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Effects of high night temperature on yield and agronomic traits of irrigated rice under field chamber system condition

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Abstract

Temperature during night is greater than daytime and tends to be further increased in the future as a result of global warming. However, little information is known about genotypic responses to warm nighttime temperatures *in situ*. Field experiments were conducted in 2009 wet season (WS), 2010 dry season (DS), 2010WS and 2011DS at IRRI to determine the genotypic variation in sensitivity to warm nighttime temperature. Thirty-six varieties, originated from different countries, were grown in temperature-controlled field chambers. An increase of 4.8 °C, 4.0 °C, 3.9 °C and 3.8 °C in night temperature was imposed on the plants from 40 to 120 days after transplanting (DAT) from 1900h to 0600h. Significant difference of grain yield between low night temperature (LNT) and high night temperature (HNT) treatment was observed in all experiments. Grain yield in HNT was decreased by 16.7%, 9.1%, 9.6% and 8.0% than LNT in the four consecutive seasons, respectively. The negative effect of HNT on grain yield was partially due to low biomass and low harvest index (HI). Plants in LNT achieved higher total dry weight because of higher crop growth rate (CGR). Mild increase in night temperature during the reproductive growth stage reduced yield which was attributed to decrease in grain weight, harvest index, grain filling (2009WS), and spikelets number per panicle (2010DS and 2011DS). Our study showed that ~4°C differences between HNT and LNT in the field chamber system causes 11% grain yield decrease on average of four consecutive seasons. Genotypes N22, PSBRc52, Swarna and IR8 were tolerant to high night temperature.

Keywords: Grain yield, night temperature, rice, temperature-controlled field chambers, yield components.
Abbreviations: DAT_days after transplanting, DS_dry season, HNT_high night temperature, LNT_low night temperature, RH_relative humidity, WS_wet season.

Introduction

Global mean surface air temperature increased by ~0.5 ºC in the 20th century and will be likely further increased by 1.5 to 4.5ºC in this century (IPCC, 2001). IPCC predicted continuous warming of 0.2°C per decade in the coming few decades (IPCC, 2007). The overall global trend of maximum temperature increased 0.141ºC per decade and 0.204ºC per decade of minimum temperature from 1950 to 2004 (Vose et al., 2004). Recent increase in night temperature has been approximately three times higher of the corresponding day temperatures in the earth's surface (Karl et al., 1991).

Global warming could increase agriculture production in some temperate countries, but possibly decrease production in most Asian countries (Rosenzweig et al., 1993). Rice (*Oryza sativa* L.) is one of the most important crops in the world. Approximately, 90% of rice yield are produced and consumed in tropical Asia (FAO, 2008). Rice is extensively grown in wide range of cropping systems and environments, much of which is experiencing increase in daytime and nighttime temperature (Khush et al., 2005). Most of rice yield is being grown in regions, where current temperature is already close to optimum for production. As a C_3 crop species, rice responds favorably to high air temperature under carbon dioxide enrichment which increases assimilation rates and final grain yield (Baker et al., 2004). Achieving higher yield depends on increasing total biomass. Total crop biomass is determined mainly by crop photosynthesis and respiration losses, both of which are sensitive to temperature (Peng et al., 2004).

Recently, more attention has been paid on rice yield under night temperature stress. It is reported that the grain yield is declined by 10% with any 1ºC minimum temperature increase, while this effect of maximum temperature increase on crop yield is insignificant (Peng et al., 2004). Lobell et al. (2005) analyzed a 15-year historical data set (1988-2002) from two major wheat growing areas in Mexico and found that wheat yield was associated with growing-season mean minimum temperature, not with mean maximum temperature or daily radiation. Mohammed et al. (2009) confirmed that high nighttime temperature affected rice productivity through altered pollen germination and spikelet fertility. Kanno et al.

(2010) indicated that the relative growth rate in the night temperature of 27 °C treatment caused increase in leaf area ratio, leaf weight ratio and specific leaf area during the vegetative stage of rice plant. Welch et al. (2010) used a multiple regression model to analyze data from 227 intensively managed irrigated rice farms in six important rice producing countries and found that higher minimum temperature reduced grain yield but higher maximum temperature improved it. Meanwhile, Kanno et al. (2010) found grain yield and biomass allocation of rice increased under cool night temperature.

Adopting high temperature-tolerant cultivars is one of the most effective countermeasures to maintain high productivity and stability of rice under anticipated climate change (Horie et al., 1996). Genetic variability to high temperature tolerance *per se* has been reported in rice as early as in the late 1970s. Jennings et al. (1979) found some varieties, such as Hoveyzeh from southern Iran, which still remained fertile at the temperature over 45^{o}C, while other varieties were already completely sterile. Baker (2004) indicated that tropical japonica variety from the southern US were more sensitive to high temperature than indica and temperate japonicas varieties. Prasad et al. (2006) did not find clear species or ecotype difference in 14 diverse cultivars, but identified N22 as the heat tolerant variety and noted its potential for genetic improvement in heat tolerance based on existing variation. Genotypes N22 (Satake, 1995; Prasad et al., 2006) and Akitakomachi (Matsui et al., 2001) are the most tolerant genotypes between indica and japonica.

