



A Review: Elevated Nighttime Temperature Impacts on Rice

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Authors' contributions

This work was carried out in collaboration among all authors. Author DK conceptualized and designed, and drafted the manuscript. Author BB reviewed the literature, and did critical revision of the manuscript and intellectual content. Author DB contributed to the manuscript. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

High nighttime temperatures adversely affect rice grain yield and quality by causing early panicle emergence, decreased pollen germination, increased spikelet sterility, and chalkiness. The severity of these effects depends on genotype, growth stage, stress period, and temperature. High nighttime temperature leads to structural abnormalities in starch granules, modify the amounts of amylose and amylopectin, and disturb the expression pattern of genes involved in starch biosynthesis and accumulation, ultimately affecting the cooking properties of rice grains. To ensure sustainable rice production in the context of global warming, rice breeding efforts must consider yield attributes focusing on the interactions between heat stress, genetic variables, and grain quality. This article provides an overview of current research on the significant impacts of high nighttime temperatures on rice grain production, starch granularity, physiochemical characteristics, and cooking properties.

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Keywords: Chalkiness; high nighttime temperature; rice grain; starch granules.

1. INTRODUCTION

Rice is a staple food for most people almost half of the world's population [1,2] and with improving living standards and food culture, more attention is on quality rice, which is more concerned with appearance (grain shape, chalkiness, and translucency) and taste: a significant goal of rice research today [3]. The decline in rice production in recent years is due to climate alternation, and understanding its mechanism helps to adapt climate change impacts on rice farming [4]. The effect of heat stress on the vegetative stage of the rice plants is non-significant; however, the reproductive stage is susceptible to higher temperatures, and it has a higher impact on rice grain yield than plant biomass [5]. Compared to low night temperature, high nighttime temperature (HNT) shortens the crop duration period and results in taller plants, but it does not impact leaf area and above ground biomass [6]. HNT also causes a slight increase in leaf-dark respiration, significantly negatively correlating with spikelet number per panicle and showing negative trends with biomass and harvest index [7]. Increasing night temperature (33 °C) combined with higher day temperature reduces average grain weight and can cause a 100 percent infertile spikelets [8]. Several research projects have recorded that HNT reduces rice grain yield, distorts grain dimensions, and deteriorates grain quality and appearance are explained below Table 1.

The reduction in rice grain yield under HNT is not due to reduced photosynthesis but rather early panicle emergence by two days, reduced crop growth duration, and decreased pollen germination by 20%. These effects may be due to weak anther dehiscence, pollen receptivity, reduced pollen swelling, and decreased anther pore size, leading to decreased spikelet fertility by 72% [12]. Rice plants grown under nighttime heat stress experience significant impacts on rice grain yield and harvest index for both wet and dry seasons, possibly due to increased temperature sensitivity, dark respiration, and reduced carbohydrate supply to the panicle [13]. High day and night temperatures reduce the total weight of the panicle due to the decreased number of filled spikelets in each panicle and decreased dimensions of the rice kernel [14]. The significant differences between daily day and night temperatures can cause adverse impacts such as chalkiness, poor rice grain quality, and decreased final grain weight [15]. HNT decreases grain growth duration, and the reduced grain weight is not due to decreased photosynthesis but due to decreased grain growth duration (Morita et al., 2005). Higher imperfect rice rates for rice grown under HNT may be due to decreased duration of dry matter accumulation in elevated night temperatures [16]. Not only grain yield but HNT is also associated with several other harmful impacts on the rice plants, as mentioned in Fig. 1.

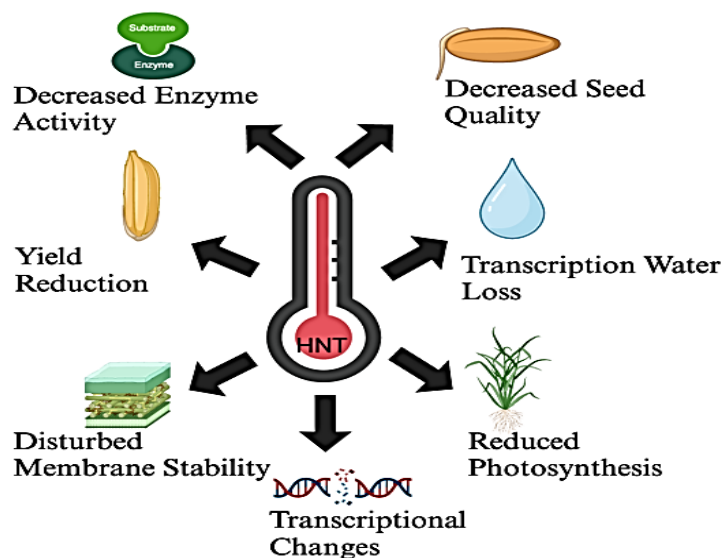


Fig. 1. Effects of HNT on rice plants

Table 1. The major research and its findings on impacts of elevated nighttime temperatures in rice plants

