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Impact of high temperature stress on photosynthetic characteristic and yield of rice (*Oryza sativa*) at heading

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ABSTRACT

To estimate impact of high temperature stress on photosynthetic characteristic and yield in rice (*Oryza sativa* L.), a pot experiment was conducted during 2008 in environment-controlled chambers with two rice cultivars (Yangdao 6 and Nanjing 44) under high temperature stresses (35°C/3d, 35°C/5d, 39°C/3d and 39°C/5d) at heading. The results showed that rice grain yield, chlorophyll content, net photosynthetic rate (NPn), superoxide dismutase content (SOD) and leaf area index (LAI) presented a sharply decline, and the relative conductivity, malondialdehyde content (MDA) increased gradually with the elevation of stress temperature and extension of stress time. The increasing rate (reduction rate) of some physiological and biochemical indexes in Yangdao 6 were lower than that in Nanjing 44 compared with the CK under the same temperature stress. It was showed that response of Nanjing 44 to high temperature was stronger than that of Yangdao 6. In accordance with correlation analysis, the rice grain yield showed a positive correlation with NPn and LAI ($P<0.01$), and the correlation coefficients of them were 0.93 and 0.89 respectively. Further, the correlation between rice grain yield and DW after early stage of maturing, the export percentage of the matter in stem-sheath (EPMSS) and the transformation percentage of the matter in stem-sheath (TPMSS) were not significant. It was showed that rice grain yield under high temperature stress originated mainly from leaves photosynthesis and LAI after heading.

Key words: Heading, High temperature stress, Photosynthetic characteristic, Rice, Yield

Photosynthesis is the foundation of grain yield in plants. In rice (*Oryza sativa* L.), 90% of grain yield originates from the photosynthetic production of leaves after heading (Wei *et al*. 2009). Although photosynthetic characteristics and their effects on dry matter accumulation and grain yield have been reported for different rice varieties in recent years, but it was up to now be rarely reported for the relationship between dry matter accumulation and photosynthetic characteristics of flag leaf under high temperature stress at home and abroad (Chen *et al*. 2007, Pand *et al*. 2008, Zhu *et al*. 2008,). With growing changes of presently global climate resulting in continually occurrence of extreme and sustained high temperature in summer, the frequency of high temperature damage in rice and damage content in Yangzi river basin of China are thus increased, which further causes increasingly damage severity for rice yield (Zheng *et al*. 2007, Shi *et al*. 2008). As is well-known, the heading is the most temperature-sensitive period during growth and development of rice (Zhang *et al*. 2007). High temperature at heading, usually over 35°C, often causes floret sterility, which results in yield reduction at maturity. Many reports have focused on the mechanisms of high temperature-induced sterility, effects of high temperature on seed setting and yield, as well as differences in response among varieties (Prasad *et al*. 2007), but mechanisms of high temperature-induced photosynthetic characteristics of flag leaf under high temperature stress at heading are still not clear (Matsui *et al*. 2007, Andrew *et al*. 2010, Zhang *et al*. 2011). In this case, Yangdao 6 and Nanjing 44 widely-planted in Yangtze River Basin were selected as research objectives, and then after those selected rice were subjected to high temperature stress at heading, photosynthetic characteristics and the amount of dry matter accumulation in flag leaves as well as yield were respectively measured. This result could act as an important basis for cultivation of high yield and breeding in Yangtze River Basin.

MATERIALS AND METHODS

The room experiment was carried out in Nanjing, China during 2008, using Yangdao 6 (conventional Indica rice, almost 130 days for total growth stage) and Nanjing 44 (conventional Japonica rice, almost 150 days for total growth stage) as test samples. Two samples were raised as follows:

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sowed on 15May, transplanted to plastic cases with specification of 30 cm × 20 cm × 10 cm on 18 June, six hills for each case, and double seedlings/hill, as well as the cases were positioned in a mesh room. Yangdao 6 started for heading at 18 August, and Nanjing 44 at 24 August. When two above rice cultivars were at heading, five cases of rice were randomly selected to be transplanted to RXZ environment-controlled chambers, and treated with high temperature of 35°C and 39°C respectively for 3d and 5d, and 5 hr/day (09:00-14:00). The temperature error of RXZ environment-controlled chambers was ±0.5°C, and the natural condition was used as the control (CK).

