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Effect of asymmetric warming on rice (*Oryza sativa*) growth characteristics and yield components under a free air temperature increase apparatus

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ABSTRACT

Climate warming shows great diurnal variations with higher warming rate at nighttime, and consequently causes significant impacts on rice growth and grain yield. The objective of this study was to determine the effects of asymmetric warming (all-day warming, AW; daytime warming from 7:00 to 19:00, DW; and nighttime warming from 19:00 to 7:00, NW; and a control, CK) on rice growth characteristics and yield. Two bucket warming experiments were performed in Nanjing in Jiangsu Province, China under Free Air Temperature Increases (FATI) in 2013 and 2014. The daily mean temperatures in the rice canopy in the AW, DW and NW plots were 2.0°C, 1.1°C and 1.3°C higher, respectively, than those in the CK plots. Asymmetric warming reduced the maximum tillers and effective tillers in the order CK>DW>NW>AW. In the AW, DW and NW treatments, the effective tillers were decreased by18.57%-37.77% in both years. Asymmetric warming also decreased plant height, the Absolute Growth Rate (AGR), the Soil and Plant Analyzer Development (SPAD) value, the Leaf Area Index (LAI) and the Net Photosynthetic Rate (Pn). The order of the plant height and Pn values were also in the order CK>DW>NW>AW. The warming treatments affect the length of rice growth. The length from the transplanting date to the heading date was shortened by 3.5 days, 2.5 days and 3.0 days on average in the AW, DW and NW plots, respectively, in both years, while the length from the heading date to the maturation date did not show obvious changes. The aboveground biomass in the maturation stage declined by 13.38%, 3.56% and 6.22%, and the grain yield was decreased by 10.07%, 5.06% and 7.89% on average in the AW, DW and NW plots, respectively, in both years. There was a decreasing trend in the panicle number, grain number per panicle and grain filling rate, whereas irregular changes in the 1000-grain weight were observed in the warmed plots. Our results suggested that under the predicted climate warming, rice productivity would be further declined in the Yangtze River Basin.

Key words: Asymmetric warming, Free air temperature increase (FATI), Grain yield, Growth characteristic, *Oryza sativa*

Climate warming is one of the most significant environmental problems in the modern world. The global average temperature has increased by 0.56 to 0.92°C over the past century, and it is now predicted that the global temperature will be 1.4 to 5.8°C warmer by the year 2100 (IPCC 2007). The air temperature increases rapidly, accompanied by an obvious asymmetry of its increment. The increment of the minimum temperature at night is nearly twice that of the maximum temperature in the daytime (Harvey 1995, Easterling *et al*. 1997). Such unprecedented changes in the differential increments of the daytime/nighttime temperature could have important effects on crop growth and development (Lobell and Asner 2003, Zhang *et al*. 2013).

Rice (*Oryza sativa* L.) is one of the most important crops in the world and the most important food in Asia. Projected changes in rice production in Asian countries have quite a wide range, depending on the crop models and global climate change scenarios (Lal *et al*. 1998, Krishman *et al*. 2007, Tao *et al*. 2008). For instance, Peng *et al.* (2004) showed that an increase of 1°C under the daily minimum temperature decreased rice yield by 10%. Sheehy *et al*. (2006) found that the rice yield declined by 13.70% under a 1°C elevation of the daily minimum temperature. However, Lobel *et al*. (2008) reported that arising air temperature increased the rice yield. These studies showed that there was great uncertainty in model forecasting analyses. To apply such models expediently, scholars in both China and abroad have only considered how the daily average temperature (but not asymmetric temperature differences between daytime and nighttime) affects crop growth and development, which has resulted in nonconformity between many prediction results

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and actual crop yields (Dong *et al*. 2011). To lessen the uncertainty of crop model predictions and reflect the real effects of climate warming on crop systems, experimental field observation data are needed to modify the existing crop model parameters to more accurately simulate changes in crop yields in the future. Artificial simulation experiments have recently been carried out in plant growth chambers or greenhouses, but the increments in the above devices are set in a manner that is inconsistent with actual climate warming. It is notably difficult to simulate the features of real climate warming (Klein *et al*. 2005, Cheng *et al*. 2009, Yang *et al*. 2010).