Although the physiological effects of increasing day temperature at extreme level on rice are well established, the effects of HNT associated with slight increase in night temperature from global warming on rice production are poorly understood. No study has been conducted on the genetics of high night temperature tolerance in rice, especially during rice reproductive stage. Most previous researches on the effect of temperature on crop plants have been conducted in two ways. One is doing temperature controlled chambers experiment, in which pot-grown plants were used. The other is analyzing correlation and regression, or historical data sets from yield records and long-term field experiments. These approaches have some weakness, because they do not necessarily reproduce field condition or possible confounding effects of other factors aside from temperature. The objectives of this study were (1) to elucidate the effect of night temperature on the biomass production and growth of rice plants under field condition, (2) to focus on understanding the fundamental effects of night temperature on yield and yield components, (3) to screen breeding materials with more tolerance to high night temperature for development of new varieties for a warmer world.

Results

Temperature and relative humidity

Mean seasonal nighttime (1900-0600h) temperature during the treatment were 22.6 ^{o}C in low night temperature (LNT) and 27.4 ^{o}C in high night temperature (HNT) in 2009WS; 22.0^{o}C and 26.0^{o}C in 2010DS, 22.9^{o}C and 26.8^{o}C in 2010WS; 22.1^{o}C and 25.9^{o}C in 2011DS, respectively. Difference between LNT and HNT were 4.8 ^{o}C, 4.0 ^{o}C, 3.9 ^{o}C and 3.8 ^{o}C in the four consecutive seasons, respectively. Relative humidity (RH) was 95.5% in LNT and 86.2% in HNT in 2009WS; 93.3% and 85.9% in 2010DS; 92.9% and 85.4% in 2010WS, 95.9% and 84.6% in 2011DS, respectively (Fig 1). RH of LNT was found to be higher than the ambient and HNT treatments. The carbon dioxide concentration of the chamber and ambient was almost the same during the treatment period. The water temperature of HNT was slightly higher than ambient, while LNT was lower than ambient (data not shown).

Plant height and panicle number

Plant height was significantly different between LNT and HNT in the three experiments except 2011DS (Table 3). There were no significant interactions between temperature and cultivars on plant height (Table 2). The average plant height of the 36 varieties was 109.6 cm in the LNT and 115.5 cm in the HNT in 2009WS; 104.9cm and 107.1 cm in 2010DS, 116.4 cm and 118.9 cm in 2010WS, respectively. The LNT plants were shorter than HNT by 5.9 cm, 2.2 cm, and 2.5 cm in the three consecutive seasons, respectively.

There were no significant effects of temperature on crop phenology. Varietal difference in growth duration was significant in all the four experiments (Table 3). The heading stage and physiological mature stage in LNT were one or two days later than that of in HNT in the four seasons. Significant difference in panicle number per m^2 between HNT and LNT treatments was only observed in 2011DS, whereas the other three seasons were not significant.

Dry weight and crop growth rate

Significant difference in total dry weight between LNT and HNT treatment was observed in all the four experiments (Table 3). Total dry weight of all cultivars was significantly decreased from 1103 g.m^{-2} to 1002 g.m^{-2} on average during 2009WS, from 1438 g.m^{-2} to 1362 g.m^{-2} during 2010DS, from 1150 g.m^{-2} to 1087 g.m^{-2} during 2010WS, and from 1320 g.m^{-2} to 1266 g.m^{-2} during 2011DS, respectively. Biomass in HNT was decreased by 9.2%, 5.3%, 5.5% and 4.1% than LNT in the four consecutive seasons, respectively. There was no significant interaction effect on variety and temperature in all the four experiments. There was significant effect of temperature on crop growth rate (CGR). Plants in the LNT achieved higher total dry weight because of their higher CGR than HNT (Table 3).

Grain yield and yield components

Significant difference in grain yield between LNT and HNT treatment was observed in all the experiments (Table 4). Varietal difference in grain yield was significant in all the four experiments, but there were no statistically significant temperature×variety interactions (Table 2). Average yield of LNT was 455.6 g.m^{-2}, 681.3 g.m^{-2}, 487.6 g.m^{-2} and 579.0 g.m^{-2} in the four consecutive seasons, respectively. Average yield of HNT was 379.3 g.m^{-2},619.2 g.m^{-2}, 440.7 g.m^{-2} and 532.9 g.m^{-2} in the four consecutive seasons, respectively. Grain yield in HNT was decreased by 16.7%, 9.1%, 9.6% and 8.0% than LNT in the four consecutive seasons, respectively.

Significant difference in grain filling between LNT and HNT treatment was observed in 2009WS, with values of 73.8% in LNT and 69.7% in HNT, respectively. Significant difference in spikelets per panicle was observed between LNT and HNT in 2010DS and 2011DS. The average of spikelets in LNT was 89.3 and 89.2 per panicle in 2010DS and 2011DS, which was 7.2% and 7.8% higher than HNT in the two dry seasons. The negative effect of HNT on grain yields were much greater than on biomass, which led to significant lower harvest index in HNT (Table 3). Grain

Table 1. Details on year of release and origin of thirty-six rice cultivars in the four experiments.

