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Physiological Responses of Rice to CO_2 Enrichment and Rising Temperature

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Abstract: The increase of atmospheric CO_2 concentration, observed in recent years, will continue and may reach 550 ppm by 2050s. The increase of atmospheric CO_2 has the potential to enhance the crop yields, as it is one of the main sources for plant photosynthesis. However, rising temperatures are likely to adversely affect physiology and development of crop. The integrated impacts on crops, caused by increases in atmospheric CO_2 concentration and temperatures over the long term have not been clearly understood so far. CAAS designed the gradient experiment to reveal the effect of rising atmospheric CO_2 and temperatures on growth, development and yield of rice (*Oryza sativa* L.) in Northern China. In this experiment, physiological characteristics of rice were measured during the season (after transplanting) in a half-open CO_2-temperature Gradient Chamber (CTGC). The CTGC was used to treat the rice crop with different CO_2 concentrations and temperatures in the field. The results showed that, the grain filling dry matter accumulation and yields increased signficantly at 550 ppm CO_2 +1.0°C and 650 ppm CO_2 +1.5°C compared to the CK. The harvest index (HI) at elevated CO_2 was lower than that of CK. The treatments 550 ppm CO_2 +1.0°C and 650 ppm CO_2 +1.5°C increased the chlorophyll content of the rice leaves to 13.41%-16.74% above the CK (outside ambient plots), and increased further in later growth stages. The chlorophyll a/b ratio remained unaffected. The soluble sugar and soluble protein contents increased in plants grown at 550 ppm CO_2 +1.0°C and 650 ppm CO_2 +1.5°C compared to CK. The results indicate that CO_2 fertilization effect also had potential to increase rice grain yield.

Key words: CO_2 enrichment, temperature rise, rice (*Oriza sativa* L.), growth and yield, physiological indices.

Over the last 200 years, the atmospheric CO_2 concentration has increased from 280 ppm before the industrial revolution to more than 380 ppm today. A special report of the IPCC (IPCC, 2007) estimated that depending on the future emissions the atmospheric CO_2 concentration might reach between 470 ppm and 560 ppm by 2050. As a result, the mean global temperature may increase by 1.0°C-3.0°C (Lin *et al.*, 2005; 2007).

CO_2 enrichment increases the crop photosynthesis rate, dry matter accumulation and crop yield in the short term. Under non-limiting irrigation and fertilization, 550 ppm CO_2 increases wheat and cotton (C_3 crops) yields by 8-28% (Wang *et al.*, 1998). CO_2 enrichment also affected some physiological characteristics of the rice, such as enhancing C-content in the stalk, decreasing N-content, reducing stomatal parameters and changing the grain quality (Wang *et al.*, 1998, Uprety *et al.*, 2002). However, in the long term under some circumstances, acclimation to elevated CO_2 can attenuate such responses. For example, when rice seedlings were treated with 600 ppm CO_2, the net photosynthetic rate of the leaf was 45% higher than that under 300 ppm CO_2 after 1 day, but were lower by 14% and 23% after 7 days and 14 days (Tang *et al.*, 1998). Many experiments using controlled-chamber have demonstrated that elevated CO_2 can increase dry matter accumulation by 14% at 550 ppm and 25% with a doubling of CO_2 concentration under field conditions. But this response is also dependent on the nitrogen level, air temperature and cultivars (Baker *et al.*, 1996; Ziska *et al.*, 1997; Moya *et al.*, 1998; Nakagawa and Horie, 2000).

On the other hand there is concern that global warming, owing to the greenhouse effect, may decrease crop yields and therefore, threaten food safety and security (Greg *et al.*, 2007). It is necessary therefore to quantify the combined effects of atmospheric warming and elevated CO_2 concentration on crop yield by experimental studies of different crops in different regions.

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Significant research has been conducted in recent years, but has not focused on the combined effect of both rising CO_2 and temperature on rice (Zavaleta *et al.*, 2003; Sujatha *et al.*, 2008). Provided here is a new perspective on this research field, accomplished through the development of the gradient chamber, in which both CO_2 and temperature treatments are imposed. In this experiment, we attempted to find out physiological, metabolic and yield responses of local rice to rising atmospheric CO_2 concentration and temperature in Northern China under the situation of climate scenario in 2050.

