Physiological and molecular attributes contribute to high night temperature tolerance in cereals

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Abstract
Asymmetric warming resulting in a faster increase in night compared to day temperatures affects crop yields negatively. Physiological characterization and agronomic findings have been complemented more recently by molecular biology approaches including transcriptomic, proteomic, metabolomic and lipidomic investigations in crops exposed to high night temperature (HNT) conditions. Nevertheless, the understanding of the underlying mechanisms causing yield decline under HNT is still limited. The discovery of significant differences between HNT-tolerant and HNT-sensitive cultivars is one of the main research directions to secure continuous food supply under the challenge of increasing climate change. With this review, we provide a summary of current knowledge on the physiological and molecular basis of contrasting HNT tolerance in rice and wheat cultivars. Requirements for HNT tolerance and the special adaptation strategies of the HNT-tolerant rice cultivar Nagina-22 (N22) are discussed. Putative metabolite markers for HNT tolerance useful for marker-assisted breeding are suggested, together with future research directions aimed at improving food security under HNT conditions.

KEYWORDS
cereal crops, high night temperature, HNT tolerance, metabolomics, natural variation, proteomics, respiration, transcriptomics, yield

INTRODUCTION

Global climate change presents a significant threat to food security by increasing abiotic stressors, which have a negative impact on the yield of all major crops (FAO, 2014; IPCC, 2014). The global surface temperature has increased by an average of 0.85°C during the past century and a further increase by up to 3.7°C is expected by 2100 (IPCC, 2014). This temperature increase occurs asymmetrically, with a larger increase of night compared to day temperatures, resulting in high night temperature (HNT) and a decrease of the diurnal temperature range (DTR) (Davy, Esau, Chemokulsky, Outten,
Zilitinkevich, 2017; Donat & Alexander, 2012; Easterling et al., 1997; Jin & Dickinson, 2002; Karl et al., 1991; Sillmann, Kharin, Zhang, Zwiers, & Bronaugh, 2013; Vose, Easterling, & Gleason, 2005). The rise of night temperatures is influenced by various factors, such as increased cloud cover resulting in reduced back radiation (Alward, Detting, & Milchunas, 1999; Braganza, Karoly, & Arblaster, 2004; Huang, Dickinson, & Chameides, 2006), desertification and changes in land use (Gallo, Easterling, & Peterson, 1996; Karl et al., 1991), aerosols (Ramanathan et al., 2007), higher evaporation and precipitation (Dai, Fung, & Del Genio, 1997) or the differential depth of the planetary boundary layer (Davy et al., 2017). The night temperature increase is especially severe in crop-growing regions such as Central and South Asia or North America (Du, Zhao, Pan, Wu, & Zhang, 2019; Klein Tank et al., 2006; Ma, Xia, & Meng, 2019; Peng et al., 2004; Peng et al., 2013; Rao, Chowdary, Sandeep, Rao, & Venkateswarlu, 2014; Welch et al., 2010; Zhao & Fitzgerald, 2013; Y. Zhou & Ren, 2011).

Asymmetric warming has a negative influence on plant species (Peng et al., 2013) and has been intensively investigated over the last decade. A significant challenge is the screening of a large number of cultivars for the identification of HNT-tolerant varieties for different cereal species. Extensive efforts are taken to improve the reproducible experimental setup of HNT conditions to characterize natural variation. Cereals were grown using overhead infrared heaters in greenhouse experiments (Mohammed & Tarpley, 2009c), in situ temperature-controlled field chambers (S. Chen et al., 2013) and tents with heaters and ventilation under field conditions (Hein et al., 2019; Hein et al., 2020). Recent reviews compare the quantification of HNT responses on grain yield in controlled environmental chambers versus field experiments (Impa et al., 2021) and summarize methods in thermal tolerance research (Geange et al., 2020).

As crops show contrasting effects in response to HNT and HNT research facilities mentioned above are difficult to be established in all stress-prone regions, alternatives are needed for the development of HNT-tolerant cultivars. In our opinion, it is of high importance to intensify omics approaches for the development of molecular markers applicable for marker-assisted breeding or molecular engineering of HNT-tolerant cultivars. This approach will complement on-going efforts for developing of HNT-tolerant cultivars through conventional and molecular breeding approaches.

In this review, differences between sensitive and tolerant rice and wheat cultivars in their physiological and molecular responses to HNT, which contrast from the effect of elevated day temperatures, will be discussed. This review concentrates on studies that have investigated increased night time temperature with reduced DTR, and not on studies having constant DTR (Y. Wang et al., 2019; Yamakawa & Hakata, 2010); or generating even an increased DTR (e.g., Liao et al., 2015). Furthermore, studies on the effect of increased soil temperatures by HNT (Fukayama et al., 2011) are not considered.

It is nevertheless a challenge to extract general patterns of HNT responses from complex studies with a large set of genotypes from controlled growth chamber or field experiments on different organs and with varying temperature changes. Therefore, we discuss general aspects and, as an example, the specific physiological and molecular HNT adaptation strategies employed by the highly heat and HNT-tolerant Nagina-22 (N22) rice cultivar in more detail. In addition, suggestions for metabolic markers for HNT tolerance are presented.

## 2 | PHYSIOLOGICAL RESPONSES TO HNT

### 2.1 | HNT causes devastating yield losses and reduces grain quality

Since a reduction of 10% in rice grain yield per 1°C night temperature increase was reported at the International Rice Research Institute (IRRI) in the Philippines (Peng et al., 2004), many studies have confirmed the substantial effect of HNT on grain yield (J. Xu, Henry, & Sreenivasulu, 2020). Rice yield reductions ranged between 55% and 90% compared to control conditions (Mohammed & Tarpley, 2009b; Mohammed & Tarpley, 2010; Yang et al., 2017), wheat yield was reduced by up to 41% (Hein et al., 2019), and barley yield decreased between 2% and 9% per 1°C night temperature increase (García et al., 2018; García, Dreccer, Miralles, & Serrago, 2015; García, Serrago, Dreccer, & Miralles, 2016). Moreover, HNT had a stronger impact on grain yield compared to high day temperatures (HDT) (Coast, Ellis, Murdoch, Quíñones, & Jagadish, 2015; Morita, Yonemaru, & Takanashi, 2005; Rehmani et al., 2014; Shi et al., 2017).

Reduction of grain yield in rice was mainly attributed to reduced spikelet fertility and/or grain weight, especially grain width, most likely generated by a disturbed translocation of photoassimilates into the grains (Bahuguna, Solis, Shi, & Jagadish, 2017; Coast et al., 2015; Mohammed & Tarpley, 2010; Mohammed & Tarpley, 2011; Nagarajan et al., 2010; Rehmani et al., 2014; Shi et al., 2013; Shi et al., 2016; Wu et al., 2017; Zhang et al., 2013). Temperature-driven decrease of pollen viability was indicated as major cause for HNT-driven spikelet sterility in rice (Mohammed, Cothren, & Tarpley, 2013; Mohammed & Tarpley, 2010; Yang et al., 2017). In wheat, HNT decreased spikelet fertility, grains per spike, grain size and reduced the grain filling period (Narayanan, Tamura, Roth, Prasad, & Welti, 2016; Prasad, Pisipati, Ristic, Bukovnik, & Fritz, 2008).

In rice, decreased yield under HNT was combined with lower grain quality or altered grain growth dynamics (Ambardkar, Siebenmorgen, Counce, Lanning, & Mauromostakos, 2011; Lanning, Siebenmorgen, Counce, Ambardkar, & Mauromostakos, 2011; Mohammed & Tarpley, 2011; Nagarajan et al., 2010; Shi et al., 2016; Shi et al., 2017). Grain quality parameters negatively affected by HNT included grain length, grain width, grain area, head rice percentage and milled rice percentage. Additionally, chalkiness was increased (Cooper, Siebenmorgen, & Counce, 2008; Fahad et al., 2016; Rehmani et al., 2014; Shi et al., 2016; Shi et al., 2017). Again, HNT had a more devastating effect on grain quality compared to HDT (Fahad et al., 2016).

Physiological and phenological aspects of HNT on rice and wheat have been extensively covered in recent reviews (Impa et al., 2021; J. Xu et al., 2020 and references within). A summary of general
Physiological changes under HNT is exemplarily shown for rice in Figure 1. However, none of the previous reviews have focused on integrating HNT responses using physiological and molecular knowledge on determining what parameters convey HNT tolerance.

2.2 The magnitude of the yield decrease depends strongly on the HNT tolerance of the cultivar

Recent studies focused intensively on the investigation of natural variation for the identification of HNT-tolerant varieties. Classification of rice or wheat cultivars for HNT sensitivity or tolerance was either based on grain yield (Bahuguna et al., 2017; Impa et al., 2019; Impa et al., 2020; Rao et al., 2014; Shi et al., 2013; Yang et al., 2017; Zhang et al., 2013), yield-related parameters such as seed size and chalkiness (Dhatt et al., 2019), or chlorosis of leaves in the vegetative stage (Glaubitz et al., 2014). For an overview about cultivars, classification parameters, tolerance classes and references, see Table S1 for rice and Table S2 for wheat. The classification of cultivars is restricted to a limited number used in the respective study and might not represent a wide and general overview about HNT tolerance. The largest study investigating 36 rice cultivars with different origins under four night temperature regimes was done in temperature-controlled field chambers at the IRRI (Zhang et al., 2013).