The objective of this study was to determine the effects of asymmetric warming on rice growth and grain yield. We carried out a field experiment in Nanjing, China, to investigate the effects of asymmetric warming on the growth and yield of the Huaidao 5 rice cultivar using a Free Air Temperature Increase (FATI) apparatus.

MATERIALS AND METHODS

Two experiments (Experiment 1 in 2013 and Experiment 2 in 2014) were conducted at the agro-meteorological experimental station (32º07′N, 118º50′E) of Nanjing University of Information Science and Technology in Jiangsu Province, China, during the rice growing season from mid-May to October. This region has a warm, semi-humid monsoon climate. The average annual precipitation is 1100 mm. The average air temperature from 2000 to 2010 was 16.6°C, which is 1.4°C and 0.7°C warmer than that in the 1980s and 1990s, respectively. The average sunshine period is over 1900 hours, and the frost-free period is 237 days.

The rice cultivar used in this study was Huaidao 5 (conventional Japonica rice), which is widely cultivated in Nanjing, China. In both study years, sowing was carried out on 18 May. One seedling was transplanted in each plastic bucket (25 cm diameter, 28 cm height) on June 20th filled with 8.0 kg Hapli-stagnicgleysol. The soil was collected from the plough layer (~15 cm of the top layer) of a rice field in Pukou, Nanjing, China, that contained 9.28 g/kg organic C, 1.06 g/kg total N, 6.89 mg/kg available P and 125 mg/kg exchangeable K. A total of 0.68 g N per bucket ($CO(NH_2)_2$) was split-applied: 50% applied at transplanting, 25% at jointing and 25% at booting. Phosphorus and potassium were applied after planting as calcium superphosphate and potassium chloride at a rate of 0.15 g P per bucket and 0.37 g K per bucket, respectively. Hand weeding was conducted before sowing to control weeds. Pesticides (imidacloprid) and fungicides (tebuconazole) were sprayed to control pests and diseases as needed.

Following the Free Air Temperature Increased (FATI) apparatus design developed by Nijs *et al.* (1996), Kimball (2005) and Dong *et al*. (2011), we designed an experimental warming apparatus with two 1-KW far-infrared heating tubes (1.5 m long, 60 cm apart). They were placed 0.5 m (seeding stage) to 1.7 m (flowering stage) apart on steel column pipe supports and, surrounded by a resin film allowing 98% light transmittance and open on the top. The experiment included four treatments (all-day warming, AW; daytime warming from 7:00 to 19:00, DW; night time warming from 19:00 to 7:00, NW; and a control, CK) for the entire period from transplanting to maturation. Each treatment included three replicate plots, which were placed in a randomized block design. Twenty-four buckets rice (four buckets rice were placed in width, six buckets rice were place in length) were grown in one block (1.2 m width × 2.0 m length). Also, all buckets positions were not changed during growth period. The apparatus had a 4-m^2 heating area and was able to induce remarkable increases in temperature (Dong *et al.* 2011). The daily mean temperatures of the crop canopy in the AW, DW and NW plots were 2.0°C, 1.1°C and 1.3°C higher than those in the CK plots (Experiment 1), respectively, and 2.0°C, 0.9°C and 1.2°C higher than those in the CK plots (Experiment 2), respectively. The canopy temperature data were obtained using a temperature recorder instrument, which automatically recorded the temperature value at every 30 min.

The main morphological characteristics related to rice growth and development, including the maximum tillers, effective tillers, plant height, Leaf Area Index (LAI) and Soil and Plant Analyzer Development (SPAD) values, were measured. The maximum tillers corresponded to the greatest number of tillers present from the tillering stage to the heading stage. The effective tillers per land area were determined at the harvesting stage. Plant heights were measured from surface soil to the leaf opex of the longest leaf for ten replications during the tillering stage to the maturation stage.