Representative plants with high temperature stress were labeled for measuring Npn (μmolCo_2/m^2/s) and chlorophyll content (mg/g FW) of flag leaves at 3d and 5d at heading. The NPn of flag leaf was measured in clear morning from 8:30–11:30 using LI 6400 portable photosynthetic system under the conditions of light intensity of 1 000 E/m^2/s and chamber CO_2 concentration of 380 μmol/mol^{-1}. Each measurement was repeated for 5 times with different plants.

LAI was measured using LI 6400 portable leaf area meter, and computed as the leaf area per unit land area. Dry weight of leaves, stems and spikelet at heading and maturing was determined by oven drying at 80°C until a constant weight was achieved. The export percentage of the matter in stem-sheath (EPMSS) and the transformation percentage of the matter in stem-sheath (TPMSS) were referred to methods of Tong (Tong *et al*. 2008).

$$\text{EPMSS}\ (\%) = (A-B)/A*100\% \quad (1)$$

$$\text{TPMSS}\ (\%) = (A-B)/C*100\% \quad (2)$$

Where A is dry weight of stem at heading, B is dry weight of stem at maturing, C is dry weight of spikelet at maturity.

Npn response curves of flag leaves to light intensity in Yangdao 6 and Nanjing 44 were measured using LI 6400 portable photosynthetic system. The order of light intensity of chamber was set at 0°C, 30°C, 50°C, 100°C, 200°C, 400°C, 800°C, 1 000°C, 1 200°C, 1 500 and 2 000 μmol/m^2/s, and chamber CO_2 concentration of 380 μmol/mol. Each measurement was repeated for five times with different plants.

Representative plants with high temperature stress were labeled for measuring relative conductivity (%), MDA content (μmol/g FW) and SOD content (U/mg FW). MDA content assay was performed by thiobituric acid (TBA) method, and SOD content assay was performed by nitroblue tetrazolium (NBA) method.

Two rice cultivars were harvested in cases and inspected at maturing. Spikelet number/panicle (no.), filled grain (no.), seed setting (%) and 1 000-grain weight (g) were determined. Actual yield (kg/hm^2) was determined by all harvested hills per case.

Analysis of data was carried out using data processing system (DPS).

RESULTS AND DISCUSSION

Impact of high temperature on rice grain yield and yield components

With elevation of stress temperature and extension of stress time, the grain yield of Yangdao 6 and Nanjing 44 presented a sharply decline (Table 1). Compared with CK, the difference of grain yield of two rice cultivars was not significant at 35°C/3d, the difference of other three high temperature stress (35°C/5d, 39°C/3d and 39°C/3d) were significant ($P < 0.05$ or $P < 0.01$). The yield reduction rate in Nanjing 44 and Yangdao 6 were 8.3%, 28.3%, 4.0% and 20.2% respectively at 35°C/3d and 39°C/3d. The reduction rate in Yangdao 6 was thus little higher than that in Nanjing

Table 1 Change of rice grain yield and yield components under high temperature tress at heading