Cultivars	Year of release	Origin	Cultivars	Year of release	Origin
IR6	1966	Philippines	NSICRc158	2007	Philippines
IR8	1966	Philippines	NSICRc112	2000	Philippines
IR20	1969	Philippines	NSICRc122	2003	Philippines
IR22	1969	Philippines	IR62266-42-6-2	2001	Philippines
IR24	1971	Philippines	BRRI dhan29	2001	Bangladesh
IR26	1973	Philippines	Cibogo	2003	Indonesia
IR30	1974	Philippines	Cigeulis	2002	Indonesia
IR36	1976	Philippines	Ggarib	1975	Iran
IR42	1977	Philippines	N22	1991	India
IR50	1979	Philippines	OM2517	2001	Vietnam
IR56	1982	Philippines	Swarna	1982	India
IR60	1983	Philippines	Mestizo1	1997	Philippines
IR64	1985	Philippines	Ciherang	2000	Indonesia
IR72	1988	Philippines	MTU1010	1999	India
PSBRc4	1991	Philippines	Sambha Mahsuri	1971	Malaysia
PSBRc18	1994	Philippines	Saunfi	1974	Paskistan
PSBRc52	1997	Philippines	Tchampa	1988	Iran
PSBRc82	2000	Philippines	X21	1996	Vietnam

weight was significantly higher in LNT than in HNT in all the four experiments. Both grain weight and HI were higher in LNT than in HNT.

Discussion

Effect of high night temperature on rice growth

Plant height of rice was significantly increased by HNT in all the four experiments except 2011DS. One possible explanation was that the elongated rice stems retained more photosynthate than the ears did under high night temperature (Cheng et al., 2009). Panicle number was not significantly affected between HNT and LNT. Previous work indicated crop growth duration was shortened under HNT, but this study did not find such significant difference. The different results may be caused by different treatment periods. Most previous temperature treatments were just conducted in vegetative stage, while the temperature treatments in this study started from 40 days after transplanting. It is possible that vegetative stage is more sensitive than reproductive stage for crop growth duration under high temperature (Mohammed et al., 2009).

Biomass in HNT decreased by 9.2 %, 5.3 %, 5.5 % and 4.1 % than LNT in the four consecutive seasons, because HNT received lower biomass due to its lower CGR. Rice biomass production was determined by the balance between net photosynthesis rate and night respiration (Sakai et al., 2001). High temperature increased respiration but decreased membrane stability, and it could potentially reduce biomass production (Peng et al., 2004) but improve the overall anti-oxidant status and physiological performance of rice (Shah et al., 2011). Plant CO_2 uptake and dark respiration were higher in HNT than in LNT (Pearcy, 1977). On the other hand, Culter et al. (1980) reported that elevated low night temperature accelerated the leaf elongation of rice period. Elevated low night temperature improves the plant biomass, which is associated with morphology change at the whole plant level (Cheng et al., 2009). High night temperature increases C assimilation owing to the increased N concentration in the living leaves and to increased leaf area per unit weight (Cheng et al., 2010). However, some researchers reported different results that total dry weight is significantly greater in the HNT grown plants than in the LNT grown plants, because plants in HNT had an increase of

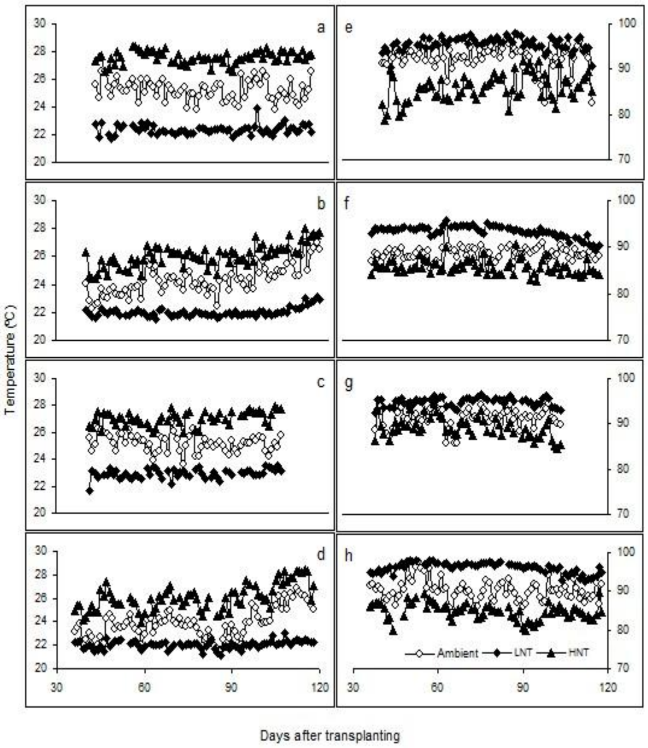

Fig 1. Daily nighttime temperature (a-d) and relative humidity (e-h) in 2009WS (a, e); 2010DS (b, f); 2010WS (c, g) and 2011DS (d, h) at IRRI farm.

leaf area and tiller number (Kanno et al., 2009).