LAI and SPAD values were measured during the tillering stage, booting stage, flowering stage, filling stage and maturation stage. The LAI values were destructively measured using an LAI-2000 Plant Canopy Analyzer and computed as the leaf area per land area. The SPAD values were non-destructively measured on the fully expanded uppermost leaf with a SPAD-502 chlorophyll instrument. The Net Photosynthetic Rate (Pn) was measured on the fully expanded uppermost leaf at the same growth stages as SPAD value. Pn values were non-destructively measured in clear morning from 9:30-11:30 using LI-6400 portable photosynthetic system under the conditions of light intensity of 1000 μmol/m^2/s, and chamber CO_2 concentration of 380 μmol/mol. The LAI, SPAD and Pn values were collected by five replications.

The Huaidao 5 plants were harvested from each treatment and measured at their maturity. To measure the aboveground biomass, Three buckets rice for each treatment (one bucket rice was selected from one plot) were collected, the soil was carefully washed away from roots by running water, and roots were cut off. The stems, leaves and ears were oven-dried under 80°C for 24 hours to constant weight for the aboveground biomass. The yield and yield components in each plot were determined by harvesting remaining buckets of rice ears after maturity. These rice ears were further air-dried for 3 weeks to constant weigh, and counted the number of panicles and carefully threshed. The

1000-grain weight was determined by randomly weighting 1000 grains. Actual yield was determined by weighting all grains for three replications. Afterwards, the grains were soaked in tap water, and the numbers of sunken and floating grains were counted to determine the grain-filling rates.

Statistical analyses were performed with SPSS 12.0 (SPSS Inc., Chicago, IL, USA). Statistically significant differences were identified via LSD calculations at level of P=0.05. The standard errors of the means were also calculated and presented in the graphs as error bars.

RESULTS AND DISCUSSION

Diurnal mean temperature variation

There were trends of canopy temperature variation during the flowering stage. It was found that the changes of canopy temperature under three warming treatments were similar to CK, which showed that warming systems did not change diurnal variation feature of field temperature. The order of canopy temperature under various scenarios was AW>NW>DW>CK, and temperature variation trends for the remaining development stages were similar to the flowering stage. The daily mean temperatures of crop canopy during the whole growth stage in AW, DW and NW plots were 2.0°C, 1.0°C and 1.3°C, higher than those in CK plots, respectively.

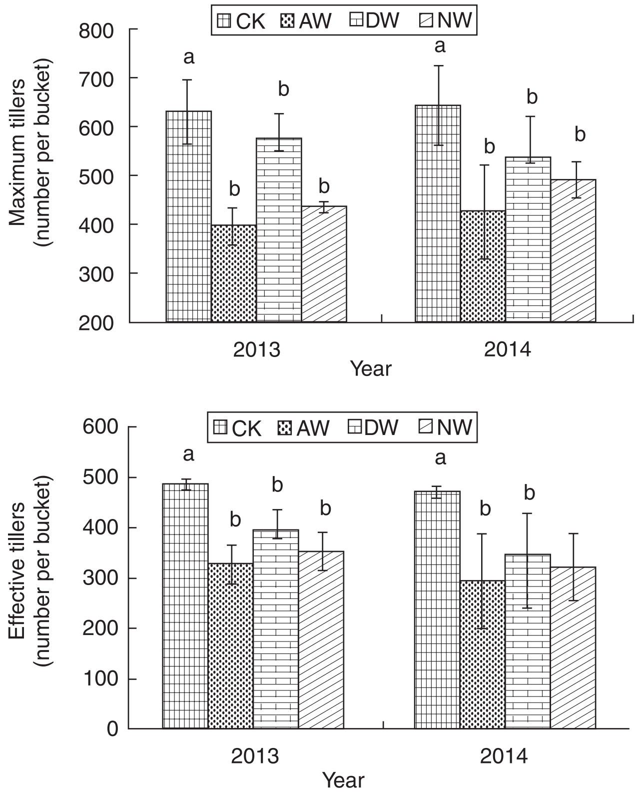

Fig 1 Effect of asymmetric warming on the rice maximum tillers and effective tillers in both years, the vertical bars indicate the standard error (n=10). Different letters between the treatments in each growth stage indicate significant differences at P<0.05.