Rice cultivar	Temperature stress	Spikelet/ panicle (no.)	Filled grain (no.)	1000-grain weight (g)	Seed setting rate (%)	Yield (kg/hm^2)	Yield reduction rate (%)
	CK/3d	180.0^{a} ± 3.5	170.2^{aA} ± 3.3	26.5^{a} ± 0.8	95.5^{aA} ± 1.5	7614.2^{aA} ± 203.1	
	35°C/3d	169.0^{a} ± 29	148.2^{bA} ± 2.5	24.9^{a} ± 0.7	87.8^{bB} ± 1.6	7312.1^{aA} ± 180.3	4.0
	39°C/3 d	154.0^{a} ± 1.7	103.4^{bB} ± 1.1	24.1^{a} ± 0.9	68.1^{cC} ± 1.3	6075.3^{bA} ± 120.1	20.2
Yangdao 6	CK/5d	176.0^{a} ± 2.4	165.4^{aA} ± 1.9	26.0^{a} ± 1.1	95.4^{aA} ± 2.0	7920.4^{aA} ± 200.5	
	35°C/5d	151.0^{b} ± 2.0	120.3^{bB} ± 1.6	23.4^{a} ± 0.5	80.8^{bB} ± 1.1	6883.3^{bA} ± 159.3	13.1
	39°C/5 d	149.0^{b} ± 1.9	72.6^{cB} ± 0.9	24.2^{a} ± 1.1	50.1^{cC} ± 0.9	5668.1^{bB} ± 182.4	28.4
	CK/3d	172.0^{a} ± 2.2	163.1^{aA} ± 1.9	24.5^{a} ± 1.0	95.25^{aA} ± 1.5	7353.0^{aA} ± 205.9	
	35°C/3d	168.0^{a} ± 2.9	140.1^{bA} ± 1.5	24.1^{a} ± 1.2	84.29^{bA} ± 1.4	6744.1^{aA} ± 149.5	8.3
	39°C/3 d	166.0^{a} ± 2.5	117.8^{bB} ± 1.1	24.2^{a} ± 1.1	73.50^{cB} ± 1.3	5275.1^{bB} ± 160.3	28.3
Nanjing 44	CK/5d	170.0^{a} ± 2.8	153.3^{aA} ± 1.2	23.9^{a} ± 1.2	94.5^{aA} ± 1.6^{aA}	7303.0^{aA} ± 225.9	
	35°C/5d	172.0^{a} ± 2.2	129.1^{bA} ± 2.0	24.5^{a} ± 0.9	78.97^{bB} ± 1.5	6269.5^{bB} ± 187.4	14.2
	39°C/5 d	165.0^{a} ± 2.3	67.7^{bB} ± 1.3	24.2^{a} ± 1.1	48.51^{cC} ± 0.5	4919.1^{cC} ± 145.9	32.2

The same letters represent insignificant, different small letter represent significant difference at 0.05, and different capital letter represent significant difference at 0.01

Table 2 Change of rice dry matter accumulation and transportation under high temperature stress at heading

Rice cultivar	Temperature stress	Dry weight (g/plant)			Transport of culum and sheath		
		DW of culm and sheath at initial heading	DW of culm and sheath at	DW of spike at maturing	DW after early stage of maturing	EPMSS (%)	TPMSS (%)
Yangdao 6	CK/3d	42.6	25.6 ^{a} ± 2.1	50.7 ^{a} ± 3.1	36.6 ^{a} ± 1.8	40.0 ^{a} ± 2.1	33.5 ^{a} ± 0.9
	35°C/3d		23.1 ^{a} ± 1.5	48.9 ^{a} ± 2.1	27.1 ^{b} ± 1.1	45.7 ^{a} ± 2.2	39.8 ^{a} ± 1.2
	39°C/3 d		23.1 ^{a} ± 1.2	47.1 ^{a} ± 1.9	30.2 ^{a} ± 1.5	45.8 ^{a} ± 2.4	41.4 ^{a} ± 1.1
	CK/5d		22.3 ^{a} ± 1.3	49.1 ^{a} ± 2.0	28.5 ^{a} ± 0.8	45.2 ^{a} ± 2.3	39.2 ^{a} ± 1.1
	35°C/5d		22.5 ^{a} ± 1.1	46.4 ^{a} ± 2.2	27.4 ^{a} ± 0.7	47.2 ^{a} ± 2.2	43.3 ^{a} ± 1.3
	39°C/5 d		21.3 ^{a} ± 0.9	44.9 ^{a} ± 2.5	20.0 ^{b} ± 0.8	50.0 ^{a} ± 2.5	47.4 ^{a} ± 1.4
Nanjing 44	CK/3d	36.9	23.7 ^{a} ± 1.5	46.0 ^{a} ± 2.0	25.3 ^{a} ± 1.3	35.7 ^{a} ± 1.5	28.6 ^{a} ± 0.7
	35°C/3d		22.9 ^{a} ± 1.1	44.5 ^{a} ± 2.1	20.0 ^{a} ± 1.0	37.8 ^{a} ± 1.7	31.2 ^{a} ± 0.5
	39°C/3 d		22.4 ^{a} ± 0.6	43.0 ^{a} ± 1.9	25.3 ^{a} ± 1.0	39.2 ^{a} ± 1.5	33.6 ^{a} ± 0.9
	CK/5d		23.5 ^{a} ± 1.2	44.9 ^{a} ± 2.2	12.0 ^{a} ± 0.8	36.4 ^{b} ± 2.0	29.8 ^{b} ± 1.1
	35?/5d		19.0 ^{a} ± 0.7	40.1 ^{a} ± 2.2	11.9 ^{a} ± 0.7	48.4 ^{a} ± 2.1	44.7 ^{a} ± 1.5
	39?/5 d		18.0 ^{a} ± 1.1	38.0 ^{b} ± 1.9	11.0 ^{a} ± 0.6	52.0 ^{a} ± 2.9	50.2 ^{a} ± 2.6

