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Response of phytohormone homeostasis to heat stress and the roles of phytohormones in rice grain yield: a review

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Rice is highly susceptible to heat stress at the reproductive stage. In this review, we first summarize recent progress in heat effects on rice grain yield during different reproductive stages. Different responses of yield traits of rice to heat stress during different reproductive stages are identified. The number of spikelets per panicle is reduced by heat stress during the early reproductive stage but is not affected by heat stress during the mid-late reproductive stage. Spikelet sterility induced by heat stress can be attributed primarily to physiological abnormalities in the reproductive organs during flowering but attributed to structural and morphological abnormalities in reproductive organs during panicle initiation. The lower grain weight caused by heat stress during the early reproductive stage was due to a reduction in non-structural carbohydrates, undeveloped vascular bundles, and a reduction in grain length and width, while a shortened grain filling duration, reduced grain filling rate, and decreased grain width affect grain weight when heat stress occurs during grain filling. Phytohormones play vital roles in regulating plant adaptations against heat stress. We discuss the processes involving phytohormone homeostasis (biosynthesis, catabolism, deactivation, and transport) in response to heat stress. It is currently thought that biosynthesis and transport may be the key processes that determine phytohormone levels and final grain yield in rice under heat stress conditions. Finally, we prospect that screening and breeding rice varieties with comprehensive tolerance to heat stress throughout the entire reproductive phase could be feasible to cope with unpredictable heat events in the future. Studies in phytohormone homeostatic response are needed to further reveal the key processes that determine phytohormone levels under heat condition.
Response of phytohormone homeostasis to heat stress and the roles of phytohormones in rice grain yield: a review

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Abstract

Rice is highly susceptible to heat stress at the reproductive stage. In this review, we first summarize recent progress in heat effects on rice grain yield during different reproductive stages. Different responses of yield traits of rice to heat stress during different reproductive stages are identified. The number of spikelets per panicle is reduced by heat stress during the early reproductive stage but is not affected by heat stress during the mid-late reproductive stage. Spikelet sterility induced by heat stress can be attributed primarily to physiological abnormalities in the reproductive organs during flowering but attributed to structural and morphological abnormalities in reproductive organs during panicle initiation. The lower grain weight caused by heat stress during the early reproductive stage was due to a reduction in non-structural carbohydrates, undeveloped vascular bundles, and a reduction in grain length and width, while a shortened grain filling duration, reduced grain filling rate, and decreased grain width affect grain weight when heat stress occurs during grain filling. Phytohormones play vital roles in regulating plant adaptations against heat stress. We discuss the processes involving phytohormone homeostasis (biosynthesis, catabolism, deactivation, and transport) in response to heat stress. It is currently thought that biosynthesis and transport may be the key processes that determine phytohormone levels and final grain yield in rice under heat stress conditions. Finally, we prospect that screening and breeding rice varieties with comprehensive tolerance to heat stress throughout the entire reproductive phase could be feasible to cope with unpredictable heat events in the future. Studies in phytohormone homeostatic response are needed to further reveal the key processes that determine phytohormone levels under heat condition.
Key words: Rice grain yield; Heat stress; Spikelet fertility; Grain weight; Spikelets per panicle;
Phytohormone homeostasis
Introduction

Human activities have triggered climate change, which is characterized by global warming. The global change in climate represents one of the most serious challenges that humans have had to face (Marsicek et al., 2018). Crop production and food security are essential components of agriculture, and each is directly and seriously affected by climate change. Rice is a staple food for approximately half of the world’s population. Frequent heat waves have had serious impacts on rice production (Zhang et al., 2014). An analysis of historical data showed that rice grain yield decreased by 14% for every 1°C increase in the daily average temperature (Aggarwal, 2009).