Tillers

Field warming using the FATI system significantly reduced the maximum tillers and effective tillers of the Huaidao 5 cultivar in both years (P<0.05). In the AW, DW and NW treatments, the maximum tillers were decreased by 37.30%, 8.90% and 31.00% in 2013 and by 33.73%, 16.67% and 23.53% in 2014, respectively, while the effective tillers were decreased by 32.57%, 18.58% and 27.27% in 2013 and by 37.77%, 26.84% and 31.83% in 2014 (Fig 1). The results showed that climate warming inhibited rice tillers.

Plant height

The three warming treatments reduced the plant height of the Huaidao 5 cultivar at the maturation stage, resulting in the following order of plant height values: CK>DW>NW>AW (Fig 2). In the AW, DW and NW treatments, the plant heights were decreased by 9.35%, 2.47% and 3.18% in 2013 and by 11.59%, 2.64% and 5.55% in 2014, respectively. Plant height had significant difference detected between warming treatments and CK (P<0.05).

SPAD value and LAI

SPAD value can directly represent chlorophyll content changes in plant leaves, with lower SPAD values corresponding to lower chlorophyll contents (Bannari *et al.* 2007). The warming treatments reduced the SPAD and LAI values in the Huaidao 5 plants (Fig 3). The SPAD and LAI were maximal at the flowering stage and minimal at the maturation stage. In the AW, DW and NW treatments, the SPAD was reduced by 6.72%, 5.21% and 4.56% in 2013 and by 9.20%, 5.12% and 3.68% in 2014 at the flowering stage, respectively; while the LAI was decreased by 33.03%, 24.00% and 28.38% in 2013 and by 20.38%, 17.41% and 6.16% at the filling stage. SPAD values had significant difference under warming treatments during booting and flowering stages compared with CK, while LAI values had significant difference during booting, flowering and filling stages (P<0.05). Many nutrients of rice leaves are

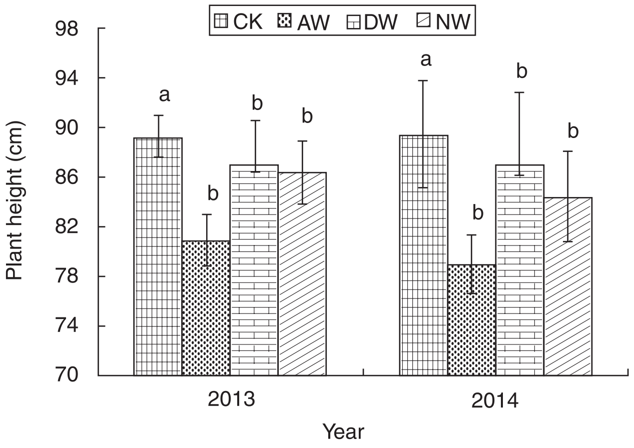

Fig 2 Effect of asymmetric warming on rice plant height in both years, the vertical bars indicate the standard error (n=10). Different letters between the treatments in each growth stage indicate significant differences at P<0.05.

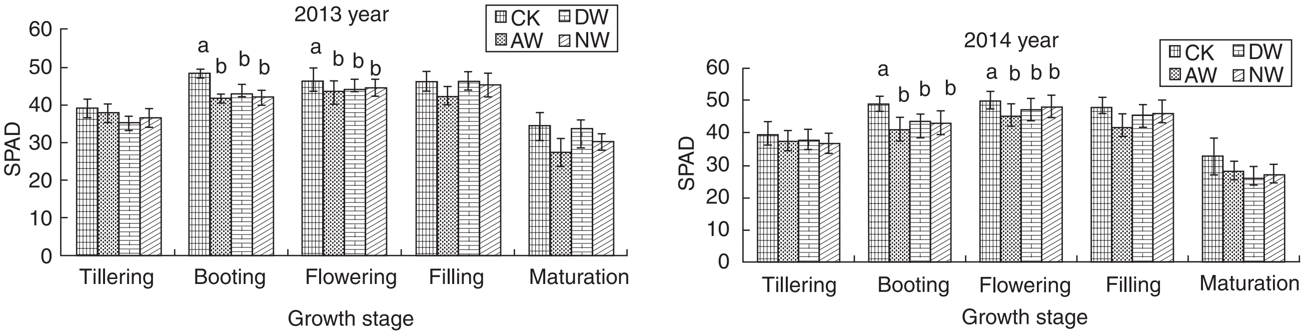

Fig 3 Effect of asymmetric warming on soil and plant analyzer development (SPAD) in the Huaidao 5 cultivar in both years, the vertical bars indicate the standard error (n=5). Different letters between the treatments in each growth stage indicate significant differences at P<0.05.