44. The yield components of two rice cultivars under high temperature stress were decreased significantly compared with CK, but the difference of seed setting rate and filled grain was significant (P<0.05), and the difference of 1000-grain weight and spikelet number/panicle was not significant. It was further showed that seed setting rate and filled grain were the important factors for affecting grain yield, as well as 1000-grain weight and spikelet number/panicle were slightly affected by high temperature.

Impact of high temperature on photosynthetic production, transportation and distribution of photosynthetic outcome

The production and accumulation speed of rice dry matter were reduced, and accordingly the accumulation amount of dry matter was reduced under high temperature stress at heading. With elevation of stress temperature and extension of stress time, EPMSS and TPMSS of Yangdao 6 and Nanjing 44 were increased sharply, and the increasing rate of two rice cultivars were distinct (Table 2). Compared with CK, at 35°C/5 d and 39°C/5d stress, the increasing rate of EPMSS in Yangdao 6 were 4.5% and 10.7%, one of TPMSS of Yangdao 6 by 10.6% and 21.0%, one of EPMSS of Nanjing 44 by 33.3% and 43.0%, and one of EPMSS of Nanjing 44 by 50.1% and 68.4%. It was shown that the production of ground dry matter after heading was mainly used to maintain the growth of rice leaves and stems under high temperature stress with lower proportion of distributing to grain. It was usually possible for self-adjusting and maintaining the growth of rice.

Chlorophyll content, LAI and Npn

The chlorophyll content in flag leaves is an important index for photosynthetic capability. The chlorophyll content reduction of both Yangdao 6 and Nanjing 44 under high temperature stress were faster than the CK, and the difference in all treatments was significant (P<0.05). Compared with CK, the chlorophyll content of two rice cultivars in flag leaves presented a sharply decline with elevation of stress temperature and extension of stress time, but the reduction rate of two rice cultivars was different. The reduction rates in Yangdao 6 and Nanjing 44 were 9.1%, 8.0%, 8.6% and 9.9% respectively at 39°C/3d and 39°C/5d stress (Fig 1).

The LAI of two rice cultivars under high temperature were also obviously lower than that of the CK (Fig 2). The reduction rates in Yangdao 6 were 1.7%, 8.2%, 2.6% and 12.6% respectively at stress of 35°C/3d, 39°C/3d, 35°C/5d and 39°C/5d, and the reduction rates in Nanjing 44 were 5.5%, 10.5%, 6.0% and 15.1% respectively at the same above stress. It was thus shown that high temperature affected LAI of rice, but differences between high temperature stress

