental stages, including seedling, booting, flowering, and grain filling. The most promising QTLs for heat tolerance across various genetic origins and regions have been found on chromosomes 1 and 4 among the numerous QTLs discovered [14]. Different populations of the heat-tolerant rice varieties 996, N22, Milyang23, and Giza178 were found to carry the heat-tolerant QTL (qHTSF4.1) on chromosome 4 [43]. OsHTAS, a dominant major QTL on chromosome 9, has been cloned and verified, and confers tolerance to 48°C temperatures in rice seedlings [46]. Kilasi *et al.* (2018) [19] detected numerous QTL for seedling growth under HS and identified one QTL, RLHT5.1, for root length under HS with phenotypic contribution up to 20.4%.

Through marker-assisted breeding, the heat-tolerant QTLs qHTSF1.1 and qHTSF4.1 [46] from Nagina 22

were introgressed into the rice variety known as Improved White Ponni (IWP) to boost IWP's heat tolerance. The progenies harboring both *qHTSF1.1* and *qHTSF4.1* showed higher fertility percentages under high-temperature stress at the flowering stage. The results confirmed that these QTLs were responsible for maintaining membrane integrity and yield under elevated-temperature conditions. Therefore the aim of thermo-tolerance breeding includes identification and validation of thermo-tolerance QTL with stable effects across various genetic backgrounds and settings, as well as pyramiding of these non-allelic QTL.

4. CONCLUSION

With the increase in global temperature, there will be more instances of unexpectedly high temperatures, which might put the food supply in danger. Thus, by identifying the management strategies, choosing tolerant genotypes, and breeding suitable rice cultivars, losses in rice production might be prevented. Therefore, it is necessary to understand the physiological and genetic mechanisms and create heat-tolerant rice varieties to increase rice production quality, quantity, and stability under a variety of environmental conditions. The yield losses will also be lessened through the adaptation of resistant genotypes of rice cultivars. However, care should be taken to ensure that increasing plant tolerance does not negatively impact the yield or the quality features. High temperatures negatively impact all stages of rice growth, but the anthesis stage is the most vulnerable because even a small rise in temperature can have a big influence on yield. In addition to these effects, high temperatures also cause pollen to become sterile, assimilate partitioning to be less efficient, grain filling to be affected, structural changes to cell organelles, oxidative stress, lipid peroxidation of cell membranes, disruption of leaf water relations, and a decrease in photosynthesis. Plant hormones and exogenous osmoprotectants are applied together to trigger a short-term acclimatization response. When used at a crucial growth stage, such priming or exogenous applications have been demonstrated to be effective for reducing the consequences of high temperature stress. Only a few reports on growth regulators are currently available, thus further research is needed to determine the effectiveness of utilizing these regulators in heat stress situations. Now, a variety of methodologies, including molecular methods like genomics, proteomics, and transcriptomics, are necessary for the adaptation and implementation of a variety of contemporary methods, including the use of climatology tools and GIS. Trait dependence and variation must be carefully taken into account because a specific genotype is only tolerant to certain circumstances.

REFERENCES:

1. Mahajan G, Sekhon NK, Singh N, Kaur R, Sidhu AS. Yield and nitrogen use efficiency of aromatic rice cultivars in response to nitrogen fertilizer. *J New Seeds*.2010; 11:356–368.
2. Peng S, Huang J, Sheehy JE, Laza RC, Visperas RM, Zhong X, Centeno GS, Khush GS, Cassman KG. Rice yields decline with higher night temperature from global warming. *Proceedings of the National Academy of Sciences*. 2004; 101(27):9971-5.
3. Shah F, Huang J, Cui K, Nie L, Shah T, Chen C, Wang K. Impact of high-temperature stress on rice plant and its traits related to tolerance. *The Journal of Agricultural Science*. 2011; 149(5):545-56.
4. Ricepedia. Food security - Ricepedia.2020; <http://ricepedia.org/challenges/food-security>.
5. Chaturvedi AK, Bahuguna RN, Shah D, Pal M, Jagadish SV. High temperature stress during flowering and grain