An outstanding HNT-tolerant rice cultivar, already identified as heat tolerant before (Jagadish et al., 2010), is N22, without any grain yield reduction after HNT exposure from panicle initiation to physiological maturity, compared to yield reductions of 16% and 9% for a susceptible and a high yielding cultivar, respectively (Bahuguna et al., 2017). N22 was also identified in other studies as highly HNT-tolerant (Moura et al., 2017; Shi et al., 2013; Wu et al., 2017; Zhang et al., 2013). Furthermore, the rice genotypes PSBRc52, Swarna and IR8 were described as HNT-tolerant in the field (Zhang et al., 2013), while IR72, Nipponbare, Taipei 309 and LC-93-4 were HNT-tolerant in the vegetative stage in controlled chamber experiments (Glaubitz et al., 2014). The cultivar Shanyou 63 (SY63) showed a very low yield

![Figure 1: Scheme of main physiological responses to HNT in vegetative and reproductive organs exemplarily shown for a rice plant. The illustration of the rice plant was taken from © Pflanzenforschung.de](image-url)
reduction (1%) in greenhouse experiments during the early reproductive phase after a HNT treatment at 31.9 °C (4.7 °C higher than control conditions), which was even smaller than that of N22 (Wu et al., 2017). SY63 was also classified as tolerant based on 1,000-grain weight and grain yield, compared with the susceptible Teyou-559 in two consecutive years under field conditions (Rehmani et al., 2014).

In wheat, the cultivars SY Monument and Larry were classified as tolerant based on grain yield in controlled environmental chambers (Impa et al., 2019), whereas under field conditions Everest, WB 4458, WB-Cedar and P1X060725 were the most HNT-tolerant cultivars (Hein et al., 2019). The cultivars Jagger X060724, K5070729 K-26 and KS070717 M-1 were in both studies HNT-susceptible.

Spikelet fertility varied among cultivars with N22 having the highest spikelet fertility compared to Azucena, WAB56–104, Moroberekan, IR64 and Lemont (Coast et al., 2015). The ability for spikelet cooling was discussed as an important precondition for coping with HNT, but seemed to be not the only adaptation strategy for maintaining fertility as the tolerant cultivar Bala also recorded a high spikelet temperature (Coast et al., 2015). Differences in grain-filling rate between the tolerant N22 and the sensitive Gharib were recorded with an increased initial grain-filling rate for both, but lower maximum and mean grain-filling rates for the sensitive cultivar. In addition, the grain-filling rate was especially reduced in spikelets in the middle and at the top of the panicle in Gharib (Shi et al., 2013). A slight reduction in spikelet number per square meter in N22 was compensated by sufficient assimilate transport (Shi et al., 2013).

Grain quality is affected by HNT in a cultivar-specific manner as was shown for milling quality (Ambardar et al., 2011; Counce et al., 2005; Lanning et al., 2011) and impact on starch composition and branching. Amylose content reduction in rice grains was reported only for HNT-sensitive (Azucena, IR64, WAB56–104) but not HNT-tolerant cultivars (CG14, N22) when HNT was applied from microsporogenesis to anthesis (Coast et al., 2015) or panicle initiation till physiological maturity (Bahuguna et al., 2017). The most tolerant rice cultivars with minimal chalkiness under HNT were Bengal, Cypress and Jupiter (Ambardar et al., 2011; Lanning et al., 2011). HNT-susceptible cultivars were negatively affected in yield, grain width and protein content, and showed shorter grain length and increased chalkiness, due to a higher amount of long-chain amylopectin accumulation (Cooper et al., 2008; Shi et al., 2013). Increased chalkiness could be caused by reduced translocation of photoassimilates to the grain increasing fissures and breakage during processing, which results in decreased head rice yield (Fahad et al., 2016).

2.3 Growth parameters and photosynthesis rates do not, but post-flowering respiration rates distinguish between differentially tolerant cultivars

Despite yield reductions, biomass production is often increased under HNT (Mohammed & Tarpley, 2010), for example, in rice, stem dry weight or shoot fresh weight were increased (S. Chen et al., 2013; Cheng, Sakai, Hartley, Yagi, & Hasegawa, 2008; Cheng, Sakai, Yagi, & Hasegawa, 2009; Kanno, Mae, & Makino, 2009). Higher biomass production might be the result of an accelerated development at HNT conditions due to higher growth thermal-time (García et al., 2015), as shown for rice panicle emergence (Mohammed & Tarpley, 2009a) and maize endosperm after long-term HNT exposure (Boehlein et al., 2019). HNT-tolerant cultivars were characterized by higher fresh and dry weight of biomass during the vegetative stage and no decrease in plant height compared to sensitive cultivars in climate chamber experiments (Glaubitz et al., 2014). Under field conditions, no clear evidence for an increased biomass in HNT-tolerant cultivars was observed as investigations of a large number of cultivars are lacking and some studies even report a decreased biomass in certain rice cultivars including the susceptible Gharib and the HNT-tolerant N22 (Shi et al., 2013).

Photosynthesis is mainly influenced by maximum daily temperature (Tmax), whereas plant respiration occurs throughout the day and is affected by both Tmax and minimum daily temperature (Tmin) (Peng et al., 2013). Higher night respiration rates could support assimilate translocation to the grains to maintain or increase biomass and enzyme activities for sugar unloading to generate starch in grains (Bahuguna et al., 2017). A frequently reported HNT response is an increased nocturnal maintenance respiration in leaves or whole plants on the expense of transitory starch, which alters the carbon balance leading to carbon limitation (Bahuguna et al., 2017; Kanno et al., 2009; Laza et al., 2015; Mohammed et al., 2013; Mohammed, Cothren, Chen, & Tarpley, 2015; Mohammed & Tarpley, 2009b). A negative association between leaf dark respiration and grain yield was found in a multi-parent advanced generation inter-cross population developed for heat tolerance (MAGICheat) under HNT conditions (J. Xu, Misra, Sreenivasulu, & Henry, 2021). Contrarily, in the vegetative stage, no carbon depletion was detected in rice leaves under HNT and negative correlations of a chlorosis-related HNT sensitivity rank with respiration rates excluded higher respiration rates in sensitive cultivars as a primary cause for HNT sensitivity (Glaubitz et al., 2014). Similarly, HNT increased respiration up to 20% at the vegetative stage but had no effect on rice growth (Laza et al., 2015). Genotypic variation for whole plant dark respiration rate was observed when HNT was applied at 15 days after panicle initiation with the lowest value for the most HNT-susceptible IR72 followed by IR36 and Nipponbare with the lowest number of degenerated spikelets (Laza et al., 2015). Under field conditions, the susceptible cultivar Gharib was characterized by the highest night respiration/photosynthesis (Rn/Pn) ratio followed by IR64 while the tolerant cultivar N22 showed no change of Rn/Pn (Bahuguna et al., 2017). Higher respiration rates under HNT were also reported for the susceptible rice cultivar Vandana 5 days after anthesis together with a simultaneous decrease of starch caused by increased activity of β-amylase through enhanced expression of OsBAM2 in flag leaves (Sharma et al., 2017).

The effect of HNT on photosynthesis in cereals is less clear. No change in photosynthetic yield was measured in leaves (Glaubitz et al., 2014) or after a long-term HNT treatment in rice and wheat during the vegetative stage (Mohammed & Tarpley, 2009a;
Mohammed & Tarpley, 2010; Nagai & Makino, 2009). Nevertheless, chlorophyll content was reduced in the leaves (Mohammed & Tarpley, 2009a). HNT had also no effects on creeping bentgrass in the vegetative stage (J. Fu & Huang, 2003). However, an impaired photosynthesis accompanied by a damage of thylakoid membranes was reported for wheat when HNT was applied during the reproductive phase until maturity (Narayanan et al., 2016; Prasad et al., 2008), and rice with stress applied after anthesis (Dong et al., 2014). On the other hand, photosynthesis was stimulated by HNT in rice during vegetative growth (Cheng et al., 2009; Cheng, Sakai, Yagi, & Hasegawa, 2010; Kanno et al., 2009) and in winter wheat when applied from tillering to jointing or jointing to booting (Fan et al., 2017). A compensatory stimulation of photosynthesis at HNT due to higher respiratory carbohydrate consumption during the night was previously discussed during the vegetative stage (Bahuguna et al., 2017). In a meta-analysis on HNT comparing data on plant species grouped by their photosynthetic pathways, a stimulating effect on photosynthesis was only reported for C3, woody and non-crop species, but not for herbaceous species or crops. The HNT effect on yield was attributed to lower biomass allocation to reproductive organs, flower development and seed maturation (Jing, Wang, Zhu, & Chen, 2016).

### 2.4 HNT affects yield of sensitive cultivars stronger in the wet than dry season

Only a few publications compare warming during different seasons, for example, comparing winter with spring night warming (Fan et al., 2017) or HNT treatments during dry or wet season (Schaarschmidt, Lawas, et al., 2020; Shi et al., 2016; Zhang et al., 2013; Zhao & Fitzgerald, 2013). Source- and sink capacities were improved by winter night warming in winter wheat compared to spring night warming (Fan et al., 2017). When 36 rice cultivars were grown during wet and dry seasons at IRRI in temperature-controlled field chambers at four different HNT conditions, yield reductions were larger in wet than in dry season (Zhang et al., 2013). The authors concluded that higher Tmax, DTR and radiation could be reasons leading to lower damage in the dry season compared to wet season. Rice grown during the wet season under HNT had a high chalk content compared to dry season, wherein low relative humidity and high vapour pressure lead to low chalk formation (Zhao & Fitzgerald, 2013).