Rice plants are vulnerable to heat stress during the reproductive phase (Boote et al., 2005). Heat stress will occur more frequently and unpredictably as global warming continues to worsen, which may cause rice plants to suffer heat stress at any time during their reproductive stages (Marsicek et al., 2018). Previously, most of the studies evaluated the responses of heat stress and the underlying mechanisms during the mid-late reproductive phase (Wu & Cui, 2014). A risk assessment of the spatiotemporal variation of high temperature events during the past 20 years indicated that heat events occurred in the middle and lower reaches of the Yangtze River, one of the major paddy rice production areas in China, as early as mid-early July (Lin et al., 2016), during which panicle formation of midseason rice occurs, resulting in disrupted panicle development and finally yield loss (Wu et al., 2016). It was previously reported that rice plants respond differently to heat stress during different developmental stages (Shi et al., 2015). However, few articles reached conclusions concerning the different effects of heat on rice grain yield at different reproductive stages (Fahad et al., 2018). Therefore, the present review offers a full conclusion regarding the effects of heat on rice grain yield during the reproductive phase (panicle initiation, flowering, and grain filling), and the distinct variations in rice grain yield based on the timing of the heat stress during the three reproductive stages are also identified.

Phytohormones play an important role in coordinating the response to heat stress in rice plants. Most of the previous studies have explored the phytohormonal mechanisms of the effects of heat stress on rice grain yield by analysing phytohormone levels in rice (Fahad et al., 2015). Phytohormone levels in target organs are associated with processes involved in phytohormone homeostasis, e.g., biosynthesis, catabolism, deactivation, and transport (phytohormones acting as mobile signals should be considered) (Sakakibara, 2010), but our work on the responses of phytohormone homeostasis to heat stress is far from adequate. This review provides insights into the physiological mechanisms of the rice heat stress response by considering the roles of homeostasis of phytohormones (cytokinin, CTK; Indole-3-acetic acid, IAA; gibberellins, GAs; abscisic acid, ABA) in grain yield.

Survey Methodology
Research papers published both in English and in Chinese were searched from the Web of Science and the China National Knowledge Infrastructure (CNKI, the largest Chinese Academic Journals database) from 1950-2018, respectively. There are six search terms: “rice AND high temperature/heat/warming” and “high temperature/heat/warming AND phytohormone”. An initial search resulted in 26618 articles, which were reduced to 8813 by limiting research to plant science, agronomy, cell biology, physiology, biology, developmental biology, and environmental science. We focus mainly on response of physiological and molecular aspects involving phytohormone homeostasis in rice varieties to heat stress. Then, we examined the article titles, abstracts, key words to judge their relevance, and 2115 articles were considered relevant. There were 15 studies in other crops (barley, wheat, tomato, etc) and Arabidopsis which were highly relevant to the topic of this review, were also included.

Effects of heat stress on grain yield and yield components

Heat stress definition and the maximum temperature for rice

Heat stress is defined as an increase in temperature beyond a critical threshold and for a certain period of time that results in irreversible damage to plant growth and development (Wu, 2016). Heat injury depends on the intensity and duration of exposure to high temperatures and can be subdivided into two categories: (i) short periods of exposure to extreme high temperatures and (ii) long periods of exposure to sub-high temperatures (Berry & Bjorkman, 1980). Rice plants are highly susceptible to heat stress during their reproductive phase. The early reproductive phase in rice is referred to as the period from panicle initiation to booting (stages R0-R3 in Figure1), during which the maximum temperature for rice growth is 33.1°C. The mid-late reproductive phase represents the period from heading to physiological maturity and includes flowering (stage R4 in Figure1) and grain filling (stages R5-R9 in Figure1), the maximum temperature for rice growth is 37°C and 31.3 °C during flowering and grain filling, respectively (Counce et al., 2000; Itoh et al., 2005; Sánchez et al., 2014). Heat stress reduces rice grain yield during the reproductive phase, but the impacts on grain yield and its components differ when heat stress occurs at different reproductive stages (Shi et al., 2015).

Effects of heat stress on the number of spikelets per panicle

The reduction in the number of spikelets per panicle in heat-stressed plants is due to the attenuated differentiation of secondary branches and their attached florets as well as the promotion of their degradation during the early reproductive phase, but heat stress does not affect the differentiation of primary branches and their attached florets (Wu et al., 2016). The differentiation of secondary branches and their attached florets is more sensitive to environmental factors than that of primary branches and their attached florets (Ding et al., 2014). Heat stress does not affect the number of spikelets per panicle during the mid-late reproductive phase.

