



Heat stress-reduced kernel weight in rice at anthesis is associated with impaired source-sink relationship and sugars allocation



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ARTICLE INFO

Keywords:

Oryza sativa L.
Heat stress
Kernel weight
Sugars allocation
Phytohormones
Source-sink relationship

ABSTRACT

Heat stress is one of the most limiting factors in rice plant growth and development. However, the impairment in the whole-plant carbohydrate partitioning at anthesis caused by heat stress is seldom documented. Two rice genotypes with different heat tolerance, namely Nipponbare (NIPP) and its high-temperature susceptible (HTS) mutant were subjected to heat stress of 40 °C for 12 d at anthesis. Heat stress significantly decreased the spikelet fertility and kernel weight, and a larger decline was found in HTS than in NIPP plants compared with their respective controls. However, there was no significant difference in photosynthesis in flag leaf and starch branching enzyme activity in grain between the control and heat-stress groups. Thus, heat stress-induced decline in kernel weight was most likely due to the inhibition of the assimilate distribution rather than the limitation of the source and sink. This assumption was confirmed by the distribution of dry matter weight, nonstructural carbohydrates (NSC) and starch in grain, leaf and sheath-stem observed under heat stress. Indeed, the *sucrose transporter (SUT)* genes, *sucrose synthase (SUS)* genes and phytohormones in grain and the callose deposition in plasmodesmata of leaf and sheath were involved in the process. However, the patterns of change in phytohormones in leaf and sheath-stem were different from those of carbohydrates, but exogenous sucrose alleviated the heat-stress effect on the spikelet fertility, kernel weight, dry matter weight accumulation and allocation. Thus, sugars rather than phytohormones might act as a signal molecule to mediate the source-sink relationship in rice under heat stress.

1. Introduction

Extreme heat events are expected to become more severe, frequent, and persistent as the greenhouse gas emissions increase due to the human activity (Meehl and Tebaldi, 2004). It is estimated that global warming and extreme heat events will exert negative effects on agricultural production in the future (Rosenzweig et al., 2014), which can severely reduce crop yield and quality, especially for rice (Deryng et al., 2014; Lobell et al., 2011). As one of the major staple cereals in the world, rice provides essential caloric requirement for billions of people (Khush, 2005). However, rice is susceptible to heat stress at the

reproductive stage, the grain yield always suffers heavy losses and may even produce no harvest when high temperature climate occurs at anthesis (Jagadish et al., 2011; Fu et al., 2016).

Heat stress at anthesis not only causes spikelet sterility in rice, but also markedly reduces the kernel weight (Fu et al., 2016; Zhang et al., 2016), which is mainly due to the inhibition of photosynthesis in leaves and the activity of key enzymes of starch synthesis in grains (Hermann and Gabriel, 2013; Kato et al., 2007; Long et al., 2015; Wang et al., 2012). It has been established that the reduction of photosynthesis by heat stress leads to insufficient sucrose in leaves and decreases export into the phloem. Additionally, the activity of key enzymes of starch

Abbreviations: DAA, days after anthesis; ELISA, enzyme-linked immunosorbent assay; SUT, sucrose transporter; Fv/Fm, maximum fluorescence quantum yield of photosystem II; HTS, high temperature susceptible mutant; NIPP, Nipponbare; NSC, nonstructural carbohydrates; PD, plasmodesmata; P_N, net photosynthetic rate; SPS, sucrose phosphate synthase; TEM, transmission electron microscopy; INV, invertase; VIN, vacuolar invertase; CWIN, cell-wall invertase; SUS, sucrose synthase; IAA, indole-3-acetic acid; ABA, abscisic acid; GAs, gibberellins; ZRs, zeatin riboside; Y(II), actual fluorescence quantum yield of photosystem II

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<https://doi.org/10.1016/j.envexpbot.2018.08.021>

Received 7 February 2018; Received in revised form 8 July 2018; Accepted 16 August 2018