In general, HNT appears to have lesser effect on sensitive rice cultivars during the dry season compared to wet season. The reduction of rice grain yield was 5.2% lower in the dry season compared to the wet season (Shi et al., 2016). Although wet and dry seasons had an effect on plant height, 1,000-grain weight and harvest index of different rice cultivars, the total grain yield was only reduced in the wet season (Schaarschmidt, Lawas, et al., 2020). Lower irradiance levels causing lower photosynthesis rates and lower overall carbon supply for grain-filling together with impaired glycolysis and higher carbon losses through respiration were suggested to be responsible for the more pronounced effect of HNT in the wet season (Schaarschmidt, Lawas, et al., 2020). A compensation of negative HNT effects in the dry season was possible by the contribution of an improved N-assimilation and an effective cyanide detoxification (Schaarschmidt, Lawas, et al., 2020).

### 2.5 HNT intensifies negative effects on plants when combined with other stresses

Increasing attention is directed to the effects of elevated night temperatures in combination with other stress treatments, as HDT (Coast et al., 2015; Fahad et al., 2016; Y. H. Fu et al., 2016; Li et al., 2011; Narayanan et al., 2016; Schoppach & Sadok, 2013; Shi et al., 2017; Wu et al., 2016; Wu et al., 2017; Yang et al., 2017; Ziska & Manalo, 1996) and elevated CO₂ (Cheng et al., 2008; Cheng et al., 2009; Cheng et al., 2010; Qiao et al., 2014; Volder, Gifford, & Evans, 2015).

While elevated temperatures often cause additional damages to plants, elevated CO₂ concentrations are mostly beneficial in terms of yield increase. In wheat, elevated CO₂ concentrations compensated the detrimental effects of asymmetric temperature changes and resulted in 9.1% higher grain yield versus 15.6% lower yield without CO₂ (Qiao et al., 2014). On the contrary, HNT reduced the stimulatory effects of elevated CO₂ on rice production (Cheng et al., 2008; Cheng et al., 2009). Due to the complexity of the stress conditions, such studies were only performed with a limited number of cultivars, lacking the opportunity to classify cultivars based on their HNT-tolerance. The investigation of the combined effect of HNT with other abiotic stresses using larger and diverse sets of cultivars is definitely necessary.

### 3 MOLECULAR RESPONSES TO HNT

The phenotype of an organism is the result of the combination of interactions between the genome, transcriptome, proteome and metabolome together with environmental impacts and the developmental stage (Arbona, Manzi, Ollas, & Gómez-Cadenas, 2013). With the development of high-throughput technologies, molecular responses to abiotic stresses have been successfully investigated. However, only a limited number of omics studies on HNT has been published and is only available for rice and wheat. For an overview on molecular studies on the effects of HNT stress in cereals published during the last decade, see Table 1.

Only one transcriptomic study using microarrays is available for rice under HNT stress analysing gene expression in specific organs such as leaves or seeds (Glaubitz et al., 2017). On the proteome level, studies revealed different accumulation patterns of proteins during HNT in rice using two-dimensional polyacrylamide gel electrophoresis (Li et al., 2011; Shi et al., 2013). Furthermore, targeted enzyme activity measurements were performed (Bahuguna et al., 2017; Shi et al., 2017). Additionally, lipid composition and structure were analysed in wheat leaves (Narayanan et al., 2016).
Most closely connected to the phenotype are metabolites, which reflect the integration of gene expression, protein interactions and other regulatory processes (Arbona et al., 2013). Changes in metabolite levels under HNT were mainly measured by gas-chromatography–mass-spectrometry (GC–MS) under controlled environmental conditions for rice (Dhatt et al., 2019; Glaubitz et al., 2015; Glaubitz et al., 2017) and winter wheat (Impa et al., 2019), and under field conditions for rice (Schaarschmidt, Lawas, et al., 2020). Metabolites were also determined in inner endosperm cells of intact seeds of the rice cultivar Koshihikari by picolitre pressure-probe-electrospray-ionization mass spectrometry (Wada et al., 2021).

For a deeper insight into the response to HNT, different omics approaches were combined to understand the interplay of molecular components, such as transcriptomics and metabolomics (Glaubitz et al., 2017). Especially grain yield is negatively affected under HNT by a dysregulated starch metabolism, and hence several studies investigated the expression of starch-related enzymes and sugar accumulation (Bahuguna et al., 2017; Glaubitz et al., 2014; Impa et al., 2020; Sharma et al., 2017; Shi et al., 2017). Finally, as HNT normally does not occur as a single stressor, some studies also investigated the impact of HDT and high day and night temperature (HDNT) stress in direct comparison (Li et al., 2011; Narayanan et al., 2016; Shi et al., 2017) and identified different responses between heat (HDNT) and HNT stress.

Recently, a clear evidence for a positive role of the locus Fertilization Independent Endosperm (Fie1), a component of the Polycomb Repressive Complex 2 (FIS-PRC2) complex, for mature grain size under HNT was reported identified by genome-wide association studies and by testing overexpression lines and knockout mutants (Dhatt et al., 2021).

### 3.1 HNT affects gene regulation, metabolic pathways and hormone metabolism differently in sensitive and tolerant cultivars

Studies investigating HNT stress on transcriptomic and metabolomic levels were performed in rice and wheat, mainly focusing on the source-and-sink organs such as leaves and seeds. The only transcriptomic study in rice leaves at the vegetative stage using six different cultivars identified a general up-regulation of six genes involved in transcription regulation, signal transduction, protein–protein interactions, jasmonate (JA) response and biosynthesis of polyphenols such as phenylalanine ammonia-lyase (PAL) as central for the HNT response (Glaubitz et al., 2017). PAL catalyses the first step in the biosynthesis of phenylpropanoids, secondary metabolites accumulating in response to different stresses (Winkel-Shirley, 2002). The increase under HNT suggests that the synthesis of secondary metabolites is activated. An in-depth analysis of the PAL activity in rice leaves revealed stable enzyme activity in the tolerant cultivar N22 for control and HNT conditions, while for a sensitive cultivar an up-regulation was only reported under HNT (Moura et al., 2017).

Metabolomic approaches indicated a highly activated TCA cycle, increased related enzyme activities and a corresponding higher accumulation of its intermediates due to enhanced night respiration and of amino acid biosynthesis pathways branching off in leaves of sensitive rice cultivars (Glaubitz et al., 2015; Glaubitz et al., 2017) and winter wheat leaves (Impa et al., 2019). Positive correlations of enzyme activities from the TCA cycle, such as fumarase or citrate synthase, with HNT sensitivity or the log2 fold change between HNT and control conditions underlined these findings for sensitive cultivars (Glaubitz et al., 2015). Additionally, integrated data analysis revealed correlations between TCA cycle-related transcripts and metabolites and identified contrasting sensitivity and tolerance profiles for different rice cultivars (Glaubitz et al., 2017). For sensitive cultivars, especially GABA signalling was involved, thus providing a link to the TCA cycle. On the contrary, no changes in the TCA cycle under HNT stress were reported for rice seeds (Dhatt et al., 2019) or wheat spikes (Impa et al., 2019).

During HNT stress, an accumulation of amino acids and the regulation of related pathways were reported, such as for the shikimate pathway providing the amino acids tryptophan, phenylalanine and tyrosine. It has been shown previously that this pathway contributes to biotic and abiotic stress responses through the synthesis of protective compounds such as anthocyanins (Dewick, 1995). An increased accumulation of alanine and phenylalanine was observed in developing rice seeds (Dhatt et al., 2019) and wheat spikes (Impa et al., 2019) upon HNT stress. Field studies in rice revealed higher amounts of alanine and cyano-alanine in panicles grown in the dry season that may have contributed to improved nitrogen assimilation and more effective detoxification of cyanide (Schaarschmidt, Lawas, et al., 2020). Metabolites related to the shikimic acid pathway, including tyrosine, shikimic acid and quinic acid, were also significantly affected by HNT treatment in winter wheat leaves (Impa et al., 2019) and rice leaves (Glaubitz et al., 2015). Both species showed higher accumulation of these compounds in tolerant cultivars. For developing rice seeds however, a general decrease in these intermediates was reported, which was in line with the lower expression of different shikimate kinases (Dhatt et al., 2019).

The activity of aspartate amino transferase (AAT) was positively correlated with HNT sensitivity in leaves (Glaubitz et al., 2017).

