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Increase in night temperature in rice enhances respiration rate without significant impact on biomass accumulation

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ABSTRACT

Night temperature (NT) increases faster than day temperature with global warming and this may have strong implications for crop yield. One of the assumptions is the increase in night respiration and thus the increase in carbon losses over time. Some rice cultivars (indica, aus and japonica types) were grown in the field in the Philippines and in heated greenhouses in Montpellier, France, to quantify the response of respiration to increased NT and its implication at crop level. Increased NT by 3.8 and 5.4 °C over the whole crop cycle in two greenhouse experiments and by 1.9 °C in the field from 33 days after transplanting up to maturity using a free-air-controlled enhancement increased night respiration rate significantly. Overall, the cost in CH_2O of night respiration over crop duration was 17 to 20% (field) and 8 to 18% (greenhouse) of the potential shoot dry matter (including that lost by respiration). Additional respiratory burden due to increased NT was only 1 to 7% of the potential shoot dry matter at maturity, and was not associated with significant loss in additional dry matter. The absence of any dry matter reduction with increased NT within indica cultivars questions the assumptions of recent papers.

1. Introduction

The global mean surface temperature is projected to increase by 0.3 to 0.7 °C for the period 2016–2035 and by 0.3 to 4.8 °C for 2081–2100 compared to the 1986–2005 period (IPCC, 2013). Near-term increases in temperature are expected to be larger in the tropics and subtropics (IPCC, 2013), which correspond to the main rice production area, than at mid-latitudes. Night temperature already increased faster than day temperature, lowering the day-night temperature amplitude in many parts of the world, e.g. annual mean maximum temperature have increased by 0.35 °C from 1979 to 2003, while annual minimum temperature have increased by 1.13 °C during the same period in the Philippines (Alward et al., 1999; Easterling et al., 1997; Karl et al., 1991; Peng et al., 2004). In this context, a reduction in grain yield of tropical irrigated rice (*Oryza sativa* L.) has been reported by Peng et al. (2004) based on field data collected over eleven years, between 1992 and 2003. This decline was associated with decreasing radiation and increasing day and night temperatures. Minimum night temperature (NT) was the single most predictive environmental variable for grain yield change (Nagarajan et al., 2010), with a reduction in grain yield of 10% with every degree Celsius increase in minimum NT in the range of 22 to 24 °C (Peng et al., 2004). The observations from Peng et al. (2004), the on-going climate changes and the climate projections suggest the increase in NT to be a strong factor affecting rice yield in the tropics. The role of NT *per se* in crop performance is, however, not well understood.

Reductions of rice grain yield under increased mean NT were also reported under 27 °C compared to 22 °C in hydroponic culture (Kanno and Makino, 2010); under 28 °C compared to 22 °C in field conditions with plants grown under natural conditions during day time and under shelters during night time (Shi et al., 2012); and under 32 °C in controlled environments compared to 27 °C (Mohammed and Tarpley, 2009a). Similar observation was reported by Cheng et al. (2009) under 32 °C compared to 22 °C but with the mean night temperature calculated over the night time period excluding the transition time from daytime to night time and from night time to daytime. On one hand, a decline in

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grain yield under increased NT was reported in studies where mean NT was (i) similar to day temperature (Kanno and Makino, 2010; Mohammed and Tarpley, 2009a), (ii) higher than day temperature (Li et al., 2011) or (iii) modified together with day temperature, thereby confounding day and night temperature effects (Glaubitz et al., 2014). On the other hand, the susceptibility of japonica cultivars and related groups, i.e. sadri and basmati (Glaszmann, 1987), to increased mean NT, including the transition time between day and night, was largely reported (cv. Notohikari in Kanno et al., 2009; cv. Akita-63 in Kanno and Makino, 2010; cv. Cocodrie in Mohammed and Tarpley, 2009a; cvs. Super Basmati, Pusa 1121 and Pusa Sugandh-2 in Nagarajan et al., 2010; cv. Gharib in Shi et al., 2012). In contrast, the response of indica cultivars and related groups, i.e. aus and boro (Glaszmann, 1987), to increased mean NT is unclear (cv. IR72 in Cheng et al., 2009; cv. N22 in Shi et al., 2012). However, grain yield of indica cultivars declined when the minimum temperature was above 22 °C in field conditions (cvs. Pusa-44 and IR64 in Nagarajan et al., 2010; cv. IR72 in Peng et al., 2004) whereas, in control environments, it increased when mean NT was elevated from 21 to 28 °C, but with also a concomitant increase in day temperature by 2 °C (cv. IR72 in Glaubitz et al., 2014). These observations raise the question whether NT in the range predicted by climate projections in the tropics, where the indica group is dominant, will have a detrimental effect on grain production.

An increased loss of biomass through enhanced respiration rate was one of the hypotheses proposed by Peng et al. (2004) to explain the rice yield decline reported under increased NT. Many studies reported an increase of dark respiration rate under increased mean NT over the whole night or part of the night, e.g. at plant scale for cotton (Loka and Oosterhuis, 2010), lettuce, tomato and soybean (Frantz et al., 2004) and rice (Cheng et al., 2009), and at leaf scale for temperate steppe species *Stipa krylovii* Roshev. (Chi et al., 2013a,b) and rice (Mohammed and Tarpley, 2009b). The increase in night respiration rate would reduce carbon accumulation with lower starch and soluble sugar concentration on pre-dawn (Turnbull et al., 2002) but could be partly offset by an increase of the assimilation rate (Kanno et al., 2009). Although higher respiratory rates under conditions of moderately increased NT may affect rice production, this has never been demonstrated.

