



Evaluating Heat Stress Impacts and Management Strategies in Rice: A Review

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ABSTRACT

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Rice, a staple crop in Nepal and a critical component of the national economy has experienced severe yield declines due to temperatures rise. This paper digs into numerous strategies to improve rice heat tolerance, analyzing the impact of heat stress on rice productivity and the mechanisms by which plants adapt. Elevated temperatures impair rice, particularly during the flowering stage, resulting in spikelet sterility and decreased yields. Early flowering to avoid high temperatures, panicle cooling through improved transpiration to reduce heat, and genetic modifications conferring heat tolerance are all important mechanisms for handling heat stress. Recent advances in genetic modification, sustainable agriculture practices, and agronomic techniques offer great promise for improving rice resilience to heat stress. Particularly, marker-assisted selection (MAS) and mutations that increase heat shock proteins (HSPs) play critical roles in developing heat-resistant rice variants. Furthermore, improvement in water management procedures and the application of growth regulators can dramatically reduce the detrimental effects of heat stress. This study underlines the crucial importance of current researches in incorporating stress-tolerance features into high-yielding rice cultivars and advancing genomic methods. Such efforts are critical for guaranteeing global food security in the face of climate change problems and sustaining rice output as temperatures rise.

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INTRODUCTION

Rice, the primary staple food crop in Nepal, constitutes a significant portion of the national economy and the livelihoods of the vast majority of people. In terms of cultivated area, production, and people's livelihoods, rice is the most important crop in Nepal. With 1.46 million hectares under cultivation, rice production stands at 5.56 million metric tons, with a productivity of 3.81 metric tons per hectare (MOALD, 2019). The daily mean temperature has increased by 0.7 °C between 2009

and 2018, although rice yield decreases by 8–10% for every 1°C increase in temperature (Song et al., 2022). The ideal temperature range for rice growth is 23–33 °C; however, the minimum temperature required for rice seedlings is 35 °C. The maximum temperature that supports healthy growth is also 35 °C. Rising temperatures have exceedingly strong detrimental impacts on rice production (Moore et al., 2021). Heat damage induced by climate change is one of the most significant abiotic factors impacting rice production. HS (heat stress) causes a significant loss of rice yield, a drop in quality, and a lower harvest index. Rice is extremely sensitive to high temperatures throughout the reproductive growth stages, which include the booting, heading, and grain-filling stages. HS inhibits rice flowering and fertilization, limiting seed-setting rates and yields (Nubankoh et al., 2020).

The earth's surface temperature has risen more rapidly in the last three decades than in any previous period since 1850, with the worst-case scenario predicting a 4.8-degree increase in global mean surface temperature by the end of the century compared to the 1986–2005 period (Stocker et al., 2014). As climate change intensifies, summer heat stress has become an important environmental factor in limiting rice yield (Espe et al., 2017). Most rice is cultivated in regions where temperatures are close to the optimal range for its growth. As a result, any further rises in mean temperatures or brief periods of extreme heat during sensitive stages may significantly reduce grain production. Rice yields are expected to decline by 41% by the end of the twenty-first century due to rising temperatures (Shah et al., 2011). In rice, phytohormones significantly coordinate yield characteristics' responses to heat stress. For example, cytokinin (CTK) and abscisic acid (ABA) regulate floret differentiation and the number of spikelets per panicle, while indole-3-acetic acid (IAA) and gibberellin (GA) are involved in the development of reproductive organs and pollination and fertilization activities, thus affecting spikelet fertility. Under heat stress, IAA, GA, ABA, and CTK moderate grain weight (Wu et al., 2016). The increased mean temperatures during sensitive growth phases may severely damage rice production, leading to a substantial decline in grain yield. Rice yields are predicted to be reduced by 41% by the end of the twenty-first century due to temperature stress (Ceccarelli et al., 2010). Furthermore, for every 1°C increase in the growing season mean temperature, dry season rice crop yields are expected to decrease by 15%. Research from 1979 to 2003 shows that rising nighttime temperatures, linked to global warming, have contributed to yield declines (Peng et al., 2004).