The main facilities required for field evaluation of CO_2 effects on crop are CO_2-temperature gradient chambers (CTGC), Open top chamber (OTC) and Free-air CO_2 enrichment (FACE). Each method has its advantage and disadvantage when compared with the others (Long *et al.*, 2004; Ziska and Bunce, 2007). OTCs have given good results at comparatively low cost, but suffer from being partially enclosed and hence do not fully replicate field conditions. FACE, fully represents field conditions, but is expensive due to the large amount of CO_2 consumed. Temperature treatment can also be problematic. CTGC control CO_2 gradients and temperatures at the same time, and are relatively economic to use (Horie *et al.*, 1995, 2000; Kim *et al.*, 1996), but as with OTC, they do not exactly represent field conditions. This study was aimed to apply CTGC treatment to rice over the entire growing season, monitoring physiology, biochemistry, growth, development and yield of rice crop under CO_2 enrichment and increased temperature.

Materials and Methods

Experimental materials and designs

The experiment was carried out on the Experimental Station of the Institute of Environment and Sustainable Development in Agriculture (IEDA), Chinese Academy of Agricultural Sciences (CAAS), China (40°13′N, 116°14′E) in 2006-2007

Rice (variety Zhongzuo 93, mid to late maturing Japonica rice) was sown in late April and transplanted in late May. The growth duration is 160 d, and is usually planted as 30 cm x 9 cm length and space.

A CTGC (Fig. 1), deployed in the field, was CO_2 enriched during entire growth season. The clay loam soil within the chamber was flat and uniform. The CTGC frame was made from steel and was covered with 0.03 mm transparent plastic film (Beijing Sanxin Film Limited Company, 90% PAR transmission) and the chamber was 26.0 m long, 4.2 m wide and 2.4 m high. There were four exhaust fans and a wet curtain (3.2 m x 1.8 m) on the air inlet side. The wet curtain provided an evaporative cooling for the chamber so that the temperature in the tunnel could be controlled.

Three CO_2 and temperature sensors (Vaisala, Finland) were set up in the CTGC, at 7 m apart in the center of the tunnel, to monitor CO_2 concentration and temperature. CO_2 was released from 15 cm PVC pipes, which were deployed along two-sides of the chamber. Air was blown through these pipes and CO_2 injected into the air flow, which was then distributed along the tunnel. The control system could open or shut CO_2 flow valves to adjust the CO_2 volume according to CO_2 sensor feedback: CO_2 concentrations at 3 monitoring points could be maintained at 450 ppm, 550 ppm and 650 ppm at 7 m, 14 m and 21 m along the tunnel (Fig. 2).

The control system developed could change the speed of fans near the evaporative curtain to provide a temperature gradient along the tunnel. The temperatures at the three monitoring points were 0.5°C, 1.0°C and 1.5°C above ambient, respectively. The CO_2 concentration error was no more than 15% for 80% of the daytime period, while the temperature error was no more than 0.2°C during daytime. The tunnel was operated during the night, but CO_2 concentration increased and temperature decreased a little more than during the day.

The tunnel therefore provided a continuous temperature and CO_2 gradient from 450 ppm CO_2 and +0.5°C, 7 m from one end to 650 ppm and +1.5°C, 7 m from the other end of the CTGC. In the middle of the tunnel, the CO_2 and temperature were 550 ppm and +1.0°C. Duplicate plots were used to collect data on the growth of rice plants from six positions within the tunnel. These paired plots correspond to 675 ppm, 625 ppm, 575 ppm, 525 ppm, 475 ppm and 425 ppm of CO_2 and a temperature gradient of +1.75°C to +0.25°C above ambient along the tunnel. Each plot was 3.5 m x 1.5 m in size, and there was an access aisle in the middle of the CTGC (0.4 m) and a 0.4 m space along both sides. The pH values both inside and outside chambers were 7.0.

