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Photosynthesis enhanced oxidative stress tolerance in high-yield rice varieties (*Oryza sativa* var. *japonica* L.) in the field

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ABSTRACT. The objective of this study was to understand varietal differences in photosynthetic characteristics, chlorophyll fluorescence, antioxidant capability, and yield of *japonica* rice varieties. Nanjing 44, *Oryza sativa* var. *japonica* (average yield of 12.7 t/ha), Nanjing 46, and Nanjing 5055 (average yields of 11.3 and 11.5 t/ha) were included as "super" and high-yield varieties, respectively, whereas Wuyunjing 7 (average yield of 10.2 t/ha) was included as a control variety. These varieties were grown under field conditions in Jiangsu Province, China, in 2010-2012. Different organs (panicle, grain, etc.) were measured, before and after flowering, to identify differences of dry matter accumulation and transformation properties. Photosynthesis, the chlorophyll content, and antioxidant enzyme activities of the flag leaf in the days after flowering (DAF) were also investigated. The results showed that, compared with the other three rice varieties, Nanjing 44 had the highest plant dry weight and number of grains per panicle. It also had a relatively high net flag leaf photosynthetic rate and showed the least inhibition of photosynthesis at noon in DAF, which probably explains the higher yield in this variety. Furthermore, Nanjing 44 also had the highest stem export and conversion rate from stem to grain, exhibiting a strong ability to convert and distribute photosynthetic products. After DAF 42, Nanjing 44 still maintained a high-soluble protein content and a high antioxidant ability in the leaves to clear peroxidation products, which could protect the photosynthetic apparatus of the flag leaves, and maintain the grain-filling activity for longer. The high-yield capability of Nanjing 44 was attributed to its photosynthetic advantages in the leaves during the late developmental stage.

Key words: Rice (*Oryza sativa* var. *japonica* L.); Photooxidation; Net photosynthetic rate; Yield component; Antioxidant enzyme

INTRODUCTION

To satisfy population growth and economic development requirements, a required increase in global average food yields by more than 1.2% per year was suggested by Normile (2008). To achieve this goal, great efforts should be made to breed new rice varieties using new planting patterns with higher yield potentials, to enhance average farm yields (San-oh et al., 2006; Peng et al., 2008). The development of semi-dwarf varieties in the late 1950s in China and in the early 1960s at the International Rice Research Institute, dramatically increased the yield potential of irrigated rice. The yield potential was further increased by the development of hybrid rice in 1976. China has been successful in breeding hybrid rice strains, but is now facing challenges to develop new hybrids with high-yielding potential, better grain quality, and tolerance to biotic and abiotic stresses (Cheng et al., 2007; Tester and Langridge, 2010).

Yield potential is defined as the yield of a variety when grown in environments to which it is adapted (Evans, 1993). In China, a nationwide mega-project on the development of modern rice (*Oryza sativa* L.) cultivars, especially the newly bred “super” rice based on the ideotype concept, has been established trying to combine the ideotype approach with the use of intersubspecific heterosis (Xiao et al., 1996; Yuan, 2001). Green Super Rice should possess resistance to multiple insects and diseases, high nutrient efficiency, and drought resistance, promising to greatly reduce the consumption of pesticides, chemical fertilizers, and water (Kato et al., 2004; Zhang, 2007). “Super” rice varieties have numerous spikes per panicle resulting in a larger yield capacity. It was reported that by 2010, the Chinese Ministry of Agriculture had released 80 varieties of “super” rice varieties, including inbred *indica*, *japonica*, and hybrid rice varieties (Wu et al., 2010). Under field conditions, it was found that many “super” rice varieties could not reach their yield potential with lower grain-filling rate, because they were not adapted to the changing environment (Yang and Zhang, 2010; Li et al., 2010b).