Advancements in genetic modifications and sustainable practices, such as optimized water management, bolster crop resilience. International collaborations aid in resource sharing and strengthen global food security by developing stress-tolerant rice varieties. Future research should focus on integrating stress-tolerance

traits into high-yielding varieties and advancing genomic technologies (Mthiyane et al., 2024).

MATERIALS and METHODS

All of the data and information presented derived from a secondary source and primary data collection methods were not employed in this review. Instead, the review draws upon various national news portals, government websites, thesis, published articles, and research papers.

RESULTS and DISCUSSION

Heat Stress

The term "heat stress" refers to a temperature increase that is sustained for some time sufficient to permanently impair plant growth and development (Wahid et al., 2007). This stress can severely reduce agricultural output, leading to societal instability and increasing the risk of widespread food insecurity. Previous research has shown that the expression of heat shock proteins (HSPs) in transgenic plants enhances resistance to heat shock (Mishra and Grover, 2015). Recently, two essential genes, *OgTT1* and *ERECTA*, which are involved in thermotolerance, were identified in rice (Shen et al., 2015). Heat stress during the reproductive stage results in significant rice yield loss, with major concerns being inadequate anther dehiscence, delayed blooming, limited pollen dispersal, low pollen yield, spikelet sterility due to poor anther dehiscence, and impaired starch synthesis during grain formation (Arshad et al., 2017). Plant processes such as germination, growth, development, reproduction, and yield are all affected by heat stress (Mittler and Blumwald, 2010). The rice flowering stage is the most sensitive period to high stress, and heat stress has occurred from time to time in the past 15 years. In 2003, heat stress caused a loss of 5.18×10^7 t in rice yield (Tian et al., 2007).

Temperature Indices

A gradient high-temperature treatment above 35°C has been shown to effectively distinguish heat tolerance variations among nine japonica rice cultivars (Matsui et al., 2001). Mild heat injury occurs when high temperatures persist for 3–5 days, moderate injury after last for 5–7 days, and severe injury when temperatures remain high for over 8 days (Wei et al., 2008). The heat tolerance threshold for current rice cultivars has increased beyond the traditional heat stress index of 35°C, suggesting that this threshold for heat stress should be raised from 35°C to 38°C (Ministry of Agriculture of the People's Republic of China, 2017). As temperatures continue to rise, it is expected that heat waves will become more frequent, prolonged, and intense in China (Gourdji et al., 2013). Predictions indicate that the global rice-

growing area exposed to heat stress will increase from 8% in the 2000s to 27% by the 2050s (Zhao et al., 2017). For an individual rice spikelet, the period from spikelet opening to pollination lasts only 0.5–1.0 hours, making this the most sensitive phase. Additionally, higher temperatures during this period lead to greater heat damage and reduced spikelet fertility (Das et al., 2014).

Meteorological Pattern

The intense heat and westward expansion of the subtropical high-pressure system in the western Pacific Ocean, attributed to global warming, directly contribute to the extreme hot conditions. Since air temperature is not a reliable indicator of an object's temperature, particularly the temperature of plant organs, it has been proposed that organ temperature, rather than air temperature, should be used to assess thermal damage (Yang and Li, 2005). For instance, when the panicle temperature exceeded 38°C, the flag leaves temperature were only around 34°C, indicating that moderate heat stress at 40°C had minimal effect on photosynthesis in flag leaves during anthesis. This highlights that the extent of heat stress-induced damage to rice plant organs varies primarily with their respective temperatures (Zhang et al., 2016). When flag leaves were removed, the temperature differences between superior and inferior spikelets were reduced. Under normal conditions, the temperature difference between superior and inferior spikelets in V20 and Zhong9 was approximately 1.75°C and 1.27°C, respectively. Under heat stress, these differences increased to 2.03°C and 2.54°C. Generally, removing the flag leaves led to an increase in spikelet temperatures, especially in the inferior spikelets (Fu et al., 2016).