### TABLE 1 Selected molecular studies with omics data on the effects of HNT stress in cereals published during the last 10 years

| Area | Reference |
|------|-----------|
| Transcriptome | (Glaubitz et al., 2017)* |
| Proteome/Lipidome | (Li et al., 2011)*, (Shi et al., 2013)*, (Narayanan et al., 2016)* |
| Metabolome | (Glaubitz, Erban, Kopka, Hincha, & Zuther, 2015)*, (Glaubitz et al., 2017)*, (Dhatt et al., 2019)*, (Impa et al., 2019)*, (Schaarschmidt, Lawas, et al., 2020)*, (Wada et al., 2021)* |

*Rice.  
Wheat.  
Note: Bold for studies on the field; italic for studies using more than one omics approach.
Furthermore, amino acids synthesized from aspartic acid were correlated with HNT sensitivity or yield decline, such as asparagine (Glaubitz et al., 2015; Glaubitz et al., 2017; Schaarschmidt, Lawas, et al., 2020), threonine (Glaubitz et al., 2015; Glaubitz et al., 2017) and methionine (Glaubitz et al., 2017). An accumulation of aspartic acid under HNT was also discovered in developing grains of six rice cultivars without genotype-specific alterations regarding their HNT tolerance on metabolite or yield parameter levels, but no changes of the other amino acids were reported (Dhatt et al., 2019). Furthermore, a greater content of aspartic acid together with ascorbic acid, fumaric acid, glycerol and 3-cyano-l-alanine was discovered in HNT-treated rice endosperm cells during the day (Wada et al., 2021). During the night instead, cell wall related metabolites, redox-related metabolites and stress response plant hormones were increased compared to control conditions (Wada et al., 2021). Increased accumulation of aspartic acid could be related to higher activity of AAT under HNT (Glaubitz et al., 2017) catalysing a reversible transamination to generate aspartic acid and 2-oxoglutarate.

Previous research has shown that polyamines play an important role in the abiotic stress response in plants (D. Chen, Shao, Yin, Younis, & Zheng, 2018). Three common polyamines in plants are putrescine, spermidine and spermine (Minocha, Majumdar, & Minocha, 2014). For rice leaves, a higher accumulation of polyamines in sensitive cultivars and a strong down-regulation of polyamine biosynthetic genes in tolerant cultivars were observed (Glaubitz et al., 2015). Additionally, correlation studies showed that the expression levels of eight polyamine biosynthesis genes, including ADC2 and ODC1, indicate that the first step of polyamine biosynthesis was highly connected with HNT sensitivity.

Changes in sugar, sugar alcohol and monosaccharide levels in plants under elevated night temperatures have been frequently reported, for example, higher sugar levels in developing rice seeds (Dhatt et al., 2019) and winter wheat spikes (Impa et al., 2019). A significant increase of trehalose under HNT compared to control was observed at later time points in developing rice grains (Dhatt et al., 2019). Trehalose is the primary compound for the synthesis of trehalose-6-phosphate, a signalling molecule involved in partitioning and plant development. Sugar alcohols accumulated when HNT was applied during early stages of grain-filling, which is in agreement with the changes observed in wheat spikes (Impa et al., 2019) for a tolerant genotype. In a field study investigating season-specific effects of HNT on rice panicles, decreased abundance of sugar phosphates and sucrose, and higher abundance of monosaccharides indicated impaired glycolysis and higher respiration-driven carbon losses in the wet season (Schaarschmidt, Lawas, et al., 2020). Based on the above studies, it can be suggested that the response of carbohydrate levels to HNT stress is organ-specific.

Furthermore, a pre-adaptation of tolerant cultivars to HNT already under control conditions represented, for example, by higher levels of potential protective compatible solutes in leaves as stabilizers of protein and cellular structures was suggested (Glaubitz et al., 2015). Metabolites with higher levels in tolerant compared to sensitive cultivars at control conditions included the organic acids shikimic and quinic acid, as well as the sugars glucose, fructose and 1-kestose and myo-inositol, a component of the raffinose biosynthesis pathway, and a member of the HNT tolerance profile identified in a later publication (Glaubitz et al., 2017). In contrast, a higher content of salicylic acid-glucopyranoside in sensitive cultivars under control conditions was hypothesized to be linked to autophagy reactions under HNT (Glaubitz et al., 2017).

Phytohormones such as JA as well as auxins, ethylene or gibberellins play an important role in the abiotic stress defence in plants (Wani, Kumar, Shriram, & Sah, 2016). An integrated analysis of transcript and metabolite data of six cultivars with contrasting HNT tolerance identified a tolerance profile including inositol phosphates, thereby linking JA to the HNT response (Glaubitz et al., 2017). In the same study, gene expression changes in sensitive cultivars were linked to ABA signalling.

Cytokinin concentrations were measured under HNT during the early reproductive stage in panicles of four rice cultivars with N22 and SY63 having the highest spikelet number per panicle under these conditions (Wu et al., 2017). For these two tolerant cultivars, the abundance of selected cytokinin species was significantly increased in panicles compared to the two sensitive cultivars Huanghuazhan and Lianyoupeiji. This observation was accompanied by higher expression of genes encoding enzymes involved in cytokinin metabolism as cytokinin riboside 5’-monophosphate phosphoribohydrolase (LOG), isopentenytransferase (IPT) and cytokinin hydroxylase (CYP735A) in the tolerant cultivars (Wu et al., 2017).

For a general overview on molecular changes in vegetative and reproductive organs in response to HNT, see Figure 2.

3.2 Lower gene expression and activity of key enzymes of starch metabolism and increased starch degradation affect grain yield in sensitive cultivars

As proteomic studies on HNT responses in cereals are rare, we have included studies on enzyme activities of sugar and starch metabolism as they provide information on protein activity and interface between gene expression, protein abundance and metabolic changes. Under HNT, a sustained carbon supply from the leaves is disturbed, which might be intensified by a high vapour pressure deficit during the night, causing reduced water and carbon supply to the grains (Sadok & Jagadish, 2020). Higher respiration rates and varying photosynthetic responses have differential effects on the carbohydrate content of diverse genotypes with a clear indication of higher carbohydrate levels in more HNT-tolerant cultivars. Furthermore, remobilization of stem non-structural carbohydrates (NSC) was positively associated with yield and harvest index under field conditions in 432 genotypes of the MAGICcoat population (J. Xu et al., 2021). Significant attention is drawn to differences in carbohydrate translocation under HNT during the ripening period in rice, causing an assimilate shortage in sensitive cultivars, indicating a source limitation, whereas NSC (total soluble sugars and starch) levels in leaf, stem and panicle were unaffected in tolerant N22 (Shi et al., 2013).
Key starch metabolism enzymes are starch synthase (SS), cytosolic invertase, vacuolar invertase (VI), cell wall invertase (CWI) and sucrose synthase (SuSy). A study in developing rice grains analysed the activity of these enzymes in three contrasting cultivars for the response to HNT (Bahuguna et al., 2017). Lower starch accumulation in developing grains of susceptible cultivars was caused by a reduction of sink strength by HNT. This was indicated by lower CWI activity causing reduced phloem loading, slower cell expansion due to lower VI activity and reduced substrate supply for starch synthesis through lower SuSy activity catalysing the first step of sucrose to starch conversion. Starch content in developing seeds was reduced by up to 22% in these cultivars leading to reduced grain weight and quality compared to the tolerant cultivar (Bahuguna et al., 2017). Similar findings were reported for five contrasting rice cultivars with significantly reduced activity of VI and SS in grains of sensitive cultivars but a lower reduction or an increase in tolerant cultivars (Shi et al., 2017). In contrast, SuSy activity remained stable or was increased by HNT in all genotypes (Shi et al., 2017). Interestingly, these enzyme activity changes did not result in a reduction of single-grain weight or NSC content in superior spikelets due to a higher grain-filling rate and a shorter grain-filling period (Shi et al., 2017).

In contrast, a study in winter wheat showed an increased SuSy expression in both, the tolerant and sensitive cultivar, at HNT compared to control temperature, which was significantly higher only in the sensitive cultivar (Impa et al., 2020). Invertase activities were more decreased in the sensitive wheat cultivar compared to the tolerant one similar to HNT-sensitive rice cultivars (Bahuguna et al., 2017).

Enzyme activity of the starch synthesizing enzyme cytosolic ADP-glucose pyrophosphorylase (AGPase) was measured for winter wheat (Impa et al., 2020). While the expression of SuSy encoding genes was increased under HNT in each wheat genotype, the expression of the small subunit of AGPase was more decreased in the sensitive cultivar and hence may have a negative effect on its ADP-glucose production. Genes encoding enzymes catalysing the synthesis of amylose (granule bound starch synthase GBSSI and GBSSI) and amylopectin (starch synthase isoforms SSI, SSII) from ADP-glucose showed an increased expression in grains of the tolerant wheat cultivar under HNT contributing to a more efficient amylose and amylopectin production (Impa et al., 2020). Contrarily, in mature seeds of rice, GBSSI, SSII and SSIV were down-regulated and starch showed structural abnormalities, which might point to a more sensitive response to HNT of this whole cultivar selection (Dhatt et al., 2019).

