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Quantifying source-sink relationships of rice under high night-time temperature combined with two nitrogen levels

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ABSTRACT

High night-time temperature (HNT) disturbs processes of both assimilate production (source) and assimilate accumulation (sink), and as a result substantially reduces yields of cereal crops. There have been reports that increasing nitrogen application can alleviate the negative impact of high-temperature stress on yield in rice (*Oryza sativa* L.). However, little is known about the interactive effect of HNT and nitrogen (N) supply on rice grain yield and its underlying source-sink relationships. We conducted two field experiments at the International Rice Research Institute in both the dry (DS) and wet (WS) season of 2012, in which three cultivars with contrasting responses to HNT were grown under two levels of night-time temperature and two levels of N application. HNT significantly decreased grain yield of cv. Gharib at both N levels and in both seasons, while grain yield of cv. PSBRc4 was significantly reduced by HNT at the higher N level only. Among the yield components, grain weight was consistently reduced by HNT in all three cultivars across two seasons while spikelets m^{-2} and seed-set were affected by HNT during DS and WS, respectively. In most cases, higher N application reduced grain yield and its components. Thus, in our study, increasing the total N fertilizer did not alleviate the adverse effects of HNT on rice yield. Using a novel modelling approach that quantifies source-sink relationships during grain filling, we found that increased nitrogen did not alleviate the negative impact of HNT on source-sink interactions during grain growth across cultivars and seasons. Nevertheless, the model showed that there were significant differences among cultivars in grain filling duration, grain filling rate and total sink size, modulated by their source-sink relationship in response to HNT, suggesting that breeding programs should select for sink-related traits to improve rice tolerance to HNT.

1. Introduction

While global climate models predict mean temperature increases of 1.0–3.7 °C by 2100 (IPCC, 2013), a greater increase in night-time minimum temperature than day-time maximum temperature is an increasingly common global phenomenon (Easterling et al., 1997; Vose et al., 2005). Night-time temperature is predicted to increase further, by up to 3 °C by 2050 (Chotamonsak et al., 2011), thereby reducing the diurnal temperature amplitude. At a smaller geographic scale, this trend has been detected across major rice-producing countries such as the Philippines (Peng et al., 2004), China (Tao et al., 2006), and India (Rao et al., 2014). Large reduction in rice yield resulting from increasing night temperature has been documented across South Asia, Southeast Asia and in the USA (Welch et al., 2010; Mohammed and Tarpley, 2014), resulting in significant economic losses (Lyman et al., 2013).

Grain yield in rice depends on both the supply of assimilates (source) and the capacity of the grains to accumulate available carbohydrates (sink), and critical yield-determining components spikelets per panicle, spikelet fertility and individual grain weight are mainly determined between panicle initiation and maturity. The yield losses under high night temperature (HNT) have been attributed to a reduction in final grain weight under realistic field conditions (Shi et al., 2013, 2016; Jagadish et al., 2015) and in spikelet sterility from studies carried out under controlled environental conditions (Cheng et al., 2009; Mohammed and Tarpley, 2009a, 2010). The latter conclusion on reduced spikelet fertility is documented for response to extremely high night-time temperature (≥32 °C), which is similar to the level of high day-time temperature but not comparable to levels of

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night temperature experienced by rice grown in different geographical locations. Hence, the major conclusion drawn from these controlled-environment studies on HNT induced yield losses through increased spikelet sterility is hard to be justified under realistic field conditions. Therefore, caution needs to be taken while comparing HNT impacts across field and controlled chamber studies (Jagadish et al., 2015). Across these studies, different mechanisms for yield reduction under HNT have been indicated, i.e. poor seed-set (Cheng et al., 2009; Mohammed and Tarpley, 2009a, 2010), limited amount of assimilates (deficiency of carbohydrates) supplied as a result of higher respiration rate and drop in photosynthesis (Cheng et al., 2009; Mohammed and Tarpley, 2009b), or lower translocation efficiency of assimilates during the grain filling phase (Shi et al., 2013). On the other hand, reduced sink size, i.e. endosperm cell size (Morita et al., 2005), and sink activity, i.e. activities of key enzymes of starch synthesis (Dong et al., 2011), have also been identified to result in lower grain weight under HNT.

There have been reports that crop management approaches can be used to minimize yield reduction under high-temperature stress. Appropriate nitrogen management can (partially) alleviate the negative impact of high-temperature stress in plants (Waraich et al., 2012). Increasing the nitrogen supply at panicle initiation and/or flowering has been reported to relieve the negative effects on grain production, of exposure to short period of high day temperatures before or after flowering (Dai et al., 2009; Duan et al., 2013; Yang et al., 2014). It has also been documented that nitrogen management could lower the panicle or canopy temperature by building a better structure of the rice canopy with higher leaf area index and facilitating higher transpiration cooling, thereby reducing high temperature-induced sterility and improving high-temperature tolerance (Yan et al., 2008). These reports suggest that nitrogen management could modulate both source and sink parts of the crop. However, the effects of nitrogen in combination with HNT exposure on source-sink ratio and rice yield under field conditions have not been investigated.