Spikelet Sterility

Spikelet sterility is linked to diminished functionality of female and male organs in heat-stressed plants during the flowering stage. Under heat stress, spikelet sterility results from the impairment of female and male organs, contributing 34% and 66% to spikelet sterility, respectively (Fábián et al., 2019). High temperatures prevent spikelet development, which is linked to cytokine synthesis and degradation (Wu et al., 2017). High temperatures also lead to the accumulation of peroxides in spikelets, damaging cellular structures and reducing spikelet numbers (Fu et al., 2015). In field conditions, daily maximum temperatures above 38°C exacerbate spikelet degeneration, with japonica rice cultivars experiencing faster degeneration rates than indica cultivars. High temperatures also inhibit anther filling during the panicle initiation stage, resulting in reduced pollen production (Wang et al., 2019). Under high-temperature stress, poor anther dehiscence and fewer pollen grains on the stigma are major factors contributing to decreased spikelet fertility (Zhao et al., 2016). Pollen activity is significantly affected by high temperatures before spikelet

flowering, explaining the lack of a strong correlation between fertilization rates and pollen viability in spikelets exposed to high temperatures. High temperatures impair pollen activity by stunting pollen mother cell growth and causing abnormal tapetum disintegration (Deng et al., 2010). Additionally, high temperatures disrupt carbohydrate transport to pollen, preventing proper pollen filling and reducing activity levels (Cao, 2014). Pollen tube elongation is also inhibited by a deficiency of indole-3-acetic acid in the stigma during flowering, a condition worsened by high temperatures. However, the effects of high temperatures on rice stigma remain unclear, and further research is needed (Zhang et al., 2018).

Phenology and Physiology

Heat stress in plants is brought on by excessively high temperatures and affects their physiology, metabolic processes, enzymatic reactions, and transcriptomics. Heat stress reduces water loss and CO₂ assimilation, which also lowers stomatal conductance. In rice, reduced biomass, inhibited root elongation, and decreased yield are the outcomes of lower photosynthesis and higher photorespiration due to decreasing CO₂ concentration in leaves (Moore et al., 2021). In the same field, rice plants were grown at varying temperatures in 2018 and 2019, with different transplanting dates during the early and late off-seasons (PDI and PDII). The primary cause of either advances or delays in the phenological development of the rice plants was high temperature (Ahmad et al., 2019). Other cell compartments are also directly impacted by heat stress, with early effects including altered protein and enzyme structure and increased cell membrane permeability, leading to photochemical modification in the chloroplast, damage to the thylakoid membrane, and inhibition of important photosynthetic enzymes such as Rubisco (Bitá et al., 2013). Higher stomatal conductance was generated by slightly higher temperatures or brief heat stress, but extreme heat stress results in decreased stomatal conductance, which reduced root water uptake and nutrient absorption, particularly nitrogen (Shi et al., 2020). In addition to physiologic changes, heat stress also affects anatomical features. In rice subjected to heat stress, smaller cells and increased trichome density were observed. Although the physiological reaction of rice to heat stress is well studied, little is known about how morphological changes interact with physiological and biochemical processes, particularly in high-productivity rice varieties (Kondamudi et al., 2012). Just before or after the maximum tillering, the reproductive period begins, marked by stem elongation, flag leaf emergence, booting, heading, and spikelet filling. The length and width of the flag leaf are significantly decreased when rice is subjected to high temperatures during the early reproductive stages. In the mid-ripening stage, high temperatures can impair the photosynthetic rate by 40–60%, accelerating the senescence of the flag leaf (Oh-e et al., 2007).

