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Differential effects of temperature and duration of heat stress during anthesis and grain filling stages in rice

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ABSTRACT

Heat stress can occur during different plant development stages, and understanding the impact of post-anthesis heat stress on grain yield in rice could help to improve the predictive accuracy of growth models. We performed temperature-controlled experiments in phytotrons to investigate this using two different heat-sensitive japonica rice cultivars at four daily maximum/minimum temperature regimes of 32 °C/22 °C (T1), 35 °C/25 °C (T2), 38 °C/28 °C (T3) and 41 °C/31 °C (T4) and temperature durations of 2 (D1), 4 (D2) or 6 days (D3) at both anthesis and 12 days after anthesis (12DAA). Heat stress at anthesis caused a marked decrease in spikelet fertility and grain filling duration, but the 1000-grain weight was not obviously affected. Compared with T1D2 controls, treatment T4D3 decreased spikelet fertility and grain filling duration by 61.1% and 14 days, respectively. Heat stress at anthesis limited grain growth by inhibiting dry matter translocation rather than diminishing photosynthetic production. Heat stress (T4D3) at 12DAA was less disruptive but still decreased spikelet fertility by 29.2%, 1000-grain weight by 30.2%, and grain filling duration by 9.5 days. Leaf photosynthesis and leaf area were also diminished, which restricted the supply of materials for grain growth, although increased dry matter translocation partially compensated to reduce overall grain yield losses. Heat stress at higher temperature but shorter duration was comparable to lower temperature but longer duration. Heat stress at anthesis and 12DAA decreased average grain yield by 3.4%/°C/day and 2.3%/°C/day in Nanjing 41 and by 3.2%/°C/day and 1.7%/°C/day in Wuxiangjing 14, respectively. Heat tolerance was generally higher in Wuxiangjing 14 than in Nanjing41. These results could improve the accuracy of crop models under heat stress and assist heat tolerance rice breeding programs.

1. Introduction

Short-term heat stress events have occurred frequently across the globe during the past 20–30 years and are likely to increase with global warming (Gourdji et al., 2013; Lobell et al., 2012; Tao et al., 2013). Areas suffering heat stress have gradually spread from tropical and subtropical regions to important agricultural production areas of temperate regions, such as North America, eastern China, southwest Russia and southern Canada (Hawkins et al., 2013; Li et al., 2010; Teixeira et al., 2013). The Intergovernmental Panel on Climate Change (IPCC) has reported that heat stress is projected to increasingly responsible for rice yield reduction in tropical and temperate regions without adaptation (IPCC, 2014). China is the largest rice producer in the world, accounting for 28.1% of the world's rice production and 18.9% of the total cultivation area (FAO, 2014). Since the occurrence of heat stress events has increased rapidly in most areas of China (Wei and Chen, 2009; Shi et al., 2015b; Tao et al., 2013), heat stress is of great concern for rice production in China specifically, and food security in general.

Heat stress influences rice growth differently in different production areas, and the growth stage during which it occurs also affects the outcome. In tropical areas such as the Philippines, high night-time temperatures have a significant effect on rice growth since they exacerbate the already high daytime temperatures. Based on field experiments implemented during 1992–2003, Peng et al. (2004) found that rice grain yield decreased 10% for every 1 °C

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increase in night-time temperature. Using artificial temperature chambers to simulate field conditions, Shi et al. (2013) explored the effect of continued high night-time temperature (from panicle initiation to physiological maturity) on rice grain yield, and the results showed a decrease in grain yield under the high night-time temperature (28 °C) was mainly due to a reduction in nitrogen and non-structural carbohydrate translocation after anthesis, which resulted in decreased maximum and mean grain-filling rate and grain weight. Evidence suggests that yield losses following high night-time temperatures are caused by increased spikelet sterility and disrupted nutrient translocation rather than decreased photosynthetic production (Cheng et al., 2009; Cheng et al., 2010; Mohammed and Tarpley, 2010). In subtropical and temperate regions with relatively lower daily average temperature, such as northeast China, northern Japan and Korea, moderate increases in temperature could provide greater photosynthetic production by increasing the activities of related enzymes that might benefit rice growth and yield (Hikosaka et al., 2006), but rice growth would be restricted above the optimal temperature, above which heat stress occurs. Prasad et al. (2006) carried out an experiment using temperature-gradient greenhouses in Florida that were maintained at >34 °C/27 °C (mean maximum/minimum temperature) during flowering stage, and found that spikelet fertility, grain weight and harvest index were all reduced significantly. Oh-e et al. (2007) conducted similar research in southern Japan, and maximum air temperature of about 31.8 °C during the whole growth period of rice accelerated leaf senescence, reduced photosynthetic rate and decreased grain yield, largely due to increased spikelet sterility. Kim et al. (2011) tested different temperatures (19 °C/11 °C, 25 °C/17 °C and 31 °C/23 °C) during the rice grain filling stage using an artificial climate chamber, and observed premature termination of grain filling at 31 °C/23 °C treatment, primarily due to loss of sink capacity in panicles rather than leaf senescence.