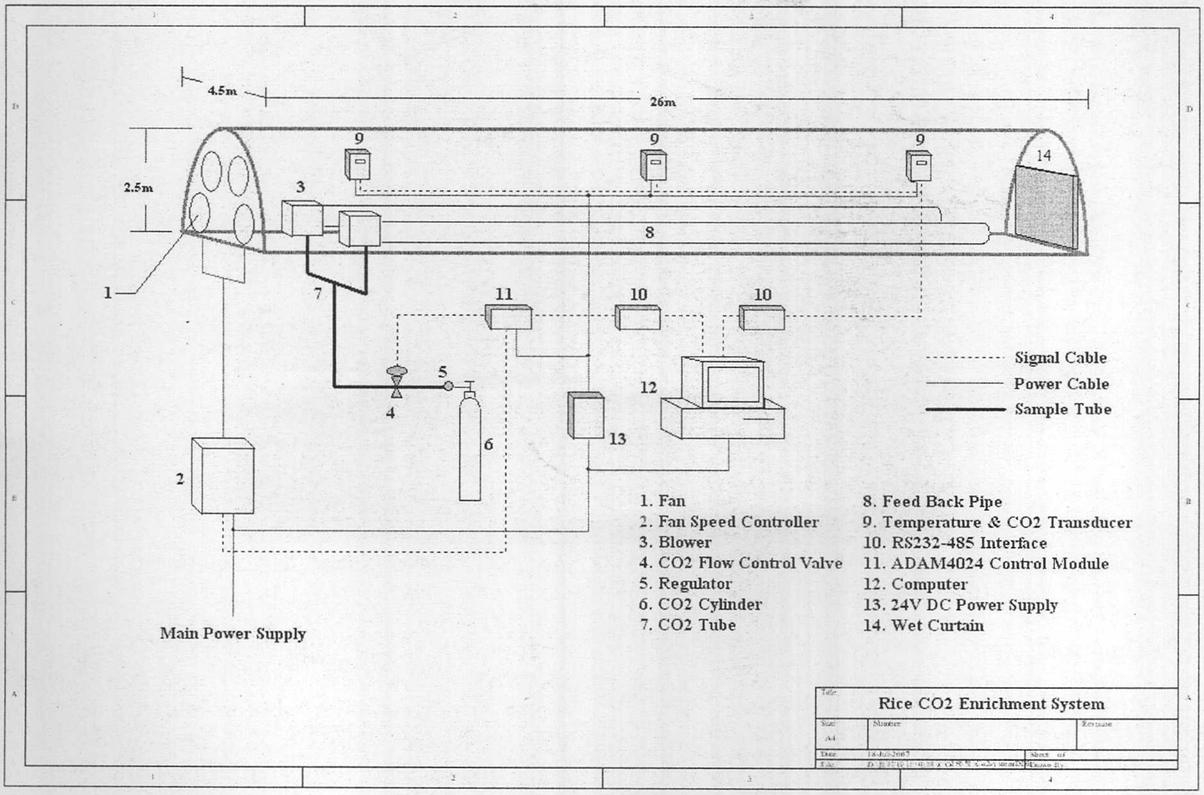

Fig. 1 Structure of the CTGCs.

Water and fertilizers were applied, both inside and outside chamber, according to recommended practices for this cultivar. The fields were submerged with water (5 cm) for 30 days after transplanting. Then drained dry several times following 25 days, and flooded with intermittent irrigation during following 55 days, until 14 days before harvest. N was supplied as urea (N, 40%) and compound chemical fertilizer ($N:P_2O_5:K_2O$ =15:15:15,%). 60% of total N was applied as basal dressing 1 day before transplanting, and others as side-dressing at panicle initiation stage (54 days after transplanting). Both P and K were applied as basal dressing 1 day before transplanting with compound chemical fertilizer at a rate of 6 g m^{-2}.

Rice seedlings (cv Zhongzuo 93) were transplanted 30 days after sowing (April 26) to CTGC on May 26 and harvested on October 28 (155 days), and they were arranged in 0.13 m hill spacing and 0.3 m row spacing.

Measurement items and methods

Above ground plant dry weight was measured every 15 days after the tillering stage of the crop. Three hills were sampled from each plot at random, and above ground biomass collected. Plants were dissected into leaf, stalk, spike and grains (after heading), were dried at 40°C and then weighed.

Grain growth was measured at six-day interval from the early grain filling stage. Ten spikes, collected from each plot, were dried and weighed. Grain yield and final biomass per plot were estimated from ten hills at maturity. The components of yield, the number of spikelets per m^2, the number of seeds per spikelet, and the seed weights were measured. The HI, which is the ratio of grain yield to total biomass, was calculated.