Source or sink limitation on grain filling in cereals is often inferred from experiments in which the source-sink ratio is manipulated by shading, defoliation or grain removal. However, interpretation of this type of experiments is usually hard, considering the possibility that a physical removal of a plant part could lead to a sudden shock and does not necessarily reflect responses to a gradual change in the source-sink relationships in intact plants. In addition, the dynamics of source activity is commonly quantified by measuring time-dependent instantaneous net canopy photosynthesis. Such measurements are time consuming and require gas-analyzer facilities. Yin et al. (2009) have created a quantitative model by using dynamics of grain weight and flag leaf area during grain filling period to quantify the source-sink relationships. However, precise source-sink relationship during grain filling often depends on the temporal changes in grain weight in response to assimilates availability per grain during the grain filling period (Borrás et al., 2004). Thus, a new modelling approach is needed to easily and accurately quantify source-sink relationships by using grain filling dynamics and associated plant biomass produced during grain filling, as dry weight is relatively easy to measure. Such an approach may help to quantify the factors involved in the reduction of grain yield under HNT and its impact on source-sink limitations and to identify physiological or agronomic traits suitable for improving rice grain yields by targeted breeding efforts.

In our study, we aim to unravel the responses in grain yield to increased N supply under HNT in rice under realistic field conditions. To that end, we extend the model of Yin et al. (2009) into a novel modelling framework to more precisely and easily quantify changes in the balance between source supply and sink demand under HNT.

2. Materials and methods

Field experiments were conducted in the 2012 dry season (DS) and wet season (WS) in the lowland farm at the International Rice Research Institute (IRRI), Los Baños (14°11′N, 121°15′E, 21 masl), Philippines. A randomized complete block design was used for these experiments, N levels used as main plot, with temperature as split plots and cultivar as split-split plots.

2.1. Crop management

Three rice cultivars with relatively similar phenology (days from transplanting to panicle initiation) and contrasting responses to high night temperature, i.e. N22 with high night-temperature tolerance (Coast et al., 2015) and Gharib with high night-temperature sensitivity (Shi et al., 2013; Zhang et al., 2013) together with PSBRc4 (a high-yielding cultivar released in the Philippines with unknown high night-temperature tolerance), were chosen for our studies. Seed dormancy was broken by exposing seeds to 50 °C for 3 days, followed by pre-germination and sowing in seeding trays. Fourteen-day-old seedlings were transplanted on 16 January during the DS and 4 July in the WS at a spacing of 0.2 × 0.2 m with four seedlings per hill to compensate for the poor tillering ability of N22 and Gharib and to ensure uniform plant density under conditions where golden apple snails are a problem during early seedling stage. The fields were flooded at 5–10 cm water depth until physiological maturity. Weeds were removed manually and chemicals were applied to control pest and diseases. Whorl maggots (*Hydrellia philippina* Ferino) during the early vegetative stage, yellow stem borers (*Scirpophaga incertulas*) and sheath blight (*Rhizoctonia solani* Kühn) at flowering stage were effectively managed by chemical spraying.

2.2. Treatments

Two levels of N fertilizer in the form of urea were applied, 150 kg N ha^{-1} (N1) and 250 kg N ha^{-1} (N2) in the DS and 75 kg N ha^{-1} (N1) and 125 kg N ha^{-1} (N2) during the WS. 150 and 75 kg N ha^{-1} are IRRI's recommended levels of N fertilizers for DS and WS, respectively. Basal nitrogen was applied at 30% of total amount and incorporated in all plots a day before transplanting, and remaining nitrogen was split-applied at mid-tillering (20%), panicle initiation (30%) and heading stage (20% of total amount), respectively. In addition, 30 kg P ha^{-1} (single superphosphate), 40 kg K ha^{-1} (KCl), and 5 kg Zn ha^{-1} (zinc sulfate heptahydrate) were applied in the DS and 15 kg P ha^{-1}, 20 kg K ha^{-1}, and 2.5 kg Zn ha^{-1} were used in the WS as basal fertilizers.

Sixteen temperature-controlled chambers were used to impose HNT stress under field conditions. The details of the set-up of the chambers were published in Shi et al. (2013). Briefly, during daytime (06:00–18:00 h), the chambers were kept open, exposing the plants to natural conditions. Chambers were manually closed at 18:00 h every day and re-opened at 6:00 h in the following morning; meanwhile, air conditioners (CW–1805 V, Matsushita Electric Philippines Corp., Taytay, Rizal, Philippines) were programmed to automatically maintain constant control temperature (22 °C) and HNT (28 °C) inside the chambers. HNT treatments of 28 °C were based on our previous experiments (Shi et al., 2013, 2016) and the current experiment, in which the ambient night temperatures on average ranged between 24 and 25 °C during the growing season and with a +3 °C increase predicted under future scenarios with warmer nights (Chotamonsak et al., 2011). Higher night-time temperature can potentially impact rice yields on a global scale, encompassing the entire crop cycle unlike the short episodic occurrence of day heat spikes (Jagadish et al., 2015). Hence, our

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