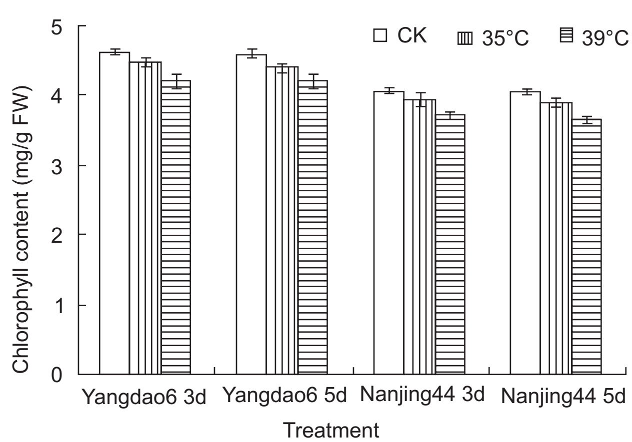

Fig 1 Change of chlorophyll content of rice leaves under high temperature stress at heading

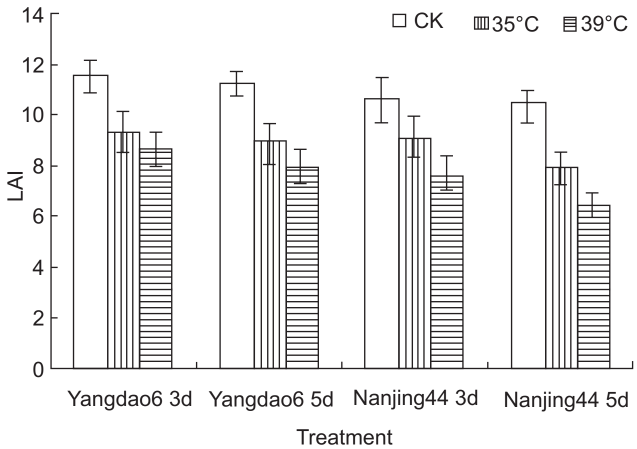

Fig 2 Change of LAI of rice under high temperature stress at heading

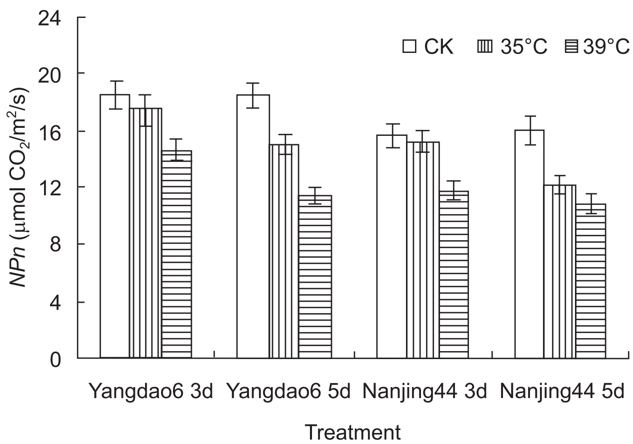

Fig 3 Change of NPn of rice leaves under high temperature stress at heading

and the CK in two rice cultivars were not significant.

NPn of two rice cultivars under high temperature was obviously lower than that of the CK (Fig 3). It was shown that rice photosynthesis was affected by high temperature. The differences between 35°C/3d stress and the CK in two rice cultivars were significant ($P<0.05$), and further differences of other treatments were significant ($P<0.01$). But the reduction rate of two rice cultivars was different compared with CK. The reduction rate of Yangdao 6 and Nanjing 44 was 5.7%, 21.0% and 9.5%, 24.7% respectively at 35°C/3d and 35°C/5d stress. And the reduction rate in Nanjing 44 was higher than that in Yangdao 6 under the same stress.

The chlorophyll is a vital pigment of absorbing, transferring and transforming photosynthetic capability (Yao et al. 2007, Rowan and David 2007). There is a close correlation between photosynthetic capability and chlorophyll content. The chlorophyll content of flag leaves was distinctly reduced compared with CK under high temperature stress, which caused more impact for the photosynthetic efficiency of the crop at the stage. The reasons for reduction of the chlorophyll content under high temperature stress were in two probabilities (Hassan 2006). On the one side, high temperature may affect the biosynthesis of 5-aminolevulinic acid (ALA) and protoporphyrin LX (PPIX), which are two intermediate products of the chlorophyll biosynthesis. This fact reduces and debases the productivity of the chlorophyll. On the other side, the productivity of active oxygen of the crops is increased under high temperature stress which accelerates oxidation of cell membrane. This case was a main reason for the reduction of chlorophyll content, which had been attempted to be improved by this study.