During the growth phases, leaf chlorophyll, soluble sugar and soluble protein contents were measured in the second upper most leaves at tillering stage, elongation stage, heading stage, early grain filling stage and mid grain filling stage (21, 54, 78, 98, and 118 days after transplanting, respectively). A UV/V spectrophotometer (Photometer UV-9200, Beijing Ruili Instrument Company) was used to measure the leaf chlorophyll content. Soluble sugars were measured by Anthrone-sulfuric acid method and soluble proteins were measured by Coomassie blue G-250 method (Zhang, 1992)

Fig. 2. Photograph of the chamber, showing rice plot, chamber frame with equipments (CO_2-temperature sensors, fans, blowers and CO_2 pipes).

Statistical analyses

The data collected were continuously variable along the length of the tunnel, and only data from one tunnel were collected. Therefore, to analyze the trends along the tunnel, the data from each pair of plots were regressed against their position in the tunnel, which corresponds to a particular CO_2 and temperature treatment.

The plot data were regressed using a simple linear model with CO_2-temperature as the independent variable and the particular data set as the dependant variable. Statistical analysis was undertaken using the MS Excel and SPSS statistical packages.

Results

Effects of treatments on yield and its components of rice

The elevated CO_2 and rising temperature had a significant effect on yield and yield components of rice (Table 1). Plant heights were 34.09%, 41.83% and 41.99% higher than CK for treatments 1, 2 and 3, respectively, while grain yields were 21.64%, 32.48% and 41.69% higher than CK, respectively. Biomass was 45.92%, 56.44% and 66.17% higher than CK, respectively. HI of treatments were lower than CK by 16.62%, 15.35% and 14.72%, respectively. The results indicated that rice with treatments had vigorous growth, but their organic matter conversion rate to grain was lower. Despite the warmer conditions that would be expected to hasten the rate of plant development, the treatments delayed maturity of rice for 10-14 days, which suggests there is huge potential to improve rice yields with elevated CO_2 and rising temperature.

Effects of treatments on dry matter increase of rice

Figs. 3 and 4 show the temporal sequence of dry matter increase and the rate of dry matter increase with treatments, respectively. Fig. 3 showed no early influence of treatments on biomass, but the situation changed after elongation stage. Biomass under treatments increased compared with CK from elongation stage till maturity, especially in treatment 3. There were significant differences among treatments and ambient (CK), which

Table 1. Yields and their components of rice with different treatments

Treatments	Average height (cm)	Panicles per hill	Stalks per hill	Ear bearing tiller (%)	Ear weight (g)	Yields (kg ha^{-1})	Biomass (kg ha^{-1})	Eco-coefficient (%)
450 ppm +0.5°C	136.10	15.75	18.33	85.92	2.30	10962	30385	36.08
550 ppm +1.0°C	143.96	15.04	15.46	97.28	2.62	11939	32575	36.63
650 ppm +1.5°C	144.12	16.63	17.67	94.11	2.56	12769	34601	36.90
CK (ambient)	101.50	14.25	15.00	95.00	2.48	9012	20823	43.27

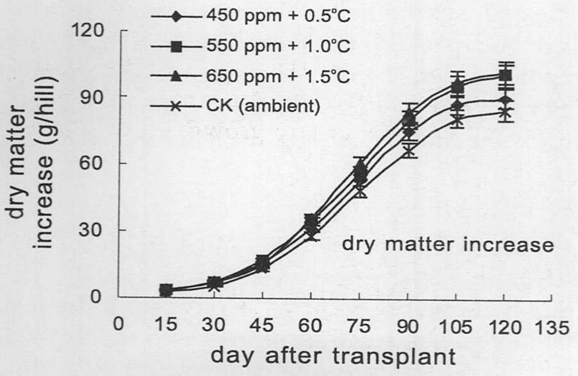

Fig. 3. Process of dry matter increase of rice.

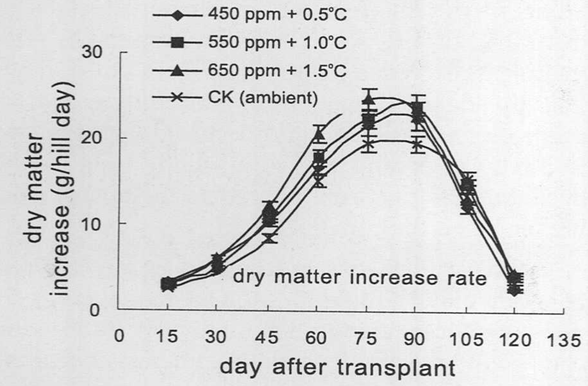

Fig. 4. Dry matter increase rate of rice.

indicates that elevated CO_2 and rising temperature accelerated photosynthetic rate of rice.