Experiment	Temperature Treatment	Stage of Imposed High Nighttime Temperature	Measurement	Findings
“Rice yields decline with higher night temperature from global warming” by Peng et al. (2004).	The average annual temperature climbed by 1.13°C and 0.35°C, respectively, for both the maximum and minimum.	Seedling stage to the Harvesting stage.	Panicle number per tiller, plant biomass, harvest index, yield attributes, straw dry weight, filled/unfilled spikelet, dry weight of rachis.	The impact of maximum temperature is insignificant, whereas each degree increases the minimum temperature in the dry season decreases grain yield by 10%.
“Rice milling quality, grain dimensions, and starch branching as affected by high night temperature” by Counce et al. [9].	The ambient temperature treatment is 18°C while the HNT (midnight to 5 am) is 24°C.	Panicle heading out at the booting stage to the harvesting stage.	Head rice yield, amylose/amylopectin content, Grain width, length, weight, dimension, and thickness.	Reduced head rice, grain width, and increased amylopectin chain length under HNT.
“Grain growth and endosperm cell size under high night temperatures in Rice (<i>Oryza sativa</i> L.)” by Morita et al. [10]	Controlled glasshouse experiment with 34°C HNT treatment and 22°C for ambient night temperature.	Heading stage to the harvesting stage.	Grain dry weight, Grain dimension, Endosperms cell number, and cell size.	Disturbed grain growth rate, cell size, and final grain weight.
“Effects of nighttime temperature during kernel development on Rice physicochemical properties” by Cooper et al. [11]	The imposed HNT is 30°C.	Throughout the kernel development stage.	Head rice yield, Kernel mass, Grain dimensions, Chalky kernels, Amylose content, Protein and Lipid content.	Head rice grain yield, grain dimensions, and amylose content decreased, chalky grain increased, but kernel mass, total lipid, and protein content remained unaffected.
“Impact of high nighttime temperature on respiration, membrane stability, antioxidant capacity and yield of Rice plants” by Mohammed et al. [12]	The ambient nighttime temperature is 27°C while the HNT is 32°C.	Twenty days after emergence to the harvesting stage.	Membrane thermal stability, total antioxidant capacity, and respirations.	Elevated nighttime temperature decreased the membrane thermal stability and yield by 90%, increasing the leaf respiration rate and electrolyte leakage but not

Experiment	Temperature Treatment	Stage of Imposed High Nighttime Temperature	Measurement	Findings
				impacting antioxidant capacity.
“Grain yield and quality responses of tropical hybrid rice to high nighttime temperature” by Shi et al. (2016).	Crops were treated with 29°C (HNT) and 23°C (control).	Panicle initiation stage to maturity: whole reproductive stage.	Spikelets per meter square, Seed set percentage, Head rice yield, Chalkiness, Grain width.	HNT significantly reduced grain yield of Gharib with a 13.4% reduction in the dry season than in the wet season (18.6%).
“Differential reaction of rice plants to high night temperatures applied at different stages of growth” by Laza et al. [6].	Plants were exposed to 21 °C (control) and 25 °C (high) night temperatures.	For the vegetative stage, transplanting to the panicle initiation stage, and for the reproductive stage, panicle initiation to the heading stage.	Photosynthesis, night respiration rates, number of spikelets per panicle.	HNT does not significantly impact the vegetative phase, and during the reproductive phase, HNT is more harmful at early phase than other times.