Available online 22 August 2018

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synthesis is susceptible to heat stress, which can significantly decrease the grain yield by inhibiting starch synthesis and accumulation in grains (Phan et al., 2013; Fu et al., 2016). Indeed, to some extent, the sink activity, rather than the source activity, is mainly responsible for the decline in grain yield under heat stress, as indicated by the remarkable increase in the plant biomass production under high temperature conditions (Suwa et al., 2010). Moreover, heat stress at 40 °C has little adverse effect on leaf photosynthesis due to the strong transpiration rate in leaves to reduce tissue temperature, whereby the leaf temperature is only about 34–35 °C (Zhang et al., 2016). Regarding the sink activity, including the starch branching enzyme activity, it was significantly decreased in grains under heat stress, but little difference was found in the decrease between the two rice cultivars with different heat tolerance compared with their respective controls (Fu et al., 2016). However, a larger decline in kernel weight caused by heat stress was found in the heat susceptible cultivar compared with the tolerant one (Fu et al., 2016). This was considered to be most likely due to the inhibition of the sucrose transport and metabolism in the phloem of leaf, sheath-stem and grains, instead of the limitation of leaf photosynthesis and sink activity under heat stress, which have seldom been reported previously.

Sucrose, the main form of sugar transported in rice, is produced by photosynthetic source tissues, such as leaf, and then transports through the phloem to the sink tissues via the apoplastic or symplastic pathway (De Schepper et al., 2013; Eom et al., 2012; Ruan, 2012; Scofield et al., 2007). Symplastic phloem loading or unloading rely on the plasmodesmata, while the apoplastic pathway requires multiple classes of sucrose transport proteins, such as sucrose transporters (SUTs) and sugar transporter family (SWEETs), for sucrose to traverse cell membranes (Ayre, 2011; Bihmidine et al., 2013; Chen, 2014; Eom et al., 2015; Yadav et al., 2015). Until now, about five *SUT* genes have been identified in rice, among them *SUT1* and *SUT2* are mainly responsible for the sucrose loading in the apoplastic pathway. It has been reported that the *SUT1* is induced during 0–25d after pollination and then transports sucrose into the developing endosperm through the aleurone layer (Aoki et al., 2003; Furbank et al., 2001). Additionally, the *INV* and *SUS* genes also play important roles in sugar unloading in the grain by hydrolyzing sucrose into glucose and fructose for starch synthesis, which in turn induces the expression of sucrose transporters (Jin et al., 2009; Wang et al., 2008). Those mutants defective in cell-wall invertase (*CWINs*) or *SUS* gene always display lower kernel weight, spikelet fertility and plant biomass (Oliver et al., 2007; Wang et al., 2008; Zanol et al., 2009). In contrast, higher seed weight, size gain and hexose level are found in tomato and rice plants when the *CWINs* is overexpressed (Wang et al., 2008; Jin et al., 2009).

Among the various possible cellular and metabolic responses, the impairment of carbon metabolism and utilization appears to be the central cause of abnormal development and yield loss under heat stress (Pressman et al., 2002; Suwa et al., 2010). In chickpea, the sucrose metabolism in anthers was impaired by heat stress, and induced reproductive failure, involving significantly decreased activity of sucrose phosphate synthase (SPSs), *SUSs*, and *INVs* (Kaushal et al., 2013). Similar findings in maize and tomato revealed that the kernel weight or pollen viability was significantly decreased by heat stress through inhibition of the *INV* activity (Cheikh and Jones, 1995; Frank et al., 2009; Pressman et al., 2006). In rice, no significant difference in the expression level of *INV1* and *INV4* was found between the control and heat-stressed spikelets of the heat-susceptible cultivar, whereas a remarkable increase was observed in the heat tolerant one (Islam et al., 2018). Thus, genetically increasing the native *CWIN* activity could sustain fruit set ability of tomato under long-term moderate heat stress by enhancing sucrose import and catabolism, HSP expression, and auxin response and biosynthesis (Liu et al., 2016). Heat stress is also reported to repress the expression of *SUT1* in grain, leaf and sheath to reduce the supply of assimilate to grains, and thus reduce the grain yield at the filling stage of rice (Phan et al., 2013). Notably, a higher increase in the expression