With increase in rate of dry matter accumulation differences in dry matter among treatments and CK were obvious during late vegetative growth stage and early floral, but disappeared during grain filling.

Statistical analysis of the average increase rate of dry matter (Table 2) showed no difference among standard deviations and coefficient of variations of treatments, which indicates that increase of dry matter and increase rate of dry matter of rice in each plot was comparable and normal.

Effects of treatments on physiological characteristics of rice

Chlorophyll contents declined until the stem elongation stage, but increased thereafter. There was little difference in chlorophyll content among treatments and CK before the elongation stage, but the content in different treatments increased with rise in CO_2 and temperature after early grain filling stage (Fig. 5a). The chlorophyll content of treatments 2 and 3 was 13.41-16.74% higher than that of CK. Excel analysis showed that there were significant differences among treatments compared with CK ($P<0.05$). Multiple comparisons further showed that difference with CK was more significant among treatments 2 and 3 than for treatment 1, which indicated that elevated CO_2 and rising temperature increased chlorophyll contents of rice leaf, and accelerated chlorophyll formation during later stages of crop growth.

Results from most of the previous studies have indicated a positive correlation between chlorophyll content and the photosynthetic rate of rice. The study, comparing Chlorophyll a/b (Table 3), showed that the ratio of Chlorophyll a/b increased a little with elevated CO_2 at tillering and elongation stages. That meant Chlorophyll a had increased more than Chlorophyll b during early growth stage. The ratio of Chlorophyll a/b was not different among treatments and with CK at heading and grain filling stages. All of the treatment data were similar to CK data, which indicated that elevated CO_2 and rising temperature did not change the ratio of Chlorophyll a/b during grain filling.

The changes in contents of soluble sugar due to treatments were similar to those observed for chlorophyll (Fig. 5b), declining during the tiller stage, and then increasing after stem elongation. There were no consistent treatment effects compared with CK. Statistical analysis indicated that there were significant differences among treatments at grain filling stage ($F=5.92>F_{0.05}=3.49$). Multiple comparisons showed that soluble sugar contents of treatments 1 and 2 were higher than that of

Table 2. Average increase rate of dry matters of rice with different treatments and variation analysis

Treatments	Average increase rate (g d^{-1} panicle)	Standard deviation	Coefficient of variation
450 ppm +0.5°C	11.8700	7.8039	0.6574
550 ppm +1.0°C	12.8038	8.2932	0.6477
650 ppm +1.5°C	13.4438	8.6487	0.6433
CK (ambient)	11.1037	7.1906	0.6476