Most previous studies have focused on the effects of heat stress over a long period of reproductive stage. However, with extreme heat stress events now occurring with increased frequency, the impact of short-term heat stress on rice is receiving more attention. The response of rice to heat stress is dependent on temperature, duration, and even temperature variability (Fukai, 1999). Jagadish et al. (2007) found that exposure to temperatures above 33.7 °C for only one hour caused infertility in indica rice (Azucena) during the flowering stage. Madan et al. (2012) reported that grain yield in hybrid indica rice was higher than that of indica rice following exposure to a temperature of 35 °C for five days during flowering, but the superior performance was lost at a temperature of 38 °C. These studies on the impact of short-term heat stress during the flowering stage provide useful guidance for heat tolerance breeding (Jagadish et al., 2010; Matsui et al., 2001). Indeed, the effects of short-term heat stress can depend on the developmental stage during which the stress is experienced. Yoshida (1981) reported that heat stress during early reproductive stages had a more serious impact on rice yield formation than an equivalent treatment during later reproductive stages. Therefore, we hypothesize that there are differential effects of heat stress on rice growth and yield formation during the different reproductive stages, with interaction effects between temperature and duration.

Moreover, considering the increasing frequency of heat stress events, the prediction on rice yield formation under heat stress is particularly important to reduce the risk of rice production in the main agricultural areas. The process-based crop model is an effective tool to estimate crop production under climate change, however, the poor prediction on heat stress effects was found in recent years (Lobell et al., 2012; Moriondo et al., 2011; Shi et al., 2015a). For the improvement of rice model under heat stress condition, reliable data in rice should be acquired by investigating the dynamic changes of physiological process and explore their relations to temperature. According to the source-sink theory, yield formation is determined both by photosynthetic production and dry matter translocation (Kato et al., 2004; Kumar et al., 2006). Therefore, the other hypothesis is that short-term heat stress affects rice yield formation through the shift of photosynthetic production after anthesis and the dry matter translocation before anthesis.

Japonica rice is widely cultivated in China on land surrounding the middle and lower reaches of the Yangtze River, especially in Jiangsu and Anhui provinces. Post-anthesis heat stress is now a major factor limiting the yield of japonica rice in these areas. Anthesis and grain filling are critical reproductive stages for determining rice grain yield, and both are sensitive to temperature (Jagadish et al., 2007; Prasad et al., 2008). Thus, the objectives of this study are (1) to investigate and quantify the impact of the temperature and duration of heat stress on grain yield in japonica rice during anthesis and grain filling stages; (2) to determinate whether heat stress affects photosynthetic production and/or nutrient translocation. The results will generate knowledge that could assist the development of improved cultivation techniques, heat tolerance breeding and in particular rice growth modelling under heat stress conditions.

2. Materials and methods

2.1. Experiment design

Temperature-controlled experiments were conducted from 2011 to 2013 at Pailou Trial Base (32.04°N, 118.78°E), Nanjing Agricultural University, Nanjing, China. The ambient maximum and minimum daily temperatures during the rice growing season (from May to October) were averagely 30.8 °C and 18.9 °C over the three years, respectively (with average daily temperature of 24.9 °C) (Fig. 1). The ambient relative humidity was 41.3–72.5% during the whole growing season. The photosynthetically active radiation (PAR) in overcast and sunny days at solar noon was about 100–600 $\mu mol\, m^{-2}\, s^{-1}$ and 1400–1700 $\mu mol\, m^{-2}\, s^{-1}$ in ambient condition, respectively. Two japonica rice cultivars, Nanjing 41 and Wuxiangjing 14, were used in the experiments, because of their different heat tolerance as indicated by previous studies (Zhang et al., 2007; Zheng et al., 2005). Seedlings were sowed in late May in nearby field and then transplanted to 600 plastic pots (height = 35.6 cm, inside diameter = 28.8 cm) in mid-June at a density of three plants per pot (about 33 plants per square meter). Each pot was filled with 20 kg air-dried paddy soil, containing an available N of 115 mg/kg, available phosphorus (P) of 18.2 mg/kg, available potassium (K) of 96 g/kg and organic matter of 21.2 g/kg in the 0–15 cm soil layer. A fertilization rate of 3.0 g N, 0.87 g P, and 1.5 g K was additionally applied in each pot. P and K were all applied as basal fertilizer before transplanting, while N was split into three applications, with 50% as basal fertilizer, 10% at mid-tillering and 40% at panicle initiation.

Plants in pots were grown in outdoor condition before temperature treatments. Pots in which 50% of panicles were flowering (anthesis stage) on the same day were selected. At anthesis and 12 days after anthesis (12DAA = early stage of grain filling), 20 pots were chosen for each treatment and transferred to phytotron rooms with the implement of different temperature levels and temperature durations. According to previous studies, the daily optimal average temperature for local rice plants during anthesis and early grain filling stages was 23 °C–26 °C (with maximum and minimum temperatures of about 29 °C–32 °C and 17 °C–21 °C, respectively), and a daily temperature >35 °C would severely affect seeds setting (Gao and Wang, 2009; Zhao et al., 2006). Thus, four temperature levels with maximum/minimum