Effect of high night temperature on rice yield

The high night temperature was strongly and negatively correlated with grain yield in all the four experiments. Grain yields in HNT decreased by 16.7%, 9.1%, 9.6% and 8.0% than LNT in the four seasons. Among the yield components, significant differences were observed in both grain weight and harvest index in the four experiments. Furthermore, significant differences were observed in grain filling in 2009WS, and spikelets pancible^{-1} in 2010DS and 2011DS, respectively.

Table 2. Analysis of variance for grain yield, aboveground total dry weight (TDW), harvest index (HI), plant height (PH), Grain filling (GF), grain weight (GW), panicles number (PN) and spikelets number (SN) at harvest at IRRI farm, Philippines.

Source of variation	Yield	TDW	HI	PH	GF	GW	PN	SN
Temperature(T)	**	**	**	**	*	**	ns	*
Variety(V)	**	**	**	**	**	**	**	**
Season(S)	ns	ns	ns	ns	*	ns	ns	*
T×V	ns	ns	ns	ns	ns	ns	ns	ns
T×S	*	ns	ns	ns	ns	ns	ns	ns
V×S	ns	ns	ns	ns	ns	ns	ns	ns
T×V×S	ns	ns	ns	ns	ns	ns	ns	ns

Within a column for each year, means followed by the same letters are not significantly different according to LSD (0.05). * Significance at the 0.05 level based on analysis of variance. ** Significance at the 0.01 level based on analysis of variance. NS denotes non-significance based on analysis of variance

Seshu and Cady (1984) predicted that rice yield would decrease by 41 g.m^{-2} when the average minimum temperature raised from 22 to 23^{o}C. Peng et al. (2004) reported that grain yield declined by 10% for each 1 ºC increase of minimum temperature. The grain yield decreased in 2009WS with a greater difference than the other seasons. In this study, ~4 ^{o}C differences was achieved between HNT and LNT, and grain yield decreased by 11% on average in the four seasons.

Rice yield is determined by panicle number per land area, spikelet number per panicle, filled spikelet percentage and grain weight. Peng et al. (2004) attributed the decrease in yield to the reduction in the total number of spikelets per plant. Yoshida showed that night temperature higher than 30 ^{o}C reduced spikelet fertility. In this study, the reduced grain yield was attributed to decrease in grain weight, harvest index, grain filling (2009WS), and spikelets number per panicle (2010DS and 2011DS).

The grain weight of rice cultivar is almost constant under stress-free environment (Yoshida, 1981). The decrease in rice grain length and width might be associated with the reduction in average endosperm cell area observed under HNT (Morita et al., 2005). High night temperature could effect both carbon and nitrogen flow to the grain (Mohammed et al., 2010). Carbohydrate deficit was possibly caused by increased respiratory loss at high temperature during the ripening period (Kanno et al., 2010).

Screening of rice cultivars for high night temperature tolerance

Adoption of high temperature-tolerant cultivars is one of the most effective countermeasures to maintain high productivity and stability of rice under anticipated climate change (Horie et al., 1996). Many methods have been used to screen rice cultivars for high temperature tolerance. Satake and Yoshida (1978) suggested that the screening temperature of 35^{o}C could be used to eliminate heat susceptible materials and the temperature of 38 ^{o}C be used to identify heat tolerance donors. Matsui et al. (2005; 2007) found that the length of basal dehiscence was closely correlated with the pollination viability or reliability under hot condition and could be also used as a marker for selecting high temperature tolerant genotypes. Mackill (1983) and Prasad et al. (2006) suggested that spikelet fertility at high temperature could be used as a screening tool in breeding for tolerance to high temperature during the reproductive phase. Decreased spikelet fertility has been the basis of cultivar differences observed at high temperature, which was due to decreased pollen production and pollen reception. There is genotypic variation in spikelet sterility at high temperature (Matsui et al., 2001; Satake and Yoshida, 1978; Prasad et al., 2006) that can be defined by different temperature thresholds.

Among all the varieties in the four experiments, the grain yield of Sambha Mahsuri, IR6, BRRI dhan29 and saunfi was sensitive to HNT, and decreased by 27.4%, 21.5%, 20.6%, and 19.5% in HNT than LNT in the four seasons, respectively. In contrast, N22, PSBRc52, Swarna and IR8 were insensitive to HNT as evidenced by their stable grain yield in HNT. Genotypes N22 (Satake, 1995; Prasad et al., 2006) and Akitakomachi (Matsui et al., 2001) are the most tolerant genotypes in indica and japonica rices.

The results of this study suggest that there is genotypic variation in sensitivity to warmer night temperatures. Cultivation of high temperature-tolerant varieties is an effective way to achieve high productivity and stability of rice under anticipated climate change.

Materials and methods

Experiment site

Field experiments were conducted for four consecutive seasons 2009 wet season (WS), 2010 dry season (DS), 2010WS and 2011DS in one unique field at the International Rice Research Institute (IRRI) farm, Los Baños (14°11′N, 121°15′E, 21 m), Philippines. The soil was an Aquandic Epiaquoll with pH 6.4; 20.0 g kg^{-1} organic C; 1.8 g kg^{-1} total N; 4.5 mg kg^{-1} Olsen P; 0.887cmol kg^{-1} exchangable K and 36.2 cmol kg^{-1} cation exchange capacity; and 59.0% clay, 32.0% silt, and 9.0% sand. The soil test was based on samples taken from the upper 20 cm of the soil before transplanting in 2010DS.