2. IMPACT OF HNT ON RICE GRAIN YIELD

HNT is a significant factor affecting rice production, causing early panicle emergence, reduced pollen germination, enhanced spikelet sterility, leaf respiration rate, and decreased grain length and width, resulting in up to a 90% loss in rice grain yield [17]. It is responsible for reduced head rice yield, smaller grain width, and overall rice grain dimension [9]. The grain weight of rice grown under HNT is 9-10% less than that under ambient conditions [10]. Rice grown under elevated night temperatures does not experience changes in panicle number, tiller number, stem length, and plant height; however, there is a 90% reduction in grain yield under HNT [12]. HNT does not impact the total number of productive tillers per plant, but spikelet sterility increases by 61% under these conditions [18]. HNT reduces the number of filled grains per panicle (25.70%), seed setting rate (22.09%), thousand-grain weight (5.17%), and grain yield (31.24%). However, there are no differences in the number of effective panicles per meter square between elevated and normal air temperature conditions [19]. Additionally, HNT increases the total number of spikelet sterility due to the decreased rate of pollen germination and enhances the rate of carbon loss due to increased respiration, but it does not affect the total leaf photosynthetic rate of rice plants [18]. HNT significantly impacts grain yield, seed setting percentage, and 1000-grain weight in rice. For instance, total dry weight, 1000 grain weight, and grain yield decreased by 13.5%, 7.9%, and 21.8%, respectively, in the sensitive rice cultivar Gharib. However, the tolerant cultivar N-22 is not

affected; the seed setting rate increased by 7.6% in the N-22 cultivar under HNT stress [20]. HNT has different growth stage-specific impacts on rice plants, ultimately reducing rice grain yield, as mentioned in Fig. 2.

HNT at the post-anthesis stage of rice decreases the 1000-grain weight, seed setting rate, and above-ground biomass accumulation, ultimately reducing grain yield [21]. Although the number of panicles and tillers increased, the number of fertile spikelets decreased, and rice grain yield under HNT, even under CO₂ fertilization, was reduced significantly by 8.5%; however, there was no impact on 1000-grain weight [22]. Temperature shifts from 24°C (ambient) to 35°C decrease rice grain yield by one-third, but grain weight per panicle varies according to the cultivar [23]. Among different stages, the spikelet differentiation stage shows the lowest number of spikelets, with 35.9% degenerated spikelets under heat stress [6]. The impact of heat stress at nighttime on spikelet fertility and rice grain yield is cultivar-dependent and varies with the period of heat stress, plant growth stage, and temperature intensity [24]. There is a significant reduction in grain yield, biomass accumulation, and harvest index for rice plants under HNT due to adverse impacts on spikelet fertility, panicle number, and spikelet number per panicle. However, there is no significant interaction between genotype and HNT for panicle number, spikelet number per panicle, and 100-grain weight [7]. How increased heat stress at nighttime alters the photosynthesis and respiration rate? and its impact on the photo-assimilate pool for the sink tissue of rice plants is mentioned below in Fig. 3.