Although there has been much research on “super” rice varieties, previous studies have mostly focused on the “super” hybrid rice (Li et al., 2010a) or “super” rice varieties in the north of China (Li and Han 2010). These studies were mostly interested in the morphological and filling characteristics of rice under different cultivation conditions, such as alternate wetting and drying, irrigation, or nitrogen levels (Peng et al., 1999; Yang et al., 2002; Mishra and Salokhe, 2008; Zhang et al., 2009a, 2012). Understanding the regulation of grain filling in the field is important for improving rice yield potential (Murchie et al., 2002).

The rice varieties from the Jiangsu Province often suffer different climate conditions, such as continuous rain (low light intensity), the first sunny day (high light intensity) after the continuous rain, a hot late-growth stage without water (water shortage), as well as other stress conditions during the whole growth stage (Li et al., 2010c). Currently, 10 rice varieties that met the “super” rice criteria were released by the Jiangsu Province. Of these, eight varieties belong to the *japonica* rice (China National Rice Research Institute and the National Rice R&D Center Industrial Technology, 2010). The “super” *japonica* rice criteria in China are that the *japonica* rice variety can get more than 11.7 tons per hectare in two consecutive years in the field. How these “super” *japonica* rice varieties are able to survive so many stresses during the life time, while, at the same time, exhibit a high-grain-filling rate, producing high yields, is yet to be understood.

In this paper, four *japonica* rice varieties with different yield levels from the Jiangsu Province in China were used in the days after flowering (DAF) in field conditions over 3 years. The objectives of this study were to understand the material accumulation, photosynthetic characteristics, and operation of varietal difference during DAF in the field.

MATERIAL AND METHODS

Experimental site

Experiments were conducted in the field at the Jiangsu Academy of Agricultural Sciences, Nanjing city, Jiangsu Province, China (32°02 N, 118°52 E, 11 m a.s.l.) on a brunisolic soil (Alfisols, USA). The rice-cropping system has prevailed in this region for more than 1000 years, and represents the typical cropping system in Asia. The relevant soil properties were as follows: total N = 2.52 g/kg, total P = 0.60 g/kg, total K = 14.0 g/kg, available P = 166.22 mg/kg, available K = 165.03 mg/kg, and soil organic C = 8.24 g/kg. The climate conditions are humid subtropical monsoon with a mean annual precipitation of 1050 mm, mean annual temperature of 16.7°C, 1900 h annual sunshine time, and a frostless period of 237 days.

Crop management

Four rice varieties (*Oryza sativa* var. *japonica*), Nanjing 5055, Nanjing 44, Wuyunjing 7, and Nanjing 46, were tested in this experiment conducted in 2010-2012. Nanjing 44, which has an average yield of 12.7 t/ha, was included as a “super” rice variety type. Nanjing 46 and Nanjing 5055, having average yields of 11.3 and 11.5 t/ha, were considered intermediate yield types. Finally, Wuyunjing 7 has an average yield of 10.2 t/ha, which is considered a low-yield type and was included in our study as a control variety. The sources of the varieties are listed in Table 1. The rice seeds were sterilized with an antiseptic and then soaked for 72 h to germinate. On May 16 of each year, the soaked seeds were directly sown in the seedbed and kept moist. Rice seedlings were transplanted manually into their corresponding field plots in mid-June with a hill space of 0.167 x 0.200 m. Rice plants were harvested in October, depending on the maturity dates of each plot. The N, P, and K fertilizers of each plot were 374, 187, and 187 kg/ha, respectively. P, K, and 50% of N, were applied as a basal dressing 2 days prior to transplanting. Half of the remaining N (25%) was applied as a side dressing at early tillering in the latter half of June and the other half was applied at panicle initiation in the latter half of August each year.

Table 1. Information about the *japonica* rice varieties used in the experiment.

Group	Variety	Subspecies type	Year of release	Female parent	Male parent
Inbred (CK)	Wuyunjing 7	*japonica*	1996	Jia 48/Xiangnuo9121	Bing 815
“Super” *japonica*	Nanjing 44		2004	45115-2/R405	NJ30125
Ordinary hybrids of good quality	Nanjing 46		2008	Wuxiangjing 14	Guandong 194
	Nanjing 5055		2005	Wujing 13	Guandong 194

CK stands for a control variety with low yield in the present study.