transferred to spike and grain after the flowering stage, so that rice leaves age rapidly (Feng *et al*. 2009). Thus, warming treatments have significant effect on SPAD values during booting and flowering stages. However, coverage of rice canopy has no significant change after the filling stage. Thus, rice LAI also has no significant change, and the warming treatments have no significant effect on LAI during filling and maturation stages (Liu *et al*. 2000).

Pn

Asymmetric warming significantly reduced the Pn in the Huaidao 5 cultivar in the order of CK>DW>NW>AW during the growing stages (Table l). In the AW, DW and NW treatments, the Pn was decreased by 26.18%, 5.84% and 19.70% in 2013 and by 26.36%, 8.95% and 25.00% in 2014 at the flowering stage, respectively. At the filling stage, the Pn was reduced by 22.46%, 10.27% and 2.09% in 2013 and by 18.87%, 7.44% and 8.40% in 2014. Similar to the SPAD and LAI, the Pn reached maximal at the flowering stage and minimal at the maturation stage. Compared with CK treatment, the Pn had significant difference during booting and flowering stages under warming treatments in both years, which were the same as the changes of SPAD values.

Length of growing period and aboveground biomass

Field warming affected the length of rice growing period (Table 2). In the AW, DW and NW treatments in 2013, the length from the transplanting date to the heading date was shortened by 3.5 days, 2.0 days and 2.5 days, while the length from the heading date to the maturation date was shortened by 1.0 day, 0.5 days and 0.5 days, and the total growing period was shortened by 4.0 days, 2.5 days and 3.0 days, respectively. In the AW, DW and NW treatments in 2014, the length from the transplanting date to the heading date was shortened by 3.5 days, 2.5 days and 2.5 days; the length from the heading date to the maturation date was shortened by 1.0 day, 0.5 days and 0.5 days, and the total growing period was reduced by 4.5 days, 3.0 days and 3.0 days, respectively. The results showed that the warming treatments shortened rice growth duration, and impact before heading was greater than that after heading.

Warming treatments reduced the rice aboveground biomass. In the AW, DW and NW treatments, the rice aboveground biomass was decreased by 12.08%, 3.34% and 3.89% in 2013 and by 14.67%, 3.79% and 8.58% in 2014. Compared with CK, the aboveground biomass had significant difference only in the AW treatment in both years (P<0.05).

Grain yield and yield components

In the AW, DW and NW treatments, the grain yield of the Huaidao 5 cultivar reduced by 13.06%, 5.23% and

Table 1 Effects of asymmetric warming on the net photosynthetic rate (Pn) of the Huaidao5 cultivar during five growth stages in both years

Year	Treatment	Net photosynthetic rate (μmol $CO_2/m^2/s$)				
		Tillering stage	Booting stage	Flowering stage	Filling stage	Maturation stage
2013	CK	20.05 ± 0.52^a	22.08 ± 0.25^a	24.62 ± 0.36^a	19.94±0.51	16.99±0.55
	AW	15.81 ± 0.66^b	16.30 ± 0.34^c	19.09 ± 0.45^c	16.91±0.42	14.06±0.36
	DW	17.39 ± 0.37^b	20.79 ± 0.57^b	22.09 ± 0.33^b	18.34±0.66	14.97±0.35
	NW	16.82 ± 0.42^b	17.73 ± 0.64^{bc}	19.60 ± 0.49^c	17.89±0.39	14.10±0.71
2014	CK	18.46 ± 0.56^a	22.12 ± 0.26^a	23.79 ± 0.41^a	20.07±0.24	14.02±0.36
	AW	13.54 ± 0.50^c	16.51 ± 0.63^c	19.30 ± 0.51^b	18.73±0.75	11.56±0.41
	DW	16.5 ± 0.72^b	20.14 ± 0.48^b	22.02 ± 0.55^b	19.74±0.63	12.97±0.55
	NW	16.24 ± 0.38^b	16.59 ± 0.37^c	21.79 ± 0.37^b	19.61±0.55	12.51±0.63

^{z}Different superscript letters in a row with indicate significant differences between growing seasons at the 5% level.