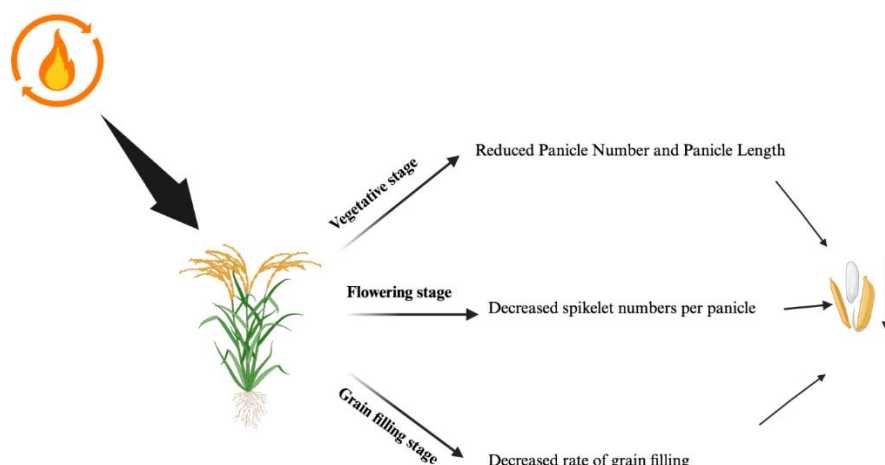


Fig. 2. Significant effects of HNT on the different growth stage of rice plants

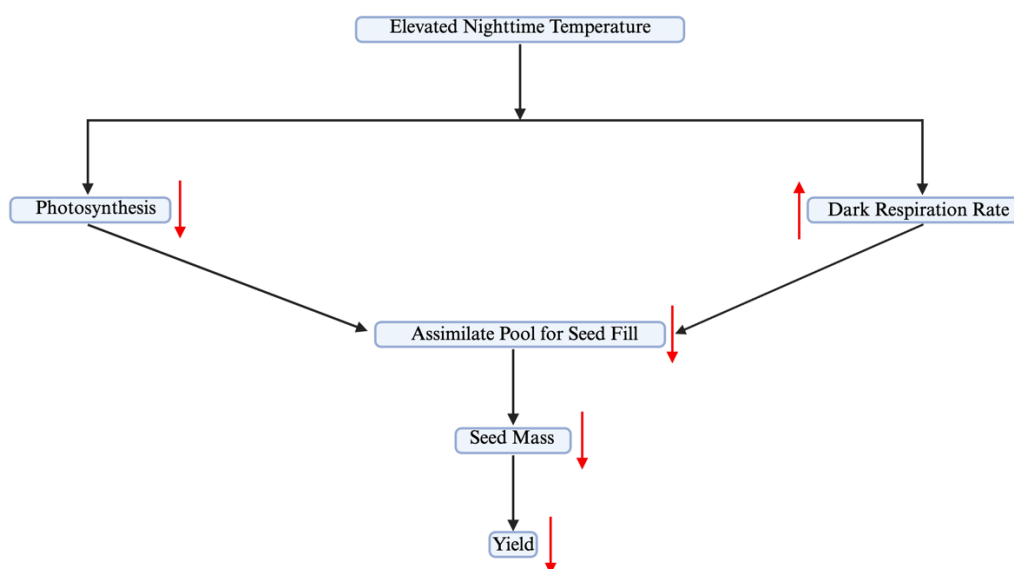


Fig. 3. Impact of HNT on rice grain yield

3. HNT INDUCED RICE CHALKINESS

Post anthesis elevated night temperature decreases rice milling quality by reducing the amount of milled rice grain and head rice grain due to increased chalkiness [21]. Rice grain grown under HNT consists of at least 80% grain chalkiness, while grains from control conditions have a perfect appearance [25]. The chalky part of the rice grain is composed of many air spaces and spherical-shaped starch granules with round corners, while the translucent part of rice grain has fewer air spaces and tightly packed starch granules with smooth surfaces [26]. Highly susceptible rice cultivars grown under HNT show a large opaque area in the endosperm, and more than 82% of grains show higher than 20% chalkiness of grain size, but tolerant rice cultivars only show 2-4% chalkiness of whole grain size by greater than 84% grains [27]. The amylose content of the chalky grains is higher than the translucent grains [28]. HNT decreases the head rice yields in long-grain hybrid cultivars, probably due to higher chalkiness in grain that makes grain prone to breakage during milling [11]. At the very starting phase of grain filling, there is no significant relationship between grain chalkiness and head rice yield to the HNT; however, when at least one of the caryopses turns yellow and brown color in the panicle, there is a direct correlation of chalk with head rice yield while inverse correlation of head rice yield to the nighttime temperature, which concludes that the impact of increased nighttime air temperature on chalkiness is growth stage-specific [29]. Up to

50% chalk content, the HNT does not have a noticeable impact; however, for the greater than 75% chalk category, the chalk content increased by 36.4% in the susceptible cultivar Gharib [20].

4. IMPACT OF HNT ON STARCH GRANULAR AND PHYSIOCHEMICAL PROPERTIES

HNT does not significantly impact the starch granules morphology, but the starch deposition rate is reduced due to HNT [30]. The starch endosperm cell numbers are higher in grain grown in HNT than in control, but the average cell area is smaller in HNT over control conditions [10]. The organization of amyloplasts is without gaps for grains grown under control conditions; however, amyloplasts are loosely packed in grains grown under HNT, creating free spaces [25]. As compared to the control condition, in HNT, the packaging of starch granules into amyloplast occurs quite in advance; the amyloplasts are compounded and tightly packed with well developed polygonal shapes in developing caryopsis for tolerant cultivars. However, for susceptible cultivars, there are round, heterogeneous sized, poorly developed starch granules under HNT, producing white belly chalky grains (31.8% to 67.0%) [30]. In translucent rice grains, amyloplasts are regular, compound type, larger (12 μm), and tightly packed with starch granules, but in the chalky part of rice grains consist of smaller size, non-systematically organized, and less tightly packed amyloplasts [28]. The starch granule structure is

compact polygonal type with well-defined edges at the early stage of grain filling for HNT due to the accelerated grain filling rate [16]. However, amylose content decreases under elevated nighttime temperatures [31]. The reduced enzymatic activity of GBSS is the reason for lower amylose content with increasing night temperature (Cooper et al., 2008). Compared to translucent rice grain, the chalky rice grain has lower amylose content and higher short-chain amylopectin but less long-chain amylopectin [26].