- filling offsets beneficial impact of elevated CO₂ on assimilate partitioning and sink-strength in rice. *Scientific Reports*. 2017; 15:7(1):1-3.
6. Li S, Jiang H, Wang J, Wang Y, Pan S, Tian H. Responses of plant growth, physiological, gas exchange parameters of super and non-super rice to rhizosphere temperature at the tillering stage. *Sci Rep*. 2019; <https://doi.org/10.1038/s41598-019-47031-9>.
 7. Aryan S, Gulab G, Habibi N, Kakar K, Sadat MI, Zahid T, Rashid RA. Phenological and physiological responses of hybrid rice under different high-temperature at seedling stage. *Bulletin of the National Research Centre*. 2022;46(1):1-9.
 8. Hasanuzzaman M, Hakim KR, Nahar K, Alharby. *Plant abiotic stress tolerance*. Springer Cham. 2019.
 9. Dias AS, Barreiro MG, Campos PS, Ramalho JC, Lidon FC. Wheat cellular membrane thermotolerance under heat stress. *J Agron Crop Sci*. 2010; 196:100–108.
 10. Agarie S, Hanaoka N, Kubota F, Agata W, Kaufman P. Measurement of cell membrane stability evaluated by electrolyte leakage as a drought and heat tolerance test in rice (*Oryza sativa*L.). Graduate School of Agriculture, Kyushu University. 1995; 40:233–240.
 11. DaMatta FM, Grandi A, Arenque BC, Buckeridge MS. Impacts of climate change on crop physiology and food quality. *Food Res. Int*. 2010; 43:1814–1823.
 12. Sujatha KB, Uprety DC, Rao DN, Rao PR, Dwivedi N. Up-regulation of photosynthesis and sucrose-P synthase in rice under elevated carbon dioxide and temperature conditions. *Plant Soil Environ*. 2008; 54:155–162.
 13. Ainsworth EA, Bush DR. Carbohydrate export from the leaf: a highly regulated process and target to enhance photosynthesis and productivity. *Plant Physiol*. 2011; 155:64–69.
 14. Jagadish SV, Muthurajan R, Oane R, Wheeler TR, Heuer S, Bennett J, Craufurd PQ. Physiological and proteomic approaches to dissect reproductive stage heat tolerance in rice (*Oryza sativa* L.). *Journal of Experimental Botany*. 2010; 61:143-56.
 15. Ahmed N, Tetlow IJ, Nawaz S, Iqbal A, Mubin M, Nawaz ulRehman MS, Butt A, Lightfoot DA, Maekawa M. Effect of high temperature on grain filling period, yield, amylose content and activity of starch biosynthesis enzymes in endosperm of basmati rice. *Journal of the Science of Food and Agriculture*. 2015; 95(11):2237-43.
 16. Kim J, Shon J, Lee CK, Yang W, Yoon Y, Yang WH, Kim YG, Lee BW. Relationship between grain filling duration and leaf senescence of temperate rice under high temperature. *Field Crops Res*. 2011; 122:207–213.
 17. Akman Z. Comparison of high temperature tolerance in maize, rice and sorghum seeds, by plant growth regulators. *Journal of Animal and Veterinary Advances*. 2009; 8:358–361.
 18. Xu Y, Chu C, Yao S. The impact of high-temperature stress on rice: challenges and solutions. *The Crop Journal*. 2021; 9(5):963-76.
 19. Kilasi NL, Singh J, Vallejos EC, Ye C, Jagadish SVK, Kusolwa P, Rathinasabapathi B. Heat stress tolerance in rice (*Oryza sativa* L.): identification of quantitative trait loci and candidate genes for seedling growth under heat stress. *Front. Plant Sci*. 2018; 9:1578.
 20. Oh-e I, Saitoh K, Kuroda T. Effects of high temperature on growth, yield and dry matter production of rice grown in the paddy field. *Plant Production Science*. 2007; 10:412-22.

21. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. *Environmental and Experimental Botany*.2007; 61: 199-223.
22. Krishnan P, Ramakrishnan B, Reddy KR, Reddy VR. High temperature stress effects on rice plant growth and yield. *Advances in Agronomy*.2011; 111:87-206.
23. Xu J, Henry A, Sreenivasulu N. Rice yield formation under high day and night temperatures-A prerequisite to ensure future food security. *Plant Cell Environ*. 2020; 43:1595–1608.
24. Yoshida S. Tropical climate and its influence on rice [periodicity, productivity and stability]. IRRI Research Paper Series (Philippines). 1978.
25. Liu G, Zha Z, Cai H, Qin D, Jia H, Liu C, Qiu D, Zhang Z, Wan Z, Yang Y, Wan B, You A, Jiao C. Dynamic transcriptome analysis of anther response to heat stress during anthesis in thermotolerant rice (*Oryza sativa* L.). *Int. J. Mol. Sci*. 2020; 21:1155.
26. Feng B, Zhang C, Chen T, Zhang X, Tao L, Fu G. Salicylic acid reverses pollen abortion of rice caused by heat stress. *BMC Plant Biol*. 2018; 18:245.
27. Sreenivasulu N, Butardo VM, Misra G, Cuevas RP, Anacleto R, Kavikishor PB. Designing climate resilient rice with ideal grain quality suited for high-temperature stress. *J. Exp. Bot*. 2015; 66:1737–1748.
28. Yoshida S, Satake T, Mackill DS. High-temperature stress in rice [study conducted at IRRI, Philippines]. IRRI Research Paper Series (Philippines). 1981.
29. Yamakawa H, Hirose T, Kuroda M, Yamaguchi T. Comprehensive expression profiling of rice grain filling-related genes under high temperature using DNA microarray. *Plant Physiology*. 2007; 144:258-77.
30. Khan IM and Tiwari RK. Effect of high temperature on physiological and yield attributes in rice genotypes. Impact of temperature stress on pollen characteristics of lowland and upland rice (*Oryza sativa* L.) genotypes. In "Agriculture Diversification, Climate Change Management and Livelihoods" (R. Prasad and Y. S. Shivay, Eds.).2012; pp 108-9.
31. Singh T, Pun K, Bhagat K, Lal B, Satapathy B, Sadawarti M, Katara J, Gautam SL. Abiotic stress in rice: Mechanism of adaptation. *Challenges and Prospective of Plant Abiotic Stress*.2015; 4436(7).
32. Setiyono TD, Barbieri M, Prasadini P, Maunahan A, Gatti L. Spatial Assessment of Heat Stress Impact on Rice Production in Two Districts of Andhra Pradesh, India. *World J. Agric. Res*. 2018; 6:10–14.
33. Zhu Z, Tan L, Fu Y, Liu F, Cai H, Xie D, Wu F, Wu J, Matsumoto T, Sun C. Genetic control of inflorescence architecture during rice domestication. *Nature communications*. 2013; 4(1):1-8.
34. Khan S, Anwar S, Ashraf MY, Khaliq B, Sun M, Hussain S, Gao Z, Noor H, Alam S. Mechanisms and adaptation strategies to improve heat tolerance in rice, a review. *Plants* 8.2019; 508.
35. Wassmann R, Jagadish SV, Heuer S, Ismail A, Redona E, Serraj R, Singh RK, Howell G, Pathak H, Sumfleth K. Climate change affecting rice production: the physiological and agronomic basis for possible adaptation strategies. *Advances in agronomy*.2009; 101:59-122.
36. Tang RS, Zheng JC, Jin ZQ, Zhang DD, Huang YH, Chen LG. Possible correlation between high temperature-induced floret sterility and endogenous levels of IAA, GAs and ABA in rice (*Oryza sativa* L.). *Plant Growth Regulation*. 2008; 54(1):37-43.
37. Jiang H, Hu J, Li Z. Evaluation and breeding application of six brown planthopperresistance genes in rice

maintainer line Jin 23B. *Rice*. 2018; 11:22

38. Morita S, Shiratsuchi H, Takahashi, Fujita K. Effect of high temperature on ripening in rice plants: analysis of the effects of high night and high day temperatures applied to the panicle and other parts of the plant. *Japanese Journal of Crop Science*.2004; 73:77–83.
39. Katiyar-Agarwal S, Agarwal M & Grover A. Heat-tolerant basmati rice engineered by over-expression of hsp101. *Plant Molecular Biology*. 2003; 51:677–686.
40. Liu JG, Qin QL, Zhang Z, Peng RH, Xiong AS, Chen JM & Yao QH. OsHSF7 gene in rice, *Oryza sativa* L., encodes a transcription factor that functions as a high temperature receptive and responsive factor. *Biochemistry and Molecular Biology Reports*.2009; 42:16–21.
41. Qi Y, Wang H, Zou Y, Liu C, Liu Y, Wang Y, Zhang W. Over-expression of mitochondrial heat shock protein 70 suppresses programmed cell death in rice. *FEBS Lett*.2011; 585:231–239.
42. Liu J, Hasanuzzaman M, Wen, Zhang J, Peng T, Sun H, Zhao Q. High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice, *Protoplasma*. 2019; 256:1217–1227.
43. Ye C, Li X, Redoña E, Ishimaru T, Jagadish K. Genetics and Breeding of Heat Tolerance in Rice. *Rice Improvement*.2021; 5:203.

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