Table 2 Effects of asymmetric warming on the rice growth stage and aboveground biomass at maturity in both years

Year	Treatment	Date of transplanting (month/day)	Date (days after transplanting)		Above-ground biomass (g per bucket)
			Heading	Harvesting	
2013	CK	06-20	08-16	10-06	95.85 ± 2.07^{a}
	AW		08-12	10-01	84.27 ± 1.96^{b}
	DW		08-14	10-03	92.65 ± 2.62^{ab}
	NW		08-13	10-03	92.15 ± 2.51^{ab}
2014	CK	06-20	08-19	10-08	93.20 ± 2.30^{a}
	AW		08-15	10-03	79.53 ± 2.31^{b}
	DW		08-16	10-05	89.67 ± 2.81^{a}
	NW		08-16	10-05	85.20 ± 0.70^{ab}

^{z}Different superscript letters in a row indicate significant differences between growing seasons at the 5% level.

Table 3 Effects of asymmetric warming on rice grain yield and components at maturity in both years

Year	Treatment	Panicle number (number per bucket)	Grain number per panicle (number)	Grain filling rate (%)	1000-grain weight (g)	Actual yield (g per bucket)
2013	CK	15.45^{a}	176.00	98.00^{a}	26.67	56.59
	AW	13.69^{b}	163.00	87.67^{b}	22.38	51.17^{b}
	NW	14.57^{a}	166.00	95.00^{ab}	25.85	52.17^{a}
	DW	14.92^{a}	171.00	97.00^{ab}	23.38	53.63^{a}
2014	CK	15.36^{a}	153.00	97.67^{a}	25.85	50.63^{a}
	AW	13.20^{b}	141.00	91.00^{b}	23.48	45.42^{b}
	NW	14.13^{a}	145.00	93.67^{ab}	24.80	46.73^{a}
	DW	14.38^{a}	149.00	94.67^{ab}	24.03	48.30^{a}

*Different superscript letters within a row indicate significant differences between growing seasons at the 5% level.

7.81% in 2013 and by 12.48%, 4.88% and 7.97% in 2014, respectively (Table 3). Furthermore, panicle number, grain number per panicle and grain filling rate decreased in the warmed plots, but the 1000-grain weight showed no consistent changes in the warmed plots. Compared with CK, the actual yield, panicle number and grain filling rate had significant difference only in the AW treatment in both years, while other yield components exhibited no significant differences among the four treatments ($P<0.05$).

Effect of asymmetric warming on growth characteristics

Environmental factors (e.g. air or soil temperature) would affect crop tillers. Li *et al.* (2010) found that elevation of soil temperatures increased the maximum and effective tillers in rice in a high altitude region. Tian *et al.* (2010) reported that warming treatments increased the effective tillers but decreased the maximum tillers in winter wheat. This study showed that asymmetric warming decreased the maximum tillers and effective tillers in the Huaidao 5 cultivar. In addition, our results showed that the warming treatments also reduced rice plant height, and there was a significant difference between the warming and CK treatments. Chlorophyll is a vital pigment for absorbing, transferring and transforming solar energy (Yao *et al.* 2007). The LAI also determines crop photosynthetic capacities and growth rates (Van *et al.* 2001). Thus, there is a close correlation between the SPAD, LAI and photosynthetic capability. Our study revealed that the SPAD and LAI of the Huaidao 5 plants were clearly reduced under the warming treatments, which further caused a reduction of the rice Pn. Although DW increased the C gain by photosynthesis and NW increased the C loss by night respiration, the higher-temperature treatment reduced the chlorophyll content of the rice, inhibited its photosynthesis and reduced its photosynthetic rate and photosynthetic product (Li 2003, Kanno and Makino 2010). The continuous daytime average temperature during three days, which was over 32°C/5h, would affect the growth and development of conventional rice varieties. An average temperature of above 32°C was commonly observed from the middle of July to the end of July in this study. This may be a primary cause of the insignificant difference in the above growth parameters among three warming treatments.