According to the method of Yang et al. (2000), panicles that headed on the second day from the onset of heading were selected and tagged. The heading period was 7 days for a line or cultivar (90 ± 10% panicles headed). A consequence of this was that the panicles sampled were mostly from main stems (approximately 70%) and the remainder from primary tillers (approximately 30%). Previous data showed no significant differences between the main stem and primary tiller in either final panicle weight or the timing or rate of grain filling within a line or cultivar if their panicles headed on the same day. Only tagged tillers were used for measurements of photosynthesis, sample collection (1 cm^2 leaf disc per sample), and panicle dry weight (DW). On each tiller, one measurement of photosynthesis was made (in the morning) and leaf discs for protein and chlorophyll (Chl) content analysis were cut from that same tiller and immediately frozen in liquid N_2. Three of the panicles were then removed for immediate assay of DW. Panicles were dried at 70°C and weighed at 2-day intervals until the weight did not change. Yield components were determined as described by Li et al. (2011).

Screening for tolerance to photooxidation

Screening for tolerance to photooxidation was determined, as described by Jiao and Li (2001). Photooxidation treatments were also conducted at the booting stage. Five detached mature leaves from rice plants that were grown under natural light conditions were cut and placed on a white tray (23 cm long, 17 cm wide) with a 2.5 cm depth of water containing equilibrated ambient levels of CO_2 and O_2. After 2 h, the O_2 concentration was increased to about 266 μM and the CO_2 concentration was decreased to minimum levels (0.75 μmol) because of leaf photosynthesis. Leaf blades were kept immersed and flat by an overlaid transparent glass plate, thus providing continuous exposure to natural sunlight. The water temperature was equilibrated with the air temperature during the day (maximum temperature 35°C) and night (average 25°C). Tolerance to photooxidation was determined by the degree of decline in Chl content and a visible score of leaf color after 6 days.

Determination of the Chl content

Five full-exhibition features of the leaves were measured during rice booting. The Chl content was determined using dimethyl sulfoxide (DMSO) as extraction solvent (Lichtenthaler and Wellburn, 1983). Plant materials were extracted at 60°C for 2 h, the temperature was maintained by a water bath with a thermostat, and light was kept out by wrapping the sample in aluminum foil. The samples were stored in the dark until all greenish remnants had been extracted by the DMSO solution. The supernatant was decanted and the absorbance was read at wavelengths of 480, 665, and 649 nm using a UV-Vis spectrophotometer UV-2550 (Shimadzu Corporation, Kyoto, Japan).

Net photosynthetic rate (P_n)

The P_n of intact rice leaves was monitored with a Li-Cor 6400 portable photosynthesis system (Lincoln, NE, USA) according to the method of Li et al. (2010c). The gas source was compressed air with a CO_2 concentration of 350 μmol/mol. The measurements were made between 9:00 and 11:00 am. Red and blue sources under the open system were used to take measurements under the following conditions: 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density, 500 μmol/s flow rate, and 30°C leaf chamber temperature. In each treatment, the first leaves under the tassel (the three youngest) were used for the measurements, and each leaf was measured five times.

Malondialdehyde (MDA) content

MDA content was measured according to the method of Sofo et al. (2004), with minor changes. In summary, 1 g leaves was homogenized in 10.0 mL 10% (w/v) trichloroacetic acid and was centrifuged at 10,000 *g* for 5 min. A 2-mL aliquot of supernatant was added to 2.0 mL 0.6% (w/v) thiobarbituric acid in 10% (w/v) trichloroacetic acid. The mixture was heated to 100°C for 15 min and then rapidly cooled in an ice bath. After centrifugation at 10,000 *g* for 10 min, the absorbance values at 532, 600, and 450 nm (A_{532}, A_{600}, and A_{450}) of the supernatant were recorded. The value for nonspecific absorption at 600 nm was subtracted, and a standard curve for sucrose (from 2.5 to 10 μmol/mL) was used to rectify the results from interference of soluble sugars in the samples (at A_{532} and A_{450}). The MDA content was calculated from the absorption coefficient of 157 mmol/cm and was expressed as nmol MDA/mg (protein).