Effects of heat stress on spikelet fertility
During the early reproductive stage, heat stress induces panicle enclosure (Wu et al., 2016). In an enclosed panicle, the spikelets in the lower region are surrounded by an enclosing sheath (the lower surrounded spikelets), while spikelets in the upper region of the panicle can successfully expand out of the sheath (the upper expanded spikelets), as illustrated in Figure 1. For the lower surrounded spikelets, spikelet sterility in heat-stressed plants was associated with failure of pollination due to the physical hindrance of the enclosing sheath (Wu et al., 2016). For the upper expanded spikelets, structural abnormalities in the anthers, disrupted function of the septum and tapetum (Wang et al., 2016a), inhibition of microsporogenesis, reductions in the starch accumulation and cytoplasm in pollen (Sakata et al., 2000), and morphological and physiological abnormalities of the stigma (Takeoka et al., 1991) collectively reduced the possibility of successful pollination in heat-stressed rice plants (Matsui & Omasa, 2002).

During the flowering stage, spikelet sterility in heat-stressed plants is associated with reduced functionality of female and male organs. Impaired female and male organs account for 34% and 66%, respectively, of spikelet sterility under heat stress conditions (Fábián et al., 2019). Behaviours of female and male organs affect pollination and fertilization, which are impacted by heat stress: (i) the septum ruptures, and stomium splits occur in the anthers. Heat stress delays or even blocks septum ruptures due to inhibition of pollen swelling (Wilson et al., 2011), which is partially attributed to a disturbance in water metabolism under heat stress conditions (Matsui & Omasa, 2002). (ii) Pollen sheds onto the stigmas. Heat stress disturbs anther dehydration, resulting in sticky pollen grains that are retained inside the locules of dehiscent anthers, as supported by our previous observation (Figure 2B). (iii) Pollen germination, pollen tube penetration, and sperm delivery to the sac are affected. Heat stress affects the balance of ions (such as K+ and Ca²⁺) (Yan et al., 2002), carbohydrate metabolism (Firon et al., 2006), and regulators (phytohormones) in pollen (Sakata et al., 2010), as well as stigma vigour (Zhang et al., 2014), which collectively reduces pollen germination and pollen tube polarized growth.

Notably, anther dehiscence is the initial step of pollination and is highly susceptible to heat stress and thus was suggested as a selective marker for screening heat tolerance (Matsui & Omasa, 2002). However, we observed that heat stress prevents the majority of pollen grains from escaping the dehisced anthers (Figure 2B), thus reducing the number of pollen grains available for successful pollination. This result may explain why the percentage of dehisced thecae (indicated by a basal or apical slit or aperture) was not always strongly correlated with spikelet fertility under heat stress conditions (Kobayashi et al., 2011). Thus, simply screening for slits or apertures in the anthers cannot ensure successful pollination in heat-stressed plants. We propose that dehisced anthers, characterized by slits or apertures, as well as low levels of residual pollen grains are guarantees for effective pollination.

In summary, spikelet sterility induced by heat stress can be attributed primarily to physiological abnormalities in the reproductive organs during flowering, and the associated mechanisms of the effects of
heat stress during the early reproductive phase are different, which is mainly attributed to structural and morphological abnormalities in reproductive organs (Figure 3).

