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Differential response of rice plants to high night temperatures imposed at varying developmental phases

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ABSTRACT

Increasing night temperatures can reduce growth and yield of rice plants, but limited information is available on the comparative effects of high night temperature (HNT) treatment at different growth stages on growth and physiological responses of rice. We conducted a study in controlled-environment chambers to determine the growth and physiological responses and spikelet differentiation of rice cultivars to HNT treatment at different growth stages. Plants were exposed to two temperatures: 30/21 °C (low) and 30/25 °C (high) day/night temperatures. At the end of the vegetative period, plants grown in the low (LNT) and high (HNT) night temperatures were further subdivided and plants were exposed to different temperature treatments in the reproductive growth period. Photosynthesis, night respiration rates, and plant growth parameters were measured at various stages. High night temperature had no significant effects on the growth of rice cultivars during the vegetative phase. Maximum photosynthesis at the vegetative phase was not significantly affected, but plant dark respiration increased (within the 14–20% range). Genotypic variation in dark respiration was observed at later growth stages. Rice plants that received HNT at the early reproductive stage had the lowest number of spikelets per panicle, presenting a 35.9% of degenerated spikelets, significantly higher than those observed in other treatment times. This study shows that the response of rice cultivars to HNT varies with time of treatment and that the occurrence of HNT during the reproductive period provided supportive evidence on how HNT might reduce yield by increasing plant's dark respiration rate and spikelet degeneration (which consequently reduced sink size), thus, decreasing biomass production.

1. Introduction

The globally averaged surface temperature has increased by 0.85 °C over the period 1880–2012 (Hartmann et al., 2013) and could increase by 0.3–4.8 °C by the end of this century (Collins et al., 2013). The advent of global warming triggered many studies that aimed to evaluate its impacts on future food production. Increases in both mean and extreme values of temperature or short episodes of high temperature were found to have an impact on the growth and development of crops in tropical and other regions (Wheeler et al., 2000; McKeown et al., 2005). For example, the simulated yield reduction from a 1 °C rise in mean daily temperature was about 5% in maize, wheat, sorghum, and soybean in central USA (Brown and Rosenberg, 1997). Both maize and soybean yields in this country decreased by 17% for each 1 °C increase in growing-season temperature for the period 1982–1998 (Lobell and Asner, 2003).

Minimum or nighttime temperature has been rising in the past (Karl et al., 1991), continuing up to the present (Alward et al., 1999; IPCC, 2007). Current predictions indicate that global averaged maximum and minimum temperatures over land have both increased by >0.1 °C per decade since 1950. Time series of average growing-season monthly temperature revealed significant positive trends in temperature since 1980 for nearly all major growing regions of maize, wheat, rice, and soybeans (Lobell et al., 2011). Changes in temperature patterns have been predicted to have important consequences on crop production (Parry et al., 2004; Lobell and Field,

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2007) affecting both plant growth and development (Barnabas et al., 2008; Challinor et al., 2007).

Rice is one of the most important crops in the world, feeding more than 3.5 billion people (Zeigler and Barclay, 2008). It is extensively grown in a wide range of cropping systems and environments (Khush, 2005), and because these environments are prone to extreme temperature increases, rice is as vulnerable as the other crops to such increases in temperature. The predicted increases in night temperature will have negative impacts on rice crop production (Challinor et al., 2007) and on the livelihood of rice farmers in many parts of the world including east Asia, southeast Asia, south Asia and in US.

The first evidence of rice yield decrease associated with increasing nighttime temperature has been reported by Peng et al. (2004) using historical data sets from field experiments from 1993 to 2004. Their analysis showed that rice grain yield declined by 10% for each 1 °C increase in minimum temperature, but that the effect of maximum temperature on crop yield was not significant. Tao et al. (2008) showed that an increase of 0.8 °C in minimum temperature has a corresponding decline in grain yield of about 3.7%. Earlier studies using controlled-growth chambers showed similar decreases in grain yield of rice grown at high night temperatures (HNTs) (Ziska and Manalo, 1996; Morita et al., 2002, 2004; Horie et al., 1995), although the mechanism behind this was unclear.

The impacts of night temperature increases on rice growth vary across growth phases (Yoshida et al., 1981; Matsui et al., 1997; Prasad et al., 2006). Growth enhancement effects such as accelerated leaf emergence and elongation and increased biomass production (Tsunoda, 1964; Tanaka et al., 1968; Cutler et al., 1980) caused by both higher night water and air temperatures were observed at the vegetative phase of rice. Kanno et al. (2009) reported strong stimulation of growth of leaf blades and tiller number at the HNT of 27 °C during the early stage of rice growth, consequently increasing biomass at the vegetative period. High night temperature stimulated whole-plant-level photosynthesis as shown by the high CO_2 uptake, which consequently increased biomass production (Kanno et al., 2009). A similar increase in the following daytime leaf photosynthetic rates by HNT was previously reported by Turnbull et al. (2002), although other studies did not show any effects of HNT on photosynthesis (Frantz et al., 2004; Mohammed and Tarpley, 2009). The rates of dark respiration increased at HNT (Kanno et al., 2009; Cheng et al., 2009), but the magnitude was much smaller than what is generally expected from the temperature dependence of respiration, *i.e.*, typical Q_{10} values of two (Yamagishi, 1994).