The activity of starch degrading enzymes (α-amylase and β-amylase) in grains of winter wheat under HNT was increased in the sensitive genotype, indicating enhanced starch degradation and conversion to maltose (Impa et al., 2020). Similarly, the susceptible rice cultivar Vandana recorded a significant effect for β-amylase under HNT in flag leaves (Sharma et al., 2017). Gene expression analysis revealed an up-regulation of α-amylase and β-amylase genes in the sensitive cultivar but a down-regulation in the tolerant cultivar. Malto-oligosaccharides, which are ultimately converted to glucose residues, were increased in flag leaves of the sensitive and reduced in the tolerant cultivar, while the glucose level was declined in both (Sharma et al., 2017).
3.3 | Specific changes in proteome and lipid composition associated with HNT tolerance

Proteins and lipids are essential for cellular functions in plants and an important nutrition source for the human diet. Major lipid alterations were identified during HDNT in wheat leaves (Narayanan et al., 2016). In the same study, HDT and HDNT had a higher impact on most lipid classes in a heat-tolerant and heat-sensitive cultivar than HNT alone. Yield traits of the two wheat genotypes did not differ under HNT conditions, making tolerance-specific conclusions difficult. Nevertheless, reactive oxygen species and malondialdehyde content were significantly increased in heat-sensitive Karl-92 but not in heat-tolerant Ventnor at HNT conditions. HDT and HDNT mainly influenced the lipid classes acylated sterol glycosides, sterol glycosides (SG), triacylglycerols and ox-lipids. Among those four classes, only SG showed a significant response also to HNT with higher levels in the heat-., but not HNT-tolerant cultivar Ventnor. Using a Random Forest approach, mainly different SG species were found to contribute to a differentiation between the three high-temperature treatments (Narayanan et al., 2016).

A change in lipid composition together with starch and protein changes was also found in the endosperm and germ of winter wheat (Impa et al., 2020). In the sensitive cultivar, a starch decrease and an increase in grain proteins and lipids were reported, whereas the protein level was significantly lower in the tolerant cultivar. HNT-induced alterations in starch–protein–lipid accumulation could be related to a negative impact on grain yield and flour quality but might also limit the mobilization of resources during germination (Impa et al., 2020).

A rice proteomic study using two-dimensional gel electrophoresis identified specific protein abundances differentiating the tolerant cultivar N22 from the susceptible cultivar Gharib (Shi et al., 2013). A combined increase of heat shock proteins (HSPs) and calcium signaling proteins as well as efficient protein modification and repair mechanisms were discussed to provide HNT tolerance in N22 (Shi et al., 2013). For example, peptidyl-prolyl cis-trans isomerase was up-regulated in N22 but down-regulated in Gharib. This protein is known to work as a tandem with HSP90 to ensure the correct folding of proteins in Arabidopsis thaliana (Z. S. Xu et al., 2012).

3.4 | Opportunities to enhance HNT tolerance in cereals

There is clear evidence for genotypic variation in response to HNT opening the possibility to identify tolerant cultivars or genomic and molecular markers for breeding of HNT-tolerant cultivars. In addition to N22 for rice, for wheat, a highly HNT-tolerant cultivar, SY Monument, was identified, maintaining grain yield, grain number and grain-starch accumulation under HNT, which was suggested as a promising donor for mapping populations (Impa et al., 2020).

Some HNT tolerance traits were suggested for plant breeding programmes to enhance resilience in warmer climates, including spikelet cooling and high spikelet fertility (Coast et al., 2015). Transpiration cooling was also identified as a key factor affecting head rice yield as well as chalkiness (Zhao & Fitzgerald, 2013), highlighting the improvement of spikelet cooling as the main trait for improved grain quality under HNT.

Another strategy is the maintenance of higher NSC pools in stem and panicles secured by efficient translocation and combined with higher biomass to prevent HNT-driven yield losses (Jagadish, Murty, & Quick, 2015; Shi et al., 2013). To reach this goal, the regulation of key sink enzymes should be explored and used for advanced breeding (Bahuguna et al., 2017). Genome-wide association studies (GWAS) identified candidate genes for stem NSC remobilization under control conditions but lost under HNT, including an invertase inhibitor, MADS box transcription factors and a UDP-glycosyltransferase (J. Xu et al., 2021). The importance of sugar remobilization is supported by the finding that HNT-tolerant cultivars have higher carbohydrate accumulation in leaves at the vegetative stage compared to sensitive cultivars (Glaubitz et al., 2014).

Sensitive cultivars were characterized by a dysregulation of central metabolism and an increased polyamine biosynthesis, whereas tolerant cultivars showed metabolic pre-adaptation already under control conditions (Glaubitz et al., 2015; Glaubitz et al., 2017).

Omics studies provided metabolites as basis for marker-assisted breeding. Threonine, asparagine, aspartic acid, glutamic acid, putrescine, pyroglutamic acid and salicylic acid-glucopyranoside in leaves harvested from controlled chamber experiments were positively correlated with the sensitivity rank of multiple cultivars under HNT (Glaubitz et al., 2015; Glaubitz et al., 2017). In field studies, four of these metabolites were verified in panicles and more were added based on significant correlations between the grain yield reduction and the corresponding metabolite change (asparagine, aspartic acid, 3-cyano-alanine, fructose-6-phosphate, glutamic acid and pyroglutamic acid) (Schaarschmidt, Lawas, et al., 2020). Summarizing this, high levels of the metabolic markers asparagine, aspartic acid, glutamic acid and pyrogulatmic acid in leaves or panicles of rice could identify more HNT-sensitive cultivars but need to be extensively tested with larger sets of cultivars under field conditions in the future. If the same metabolites are suitable as markers for wheat HNT-sensitivity remains to be investigated.

Differentially expressed transcripts under HNT were detected between tolerant and sensitive cultivars in one transcriptomic study under controlled growth chamber conditions (Glaubitz et al., 2017), but as no other transcriptomic studies exist under field conditions, suggestions for marker transcripts for HNT tolerance or sensitivity are not reliable.

CO₂ might compensate the detrimental effects of asymmetric temperature changes. Differential CO₂-temperature interaction responses for indica and japonica rice accessions might be used for introducing different gene pools in rice to enforce breeding efforts for HNT adapted crops and improve resilience to increasing temperatures (D. R. Wang et al., 2016).
The HNT-tolerant rice cultivar N22 (aus ssp.), which is also heat and drought tolerant, has several adaptation strategies to maintain productivity under harsh conditions including HNT environments (Figure 3). N22 is able to preserve high soluble sugar levels at the milky stage and has high translocation capacity for carbohydrates contributing to lower spikelet sterility and stable 1,000-grain weight (Moura et al., 2017). High sink strength and assimilate supply to spikelets for starch biosynthesis in N22 were caused by higher spikelet SuSy activity (Bahuguna et al., 2017). The activity of key enzymes of the starch metabolism was maintained under HNT (Bahuguna et al., 2017) and night respiration was unaffected (Sharma et al., 2017) (Figure 3).

Pre-adaptation mechanisms inherent under control conditions could play a role for a better performance at HNT, for example, PAL activity in leaves was stable at higher levels under control and HNT conditions in N22, whereas increased activity was only reported under HNT in a sensitive cultivar (Moura et al., 2017). Furthermore, N22 kept N-translocation constant under HNT in comparison to a reduced N-supply in sensitive cultivars (Shi et al., 2013).

At the molecular level, a combined increase of HSPs, calcium signalling proteins and efficient nucleic acid and protein modification and repair mechanisms, particularly at the early grain-filling stage, were detected at HNT. All these changes were suggested to contribute to the enhanced HNT tolerance of N22 (Shi et al., 2013) (Figure 3).

Higher gene expression of cytokinin biosynthesis genes lead to a stable cytokinin abundance in N22 and another tolerant cultivar SY-63 pointing to the importance of hormones for the HNT response (Wu et al., 2017). Furthermore, phosphatidylinositol 3- and 4-kinase family protein, involved in inositol phosphate signalling was up-regulated in N22 (Figure 3), but absent in a sensitive cultivar at the flowering stage (Shi et al., 2013). This observation was supported by the finding that myo-inositol, also involved in the inositol phosphate metabolism, was linked to HNT tolerance in leaves (Glaubitz et al., 2017).

Despite steadily growing knowledge on the HNT stress response of N22, large omics studies including transcriptomics, proteomics, metabolomics and lipidomics and their integration for identifying major HNT responsive pathways are still missing. These studies are especially interesting in comparison with comprehensive studies under heat stress.

In a recently published field study comparing HNT responses between wet and dry seasons, the cultivars N22, Gharib and IR64 were planted only in the dry season experiment and therefore not included in the published overall comparison (Schaarschmidt, Lawas, et al., 2020). In this experiment, no classification in HNT-tolerant or HNT-sensitive cultivars was possible during the dry season. Here, we analysed the metabolic response of the cultivars N22, Gharib and IR64 in panicles and flag leaves collected at the flowering stage and leaves at the vegetative stage (Figure 4). Even though no significant yield-related changes were observed in the dry season (Figure S1), comparable also to the other cultivars within this experiment (Schaarschmidt, Lawas, et al., 2020), N22 revealed significantly higher amounts of several metabolites in panicles compared to the two sensitive cultivars. Several sugars and sugar alcohols were increased in response to HNT, for example, erythritol, serving as osmoprotective...
substance or antioxidant. Furthermore, ribitol was significantly decreased in leaves of N22. High levels of this compound in flag leaves were previously identified as marker for low yield under HNT (Schaarschmidt, Lawas, et al., 2020).