It was also found that the chlorophyll content and Npn of Nanjing 44 were lower than those of Yangdao 6 under the CK, which were mainly determined by own characteristic of rice. But the reduction rate of chlorophyll content and Npn of Nanjing 44 was higher than that of Yangdao 6 under high temperature stress. It was thus proved that response of Nanjing 44 to high temperature was higher than that of Yangdao 6 again. In addition, LAI of two rice cultivars were reduced gradually with the elevation of stress temperature, but differences of different treatments were not significant. It was shown that high temperature also affected the growth of plants, accelerated the reduction of leaf LAI.

Response of light intensity to NPn

Fig 4 shows the response of NPn to light intensity under high temperature stress as an example of two rice cultivars at 5d stress. The maximum NPn of Yangdao 6 in flag leaves is 16.9 μmol $CO_2/m^2/s$, and the maximum NPn of Nanjing 44 in flag leaves is 15.2 μmol $CO_2/m^2/s$. NPn raised rapidly with elevation of light intensity under light intensity of 1 000 μmol $E/m^2/s$. Further, NPn raised to the peak value at the light intensity of 1 200 μmol $E/m^2/s$, and then decreased slowly. Compared with CK, NPn of two rice cultivars in flag leaves declined significantly. The reduction rate at 39°C stress was higher than that at 35°C stress. Light saturation

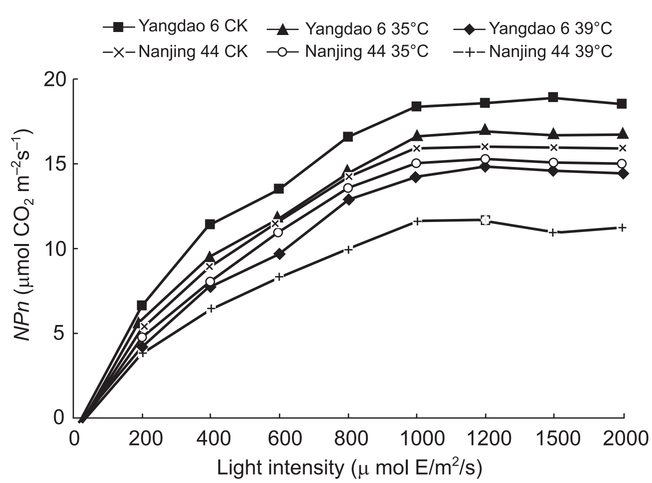

Fig 4 Response of NPn of rice leaves to light intensity under high temperature stress at heading

points of Yangdao 6 and Nanjing 44 under high temperature stress were lower than that of the CK. Many researchers considered that advance of photosynthetic production capability need advance apparent quantum efficiency of photosynthesis. The high apparent quantum efficiency was the indicator as high photosynthetic efficiency cultivars. The order of apparent quantum efficiency of six treatments was as follows: CK of Yangdao 6 > 35°C stress of Yangdao 6 > CK of Nanjing 44 > 35°C stress of Nanjing 44 > 39°C stress of Yangdao 6 > 39°C stress of Nanjing 44. It was shown the adaptive capacity of two rice cultivars were different under different treatments, and the photosynthetic production capability of them was also different.

The MDA content, relative conductivity and SOD content MDA content of leaves under high temperature stress was different. MDA content of leaves was increased gradually with extension of stress time, but differences of leaves MDA content under different treatments were significant. The increasing rate of MDA content in Yangdao 6 and Nanjing 44 were 6.3%, 6.9%, 7.5% and 13.1% at 35°C/3d and 39°C/3d stress respectively compared with CK. And the increasing rate in Nanjing 44 was significantly higher than that in Yangdao 6 (Fig 5).