Growth chambers

The field experimental area was designed with 16 temperature-controlled chambers orientated to south-north direction. The chambers were 6×3×2 m in length, width and height, respectively. The chambers were placed with 2.8 m interval for ventilation to avoid mutual shading. The framework consisted of a series of shed-type pipes. The front and back were steel structured as a skeleton covered with a layer of insulation UV-transparent film. Each chamber was equipped with an air conditioner (CW-1805V, Matsushita Electric Philippines Corp., Taytay, Rizal, Philippines). Two inlet fans were paralleled and installed at the height of 90 cm in the front frame with a horizontal space of 102cm. The two outlet fans were paralleled and installed at the height of 135cm in the back frame with a horizontal space of 102cm, too. These exhaust fans were used to minimize relative humidity and CO_2 concentration between the chamber and ambient by air exchange. During the daytime, the top and two sides of the chamber film were opened, so that the plants were exposed to the same environmental condition as the

Table 3. Growth duration, plant height, total dry weight (TDW), crop growth rate (CGR) and harvest index of thirty-six varieties grown at IRRI farm, Philippines. Data were the means across four seasons.

Variety	Growth duration (days)		Plant Height （cm）		TWD ($g.m^{-2}$)		CGR ($g.m^{-2}.d^{-1}$)		Harvest index (%)	
	LNT	HNT	LNT	HNT	LNT	HNT	LNT	HNT	LNT	HNT
BRRI dhan29	109	109	112.5	112.1	1475.1	1322.1	13.7	12.3	44.1	40.8
Cibogo	104	102	110.0	113.6	1378.2	1330.0	13.3	13.1	45.6	43.1
Cigeulis	103	100	111.0	114.7	1260.5	1230.5	12.3	12.3	44.4	42.2
Ciherang	105	104	107.9	110.7	1377.2	1290.2	13.1	12.5	45.2	40.7
Gharib	86	80	126.7	125.5	906.0	856.8	10.5	10.8	39.4	36.7
IR20	116	115	102.4	103.1	1215.5	1160.9	10.5	10.1	40.7	36.0
IR22	110	109	96.7	99.0	1052.3	1077.0	9.6	9.9	40.1	36.4
IR24	113	112	103.0	109.1	1636.2	1551.3	14.5	13.9	40.9	39.8
IR26	118	115	113.2	116.6	1659.0	1508.8	14.1	13.1	44.1	40.8
IR30	106	106	103.1	102.1	1304.3	1223.9	12.3	11.6	42.1	39.9
IR36	100	97	98.9	98.2	940.4	829.7	9.4	8.6	44.4	41.1
IR42	118	118	108.6	109.9	1618.2	1537.7	13.7	13.0	43.3	40.5
IR50	96	94	98.1	98.4	953.2	883.4	9.9	9.4	41.3	38.8
IR56	99	98	99.7	99.9	1233.4	1169.9	12.5	11.9	48.2	48.1
IR6	79	77	118.7	117.8	721.5	670.9	9.1	8.7	39.2	33.0
IR60	102	98	96.4	96.1	945.3	896.5	9.3	9.2	45.5	42.3
IR62266-42-6-2	114	113	110.6	115.1	1405.5	1082.2	12.3	9.6	35.8	37.3
IR64	103	101	106.1	109.5	1302.9	1284.4	12.7	12.7	46.5	44.3
IR72	107	105	103.7	107.8	1308.7	1245.1	12.3	11.9	42.7	39.6
IR8	118	115	100.1	106.1	1599.6	1558.6	13.6	13.6	38.8	37.2
Mestizo1	103	99	113.9	122.0	1555.9	1341.1	15.1	13.5	46.0	45.1
MTU1010	101	96	115.0	116.2	1366.9	1272.8	13.5	13.3	43.8	42.7
N22	80	79	129.8	131.0	1105.0	1086.7	13.9	13.7	41.1	42.4
NSICRc112	103	98	109.6	111.5	1410.3	1333.0	13.6	13.6	45.3	45.3
NSICRc122	102	99	112.7	116.4	1460.2	1350.8	14.1	13.5	46.7	45.1
NSICRc158	110	109	108.7	111.1	1392.2	1329.0	13.1	12.4	45.5	43.1
OM2517	100	96	112.6	115.1	1396.6	1320.8	14.0	13.7	48.7	48.0
PSBRc18	112	111	109.4	111.2	1409.0	1261.9	12.6	11.4	45.0	41.2
PSBRc4	95	93	103.3	106.1	1172.4	1109.4	12.3	11.8	43.9	42.0
PSBRc52	103	99	102.4	105.5	1052.1	1046.8	10.3	10.6	45.4	44.9
PSBRc82	103	103	113.5	117.1	1269.5	1148.7	12.2	11.2	46.7	41.6
Sambha Mahsuri	114	114	91.8	99.1	991.0	1034.9	8.5	9.1	32.7	21.1
Saunfi	98	96	140.4	147.5	1511.8	1255.3	15.4	13.1	39.9	38.7
Swarna	109	108	102.2	105.1	981.2	944.5	9.0	8.8	36.7	36.6
Tchampa	90	89	115.7	144.4	1098.5	992.9	12.2	11.2	39.0	36.4
X21	116	116	105.7	109.1	1579.3	1426.8	13.5	12.3	40.7	37.3
Mean	***104a***	***102a***	***108.7b***	***112.0a***	***1279.0a***	***1193.5b***	***12.3a***	***11.7b***	***42.8a***	***40.3b***