**Effects of heat stress on grain weight**

Rice grain weight is determined by multiplying grain volume by grain plumpness. Heat stress had adverse effects on grain volume and grain plumpness during the reproductive phase (Wang et al., 2016b). The small grain size in heat-stressed rice plants was characterized by both reduced grain width and reduced grain length when suffering from high temperature stress during the panicle initiation stage (Takeoka et al., 1991; Wu et al., 2016), but it was attributed to reduced grain thickness when suffering from high temperature stress during the grain filling stage (Mohammed et al., 2013). Grain plumpness was associated with the duration of grain filling and the grain filling rate. The reduction in grain plumpness induced by heat stress during the early reproductive phase was associated with a reduced content of non-structural carbohydrates in stems (Li, 2012) and hindered vascular bundle development (Zhang et al., 2009) but was due to the shortened duration of grain filling, although the grain filling rate was increased by moderately high temperatures during the grain filling stage (Cao et al., 2016; Dou et al., 2017). Notably, the early termination of grain filling induced by moderately high temperatures was the result of lower sink activity due to the early senescence of the panicle, not a lack of assimilation (Kim et al., 2011).

In conclusion, the lower grain weight caused by heat stress during the early reproductive phase is due to reduced non-structural carbohydrates, undeveloped vascular bundles, and reduced grain length and width, but it is attributed to a shortened grain filling duration, reduced grain filling rate, and decreased grain width when exposure to heat stress occurs during grain filling (Figure 3).

**Responses of phytohormones to heat and their role in yield components**

**Phytohormone changes affect the spikelets per panicle under heat stress**

Heat stress reduced the content of CTK. Reductions in the CTK contents of heat-stressed rice plants were due to (i) reduced long-distance transport of CTKs from the roots to the shoots; (ii) inhibited CTK biosynthesis through decreased biosynthesis of related enzymes (isopentenylation of adenosine phosphate by isopentenyltransferases, IPT; cytochrome P450 mono-oxygenase, CYP735A; LONELY GUY, LOG); and (iii) increased catabolism of CTK due to the higher activity of CTK metabolism-related enzymes (cytokinin oxidase/dehydrogenase, CKX) and CTK glycosylation (Skalák et al., 2016; Tripathi et al., 2012; Vyroubalová et al., 2009; Wu et al., 2017; Wu et al., 2016). Additional studies are necessary to understand how the membrane transport of CTK is involved in the response to heat stress (Figure 4A).

The number of spikelets per panicle is mainly affected by heat stress during panicle initiation (Figure 3).
Changes in the content of CTK and CTK homeostasis in young panicles regulated the number of spikelets per panicle in rice (Ha et al., 2012). Under heat stress conditions, heat-susceptible varieties showed significant reductions in panicle CTKs that were accompanied by reduced spikelets per panicle in response to heat stress, while a heat-tolerant variety had stable levels of panicle CTKs and a higher relative number of spikelets per panicle in response to heat stress. Changes in panicle CTKs correlated with a decrease in spikelets per panicle (Wu et al., 2016). We determined that enhanced transport of root-derived CTKs and stable CKX activity in panicles are the two key processes that play a vital role in maintaining panicle size in rice varieties (Wu et al., 2017). In Arabidopsis, reduced degradation, stable local biosynthesis, and/or enhanced transportation of CTK from the roots likely contributed to the stability of CTK in target organs and facilitated adaptations to abiotic stress (Ha et al., 2012). Genetic manipulation of CTK transport and degradation will be useful to stabilize panicle size in rice under heat stress.

**Phytohormone changes affect spikelet fertility under heat stress**

Spikelet fertility is affected by heat stress during panicle initiation and flowering (Figure 3). In rice, reduced levels of IAA in young panicles were closely related to decreased spikelet fertility, anther dehiscence and pollen vigour (Wu et al., 2016). In barley and Arabidopsis, lower levels of IAA in anthers were attributed to reduced expression of the IAA biosynthesis gene *YUCCA*, leading to anther indehiscence and lower pollen vigour that could be rescued by the application of exogenous IAA (Sakata et al., 2010). However, in cotton plants, high levels of background IAA weakened the defence response of the anthers to heat stress (Min et al., 2014). It is speculated that excessively low or high levels of IAA due to disturbances in IAA homeostasis during the response to heat stress are deleterious to anther dehiscence. Recently, it was found that heat stress during panicle initiation reduced spikelet fertility by inducing panicle enclosure, which can be mainly attributed to deficiencies in GA$_1$ and IAA (Wu et al., 2016). IAA regulates panicle expansion by regulating GA$_1$ biosynthesis (Yin et al., 2007); we speculate that panicle enclosure in heat-stressed plants may be attributed to reduced GA$_1$ biosynthesis due to the changes in IAA induced by heat stress.