5. ALTERED COOKING PROPERTIES DUE TO HNT

With increasing night temperature through different grain filling stages in rice, the amylose content, crude protein content, and setback viscosity decreased. In contrast, the total lipid content, peak viscosity, and gelatinization temperature increase, which significantly impacts the cooking quality of rice grain [32]. Changed proportions of amylose and amylopectin in rice grain grown under elevated nighttime temperatures are responsible for increased breakdown, peak, final, and total setback viscosity, impacting starch pasting properties [31]. Long chain amylopectin content interacts positively with gelatinization temperature and relative crystallinity of rice endosperm, due to which grain grown under HNT needs more time to cook well [33]. Higher gelatinization temperature for grain grown under HNT impacts cooking quality and the food industry [16]. The pasting temperature and viscosities are higher for grains grown under higher temperatures, where grains at the superior position of the panicle have higher peak viscosity while grains at the inferior position show higher chalkiness and are a little softer [28]. Chalky rice grain consists of more air spaces and a disorganized cellular structure that allows more water diffusion during cooking and causes more water absorption and more significant grain expansion than translucent rice [26]. Higher iodine index, less adhesiveness texture of cooked rice, more chewing time for cooked rice, and higher peak and final viscosity of chalky rice grains deteriorate the eating quality of rice grain [26,34].

6. HNT IMPACT ON GENE EXPRESSION

Small pit-like structures in rice grain grown under HNT are due to the loosely packed round-shaped starch granules instead of tightly packed polyhedral starch granules, which is associated with the downregulation of genes involved in

starch biosynthesis at the early reproductive stage (Dhatt et al., 2019). At the early stage of grain development, there is a two to three-fold increase in transcript levels of alpha-amylase for grain grown under high temperature; however, mRNAs for alpha-amylase are not detectable in the central chalky part of the endosperm, suggesting that rather than starch degradation by alpha-amylase, the inefficient starch synthesis is the reason for grain chalkiness in elevated temperature conditions [25]. Among different genes involved in starch biosynthesis, the starch branching enzyme-IIb (BEIIb) is highly sensitive to the elevated nighttime temperature, and suppression of BEIIb during the grain filling stage under HNT decreases branching [31]. The expression of GBSSI and SSIIA is enhanced only six days after anthesis, and lower expression starts twenty days after anthesis under HNT. In contrast, under control conditions, the expression of SSIIA and GBSSI increases gradually between six to twenty days after anthesis [14]. In susceptible lines, AGPase genes are expressed at a higher rate in the early reproductive stage; however, gradually low expression in subsequent stages occurs, at which upregulation of GBSSI and SSIIA shows consistent expression. However, in tolerant cultivars, AGPase produces sufficient ADP glucose, which GBSS and SS quickly utilize to produce amylose and amylopectin [27]. The expression of cell wall invertase, vacuolar invertase, and starch synthase genes were significantly reduced in developing rice grain under HNT fifteen days after flowering [30].

7. CONCLUSION

In conclusion, HNT's effects on rice growth, development, and grain quality underscore its profound impact on multiple physiological and biochemical processes. HNT induces detrimental alterations such as early panicle emergence, reduced pollen germination, increased spikelet sterility, and chalkiness in rice grains. These changes contribute to a substantial decline in grain yield, depending on factors like genotype and growth stage. The intricate interplay between HNT and rice physiology involves disruptions in starch granule structure, changes in amylose and amylopectin content, and variations in gene expression related to starch biosynthesis. Furthermore, the negative consequences extend to cooking properties, affecting pasting characteristics and overall eating quality. As climate patterns continue to shift, understanding these various impacts becomes increasingly

critical for developing strategies to mitigate the adverse effects of HNT on rice production. Effective adaptation must consider the intricate relationships between heat stress, genetic factors, and grain quality to ensure sustainable rice cultivation in changing environmental conditions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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