Within a column for each parameter, means followed by the same letters are not significantly different according to LSD (0.05).

ambient-grown plants. Air temperature and relative humidity (at 50 cm above the soil of the chamber) were monitored independently using standalone sensor/loggers (HOBO, Onset computer Corp., Bourne, MA, USA) in each chamber. The temperature and humidity during the nighttime (1900-0600 h) were automatically recorded every 30 minutes.

Temperature treatments

Experimental design was split-plots with eight replications in the four consecutive seasons. The main plots were two temperature regimes (HNT and LNT). The sub-plots were the 36 varieties. Detailed information about varieties is given in Table 1. During nighttime (1900-0600 hours), the chambers were closed and the air conditioner was turned on to create about 4 °C difference between high night temperature and low night temperature. HNT was set at 26 °C and 27 °C in the WS and DS. LNT was set at 22 °C and 23 °C in the WS and DS, respectively. Night temperature treatments were implemented at 40 DAT in the four seasons.

Crop husbandry

Thirty-six varieties were grown inside the chamber to study the effects of night temperature on grain yield in 2009WS, 2010DS, 2010WS and 2011DS, respectively. Pre-germinated seeds were sown in seeding trays to produce uniform seedlings. Fourteen-day-old seedlings were manually transplanted on 11 June, 16 Jan, 15 June and 23 Feb in 2009WS, 2010DS, 2010WS and 2011DS, respectively. Four seedlings per hill were transplanted at a hill spacing of 20×20cm. All fertilizers were manually broadcast and incorporated during basal application: 30 kg P ha^{-1}, 40 kg K ha^{-1}, and 5 kg Zn ha^{-1} in the DS and 15 kg P ha^{-1}, 20 kg K ha^{-1}, and 2.5 kg Zn ha^{-1} in the WS, respectively. Nitrogen in urea form was split applied: 60 kg ha^{-1} at basal, 40 kg ha^{-1} at mid-tillering, 60 kg ha^{-1} at panicle initiation and 40 kg ha^{-1} at flowering in the DS; 30 kg ha^{-1} at basal, 20 kg ha^{-1} at mid-tillering, 30 kg ha^{-1} at panicle initiation and 20 kg ha^{-1} at flowering in the WS, respectively. Crop management followed the standard cultural practices. The experimental field was kept flooded from transplanting day until 7 days

Table 4. Grain yield and yield components of thirty-six varieties grown at IRRI farm, Philippines. Data were the means across four seasons.