Given the importance of N22 as a HNT-tolerant model cultivar, the genome (Stein et al., 2018) and the transcriptome of N22 from control and abiotic stress conditions were sequenced on the PacBio Sequel platform and reconstructed as template for mapping RNA-seq reads (Schaarschmidt, Fischer, et al., 2020). This provides tools for the identification of new candidate genes that are important for HNT tolerance and are currently overlooked in molecular studies because a larger number of N22 specific genes are absent from common reference genomes and transcriptomes. These genes could then be integrated into high yielding varieties using, for example, the CRISPR/CAS technology to improve HNT tolerance. As an example, the newly identified gene B12288 was up-regulated in N22 during combined heat and drought stress (Schaarschmidt, Fischer, et al., 2020). This gene is a homolog of RAB21, a member of the dehydrin family of Late Embryogenesis Abundant (LEA) proteins controlling cellular membrane traffic, and was in N22 more similar to genes from wild rice species than from O. sativa ssp. japonica (Schaarschmidt, Fischer, et al., 2020).

4 | FUTURE DIRECTIONS

Suggestions for future research direction on HNT in cereals:

1. Exploration of more natural genetic diversity for HNT tolerance at the sensitive pre-flowering stage and from panicle initiation to physiological maturity

2. Usage of new sequencing technologies and information of specifically adapted genome regions, in combination with intensive omics studies, to explore highly tolerant cultivars, such as N22 (rice) or SY Monument (wheat), in comparison to selected sensitive cultivars

3. Discovery of QTL and mQTL for yield stability under HNT conditions with mapping populations including at least one HNT-tolerant cultivar

4. Development of molecular markers (metabolites and transcripts) for HNT tolerance for integration into on-going breeding efforts (Marker-assisted selection)

5. Investigation of other accompanying factors of HNT reducing yield and grain quality traits, for example, increases of night time evaporation demand (Sadok & Jagadish, 2020)

6. Intensification of research on combined stress with HNT and other abiotic stresses, which are predicted under future changing climate

7. Extension of research on the influence of HNT, particularly at the molecular level, on other cereal crops (e.g., maize, barley) and other crop species, as, for example, potato (Hastilestari et al., 2018) or oilseed rape (L. Zhou et al., 2018) for detection of common HNT responses

8. With increasing omics data availability for meta-analyses, utilization of bioinformatic models to develop hypotheses for targeted mechanistic research on HNT responses

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CONFLICTS OF INTEREST
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS
Stephanie Schaarschmidt, Ellen Zuther and S. V. Krishna Jagadish developed the manuscript idea. Lovely Mae F. Lawas, Joachim Kopka and S. V. Krishna Jagadish performed the field and metabolite profiling experiment. Stephanie Schaarschmidt performed data analysis. Stephanie Schaarschmidt and Ellen Zuther wrote the manuscript with contributions of all authors. All authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY STATEMENT
Data are available on request from the authors.

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REFERENCES
Alward, R. D., Detling, J. K., & Milchunas, D. G. (1999). Grassland vegetation changes and nocturnal global warming. Science, 283, 229–231.
Ambardekar, A. A., Siebenmorgen, T. J., Counce, P. A., Lanning, S. B., & Mauromoustakos, A. (2011). Impact of field-scale nighttime air temperatures during kernel development on rice milling quality. Field Crops Research, 122, 179–185.
Arbona, V., Manzi, M., Ollas, C., & Gómez-Cadenas, A. (2013). Metabolomics as a tool to investigate abiotic stress tolerance in plants. International Journal of Molecular Sciences, 14, 4885–4911.
Bahuguna, R. N., Solis, C. A., Shi, W., & Jagdish, K. S. V. (2017). Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (Oryza sativa L.). Physiologia Plantarum, 159, 59–73.
Boehlein, S. K., Liu, P., Webster, A., Ribeiro, C., Suzuki, M., Wu, S., & Myers, A. M. (2019). Effects of long-term exposure to elevated temperature on Zea mays endosperm development during grain fill. The Plant Journal, 99, 23–40.
Braganza, K., Karoly, D. J., & Arblaster, J. M. (2004). Diurnal temperature range as an index of global climate change during the twentieth century. Geophysical Research Letters, 31, L13287.
Chen, D., Shao, Q., Yin, L., Younis, A., & Zheng, B. (2018). Polyamine function in plants: Metabolism, regulation on development, and roles in abiotic stress responses. Frontiers in Plant Science, 9, 1945.
Chen, S., Zheng, X., Wang, D., Xu, C., Laza, M. R. C., & Zhang, X. (2013). The chamber for studying rice response to elevated nighttime temperature in field. The Scientific World Journal, 2013, 647897.
Cheng, W., Sakai, H., Hartley, A., Yagi, K., & Hasegawa, T. (2008). Increased night temperature reduces the stimulatory effect of elevated carbon dioxide concentration on methane emission from rice paddy soil. Global Change Biology, 14, 644–656.
Cheng, W., Sakai, H., Yagi, K., & Hasegawa, T. (2009). Interactions of elevated [CO2] and night temperature on rice growth and yield. Agricultural and Forest Meteorology, 149, 51–58.
Cheng, W., Sakai, H., Yagi, K., & Hasegawa, T. (2010). Combined effects of elevated [CO2] and high night temperature on carbon assimilation, nitrogen absorption, and the allocations of C and N by rice (Oryza sativa L.). Agricultural and Forest Meteorology, 150, 1174–1181.
Coast, O., Ellis, R. H., Murdoch, A. J., Quiniones, C., & Jagadish, K. S. V. (2015). High night temperature induces contrasting responses for spikelet fertility, spikelet tissue temperature, flowering characteristics and grain quality in rice. Functional Plant Biology, 42, 149–161.
Cooper, N. T. W., Siebenmorgen, T. J., & Counce, P. A. (2008). Effects of nighttime temperature during kernel development on rice physico-chemical properties. Cereal Chemistry, 85, 276–282.
Counce, P. A., Bryant, R. J., Bergman, C. J., Bautista, R. C., Wang, Y.-J., Siebenmorgen, T. J., … Meullenet, J.-F. C. (2005). Rice milling quality, grain dimensions, and starch branching as affected by high night temperatures. Cereal Chemistry, 82, 645–648.
Dai, A., Fung, I. Y., & Del Genio, A. D. (1997). Surface observed global land precipitation variations during 1900–88. Journal of Climate, 10, 2943–2962.
Davy, R., Esau, I., Chemokulsky, A., Outen, S., & Zilitinkevich, S. (2017). Diurnal asymmetry to the observed global warming. International Journal of Climatology, 37, 79–93.
Dewick, P. M. (1995). The biosynthesis of shikimate metabolites. Natural Product Reports, 12, 579–607.
Dhatt, B. K., Abshire, N., Paul, P., Hasanthika, K., Sandhu, J., Zhang, Q., … Walla, H. (2019). Metabolic dynamics of developing rice seeds under high night-time temperature stress. Frontiers in Plant Science, 10, 1443.
Dhatt, B. K., Paul, P., Sandhu, J., Hussain, W., Irvin, L., Zhu, F., … Walla, H. (2021). Allelic variation in rice fertilization independent endosperm 1 contributes to grain width under high night temperature stress. The New Phytologist, 229, 335–350.
Donat, M. G., & Alexander, L. V. (2012). The shifting probability distribution of global daytime and night-time temperatures. Geophysical Research Letters, 39, L14707.
Dong, W., Chen, J., Wang, L., Tian, Y., Zhang, B., Lai, Y., … Guo, J. (2014). Impacts of nighttime post-anthesis warming on rice productivity and grain quality in East China. The Crop Journal, 2, 63–69.
Du, Z., Zhao, J., Pan, H., Wu, Z., & Zhang, H. (2019). Responses of vegetation activity to the daytime and nighttime warming in Northwest China. Environmental Monitoring and Assessment, 191, 721.
Easterling, D. R., Horton, B., Jones, P. D., Peterson, T. C., Karl, T. R., Parker, D. E., … Folland, C. K. (1997). Maximum and minimum temperature trends for the globe. Science, 277, 364–367.
Fahad, S., Hussain, S., Saud, S., Hassan, S., Chauhan, B. S., Khan, F., … Huang, J. (2016). Responses of rapid viscoanalyzer profile and other rice grain qualities to exogenously applied plant growth regulators under high day and high night temperatures. PLos One, 11, e0159590.
Fan, Y., Tian, Z., Yan, Y., Hu, C., Abid, M., Jiang, D., … Dai, T. (2017). Winter night-warming improves post-anthesis physiological activities and sink strength in relation to grain filling in winter wheat (Triticum aestivum L.). Frontiers in Plant Science, 8, 992.
FAO. (2014) FAOSTAT Database 2014. Rom.
Fu, J., & Huang, B. (2003). Growth and physiological response of creeping bentgrass to elevated night temperature. HortScience, 38, 299–301.
Fu, Y. H., Liu, Y., De Boeck, H. J., Menzel, A., Nijs, I., Peaucelle, M., … Janssens, I. A. (2016). Three times greater weight of daytime than of nighttime temperature for the globe. Science, 357, 656–660.
Fukayama, H., Sugino, M., Fukuda, T., Masumoto, C., Taniguchi, Y., Okada, M., … Miyao, M. (2011). Gene expression profiling of rice
grown in free air CO₂ enrichment (FACE) and elevated soil temperature. *Field Crops Research*, 121, 195–199.

Gallo, K. P., Easterling, D. R., & Peterson, T. C. (1996). The influence of land use/land cover on climatological values of the diurnal temperature range. *Journal of Climate*, 9, 2941–2944.

Garcia, G. A., Drecrer, M. F., Miralles, D. J., & Serrago, R. A. (2015). High night temperatures during grain number determination reduce wheat and barley grain yield: A field study. *Global Change Biology*, 21, 4153–4164.