Heat stress suppressed the biosynthesis of IAA by downregulating genes involved in IAA biosynthesis, including tryptophan aminotransferase-encoding gene (*TAA1/TARs*), YUC flavin monooxygenases (*YUC*), and UDP-glucosyltransferase 74b1 (*UGT74B1*) (Guo et al., 2016; Sharma et al., 2018), and reduced IAA by upregulating the IAA-amino acid synthetase gene (*GH3*) in rice (Du et al., 2012), which positively regulates the formation of IAA-amino acid conjugates (Mittag et al., 2015). However, there is limited information on the response of genes involved in the degradation of IAA-amino acid conjugates (*ILR1, IAR3*) and the transportation of IAA (*AUX1, LAX3, PIN1*) during heat stress in rice. In peas, monitoring an isotope labelled $^{14}$C-IAA in the root tissues revealed that heat stress reduced IAA transport (Gladish et al., 2000), but the sensitivity of the diffusion component (the IAA-influx/efflux gene) to temperature and IAA concentration has not been determined. In summary, heat stress suppressed the biosynthesis of IAA and promoted the formation
of IAA-amino acid conjugates, yet information on the effects of heat on the catabolism and transport of IAA in rice plants is limited (Figure 4C).

Heat stress reduced the content of GAs in young panicles of rice varieties (Wu et al., 2016). The GA biosynthetic pathway is catalysed by several enzymes. In Arabidopsis, the GA 20-oxidase genes \((GA20ox1, GA20ox2, GA20ox3)\) and GA3-oxidase genes \((GA3ox1, GA3ox2)\) that regulate the late steps of the GA biosynthetic pathway were suppressed by heat stress (Toh et al., 2008). However, the genes that regulate the early steps of the GA biosynthetic pathway, including ent-copalyl diphosphate synthase \((OsCPS1)\), ent-kaurene synthase \((OsKS1)\), ent-Kaurene oxidase \((OsKO2)\), and ent-kaurenoic acid oxidase \((OsKAO)\), have seldom been investigated under heat stress conditions in plants. The responses of the catabolism-related genes \((GA 2-oxidases, OsGA2oxs)\) and transport-related genes \((OsNPF, OsSWEET)\) to heat stress are also limited. According to existing results, heat stress suppressed the biosynthesis and promoted the deactivation of GA, but few studies to date have documented the effects of heat on catabolism and the transport of GA in rice plants (Figure 4D).

The major cause of spikelet sterility in rice was heat stress-mediated decline in the endogenous IAA level in anthers, which was associated with the expression levels of IAA biosynthesis \((YUC)\) and transport genes \((AUX, PIN)\) in rice under high temperature (Sharma et al., 2018). In barley and Arabidopsis, the \(YUC\) gene affected spikelet fertility by regulating male sterility under heat stress (Sakata et al., 2010). GA is also a key phytohormone for spikelet fertility, but the molecular genetic and biochemical mechanisms of GA in male fertility remain largely unknown (Kwon & Paek, 2016). In thermo-sensitive genic male sterile lines, heat stress suppressed the expression of the \(EUI\) gene, which induced the deactivation of GA (Xiao et al., 2005). Further studies on the role of GA homeostasis in spikelet fertility under heat stress are needed.