Heat Resistance Characteristics

Heat resistance in rice is categorized into three mechanisms: heat defense, heat avoidance, and heat tolerance. Heat defense involves the regulation of morphological development and leaf transpiration, lowering panicle temperature and protecting the plant from heat-induced damage. Short flowering periods and early blooming are two methods of heat avoidance that are especially helpful for developing rice cultivars capable of withstanding high temperatures. Heat tolerance refers to the ability of the plant to carry on with daily activities notwithstanding the presence of high temperatures (Bheemanahalli et al., 2017). A significant quantitative trait locus, thermo-tolerance 1, identified and cloned from African wild rice, maintains cell metabolism balance and allows plants to survive in severely high temperatures (Li et al., 2015). After extensive analysis of the restorer and maintainer lines commonly used in China, it has been found that the male parent contributes significantly more to heat resistance. As a result, heat tolerance in hybrid rice is influenced by both male and female parents. Backcrossing is an effective method to improve heat resistance. Heat stress tolerance is a complex polygenic characteristic that is challenging to breed using traditional methods. To increase rice's ability to withstand heat stress, genetic factors that are less affected by the environment should be investigated (Fu et al., 2015).

Agronomic Strategies

To minimize excessive temperatures during the flowering stage, rice cropping methods can be adjusted in two ways. The first approach is to alter the single-season rice sowing date, and the second is to convert single-season rice to double-season rice. Early rice sowing boosts spikelet fertility by 5% in southwest China (Xiong et al., 2016). In the late 1990s, a new form of insurance known as agricultural weather index insurance was introduced. Meteorological data are used to calculate both the premium rate and payout of weather index insurance. As a result, reimbursements are based on a weather index which strongly correlates with actual losses experienced by policyholders (Liu et al., 2010). Early morning flowering (EMF) has recently been shown to considerably minimize heat stress damage by adopting an escape mechanism (Hirabayashi et al., 2014). Irrigation is the most efficient method for lowering canopy temperature in rice fields (Zhang et al., 2008). However, timely irrigation is problematic due to high temperatures, often accompanied by drought and a lack of irrigation infrastructure. Therefore, it is critical to maintain appropriate field moisture during the early phases of rice growth. Increased row spacing between rice plants is useful for air circulation in paddy fields, reducing canopy temperature during the flowering stage. Additionally, adjusting the rice plant population and microclimate in the field can also alleviate heat damage (Yan et al., 2007). To mitigate the effects of high-temperature stress, soil moisture conservation

plays a crucial role. This can be achieved by incorporating crop residues and manure into the soil or modifying the microclimate through shading (Krishnan et al., 2011). In Bangladesh, several strategies have been developed to promote climate-resilient farming practices. These include crop rotation, selecting suitable crop varieties, and adjusting planting dates to enhance agricultural sustainability. Additionally, effective water management techniques, such as alternate wetting and drying, have demonstrated significant benefits, reducing water usage by 30% while increasing yields by 15%, thus mitigating climate stress on crops (Bhuiyan et al., 2021).

Use of Growth Regulators and Fertilizers

Under high-temperature conditions, foliar application of micronutrient fertilizers containing silicon, KH_2PO_4 , ZnSO_4 , Na_2SeO_3 , or natural abscisic acid can boost spikelet fertilization capacity (Wu et al., 2013). Foliar spray of salicylic acid ($0\text{-}50\text{ mmol L}^{-1}$) has been shown to mitigate the negative effects of heat stress by increasing the levels of proline, sugar, and antioxidative enzymes such as POD, APX, and CAT. It also elevated concentrations of phytohormones such as GA_3 , IAA, and ABA, which ultimately increasing yield, seed setting rate, and spikelet numbers (Zhang et al., 2017). Additionally, spraying japonica rice plants with 2.3 kg ha^{-1} of α -tocopherol increased grain yield by 6% through enhanced membrane integrity, improved spikelet fertility, and lowered respiration. α -Tocopherol has been observed to play a key role in maintaining membrane integrity by reducing the formation of reactive oxygen species (ROS). Since plants boost maintenance respiration to repair damaged membranes under oxidative stress, increased membrane stability leads to reduction respiration rates (Mohammed and Tarpley, 2011). Soil boron application has also been found to mitigate the detrimental effects of heat stress, with boron-treated rice plants demonstrating enhanced cell membrane stability, improved spikelet fertility, and higher yield (Shahid et al., 2018). Similarly, treatment with calcium chloride (10 mM) alleviated heat stress-induced decreases in gas exchange, PSII efficiency, photosynthetic water-use efficiency, spikelet fertility, and leaf chlorophyll content in rice (Chandrakala et al., 2013).

