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Combined drought and heat stress impact during flowering and grain filling in contrasting rice cultivars grown under field conditions

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ABSTRACT

Combined drought and heat stress is the most common abiotic stress occurring under field conditions that negatively affects rice productivity. Systematic evaluation of the response of rice cultivars to this combined stress under field conditions has not been attempted. To fill this major knowledge gap, three rice cultivars (N22, Dular, Anjali) were exposed to combined drought and heat stress during flowering and early grain-filling stages, using rainout shelters and natural summer conditions in 2013, 2014 and 2015. By employing staggered sowing, stress was imposed at the same time across both stages and between cultivars, which helped capture temporal soil and canopy-air temperature and soil water potential without being confounded by other climatic conditions. Across experiments, soil water potential under drought reached up to -61 and -57 kPa during flowering and grain filling, resulting in up to 1.75 °C and 1.17 °C higher canopy-air temperature, respectively. Across years and cultivars, 50.0% and 74.5% lower panicle conductance under combined stress during flowering and grain filling led to an increase in panicle tissue temperature by up to 3.94 °C and 3.27 °C, respectively. The range in combined stress-induced yield reduction between flowering and grain filling was similar (approximately 20–80%), while there were clear differences among cultivars. Dular had the highest reduction in yield (73.2%) with stress exposure during flowering, while N22 recorded a similar reduction (77.6%) during grain filling. A similar differential cultivar response in parameters related to grain quality was recorded with stress imposed at both developmental stages. Our findings demonstrate the potential of using existing rainout shelters to systematically characterize rice and other crops for combined drought and heat stress impact under field conditions, and to identify novel multi stress-tolerant donors to support abiotic stress breeding programs.

1. Introduction

Current global climate models predict an increase in frequency and magnitude of hot and dry spells under future climate (IPCC, 2014). However, these anticipated climatic challenges have already started to manifest in different geographical locations leading to significant crop and hence economic losses (reviewed by Kadam et al., 2014). Among field crops, rice is extremely sensitive to heat (Bahuguna et al., 2015; Jagadish et al., 2010, 2007; Shi et al., 2016), drought (Kumar et al., 2014; Venuprasad et al., 2007) and combined drought and heat stress (Rang et al., 2011), particularly when these conditions coincide with reproductive and grain-filling stages. Heat stress (≥ 38 °C) during the flowering and grain-filling stages has induced large yield reductions across major rice-growing regions of China (Tian et al., 2010), Japan (Hasegawa et al., 2011), Laos and Southern India (Ishimaru et al., 2016). In addition, a modelling exercise using the criteria of at least five days of heat stress coinciding with reproductive stage concluded that more than 27% of the global rice-producing areas would be affected by heat stress exposure by 2050, compared with 8% in 2000 (Gourdji et al., 2013). Empirically, even a few hours of heat stress coinciding with flowering increases spikelet sterility (Jagadish et al., 2007), with a quantitative impact observed with more than one day of stress (Rang

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et al., 2011). Similarly, drought is another major abiotic stress that is projected to affect 2 million hectares of Asia's dry-season irrigated rice by 2025 (Tuong and Bouman, 2003). The anticipated increase in temperature and drought under future climate and simultaneous reduction in availability of fresh water for irrigation has led to the development of water-saving technologies such as aerobic and dry direct-seeded rice. Recent analysis has indicated that the occurrence of intermittent drought spells with direct-seeded rice can lead to significant reduction in yield (Quinones et al., 2017). Hence, co-occurrence of both drought and heat stress under field conditions in many rice-growing regions is almost inevitable, leading to increased plant-tissue temperature with progressive severity of drought (Cohen et al., 2005; O'Toole and Namuco, 1983). It has been mechanistically demonstrated that combined drought and heat stress exposure translates to a completely new response and not a mere additive effect of both stresses (Rizhsky et al., 2004, 2002). Despite acknowledging the practical relevance of combined drought and heat stress exposure on plants, knowledge generated along these lines under field conditions is limited (Lawas et al., 2018b). This can be attributed to limited field-based heating systems (Chiba and Terao, 2014; Prasanth et al., 2016; Rehmani et al., 2011; Yang et al., 2017), although the use of rainout shelters to induce drought stress is quite common across stress physiology and breeding programs in both developed and developing countries (Anyaoha et al., 2018; Nam et al., 2015; Selvaraj et al., 2017; Zu et al., 2017).

Information obtained from regional reports, experiments and modelling exercises indicates that it is timely to investigate this most prevalent combined stress impact in greater detail under field conditions. Only a few studies have investigated combined drought and heat stress impact on rice during the reproductive or grain-filling stages (Jagadish et al., 2011b; Li et al., 2015; Rang et al., 2011). However, all these studies have been carried out in controlled environment facilities, where the growth conditions could vary considerably compared with field conditions (Bahuguna et al., 2015). Hence, combining the approach of growing rice during the hotter summer months to induce heat stress under field conditions (Bahuguna et al., 2015), in combination with rainout shelters provides the opportunity to study the impact of combined drought and heat stress on rice productivity under field conditions. Therefore, by (i) using rice cultivars contrasting for drought and heat stress response; (ii) following staggered sowing technique to minimize phenological differences; (iii) strategically making sure flowering and grain filling occurred under hotter summer months and (iv) using the rainout shelter facility at the International Rice Research Institute (IRRI), Philippines, we were able to quantify the impact of combined drought and heat stress on the agronomic performance of these cultivars over three summer seasons. Specific objectives were to (i) Quantify the impact of combined drought and heat stress exposure during flowering and grain filling on grain yield and quality in contrasting rice cultivars; (ii) Compare the physiological response of rice exposed to combined drought and heat stress at flowering versus grain-filling stages; and (iii) Determine the major yield-limiting components and key quality parameters affected by combined drought and heat stress and associate the impact to changes in canopy-air temperature.