levels of the *SUT* genes and NSC content was found in spikelets induced by heat stress (Miyazaki et al., 2013; Islam et al., 2018). Accordingly, the increase in the expression level or content was found to be higher in the heat tolerant rice cultivar than in the sensitive one relative to their respective controls under non-stress conditions (Miyazaki et al., 2013; Islam et al., 2018). These results suggested that sugar transport functioned more effectively in the heat resistant cultivar than in heat sensitive one under high temperature conditions. However, those results are mainly found in reproductive organs in plants, and very few studies have been documented on the alteration of the source-sink relationship of rice at anthesis by heat stress.

It has been reported that sucrose transport and metabolism in plants is also affected by the phytohormone and plasmodesmata, especially under abiotic stress (Islam et al., 2018; Zhang et al., 2017). Indeed, the interaction between phytohormones and sugars has been found to occur during plant development under natural or stress conditions (Çakir et al., 2003; Sairanen et al., 2012). The phytohormone could regulate the source-sink relationship not only by influencing the strength of the source, but also the sink activity and their interrelation (Albacete et al., 2014). It has also been reported that ABA could enhance sugar metabolism and transport into spikelets of rice to prevent pollen abortion by increasing the expression level of the *SUT1*, *INV* and *SUS* genes, under heat stress, at the pollen mother cell meiosis stage (Islam et al., 2018). Moreover, as the symplastic pathway is also involved in the process of sucrose loading or unloading in leaf, sheath-stem and grain of rice, the frequency, number and morphology of plasmodesmata are the determinants for sucrose transport under abiotic stress (Braun et al., 2014; Zhang et al., 2006, 2004). It was reported decades ago by McNairn (1972) that the sieve pores could be occluded by callose within minutes under heat stress, and thus heat stress could induce plasmodesmata closure in leaf, sheath, stem and grain. However, the role of phytohormones and plasmodesmata in sugar transport and metabolism under heat stress at anthesis is still remains elusive.

Thus, in the present study, we determined the photosynthesis, dry matter weight and carbohydrates accumulation and distribution, expression level of *SUT*, *SUS* and *INV* genes, phytohormones effects and ultrastructure of plasmodesmata to investigate how heat stress affects the source-sink relationship of rice at anthesis.

2. Materials and methods

2.1. Experimental set-up

The study was conducted at the experimental farm of China National Rice Research Institute, Hangzhou, Zhejiang Province from May to September. Two rice genotypes differing in heat tolerance, namely the Nipponbare (NIPP) and its high temperature susceptibility (HTS) mutant, were selected for use in this study. The HTS semi-rolled leaf mutant was isolated from an ethyl methane sulfonate (EMS)-induced japonica rice Nipponbare mutant bank (Zhang et al., 2018). This mutant has been self-pollinated for more than nine generations and the semi-rolled leaf phenotype has been stably expressed in greenhouse and field conditions in Hangzhou, Zhejiang Province China. The rice seeds were sown in seedling bed, and then two seedlings with 4–5 leaves were transplanted into each pot filled with paddy soil under natural environment until flowering. Thereafter, rice plants were divided into two groups and moved into two separate plant growth chamber with an area of 10 m² using an automatic temperature control system to control the temperature and relative humidity. One group of rice plants was subjected to heat stress (40 °C from 09:00 a.m. to 04:00 p.m., 30 °C from 04:01 p.m. to 8:59 a.m., for 12 d), while the other group served as the control (30 °C from 09:00 a.m. to 04:00 p.m. and 24 °C from 04:01 p.m. to 8:59 a.m. for 12 d). Both groups were maintained under 70–80% relative humidity and natural sunlight conditions, in which the light intensity was about 50,000 lx. The samples including flag leaves, sheath-stems and spikelets from heat-stressed and non-heat-stressed

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