Breeding Strategies

Traditional selection and breeding procedures aimed at obtaining high agro-economically significant qualities have often overlooked adaptive features such as drought and heat stress tolerance. Additionally, the gene pool of domesticated rice (*Oryza sativa* L.) has only about 10-20% of the genetic diversity found in its wild progenitors, which limits its potential for cultivation in hotter climate zones. Consequently, crossing domesticated rice with wild relatives, which possess a

broader range of stress-related genes, offers an opportunity for rapid genetic improvement through breeding and transgenic techniques (Zhu et al., 2007).

Recent studies suggest that the early morning flowering (EMF) feature might be an efficient strategy to avoid heat stress-induced spikelet sterility during anthesis by allowing viable pollen to reach the receptive stigma during cooler morning hours, thus avoiding sterility-inducing temperatures later in the day. A potential EMF feature or allele has been transplanted from wild rice (*Oryza officinalis*) to mitigate heat stress damage during anthesis. Introgression lines developed from hybridization between wild rice (*Oryza officinalis*) and the indica cultivar Koshihikari (*Oryza sativa*), expressing the early morning flowering trait, showed greater spikelet fertility and yield under heat stress compared to the late-flowering genotype (Ishimaru et al., 2010).

The majority of the QTLs linked to heat stress tolerance have been discovered during the early stages of development. In rice, heat and its associated features, including yield, remaining green, and floral sterility QTLs, have been found on all 12 linkage groups, primarily on chromosomes 1, 4, 7, and 10 (Wang et al., 2011). In breeding strategies based on gene pyramiding, several QTLs have been exploited to manage heat tolerance in rice during the flowering stage (Kilasi et al., 2018). To create rice varieties that are resilient to climate change, HS-tolerance characteristics from line N22 have been successfully introduced into other cultivars (Ye et al., 2015). Both the perception of stress and the reaction to it are undoubtedly regulated by transcriptional and post-transcriptional mechanisms. These processes have been investigated at various stress levels and when comparing across different genetic resources. The traditional transcriptome technique has been widely used to examine changes in gene expression in response to stress in many crop species, including rice (Mangrauthia et al., 2017).

It is widely known that responses to abiotic stress, such as HS, in crop species take the form of a complex quantitative trait whose inheritance is governed by a synergy between genes known as QTLs, dispersed across the genome. Historically, novel genetic variability and sources of tolerance have been found via QTL mapping and introduced into breeding programs. However, the low marker density in many QTL studies has limited their relevance for breeding. QTL regions can be fairly vast and can contain numerous genes that need to be looked into as potential candidate genes. The number of markers, particularly SNPs (single nuclear polymorphisms), that are equally dispersed throughout the genome has increased recently because of genotyping-by-sequencing (GBS) (Spindel and Iwata, 2018). Marker-assisted selection (MAS) in rice breeding has made significant strides in incorporating genetic traits for heat tolerance, aiding the development of heat-resistant rice varieties suited to global climate challenges. The success of marker-assisted backcross breeding (MABB) in wheat, which can also be applied to rice,

demonstrates MAS's potential to improve heat tolerance by introducing heat-resistant traits from tolerant donors into susceptible commercial varieties (Bellundagi et al., 2022). Mutations can result in proteins that support cellular homeostasis under stress. For example, heat shock proteins (HSPs) aid in protein folding and prevent aggregation under high temperatures. Studies indicate that mutation-induced rice varieties produce higher levels of HSPs, enhancing heat stress tolerance (Cai et al., 2023). Coping with heat stress involves strategies where plants can either escape it by flowering earlier, avoid it through panicle cooling via transpiration, or tolerate it by having specific heat-resistant genes, and also from hormone application as illustrated in Figure 1 (Khan et al., 2019).