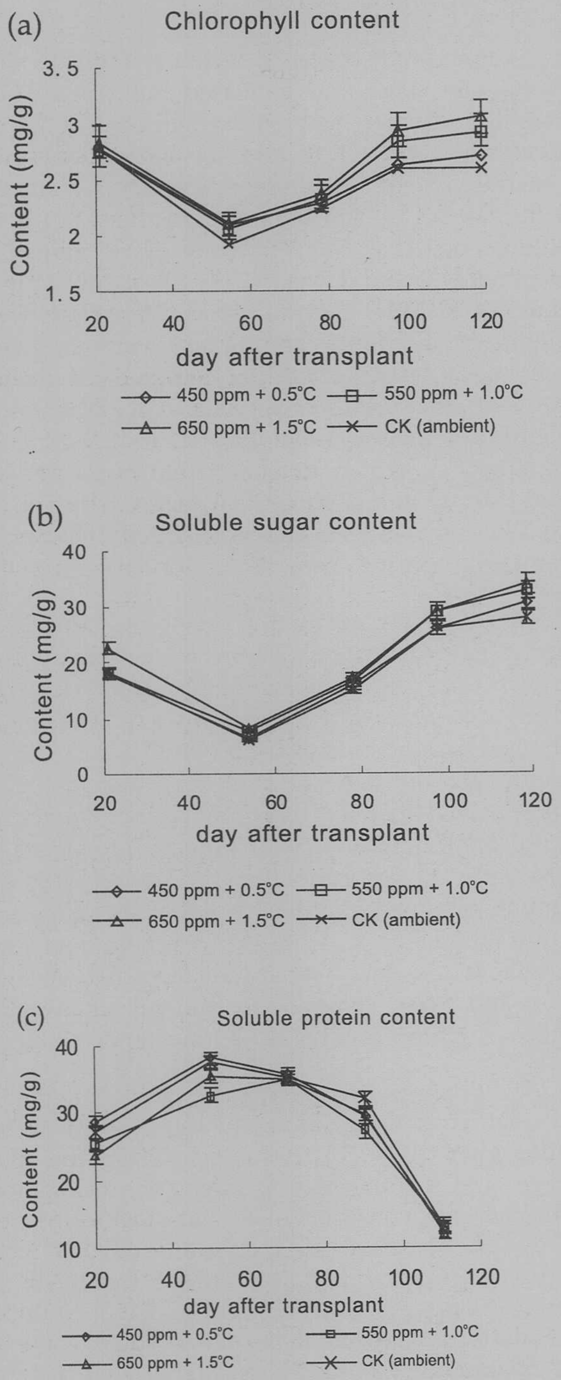

Fig. 5. Effects of rising CO_2 and temperature on physiological characteristics of rice.

treatment 3, which indicated that elevated CO_2, and rising temperature had increased soluble sugar contents of rice, but the effect would be restrained when CO_2 and temperature exceeded a certain value.

Soluble protein contents in all treatments increased substantially during the early growth stage and peaked at stem elongation stage, and then decreased. There was no statistically significant difference in soluble protein contents among treatments and CK at any growth stage (Fig. 5c).

Effects on grain filling of rice

Examination of the time-course of grain filling and grain filling rates (Figs. 6 and 7) show that grain filling in CK occurred earlier and faster than that in treatments. But these increased rapidly after grain filling, especially for treatment 3. This situation might be related to vigorous growth at elongation stage in treatment plots, because vigorous growth at elongation stage can delay heading stage. Grain filling of rice in treatment plots remained faster than that of CK so that grain production with treatments exceeded that of CK. Figure 7 also shows that the date of maximum grain filling rate of every plot was similar, and occurred between two to three weeks after mid grain filling stage before declining. Peak grain filling rate of treatments were higher than that of CK.

Statistical analysis of the average increase rate of grain filling (Table 4) showed that there were no differences among standard deviations and coefficient of variations of treatments, indicating that the process of grain filling and grain filling rate of rice in each plot was reasonable and normal.

Discussion

The study showed that elevated CO_2 and rising temperature increased chlorophyll contents of rice leaves, during later growth stages. Chlorophyll contents of rice with 550 ppm CO_2 +1.0°C and 650 ppm CO_2 +1.5°C were enhanced by 13.41% to 16.74% compared to CK (ambient). Treatments also had delayed rice maturity (10-14 days), which helped to increase rice production. The ratio of Chlorophyll a/b increased a little with elevated CO_2 and rising temperature at early stage, but the ratio was similar for treatments and CK at later stage. Over the whole growth season, the ratio of Chlorophyll a/b of treatments changed only by a small fraction. Previous studies on the photosynthesis process have shown that double CO_2 concentration might enhance chlorophyll contents and carotenoids of soybean, but varied depending on varieties (Wang *et al.*, 1997). The chlorophyll and carotenoids contents of hybrid-rice declined with high CO_2 concentration (600 ppm). High CO_2 concentration also restrained dark respiration at later stage of rice development

Table 3. Chlorophyll a/b with different treatments at each stage

Treatments	Tiller stage	Elongation stage	Heading stage	Early grain filling stage	Mid grain filling stage
450 ppm +0.5°C	3.0747	3.4034	2.5308	3.0514	3.0756
550 ppm +1.0°C	3.6894	3.6686	2.7376	3.0265	3.0054
650 ppm +1.5°C	4.4367	4.2372	2.4773	3.0467	3.0025
CK (ambient)	3.0666	3.1021	2.9922	2.9947	2.9944

because of its accelerated degradation (Liao *et al.*, 2002; De Costa *et al.*, 2007). So our results are inconsistent with those of other researchers.