2. Materials and methods

2.1. Crop husbandry

Three rice (*Oryza sativa* L.) cultivars (N22 (*aus* ssp.), drought and heat tolerant; Dular (*aus* ssp.), drought tolerant and heat susceptible; and Anjali (*indica* ssp.), drought and heat susceptible) with contrasting response to drought and heat at the flowering stage (Henry et al., 2011; Kumar et al., 2014; Rang et al., 2011; Tenorio et al., 2013) were used. These were grown at IRRI, Philippines (14° 11′N, 121° 15′E, 21 MASL) for three consecutive years (2013–2015) during the dry season. Seeds were exposed to 50 °C for three days to break dormancy, followed by pre-germination by soaking in water and incubation at 25 °C. Pre-germinated seeds were sown in seeding trays filled with clay loam soil from the farm. After 14 days, seedlings were transplanted in the field at a spacing of 0.2 m × 0.2 m with one seedling per hill. Nitrogen (60 kg ha^{-1} N as urea), phosphorus (30 kg ha^{-1} P as single superphosphate), potassium (40 kg ha^{-1} K as KCl) and zinc (5 kg ha^{-1} Zn as zinc sulfate heptahydrate) were incorporated as basal fertilizer in the plots a day before transplanting. Additional nitrogen was applied at mid-tillering (45 kg ha^{-1} N as urea) and at panicle initiation (45 kg ha^{-1} N as urea). Insects and diseases were controlled using appropriate pesticides to avoid negative effects on plant growth and productivity.

2.2. Stress treatment

Staggered sowing was employed based on phenology data collected during 2012 dry season for the flowering and early grain-filling stages of the three cultivars to occur at similar time and to coincide specifically between late-April to early-May. This specific time of the year has recorded the highest maximum air temperature together with least amount of rainfall at the IRRI experimental station over three decades (1982–2011) (IRRI Climate Unit, 2011). For drought stress, two rainout shelters designed for precise phenotyping under field conditions were used, with one shelter each used for control and stress treatments (Supplementary Image S1). Cultivars were randomly assigned in three replicate plots per treatment and separate plots were allocated for imposing stage-specific (flowering and early grain filling) drought stress. Flooded conditions were maintained in both rainout shelters until the start of the treatment. In the stress shelter, water was drained at early booting (i.e. emergence of flag leaves) and with the start of flowering to impose drought simultaneously during flowering and early grain filling, respectively (Fig. 1). Soil water potential was monitored in the drought stress treatments with tensiometers (Spectrum Technologies, Inc., Illinois, USA) installed at a depth of 30 cm. In total, 18 tensiometers were installed with nine each in flowering (3 cultivars × 3 replicates) and early grain-filling stress (3 cultivars × 3 replicates) plots, i.e. each plot had one tensiometer. Additionally, soil samples were collected at 2–3 day intervals to measure soil water content gravimetrically. Soil samples were collected at three depths, i.e. 0–10 cm, 10–20 cm, and 20–30 cm. Moist soil weight was recorded, after which the samples were oven-dried at 70 °C for three days and dry weight was determined. In the first experiment (2013), flag leaves from 2 to 3 plants per plot were collected between 13:00–14:00 to determine relative water content (RWC) following Rang et al. (2011), as an additional drought stress indicator. When the tensiometer readings registered an average soil water potential of about -50 kPa or when the plants showed severe leaf rolling, the plots were rewatered and maintained under flooded conditions until crop maturity. Control plots were fully irrigated throughout the cropping season. Canopy-air temperature and relative humidity (RH) were measured at 2-min intervals and averaged for every 10 min using data loggers (RX-350TH, As One Co., Osaka, Japan) housed in Micrometeorological Instrument for Near Canopy Environment of Rice (MINCER) (Fukuoka et al., 2012a). These parameters were also used to determine canopy vapor pressure deficit (VPD), which was calculated using the formula VPD = (1- (RH/100))*saturated vapor pressure (CronkLab, 2018; Murray, 1967). Data loggers (HOBO Pendant, Onset Computer Corporation, Bourne, MA, USA) were installed at about 20 cm depth to record soil temperature at 15-min intervals.

It should be noted however, that the control condition described here is characterized as irrigated and exposed to natural high temperatures. A true control, i.e. irrigated and with optimum air temperature, without staggered sowing was not included in the experiment. Such setup was planned and carried out during the wet season but was not feasible due to typhoon events. The flooded conditions in the control plots throughout the crop growing season alleviated the effects of possible heat stress, which was manifested by the lower canopy-air temperature compared with the stress plots (see Discussion for further details).