Phytohormone changes affect grain weight under heat stress

Grain weight is impaired by heat stress during panicle initiation and grain filling (Figure 3). Formation of grain weight is regulated by phytohormones under heat stress. (i) From a physiological perspective, grain weight is determined by multiplying the endosperm number by the endosperm weight, which is regulated by phytohormones such as CTK, ABA, and IAA (Javid et al., 2011; Nayar et al., 2013). Changes in endosperm CTK, IAA, and ABA in response to heat stress lead to changes in grain weight in rice varieties (Cao et al., 2016). In wheat, changes in grain weight are accompanied by changes in grain CTK content under heat stress, and exogenous CTK is able to increase the final grain weight under heat conditions (Banowetz et al., 1999). (ii) From an agronomic perspective, grain weight is determined by multiplying the grain filling rate by the duration of grain filling, and these metrics are regulated by phytohormones during heat stress. ① Grain filling rate. Changes in the grain filling rate are closely associated with the response of phytohormones such as ABA and GA (Liu et al., 2007). ② Duration of grain filling. Early panicle senescence in heat stress-stressed plants is the main cause of shorter periods of grain filling (Kim et al., 2011). The stay-green trait mitigated the negative
impacts of heat stress on grains due to an extended period of grain filling in rice (Kobata et al., 2015). Enhanced CTK synthesis or increased CTK transportation from the roots to the shoots via sap in the xylem delayed plant senescence (Singh et al., 1992) and may enhance heat tolerance.

ABA, which acts as an important mobile signal, is synthesized in the roots and transported to target organs via the xylem and phloem (Kuromori et al., 2010). Heat stress had no overt effects on the ABA concentration in the roots but increased the amount of continuous xylem sap flow for at least two weeks in rice plants (Wu et al., 2017). Our previous data indicated that changes in ABA transportation in rice were closely correlated with the effects of heat on the panicle ABA content ($r=0.66$, $P<0.05$, $n=12$). In aerial organs, heat exposure increased the ABA content by upregulating ABA biosynthesis-related genes, including the zeaxanthin epoxidase genes ($ABA1$, $ABA2$, $ABA4$, $AAO3$) and the 9-cis-epoxycarotenoid dioxygenase genes ($NCED2$, $NCED5$, $NCED9$), but downregulated the ABA 8’-hydroxylase gene $CYP707A$ (Toh et al., 2008), the glucosyltransferase gene $UGT75B1$, and the glucosidase gene $AtBG1$ (Dobrá et al., 2015). Figure 4B illustrates the processes involved in ABA homeostasis that respond to heat stress. However, little is known about the key processes that determine the ABA content in target organs under heat stress. ABA transport and the processes involved in ABA metabolism should be studied in parallel to understand the response of local ABA contents to heat stress.

**Perspectives**

Heat events will occur more seriously and frequently as global warming continues, and rice plants may be affected by heat events at any growth stage. Although many heat-tolerant rice varieties have been identified, most of these varieties endure heat injury only at specific reproductive stages. For example, the heat-tolerant cv. Nagina22 exhibits relatively high grain yield under heat stress at flowering but is highly susceptible to heat during the panicle initiation stage (Wu et al., 2016). Critical traits, such as high anther dehiscence (Zhang et al., 2014), low stigma exsertion (Wu et al., 2018), early morning flowering (Jagadish et al., 2007) are useful for heat tolerance at flowering, but useless to heat stress during panicle initiation or grain filling. Further studies should focus on the effect of heat stress on rice plants and the underlying mechanisms during all the reproductive stages. To cope with unpredictable heat events in the future, we should screen and breed rice varieties with comprehensive tolerance to heat stress throughout the entire reproductive phase.

The physiological and molecular mechanisms of heat effects on rice grain yield have drawn much attention. The existing studies explore the phytohormonal mechanisms of the effects of heat stress on rice grain yield by analysing phytohormone levels in rice. Most of previous studies focus on responses of biosynthesis and catabolism of phytohormones to heat stress in rice, but studies on responses of phytohormone to heat stress are relatively fewer. Full understanding of the phytohormone homeostatic response will help to reveal the key processes that determine phytohormone levels and final grain yield in rice under heat stress conditions. Thus,
future work will provide a theoretical basis for the establishment of technology for breeding heat-tolerant varieties and mitigating heat injury in rice.