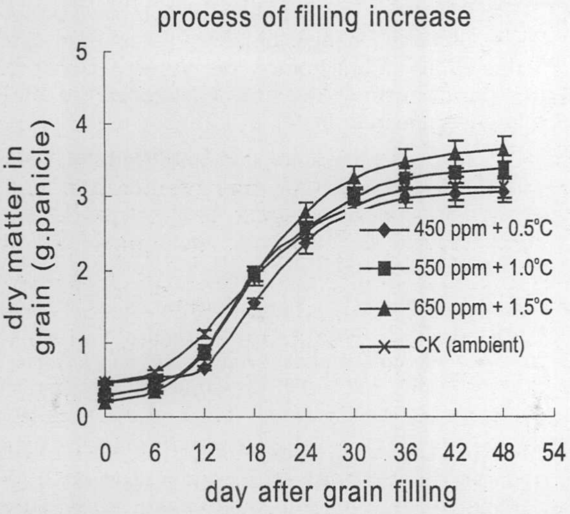

Fig. 6. Process of grain filling increase of rice.

After the elongation stage, the soluble sugar contents of rice with treatment of 550 ppm CO_2 +1.0°C and 650 ppm CO_2 +1.5°C was enhanced by 6.06% and 14.82%, respectively compared with CK (ambient). This was probably related to the process of photosynthates converting to dry matter and energy for rice growth. Because vigorous growth of rice with treatments at early stage accumulated lots of soluble sugar in rice leaves until latter stage and also delayed maturity, the soluble sugar contents of rice increased continually. Other studies have showed that elevated CO_2 might increase soluble sugar contents of rice stalks significantly (Tang *et al.*, 1998).

Soluble protein contents increased at early stage, and reached maximum value at elongation stage, then declined gradually. Soluble protein contents of all treatments were lower than that of CK from tiller stage to early grain filling stage, and they were similar to CK from heading stage to mid grain filling stage. Previous reports showed that soluble protein contents of Barn grass (C_4) declined dramatically during tiller and elongation stages (Huang *et al.*, 2002). Probably elevated CO_2 had accelerated rice growth at early stage, resulting in declined protein contents.

The study showed that elevated CO_2 and temperature changed physiological characteristics of rice, which varied at different growth stages, and changed demand of rice growth to dry matter and energy, which resulted in increased yield of rice. Elevated CO_2 and temperature increased significantly rice grain filling and maximum grain filling rate, and dry matter accumulation and accumulation rate as well as yields and biomass. The results showed that despite the expectation that warmer temperature might reduce yields, concurrent elevation of CO_2 concentration did improve rice yield potential.

The HI of rice with treatments was lower than that of CK, which means that there was unexploited rice yield potential under the treatments. Biomass of rice with treatments increased rapidly at early stages, especially in the latter stages of vegetative growth. As a consequence maturity of rice was delayed by 10-14 days compared to CK. Kim (1996) found that, with chamber, double CO_2 extended the duration from transplant to heading, but Huang (2002) found that, with FACE, CO_2 enrichment accelerates

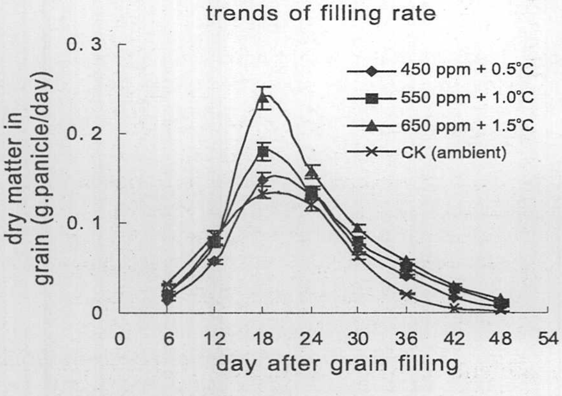

Fig. 7. Grain filling increase rate of rice.

Table 4. Average grain filling rate of rice with different treatments and variation analysis

Treatments	Average grain filling rate (g d^{-1} panicle)	Standard deviation	Coefficient of variation
450 ppm +0.5°C	0.0585	0.0557	0.9489
550 ppm +1.0°C	0.0708	0.0578	0.8164
650 ppm +1.5°C	0.0790	0.0775	0.9810
CK (ambient)	0.0580	0.0496	0.8552

growth and the development process of rice, shortening the growth season. The difference in results might be related to temperature, or rice variety or different latitudes. However, most studies have showed that elevated CO_2 increased rice production and yields (Yang *et al.*, 2006a, 2006b).

In addition, systems accuracy during night needs further improvement in order to ensure better control of CO_2 concentration and temperature.

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