The reproductive phase of rice (panicle initiation to heading) is the most sensitive stage to temperature because it is during this period that spikelet differentiation occurs and the potential number of spikelets in rice is determined (Kato et al., 2008). Satake and Yoshida (1978) showed that nighttime temperatures above 29.8 °C can increase sterility with a subsequent reduction in seed set and grain yield. Grain-filling percentage and consequently yield were significantly reduced by an increase of night temperature from 25 to 33 °C at a constant day temperature of 33 °C. The final grain weight of rice was reduced at HNT because of reduced grain growth rate (Morita et al., 2005).

Most of the studies previously conducted imposed night temperature treatments either at the vegetative or the reproductive growth phases. Enhancement effects were observed at the vegetative phase, which may increase source capacity. Biomass and yield reductions were reported but very limited information is available on the crucial stage of the onset of HNT that caused such reductions. A strong limitation on growth or sink size may be occurring if temperature treatments are applied at different stages, an approach that has not been done but may prove to be potentially valuable. We conducted an experiment in controlled-growth chambers to determine the effect of HNT imposed at different growth stages on growth and physiological processes of three different rice cultivars and identify the critical stage of HNT treatment that might shed light on the observed yield reduction in rice.

2. Materials and methods

2.1. Plant materials and pot experiment

A pot experiment was conducted using the controlled-environment growth chambers (Koitotrons, Koito Kogyo Co., Japan) of the National Institute for Agro-Environmental Sciences, Tsukuba, Japan (36°01′N, 140°07′E). Three rice (*Oryza sativa* L.) cultivars, namely Nipponbare (standard japonica cultivar, herein referred to as NPB) and IR36 and IR72 (modern indica mega varieties) were used in the study. Pregerminated rice seeds were sown on 19 June 2009 into seedling trays at one seed per cell and were grown under ambient conditions. Seventeen-day-old rice seedlings were transplanted on July 6, 2009 in 5 L plastic pots at one plant per pot. A total of 16 pots per cultivar were planted for the four temperature treatments (below) and four replications. Extra plants for the IR cultivars were maintained as stopgaps. Basal application of NPK fertilizer at the rate of 0.6 g urea supergranules, 1.91 g KCl, and 5.72 g P_2O_5 per pot was done before transplanting. Fertilizer was thoroughly mixed with the soil prior to transplanting. An additional 1.92 g $(NH_4)_2SO_4$ per pot was topdressed around the panicle initiation stage. The soil, collected from the top 20 cm plow layer of a rice field in Yawara, Ibaraki Prefecture, Japan, had an average pH of 5.8 and contained 30.1 g kg^{-1} organic carbon and 2.63 g kg^{-1} total nitrogen (Cheng et al., 2009).

2.2. Temperature treatments

Plants were grown in controlled-environment growth chambers with day/night temperatures of 30/21 °C low night temperature (LNT) and 30/25 °C HNT and 70% relative humidity (RH). The 25 °C temperature was chosen because based on the previous results in field chambers, this temperature caused 11% yield reduction (Zhang et al., 2013); thus, to understand the mechanism involved in yield reduction the same temperature settings were used. The night temperature was maintained for a 10-h period from 1900 to 0500. Air temperature and RH were measured with temperature–humidity sensors (HN-Q500-1; Chino, Tokyo) that were mounted above the rice canopy and shielded against direct solar radiation. Ambient air temperature was monitored. Pots were laid out in split plot in randomized complete block design with temperature regime (growth chamber) as main plot and variety as subplot. There were no chamber or true replicates, thus, to minimize variation, the pots in each chamber were rotated at weekly intervals and the chambers were rotated at 3-week interval, *i.e.*, pots from one chamber were transferred to the other and *vice versa* and the environment settings were changed accordingly. Fig. 1 shows the schematic diagram of the schedule of treatment and temperature condition inside and outside the growth chambers.

At the end of the vegetative period (onset of panicle initiation, PI), the LNT treatment was kept from transplanting until heading stage while the HNT was subdivided into another three treatments as follows:

(1) Control LNT (C-LNT); plants continuously grown under LNT from transplanting until heading stage.
(2) Vegetative HNT (V-HNT); HNT treatment from transplanting to PI stage.
(3) Reproductive (R-HNT); plants grown under 30/21 °C until PI and transferred to 30/25 °C (HNT) from PI to heading.