Cell membrane permeability would be changed or lost under stress conditions (eg water stress, drought stress and low temperature stress, etc). Damage degree of cell membrane and stress resistance of plant could be reflected by measuring the relative conductivity of infiltrated liquid. The relative conductivities of two rice cultivars were increased sharply with elevation of stress temperature and extension of stress time, but the increasing rate of different rice cultivars was different. The reduction rate of Yangdao 6 and Nanjing 44 was 15.2%, 34.2%, 16.3% and 48.3% respectively at 35°C/3d and 35°C/5d stress compared with CK (Fig 6).

Fig 7 shows that changes of SOD content of the CK leaves were not obvious, but changes of SOD content under high temperature stress were significantly different. SOD

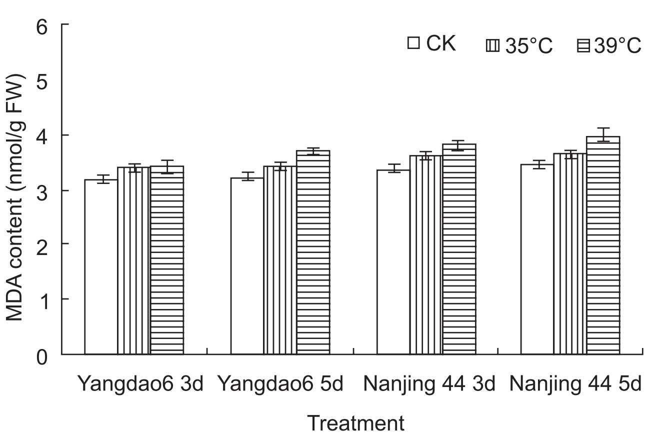

Fig 5 Change of MDA of rice leaves under high temperature stress at heading

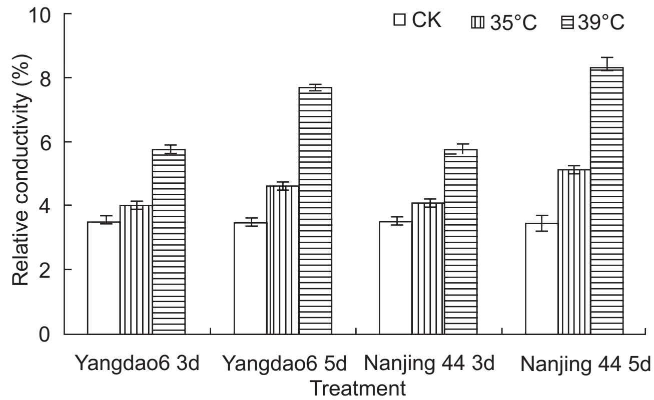

Fig 6 Change of relative conductivity of rice leaves under high temperature stress at heading

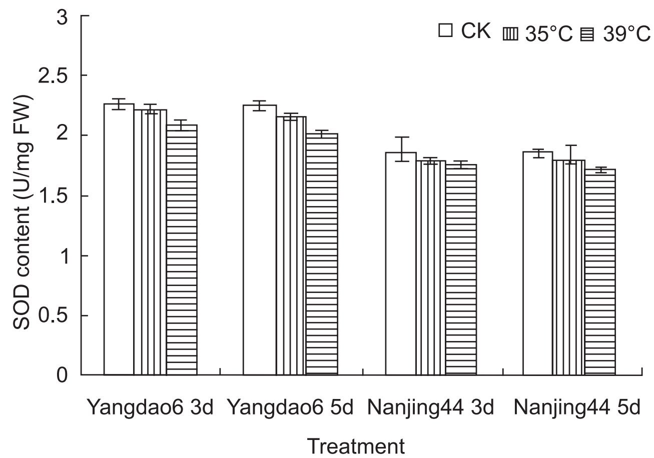

Fig 7 Change of SOD of rice leaves under high temperature stress at heading

content of leaves of two rice cultivars were subjected to a sharply decline with elevation of stress temperature and extension of stress time. The increasing rate of SOD content in Nanjing 44 was obviously higher than that in Yangdao 6 compared with CK.