The purpose of the present study was to assess whether a moderate increase in NT, while keeping day-time temperature unchanged, affects (i) night respiration rates and biomass losses, (ii) carbon accumulation and (iii) rice grain and biomass production. The study was conducted in thermally controlled greenhouses (Montpellier, France) and in the field at the International Rice Research Institute (IRRI) experimental station in the Philippines using a temperature free-air-controlled enhancement (T-FACE) system (Gaihre et al., 2014; Kimball et al., 2008). An initial greenhouse experiment (GH1) established increased NT responses of eight contrasting cultivars and compared leaf and plant scale respiration rates. The field study in 2013 concentrated three of these cultivars, and two of the cultivars were studied in the second experiment in the greenhouse (GH2). We also attempted to scale up night respiration losses to the entire crop cycle.

2. Materials and methods

The field experiment was conducted in 2013 at the International Rice Research Institute (IRRI), Los Baños (14°8′N, 121°15′E), Philippines. Two greenhouse experiments were conducted, one in 2012 (GH1) and one in 2013 (GH2) at the National Center for Scientific Research (CNRS), Montpellier (43°38′N, 3°51′E), France.

2.1. Plant management

Based on geographic origin, plant architecture and yield potential, eight rice cultivars were chosen for the GH1 experiment in which three subspecies were represented: indica (Hybrid 1, Hybrid 2, Hybrid 3 and Jamajigi), aus (Kasalath and N22) and japonica (Cocodrie as tropical and M202 as temperate). Three of these cultivars were used in the field: M202, known to be susceptible to high NT; N22, known to be tolerant to high day temperature and Hybrid 1. Two of these cultivars (Hybrid 1 and N22) were used in the GH2 experiment.

In the field experiment, seed dormancy was broken by exposure to 50 °C for three days, followed by pre-germination and sowing in seedling trays. Fourteen-day-old seedlings were transplanted on February 9, 2013 at a spacing of 0.2 m × 0.2 m with one seedling per hill. The particles size proportion of the soil was clay (37%), sand (20%), silt (43%), with pH = 6.6. Key elements as P_2O_5 (30 kg ha^{-1}), KCl (40 kg ha^{-1}) and $ZnSO_4$ (5 kg ha^{-1}) were applied one day before transplanting. Application of N fertilizer in the form of urea was done in four splits (45 kg ha^{-1} as basal, 30 kg ha^{-1} at mid-tillering, 45 kg ha^{-1} at panicle initiation and 30 kg ha^{-1} at heading). The field was flooded with 2 cm of water at transplanting and with 5 cm from crop establishment onwards. Weeding was done manually when required and insect pests were controlled using the appropriate chemicals.

In the greenhouse experiments (GH1 and GH2), seed dormancy was broken by exposure to 29 °C for four days. Pre-germinated seeds were transplanted on April 24, 2012 (GH1) and on May 28, 2013 or June 3, 2013 (GH2) for N22 and Hybrid 1, respectively. Pots were arranged within large aluminum tables where 5 cm of water level was maintained throughout the whole experiment. Pre-germinated seed was transplanted with two seedlings per pot (3 l). About one week after transplanting thinning was performed at one plant per pot. Soil EGOT 140 (17N-10P-14 K, pH = 5) (Jiffy, Norway) was used to fill each pot and Basacot 6 M+ (2 g l^{-1}, 11N-9P-19K + 2Mg) (Compo, Germany) was added and incorporated before transplanting. Four tables were used in each compartment, each containing 84 pots at the beginning of the experiment. Plant density was 30 and 32 plants m^{-2} for GH1 and GH2, respectively. Difference between both GH1 and GH2 was due to the largest pots for border plants in GH2 than in GH1. Each of the four tables within a compartment were moved and re-oriented twice a week to avoid any bias generated by the structure of the facility.

2.2. Temperature treatment

In the field experiment, as described in Kimball et al. (2008), a temperature treatment named as increased NT (INT) was set up as follow: Four rings of 4.5 m^2 were equipped with six regularly distributed thermal radiators (1000 W) located at 2 m height. Another set of four rings without thermal radiators was used for the control temperature treatment (CT). The cultivar disposition within each ring was set up in such a way that each cultivar (Hybrid 1, M202 and N22) occupied a quarter of the ring. The fourth quarter was occupied by a cultivar which was not analyzed in this study. Outside the ring, the cultivar PSBRC4 was transplanted to avoid border effects within the rings. The radiators were programmed to work at full capacity from 6 pm to 6 am (night time) from 33 days after transplanting, i.e. 20 days after panicle initiation for M202 and N22, and 10 days before panicle initiation for Hybrid 1 up to maturity (up to mid-grain filling for Hybrid 1). Temperature of the canopy was measured by the infrared thermal sensors that were placed above the ring. The increased air temperature was well distributed within the ring according to the low wind speed during night time, 0.45 ± 0.22 m s^{-1} with a maximum of 1.00 m s^{-1} (Table 2, Kimball et al., 2008).