Effects of asymmetric warming on growing length

Ge *et al.* (2002) found that the rice growing period on the South-western Plateau in China was reduced by 19 days, 42 days and 48 days in 2010, 2030 and 2050, respectively, by analyzing the CERES-rice model. Zhang *et al.* (2005) showed that the early rice and late rice growth length were decreased by 4.9 days and 4.4 days in 2100, respectively, by analyzing the WOFOST model. However, the above models could not predict the specific growth stage influencing rice growth and development. Moreover, these researchers did not consider the differences between daytime and nighttime in terms of asymmetric warming in their analyses of the above models. The present study showed that increasing the temperature by 1°C would cause the changes of rice growing length. In the AW, DW and NW treatments, the length from the transplanting date to the heading date was shortened by 3.5 days, 2.5 days and 3.0 days on average, respectively, in both years. Under actual climate warming, the temperature increases are nonlinear, and there are significant differences between daytime and nighttime. Therefore, the temperature differences between the day and night need to be considered by predicting the rice growth period, and the predicted results also need to be verified by field experiments.

Effects of asymmetric warming on grain yields

This study showed that the warming treatments reduced the actual rice yield from 4.88% to 13.05%. Similarly, a previous study found that a high temperature of 36°C significantly decreased the rice grain yield at the heading stage (Zheng *et al.* 2003). Furthermore, Mohammed and

Tarpley (2011) observed that increasing the nighttime temperature by 5°C decreased the rice grain yield by 90.00%. Grain yield is determined by the panicle number, grain number per panicle and 1000-grain weight. In our study, the warming treatments reduced the panicle number, grain number per panicle and 1000-grain weight as well as the grain filling rate. The results for the two study years were similar, and the ordering of the relative reductions was CK>DW>NW>AW. However, the actual yield, panicle number, and grain filling rate were only significantly different for AW and CK in both years ($P<0.05$). The grain number per panicle and 1000-grain weight had no significant difference among the four treatments. In addition, in both growing seasons, the aboveground biomass at maturity was lower in the warming plots than that in the CK plots, mainly due to a strong reduction in panicle number. Nighttime warming not only shortened the growth length but also increased respiration consumption (Fang *et al*. 2012). The adverse impacts of nighttime warming were greater than those of daytime warming (Peng *et al*. 2004), but less than those of all-day warming. Zhang *et al.* (2005) found that early- and late-season rice yields would be reduced by 3.60% and 2.80%, respectively, in 2100 using a crop model. Although the yield reduction trends determined by analyzing the above models were similar to that found in the present study, the extent of the reductions was associated with the significant temperature differences between daytime and nighttime. It suggests that environmental temperature differences, especially daytime and nighttime differences, should be considered when applying crop models to lessen the uncertainty of the model prediction.

Some studies have revealed that the temperature tolerance of different rice cultivars is different (Prasad *et al*. 2005, Cheng *et al*. 2010, Chakrabarti *et al*. 2012), and field management and fertilization can regulate rice canopy temperatures (Zhao 2005). Therefore, selecting new rice cultivars more tolerant to high temperatures and perfecting cultivation techniques are very important for addressing climate change in the Yangzi river basin in China.

Asymmetric warming decreased the rice growth parameters compared with CK in both years. But there had no significant differences among the three warming treatments. The rice growing periods from the transplanting date to the maturation data were different under different warming treatments. In addition, AW treatment significantly reduced rice the aboveground biomass and grain yield. Our results showed that under predicted warming, rice productivity would be further declined in the Yangtze River Basin. The elevated CO_2 associated with climate change increased rice photosynthetic rates, biomass and grain yield. To accurately assess the response of rice growth and yield to potential climate change, more complex impact study on rice growth and yield for both elevated CO_2 and air temperature needs to be conducted.

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