Garcia, G. A., Miralles, D. J., Serrago, R. A., Atzueta, I., Huth, N., & Drecrer, M. F. (2018). Warm nights in the argentine pampas: Modeling its impact on wheat and barley shows yield reductions. *Agricultural Systems*, 162, 259–268.

Garcia, G. A., Serrago, R. A., Drecrer, M. F., & Miralles, D. J. (2016). Post-anthesis warm nights reduce grain weight in field-grown wheat and barley. *Field Crops Research*, 195, 50–59.

Geange, S. R., Arnold, P. A., Catling, A. A., Coast, O., Cook, A. M., Gowland, K. M., ... Nicotra, A. B. (2020). The thermal tolerance of photosynthetic tissues: A global systematic review and agenda for future research. *New Phytologist*, 229, 2497–2513.

Glaubitz, U., Erban, A., Kopka, J., Hincha, D. K., & Zuther, E. (2015). High night temperature strongly impacts TCA cycle, amino acid and polyamine biosynthetic pathways in rice in a sensitivity-dependent manner. *Journal of Experimental Botany*, 66, 6385–6397.

Glaubitz, U., Li, X., Kühle, K. L., van Dongen, J. T., Hincha, D. K., & Zuther, E. (2014). Differential physiological responses of different rice (*Oryza sativa*) cultivars to elevated night temperature during vegetative growth. *Functional Plant Biology*, 41, 437–448.

Glaubitz, U., Li, X., Schaedel, S., Erban, A., Sulpice, R., Kopka, J., ... Zuther, E. (2017). Integrated analysis of rice transcriptomic and metabolomic responses to elevated night temperatures identifies sensitivity- and tolerance-related profiles. *Plant, Cell and Environment*, 40, 121–137.

Hasilestari, B. R., Lorenz, J., Reid, S., Hofmann, J., Pscheidt, D., Sonnewald, U., & Sonnewald, S. (2018). Deciphering source and sink responses of potato plants (*Solanum tuberosum L.*) to elevated temperatures. *Plant, Cell and Environment*, 41, 2600–2616.

Hein, N. T., Bheemanahalli, R., Wagner, D., Vennapusa, A. R., Bustamante, C., Ostmeyer, T., ... Jagadish, S. V. K. (2020). Improved cyber-physical system captured post-flowering high night temperature impact on yield and quality of field grown wheat. *Scientific Reports*, 10, 22213.

Hein, N. T., Wagner, D., Bheemanahalli, R., Šebela, D., Bustamante, C., Chiluwal, A., ... Jagadish, S. V. K. (2019). Integrating field-based heat tents and cyber-physical system technology to phenotype high night temperature impact on winter wheat. *Plant Methods*, 15, 41.

Huang, Y., Dickinson, R. E., & Chameides, W. L. (2006). Impact of aerosol indirect effect on surface temperature over East Asia. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 4371–4376.

Impa, S. M., Bheemanahalli, R., Hein, N. T., Sandhu, J., Prasad, P. V. V., Walla, H., & Jagadish, S. V. K. (2021). High night temperature effects on wheat and rice – Current status and way forward. *Plant, Cell and Environment*. https://doi.org/10.1111/pec.14028

Impa, S. M., Sunoj, V. S., J., Krassovskaya, I., Bheemanahalli, R., Obata, T., & Jagadish, S. V. K. (2019). Carbon balance and source-sink metabolic changes in winter wheat exposed to high night-time temperature. *Plant, Cell and Environment*, 42, 1233–1246.

Impa, S. M., Vennapusa, A. R., Bheemanahalli, R., Sabela, D., Boyle, D., Walla, H., & Jagadish, S. V. K. (2020). High night temperature induced changes in grain starch metabolism alters starch, protein, and lipid accumulation in winter wheat. *Plant, Cell and Environment*, 43, 431–447.

IPCC. (2014). *AR5 climate change 2014: Impacts, adaptation, and vulnerability*. Cambridge, Great Britain: Cambridge University Press.

Jagadish, S. V., Muthurajan, R., Oane, R., Wheeler, T. R., Heuer, S., Bennett, J., & Craufurd, P. Q. (2010). Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa L*). *Journal of Experimental Botany*, 61, 143–156.

Jin, M., & Dickinson, R. E. (2002). New observational evidence for global warming from satellite. *Geophysical Research Letters*, 29, 391–394.

Jing, P., Wang, D., Zhu, C., & Chen, J. (2016). Plant physiological, morphological and yield-related responses to night temperature changes across different species and plant functional types. *Frontiers in Plant Science*, 7, 1774.

Kanno, K., Mae, T., & Makino, A. (2009). High night temperature stimulates photosynthesis, biomass production and growth during the vegetative stage of rice plants. *Soil Science & Plant Nutrition*, 55, 124–131.

Karl, T. R., Kukla, G., Razuvayev, V. N., Changery, M. J., Quayle, R. G., Heim, R. L., Jr., ... Fu, C. B. (1991). Global warming: Evidence for asymmetric diurnal temperature change. *Geophysical Research Letters*, 18, 2253–2256.

Klein Tank, A. M. G., Peterson, T. C., Quadir, D. A., Dorji, S., Zou, X., Tang, H., ... Spektorman, T. (2006). Changes in daily temperature and precipitation extremes in central and South Asia. *Journal of Geophysical Research-Atmospheres*, 111, D16105.

Lanning, S. B., Siebenmorgen, T. J., Counce, P. A., Ambardar, A. A., & Maouromoustakos, A. (2011). Extreme nighttime air temperatures in 2010 impact rice chalkiness and milling quality. *Field Crops Research*, 124, 132–136.

Laza, M. R. C., Sakai, H., Cheng, W., Tokida, T., Peng, S., & Hasegawa, T. (2015). Differential response of rice plants to high night temperatures imposed at varying developmental phases. *Agricultural and Forest Meteorology*, 209–210, 69–77.

Li, H., Chen, Z., Hu, M., Wang, Z., Hua, Y., Yin, C., & Zeng, H. (2011). Different effects of night versus day high temperature on rice quality and accumulation profiling of rice grain proteins during grain filling. *Plant Cell Reports*, 30, 1641–1659.

Liao, J.-L., Zhou, H.-W., Peng, Q., Zhong, P.-A., Zhang, H.-Y., He, C., & Huang, Y.-J. (2015). Transcriptome changes in rice (*Oryza sativa*) in response to high night temperature stress at the early milky stage. *BMC Genomics*, 16, 1–14.

Ma, L., Xia, H., & Meng, Q. (2019). Spatiotemporal variability of asymmetric day and night-time warming and its effects on vegetation in the Yellow River Basin from 1982 to 2015. *Sensors*, 19, 1832.

Minocha, R., Majumdar, R., & Minocha, S. C. (2014). Polyamines and abiotic stress in plants: A complex relationship. *Frontiers in Plant Science*, 5, 175.

Mohammed, A. R., Cothren, J. T., Chen, M.-H., & Tarpley, L. (2015). 1-Methylcyclopropene (1-MCP)-induced alteration in leaf photosynthetic rate, chlorophyll fluorescence, respiration and membrane damage in rice (*Oryza sativa L.*) under high night temperature. *Journal of Agronomy and Crop Science*, 201, 105–116.

Mohammed, A. R., & Tarpley, L. (2009a). High nighttime temperatures affect rice productivity through altered pollen germination and spikelet fertility. *Agricultural and Forest Meteorology*, 149, 999–1008.

Mohammed, A. R., & Tarpley, L. (2009b). Impact of high nighttime temperature on respiration, membrane stability, antioxidant capacity, and yield of rice plants. *Crop Science*, 49, 313–322.

Mohammed, A. R., & Tarpley, L. (2009c). Instrumentation enabling study of plant physiological response to elevated night temperature. *Plant Methods*, 5, 7.

Mohammed, A. R., & Tarpley, L. (2010). Effects of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa L.*) plants. *European Journal of Agronomy*, 33, 117–123.

Mohammed, A. R., & Tarpley, L. (2011). Effects of night temperature, spikelet position and salicylic acid on yield and yield-related
parameters of rice (Oryza sativa L.) plants. Journal of Agronomy and Crop Science, 197, 40–49.

Mohammed, R., Cothren, J. T., & Tarpley, L. (2013). High night temperature and abscisic acid affect rice productivity through altered photosynthesis, respiration and spikelet fertility. Crop Science, 53, 2603–2612.

Morita, S., Yonemaru, J., & Takashani, J. (2005). Grain growth and endosperm cell size under high night temperatures in rice (Oryza sativa L.). Annals of Botany, 95, 695–701.

Moura, D., Brito, G., Campos, Â., Moraes, Í., Fagundes, P. R., & Deuner, S. (2017). Phenylalanine ammonia-lyase and source-flow-sink related attributes in rice genotypes subjected to high night temperatures. Journal of Agricultural Science, 9, 268–282.

Nagai, T., & Makino, A. (2009). Differences between rice and wheat in temperature responses of photosynthesis and plant growth. Plant and Cell Physiology, 50, 744–755.

Nagarajan, S., Jagadish, S. V. K., Prasad, A. S. H., Thomar, A. K., Anand, A., Pal, M., & Agarwal, P. K. (2010). Local climate affects growth, yield and grain quality of aromatic and non-aromatic rice in northwestern India. Agriculture, Ecosystems & Environment, 138, 274–281.