Variety	Grain yield ($g.m^2$)		Grain filling (%)		Spikelets ($Panicle^{-1}$)		Grain weight (mg)		Panicles (m^2)	
	LNT	HNT	LNT	HNT	LNT	HNT	LNT	HNT	LNT	HNT
BRRI dhan29	691.1	553.0	76.9	75.1	135.4	120.3	19.8	19.2	339.3	321.2
Cibogo	631.4	577.8	81.2	78.3	93.1	91.0	23.5	23.0	359.6	356.6
Cigeulis	560.4	522.2	78.9	79.4	98.5	92.0	23.5	22.9	309.6	313.7
Ciherang	622.0	526.9	79.1	77.9	97.8	85.9	23.8	23.1	341.0	340.6
Gharib	358.5	319.7	82.9	74.4	56.0	57.3	25.0	24.1	306.1	306.4
IR20	493.9	428.7	79.6	72.7	85.7	78.0	22.4	21.5	337.2	354.9
IR22	426.3	394.0	78.4	79.1	77.9	73.6	20.3	20.3	342.6	333.4
IR24	669.3	619.9	87.1	88.7	84.9	75.2	25.6	25.0	354.2	370.6
IR26	733.8	616.5	85.2	85.4	100.2	93.1	20.7	20.4	417.4	379.7
IR30	550.2	487.6	77.9	76.7	75.8	67.3	20.8	20.5	453.5	469.9
IR36	418.4	343.8	65.5	63.8	83.2	73.4	20.4	19.8	377.3	370.9
IR42	699.2	624.5	88.2	90.8	100.9	88.9	18.6	18.6	427.6	422.9
IR50	403.7	350.8	59.9	57.2	93.1	85.4	17.8	17.5	395.3	402.7
IR56	598.5	562.8	68.3	74.7	81.9	71.7	23.1	22.5	461.2	471.6
IR6	283.0	222.1	81.2	74.7	51.9	45.9	24.6	23.1	273.8	280.5
IR60	434.2	387.3	71.6	72.1	78.2	68.1	18.6	18.2	414.3	422.2
IR62266-42-6-2	500.2	405.7	65.5	67.0	87.5	80.1	22.0	21.7	400.5	346.7
IR64	612.6	575.0	80.4	79.5	82.5	79.7	24.2	23.7	378.8	379.7
IR72	559.5	494.1	74.0	73.5	90.2	83.7	22.0	21.7	383.6	372.9
IR8	620.7	590.1	84.2	84.8	78.0	70.7	26.4	26.3	359.1	367.2
Mestizo1	713.2	605.3	68.8	67.9	117.7	105.4	23.3	22.9	381.3	371.9
MTU1010	606.8	549.5	80.5	80.9	90.2	87.6	23.8	23.2	344.4	336.9
N22	460.8	462.2	85.1	85.8	80.2	80.5	17.5	17.4	386.2	391.7
NSICRc112	654.2	614.5	73.1	72.1	94.6	95.2	23.1	22.7	400.8	386.9
NSICRc122	679.1	606.7	84.1	81.6	90.7	85.2	22.5	21.9	390.9	396.8
NSICRc158	642.4	591.8	78.9	77.4	99.2	94.3	21.4	20.6	373.3	374.6
OM2517	686.0	634.3	83.3	79.2	92.9	92.9	22.7	22.3	388.8	386.7
PSBRc18	638.7	530.2	79.3	77.6	99.1	87.0	21.4	20.4	380.9	380.4
PSBRc4	542.3	493.5	67.4	64.7	84.5	85.2	20.8	20.2	427.3	412.8
PSBRc52	479.3	472.3	78.6	78.4	80.3	77.1	18.8	18.7	400.8	421.2
PSBRc82	597.1	489.6	78.5	72.3	90.9	84.7	23.0	22.6	365.5	347.3
Sambha Mahsuri	304.3	220.9	76.5	65.4	113.7	100.2	11.7	11.7	287.5	285.8
Saunfi	603.2	485.3	68.5	57.9	217.4	219.8	11.6	11.9	349.7	323.2
Swarna	364.4	352.1	74.8	71.4	84.8	90.2	18.7	18.1	301.9	296.4
Tchampa	428.3	360.3	85.9	80.0	62.2	62.1	23.5	22.0	339.8	329.5
X21	650.6	545.4	66.3	67.0	117.7	110.7	23.5	22.5	347.6	314.3
Mean	***553.3a***	***489.3b***	***77.1a***	***75.2a***	***93.0a***	***87.2b***	***21.4a***	***20.9b***	***369.4a***	***365.0a***

Within a column for each parameter, means followed by the same letters are not significantly different according to LSD (0.05).

before maturity. Insects were intensively controlled by chemicals to avoid biomass and yield loss.

Sampling

Twelve hills were sampled diagonally from each plot to determine aboveground total dry weight, harvest index, and yield components. Panicle number was counted in each hill to determine panicle number per m^2. Plants were separated into straws and panicles. Straw dry weight was determined after oven-drying at 70°C to constant weight. Panicles were hand-threshed and the filled spikelets were separated from unfilled spikelets by submerging them in tap water. Three subsamples of 30 g of filled spikelets and 3 g of unfilled spikelets were taken to count the number of spikelets. Dry weights of rachis, filled and unfilled spikelets were determined after oven-drying at 70°C to constant weight. Aboveground total dry weight was the total dry matter of straw, rachis, and filled and unfilled spikelets. Spikelets per panicle, grain-filling percentage (100 × filled spikelet number/total spikelet number), and harvest index (100 × filled spikelet weight/aboveground total dry weight) were calculated. Grain yield was determined from 12 hills in each plot and adjusted to the standard moisture content of 0.14 g H_2O g^{-1}. Crop growth rate (aboveground total dry weight/crop growth duration).

Statistical analysis

Data were analyzed following analysis of variance (SAS Institute, 2003) and means of varieties were compared based on the least significant difference test (LSD) at the 0.05 probability level.

Conclusions

Significant differences in grain yield between LNT and HNT treatments were observed in our study. Varietal differences in grain yield were significant in all the four experiments, but there were no statistically significant temperature × variety interactions. The results indicated that mild increase in night temperature during the reproductive growth stage reduced yield which was attributed to decrease in biomass, crop growth rate, grain weight, and harvest index. In our study, 4°C difference between HNT and LNT caused 11% grain yields decrease on average in the four seasons. Some varieties, such as N22, PSBRc52, Swarna and IR8, were insensitive to high night temperature. The most sensitive varieties were Sambha Mahsuri, IR6, BRRI dhan29 and Saunfi. Screening of breeding materials with more tolerance to high night temperature is an efficient way to develop new varieties for a warmer world.

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References

Baker TJ (2004) Yield responses of southern US rice cultivars to CO_2 and temperature. Agr Forest Meteorol 122:129-137.

Cheng W, Sakai H, Yagi K (2009) Interactions of elevated [CO_2] and night temperature on rice growth and yield. Agr Forest Meteorol 149:51-58.