As is well known, SOD is one of the important antioxidative enzymes in plants, which has important function in avoiding oxidation of cell membrane, lightening damage of cell membrane and delaying aging of the plants under negtive conditions. The MDA is the final product of membrane lipid peroxidation (Cao and Zhao 2008). It was shown in the paper that SOD (MDA) content of two rice cultivars were reduced (increased) significantly under high temperature stress. Therefore, the content of active oxygen of two rice cultivars were increased significantly with high temperature, which leaded to reduction of the chlorophyll content in rice, and accelerated leaf senescence. In addition, it was also shown that the relative conductivities of two rice cultivars were increased under high temperature stress compared with CK, and further the increasing rate of the relative conductivity was increased correspondingly with elevation of stress

Table 3 Correlation coefficients among indices related to rice grain yield

Index	Grain yield	NPn	DW after early stage of maturing	EPMSS	TPMSS	LAI
Grain yield	1					
NPn	0.93**	1				
DW after early stage of maturing	0.44	0.63*	1			
EPMSS	–0.45	–0.41	–0.21	1		
TPMSS	–0.52	–0.49	–0.25	0.96**	1	
LAI	0.89**	0.94**	0.75**	–0.60*	–0.66*	1

*$P<0.05$, **$P<0.01$

temperature and extension of stress time. The relative conductivity of leaves can directly reflect the damage degree of cell membrane and stress resistance of selected plants. Usually, the strong relative conductivity of leaves is corresponding to unstable structure of cell membrane, and weak stress resistance of the plants. Therefore, high temperature stress disturbed the osmosis equilibrium of cell membrane in leaves, destroyed the structure and function of cell membrane, and finally affected normal physiological metabolism. The increasing rate (reduction rate) of SOD content, MDA content and relative conductivity in Yangdao 6 was lower than that in Nanjing 44 compared with CK under the same temperature stress. It was shown that the response of Nanjing 44 to high temperature was higher than that of Yangdao 6.

Correlation of grain yield and photosynthetic characteristic

The positive correlation between NPn, LAI and grain yield were significant ($P<0.01$), and the correlation coefficients of them were 0.93 and 0.89 respectively (Table 3). Further, the correlation among DW after early stage of maturing, EPMSS, TPMSS and grain yield were not significant. The correlation coefficient of NPn and DW after early stage of maturing was 0.63, the correlation coefficient of NPn and LAI was 0.94, and the negative correlation among EPMSS, TPMSS and grain yield were not significant. Besides, the correlation coefficient of DW after early stage of maturing and LAI was 0.75, the negative correlation coefficient of EPMSS, TPMSS and DW after early stage of maturing were not significant. Furthermore, there were the correlation coefficient of EPMSS and TPMSS by 0.96, correlation coefficient of EPMSS and LAI by 0.60, and correlation coefficient of TPMSS and LAI by 0.66. It was shown that the grain yield originated mainly from the photosynthesis and LAI of leaves after heading. Therefore, promoting at early stage, controlling at middle stage and supplying at later stage in rice were adopted in practice in summer high-temperature area, and in particular, appropriate fertilization would be strengthened, which could be against prematurely senile of plants, better provide a support for high yield at later stage.

Many researchers considered that the reduction of grain yield was close correlation with the reduction of 1000-grain weight and setting seeding (Jasadish *et al* 2007, Xie *et al* 2009). This study showed that important factors of reduction of grain yield in two rice cultivars were the reduction of filled grain and setting seeding, and spikelet number/panicle and 1 000-grain weight were slightly affected by high temperature. In addition, the impacted degree of different rice grain yield by high temperature was different. As same as SOD content, MDA content and relative conductivity, the reduction rate of grain yield in Yangdao 6 was lower than that in Nanjing 44 under the same stress. This fact showed that the stress resistance was close correlation with the grain yield. As a result, selecting rice cultivars with high temperature-resistance and properly adopting horticultural practices had an important practice application meaning for realizing rice high yield and stable yield in high temperature area.

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