Narayanam, S., Tamura, P. J., Roth, M. R., Prasad, P. V., & Welti, R. (2016). Wheat leaf lipids during heat stress: I. High day and night temperatures result in major lipid alterations. Plant, Cell and Environment, 39, 787–803.

Peng, S., Huang, J., Sheehy, J. E., Laza, R. C., Vesperas, R. M., Zhong, X., ... Cassman, K. G. (2004). Rice yields decline with higher night temperature from global warming. Proceedings of the National Academy of Sciences, 101, 9971–9975.

Peng, S., Piao, S., Ciais, P., Myeni, R. B., Chen, A., Chevallier, F., ... Zeng, H. (2013). Asymmetric effects of daytime and night-time warming on northern hemisphere vegetation. Nature, 501, 88–92.

Prasad, P. V., Pisipati, S. R., Ristic, Z., Bukovnik, U., & Fritz, A. K. (2008). Impact of nighttime temperature on physiology and growth of spring wheat. Crop Science, 48, 2372–2380.

Qiao, Y., Liu, H., Kellomäki, S., Peltola, H., Liu, Y., Dong, B., ... Liu, M. (2014). Comparison of the effects of symmetric and asymmetric temperature elevation and CO2 enrichment on yield and evapotranspiration of winter wheat (Triticum aestivum L.). Ecology and Evolution, 4, 1994–2003.

Ramanathan, V., Ramana, M. V., Roberts, G., Kim, D., Corrigan, C., Chung, C., ... Assuring the Future of Rice Production: An Update of 2004. GeoTech Report, 1, 447–453.

Rao, B. B., Chowdary, S. P., Sandeep, V. M., Rao, V. U. M., & Rehmani, M. I. A., Wei, G., Hussain, N., Ding, C., Li, G., Liu, Z., ... Ding, Y. (2014). Yield and quality responses of two indica rice hybrids to post-anthesis asymmetric day and night open-field warming in lower reaches of Yangtze River delta. Field Crops Research, 156, 231–241.

Sadok, W., & Jagadish, S. V. K. (2020). The hidden costs of nighttime warming on yields. Trends in Plant Science, 25, 644–651.

Scharrer, S., Fischer, A., Lawas, L. M. F., Alam, R., Septiningsih, E. M., Bailey-Serres, J., ... Zuther, E. (2020). Using PacBio Iso-Seq for novel transcript and gene discovery of abiotic stress responses in Oryza sativa L. International Journal of Molecular Sciences, 21, 8148.

Scharrer, S., Lawas, L. M. F., Glaubitz, U., Li, X., Erban, A., Kopka, J., ... Zuther, E. (2020). Season affects yield and metabolic profiles of rice (Oryza sativa L.) under high night temperature stress in the field. International Journal of Molecular Sciences, 21, 3187.

Schoppach, R., & Sadok, W. (2013). Transpiration sensitivities to evaporative demand and leaf areas vary with night and day warming regimes among wheat genotypes. Functional Plant Biology, 40, 708–718.

Sharma, N., Yadav, A., Khetarpal, S., Anand, A., Sathe, L., Kumar, R. R., ... Pushkar, S. (2017). High day-night transition temperature alters nocturnal starch metabolism in rice (Oryza sativa L.). Acta Physiologiae Plantarum, 39, 74.

Shi, W., Muthurajan, R., Rahman, H., Selvam, J., Peng, S., Zou, Y., & Jagadish, K. S. (2013). Source-sink dynamics and proteomic reprogramming under elevated night temperature and their impact on rice yield and grain quality. New Phytologist, 197, 825–837.

Shi, W., Yin, X., Strulik, P. C., Solis, C., Xie, F., Schmidt, R. C., ... Jagadish, S. V. K. (2017). High day- and night-time temperatures affect grain growth dynamics in contrasting rice genotypes. Journal of Experimental Botany, 68, 5233–5245.

Shi, W., Yin, X., Strulik, P. C., Xie, F., Schmidt, R. C., & Jagadish, K. S. V. (2016). Grain yield and quality responses of tropical hybrid rice to high night-time temperature. Field Crops Research, 190, 18–25.

Sillmann, J., Kharin, V. V., Zhang, X., Zwiers, F. W., & Bronaugh, D. (2013). Climate extremes indices in the CMIP5 multimodel ensemble: Part 1. Model evaluation in the present climate. Journal of Geophysical Research-Atmospheres, 118, 1716–1733.

Stein, J. C., Yu, Y., Copetti, D., Zwickl, D. J., Zhang, L., Zheng, C., ... Wing, R. A. (2018). Genomes of 13 domesticated and wild rice relatives highlight genetic conservation, turnover and innovation across the genus Oryza. Nature Genetics, 50, 285–296.

Volder, A., Gifford, R. M., & Evans, J. R. (2015). Effects of elevated atmospheric CO2 concentrations, clipping regimen and differential day/night atmospheric warming on tissue nitrogen concentrations of a perennial pasture grass. AoB Plants, 7, plv094.

Vose, R. S., Easterling, D. R., & Gleason, B. (2005). Maximum and minimum temperature trends for the globe: An update through 2004. Geophysical Research Letters, 32, L23822.

Wada, H., Chang, F.-Y., Hatakeyama, Y., Erra-Balsells, R., Araki, T., Nakano, H., & Nonami, H. (2021). Endosperm cell size reduction caused by osmotic adjustment during nighttime warming in rice. Scientific Reports, 11, 4447.

Wang, D. R., Bunce, J. A., Tomecek, M. B., Gealy, D., McClung, A., McCouch, S. R., & Ziska, L. H. (2016). Evidence for divergence of response in indica, japonica, and wild rice to high CO2 × temperature interaction. Global Change Biology, 22, 2620–2632.

Wang, Y., Tao, H., Tian, B., Sheng, D., Xu, C., Zhou, H., ... Wang, P. (2019). Flowering dynamics, pollen, and pistil contribution to grain yield in response to high temperature during maize flowering. Environmental and Experimental Botany, 158, 80–88.

Wani, S. H., Kumar, V., Shriram, V., & Sah, S. K. (2016). Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal, 4, 162–176.

Welch, J. R., Vincent, J. R., Auffhammer, M., Moya, P. F., Dobermann, A., & Dawe, D. (2010). Rice yields in tropical/subtropical Asia exhibit large but opposing sensitivities to minimum and maximum temperatures. Proceedings of the National Academy of Sciences, 107, 14562–14567.

Winkel-Shirley, B. (2002). Biosynthesis of flavonoids and effects of stress. Current Opinion in Plant Biology, 5, 218–223.

Wu, C., Cui, K., Wang, W., Li, Q., Fahad, S., Hu, Q., ... Peng, S. (2017). Heat-induced cytokinin transportation and degradation are associated with reduced panicle cytokinin expression and fewer spikelets per panicle in rice. Frontiers in Plant Science, 8, 371.

Wu, C., Cui, K., Wang, W., Li, Q., Fahad, S., Hu, Q., ... Peng, S. (2016). Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice. Scientific Reports, 6, 34978.

Xu, J., Henry, A., & Sreenivasulu, N. (2020). Rice yield formation under high day and night temperatures - a prerequisite to ensure future food security. Plant, Cell and Environment, 43, 1595–1608.

Xu, J., Misra, G., Sreenivasulu, N., & Henry, A. (2021). What happens at night? Physiological mechanisms related to maintaining grain yield under high night temperature in rice. Plant, Cell & Environment.

Xu, Z. S., Li, Z. Y., Chen, Y., Chen, M., Li, L. C., & Ma, Y. Z. (2012). Heat shock protein 90 in plants: Molecular mechanisms and roles in stress...
responses. *International Journal of Molecular Sciences*, 13, 15706–15723.

Yamakawa, H., & Hakata, M. (2010). Atlas of rice grain filling-related metabolism under high temperature: Joint analysis of metabolome and transcriptome demonstrated inhibition of starch accumulation and induction of amino acid accumulation. *Plant and Cell Physiology*, 51, 795–809.

Yang, Z., Zhang, Z., Zhang, T., Fahad, S., Cui, K., Nie, L., ... Huang, J. (2017). The effect of season-long temperature increases on rice cultivars grown in the central and southern regions of China. *Frontiers in Plant Science*, 8, 1908.

Zhang, Y., Tang, Q., Peng, S., Zou, Y., Chen, S., Shi, W., ... Laza, M. R. C. (2013). Effects of high night temperature on yield and agronomic traits of irrigated rice under field chamber system condition. *Australian Journal of Crop Science*, 7, 7–13.

Zhao, X., & Fitzgerald, M. (2013). Climate change: Implications for the yield of edible rice. *PLoS One*, 8, e66218.

Zhou, L., Yan, T., Chen, X., Li, Z., Wu, D., Hua, S., & Jiang, L. (2018). Effect of high night temperature on storage lipids and transcriptome changes in developing seeds of oilseed rape. *Journal of Experimental Botany*, 69, 1721–1733.

Zhou, Y., & Ren, G. (2011). Change in extreme temperature event frequency over mainland China, 1961–2008. *Climate Research*, 50, 125–139.

Ziska, L., & Manalo, P. (1996). Increasing night temperature can reduce seed set and potential yield of tropical rice. *Functional Plant Biology*, 23, 791–794.

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