Cheng W, Sakai H, Yagi K (2010) Combined effects of elevated [CO_2] and high temperature on carbon assimilation, nitrogen absorption, and the allocations of C and N by rice (*Oryza sativa* L.). Agr Forest Meteorol 150:1174-1218.

Cutler JM, Steponkus PL, Wach MJ, Shahan KW (1980) Dynamic aspects and enhancement of leaf elongation in rice. Plant Physiol 66:147-152.

FAO (2008) Food outlook global market analysis. 23-28.

Horie T, Matsui T, Nakagawa H, Omasa K (1996) Effect of elevated CO2 and global climate change on rice yield in Japan. In: Omasa, K., Kai, K., Toda, H., Uchijima, Z., and Yoshino, M., eds. Climate Change And Plants In East Asia. Tokyo: Springer-Verlag 39-56.

IPCC (2001) Climate change 2001: The scientific basis. Contribution of working group I to the third assessment report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press.

IPCC (2007) Climate change 2007: The physical science basis summary for policymakers contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press.

Jennings PR, Coffman WR, Kauffman HE (1979) Rice improvement.IRRI, Los Baños, Philippines.

Karl RT, George K, Vyacheslav N, Changery MJ (1991) Global warming: Evidence for asymmetric diurnal temperature change. Geophysical Res Letters 18:2253-2256.

Kanno K, Tadahiko, Makino A (2009) High night temperature stimulates photosynthesis, biomass production and growth during the vegetative stage of rice plants. Soil Sci Plant Nutr 55:124-431.

Kanno K, Makino A (2010) Increased grain yield and biomass allocation in rice under cool night temperature. Soil Sci Plant Nutr 56: 412-417.

Khush S (2005) What it will take to feed 5.0 Billion rice consumers in 2030. Plant Mole Biol 59:1-6.

Lobell DB, Ortiz-Monasterio JI, Asner GP, Matson PA, Naylor RL (2005) Analysis of wheat yield and climatic trends in Mexico. Field Crops Res 94: 250-256.

Mohammed AR, Tarpley L (2009) High nighttime temperatures affect rice productivity through altered pollen germination and spikelet fertility. Agr Forest Meteorol 14:999-1008.

Mohammed AR, Tarpley L (2010) Effect of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa* L.) plants. Eur J Agron 33:117-123.

Morita S, Yonemaru J, Takanashi J (2005) Grain growth and endosperm cell size under high night temperatures in rice (*Oryza sativa* L.). Annals Bot 95(4): 695-701.

Matsui T, Omasa K, and Horie T (2001) The difference in sterility due to high temperatures during the flowering period among japonica rice varieties. Plant Production Sci 4: 90-93.

Mackill DJ, Coffman WR, Rutger JN (1982) Pollen shedding and combining ability for high temperature tolerance in rice. Crop Sci 22:730-733.

Pearcy RW(1977) Acclimation of Photosynthetic and Respiratory Carbon Dioxide Exchange to Growth Temperature in *Atriplex lentiformis* (Torr.) Wats. Plant Physiol 59:795-799.

Peng S, Huang J, Sheehy JE, Laza RC, Visperas RM, Zhong X (2004) Rice yields decline with higher night temperature from global warming. Proc Nat Acad Sci 101:9971-9975.

Prasad PV, Boote KJ, Allen LH, Sheehy JE, Thomas JM (2006) Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crops Res 95:398-411.

Rosenzweig C, Parry ML, Fischer G, Frohberg K (1993) Climate change and world food supply. Research Report No. 3. Oxford: University of Oxford, Environmental Change Unit.

SAS Institute (2003) SAS Version 9.1.2 © 2002-2003. SAS Institute, Inc., Cary, NC.

Sakai H, Yagi K, Kobayashi K (2001) Rice carbon balance under elevated CO_2. New Phytologist 150:241-249.

Satake T (1995) High temperature injury. In, Matsuo T, et al., eds. Science of the Rice Plant, Vol.2. Physio. Food and Agricultural Policy Research Centre, Tokyo 805-812.

Satake T, Yoshida S (1978) High temperature induced sterility in indica rices at flowering. Jap J Crop Sci 47: 6-17.

Seshu DV, Cady FB (1984) Response of rice to solar radiation and temperature estimated from international yield traits. Crop Sci 24:649-654.

Shah F, Huang JL, Cui KH, Nie LX , Shah T, Wu W, Wang K, Hayat ZK, Zhu LY, Chen C (2011) Physiological and biochemical changes in rice associated with high night temperature stress and their amelioration by exogenous application of ascorbic acid (vitamin C). Aust J Crop Sci 5(13):1810-1816.

Vose RS, Easterling DR, Gleason B (2004) Maximum and minimum temperature trend for the globe: An update through 2004. Geophysical Res Letters 32(23): Art. No. L23822.

Welch RJ, Vincent JR, Auffhammer M, Moya FP, Dobermann A, Dawe D (2010) Rice yields in tropical/subtropical asia exhibit large but opposing sensitivities to minimum and maximum temperature. Proc Nat Acad Sci 107(33):4562-4567.

Yoshida S, Satake T, Mackill DJ (1981) High temperature stress in rice. IRRI, Los Baños, Philippines. IRRI Res. Paper Series 67.