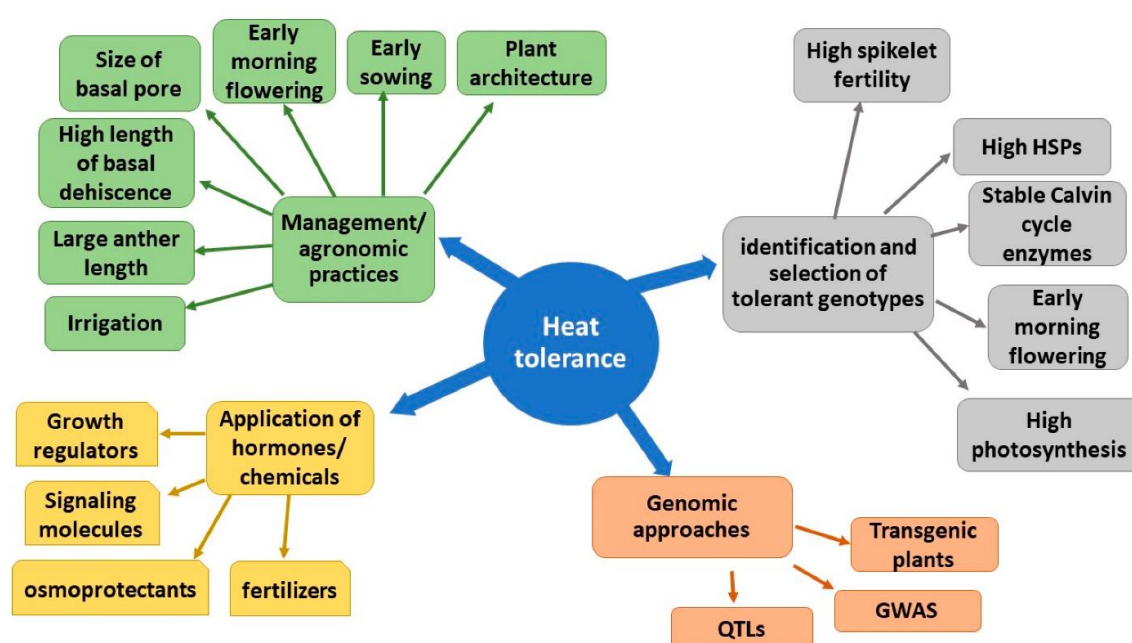


Figure 1. Strategies to tolerate heat stress in rice. (Khan et al., 2019)

CONCLUSION

Rising temperatures and heat stress pose serious threats to rice cultivation, severely reducing yields and quality. This review focuses on the various measures needed to improve heat tolerance in rice, such as genetic advances, sustainable farming practices, and agronomic changes. Early flowering, careful water management, and the application of growth regulators have all been shown to reduce heat stress effectively. Genetic enhancements through marker-assisted selection and mutation-induced heat shock proteins offer considerable potential for producing hardy rice varieties. A comprehensive strategy incorporating both technology innovations and workable farming solutions is needed to combat heat stress. To adapt to the changing environment and protect global food security, future research should concentrate on

honing these techniques, introducing stress-tolerance features into high-yielding rice varieties, and utilizing genetic techniques.

Conflict of Interest

The authors have declared that there are no competing interests.

Authors Contribution

The authors contributed equally to the article.

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