Conclusions

Rice is susceptible to heat stress during the reproductive phase, e.g., panicle initiation, flowering, and grain filling stage. The current study identified different responses of yield traits of rice to heat stress during different reproductive stages: (i) the number of spikelets per panicle is reduced by heat stress during panicle initiation stage but is not affected by heat stress during flowering and grain filling stage; (ii) spikelet sterility induced by heat stress can be attributed primarily to physiological abnormalities in the reproductive organs during flowering stage but attributed to structural and morphological abnormalities in reproductive organs during panicle initiation stage; and (iii) the lower grain weight caused by heat stress during panicle initiation stage was due to a reduction in non-structural carbohydrates, undeveloped vascular bundles, and a reduction in grain length and width, while a shortened grain filling duration, reduced grain filling rate, and decreased grain width affect grain weight when heat stress occurs during grain filling stage.

Responds of processes involving phytohormone homeostasis (biosynthesis, catabolism, deactivation, and transport) play vital roles in regulating plant adaptations to heat stress. Currently, biosynthesis and transport are supposed be the key processes that determine phytohormone levels and final grain yield in rice under heat stress. Prospectively, screening and breeding of rice varieties with comprehensive tolerance to heat stress during panicle initiation, flowering, and grain filling could be feasible to cope with unpredictable heat events in the future. In aspect of physiological mechanisms, studies in phytohormone homeostatic response are needed to further reveal the key processes that determine phytohormone levels under heat condition.

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Additional Information

Competing financial interests

The authors declare no competing financial interests.

Figure legends

**Figure 1. Illustrations of the panicle enclosure induced by heat stress, (Photo Credit: Chao Wu).**

**Figure 2. The effects of heat stress on anther dehiscence and pollen release, (Photo Credit: Chao Wu).** A: the dehisced anthers with no adhered pollen under heat stress; B: the dehisced anthers with adhered pollens inside the anthers under heat stress. Red arrow indicates residual pollen grains in anthers, and blue arrow indicates aperture of the thecae.

**Figure 3. Illustration of the effects of heat on yield components during the reproductive phase in rice.** R0: panicle development has initiated; R1: panicle branches have formed; R2: flag leaf collar formation; R3: panicle exertion from boot; R4: one or more florets on the main stem panicle has reached anthesis; R5: at least one caryopsis on the main stem panicle is elongation to the end of the hull; R6: at least one caryopsis on the main stem panicle has elongated to the end of the hull; R7: at least one grain on the main stem panicle has a yellow hull; R8: at least one grain on the main stem panicle has a brown hull; and R9: all grains that reached R6 have brown hulls. Illustration of reproductive stages with morphological makers were adapted from
Figure 4. Response of processes involving homeostasis cytokinin, indoleacetic acid, abscisic acid, and gibberellin. +, - , O , and ? indicate an increase, a decrease, and steadiness, and undefined response, respectively, in a certain trait or process under heat conditions.
Figure 1

Figure 1. Illustrations of the panicle enclosure induced by heat stress, (Photo Credit: Chao Wu).
Figure 2

Figure 2. The effects of heat stress on anther dehiscence and pollen release, (Photo Credit: Chao Wu).

A: the dehisced anthers with no adhered pollen under heat stress; B: the dehisced anthers with adhered pollens inside the anthers under heat stress. Red arrow indicates residual pollen grains in anthers, and blue arrow indicates aperture of the thecae.
Figure 3

Illustration of the effects of heat on yield components during the reproductive phase in rice.

R0: panicle development has initiated; R1: panicle branches have formed; R2: flag leaf collar formation; R3: panicle exertion from boot; R4: one or more florets on the main stem panicle has reached anthesis; R5: at least one caryopsis on the main stem panicle is elongation to the end of the hull; R6: at least one caryopsis on the main stem panicle has elongated to the end of the hull; R7: at least one grain on the main stem panicle has a yellow hull; R8: at least one grain on the main stem panicle has a brown hull; and R9: all grains that reached R6 have brown hulls. Illustration of reproductive stages with morphological markers were adapted from (Counce et al., 2000)
Figure 4

Response of processes involving homeostasis cytokinin, indoleacetic acid, abscisic acid, and gibberellin.

+ , - , O , and ? indicate an increase, a decrease, and steadiness, and undefined response, respectively, in a certain trait or process under heat conditions.