Activities of antioxidant enzymes

Determination of the activity of antioxidant enzymes and concentration of related metabolites was undertaken according to optimized protocols described previously (Habibi et al., 2010). Fresh samples were ground in the presence of liquid N_2 and measurements were undertaken using a spectrophotometer (Specord 200, Analytic Jena, Jena, Germany). Superoxide dismutase (SOD; EC 1.15.1.1) activity was estimated according to the method of Giannopolitis and Ries (1977). Enzyme was extracted in 25 mM HEPES, pH 7.8, with 0.1 mM EDTA and the supernatant was added to the reaction mixture containing 0.1 mM EDTA, 50 mM Na_2CO_3, pH 10.2, 13 mM methionine, 63 μM nitroblue tetrazolium chloride (NBT), and 13 μM riboflavin. One unit of SOD was defined as that being contained in the volume of extract that caused a 50% inhibition of the SOD-inhibitable fraction of the NBT reduction. For determination of catalase (CAT; EC 1.11.1.6) activity, samples were homogenized with 50 mM phosphate buffer, pH 7.0, and assayed spectrophotometrically, by following the degradation of H_2O_2 at 240 nm according to the method of Simon et al. (1974). The reaction medium contained 50 mM phosphate buffer, pH 7.0, and 10 mM H_2O_2. All the activities of the enzymes were expressed as U/mg (protein).

The total antioxidant capacity of non-enzymatic antioxidant was measured using a kit from Nanjing, Jiancheng. The principle of the measurement was based on whether the plant had many antioxidants. If so, then Fe^{3+} is reduced to Fe^{2+}, which combines morpholine with the Philippine morpholines forming a solid complex substance. The total antioxidant capacity of the leaves can then be determined by its colorimetry.

Leaf soluble protein content, dry weight, and conversion rate

Leaf soluble protein content was measured according to the Coomassie brilliant blue (G-250) method used by Bradford (1976). Measurements of DW and conversion rates were determined according to the method described by Yang et al. (2002).

Statistical analysis

All results reported here are the means of replicates. Data were subjected to analysis of variance (ANOVA) using the STATGRAPHICS plus 5.1 statistical software (Statistical Graphics Corp., Princeton, NJ, USA).

RESULTS

Growth parameters and yield components of *japonica* rice varieties

The average yield per ha of Nanjing 44 during 2010-2012 was significantly higher than the control Wuyunjing 7 variety (24.51% higher; $P < 0.05$) (Table 2). The yields of Nanjing 46 and Nanjing 5055 were intermediate between the control and the "super" rice varieties. Nanjing 44, produced the highest yield among the other intermediate- and low-yielding rice varieties, mainly due to the high number of panicles per plant, grains per panicle, and filled-grain percentage.

Table 2. Growth parameters and yield components of *japonica* rice varieties with different yield levels during 2010-2012 in Nanjing, Jiangsu Province, China.

Variety	Years	Height (cm)	Panicle number per plant	Grains per panicle	1000-grain weight (g)	Filled-grain percentage (%)	Tons/ha
Wuyunjing 7 (CK)	2010	100.12 ± 3.25^{Aa}	14.41 ± 1.51^{Aa}	128.19 ± 14.21^{Aa}	26.14 ± 1.31^{Aa}	86.14 ± 1.57^{Bb}	10.11 ± 0.17^{Cc}
	2011	105.33 ± 4.04^{Aa}	15.10 ± 2.00^{Aa}	126.33 ± 13.50^{Aa}	24.65 ± 1.20^{Aa}	87.52 ± 1.44^{Bb}	10.50 ± 0.18^{Cc}
	2012	104.21 ± 2.14^{Aa}	16.54 ± 1.67^{Aa}	125.45 ± 9.71^{Aa}	23.17 ± 1.62^{Aa}	85.34 ± 2.14^{Bb}	9.99 ± 0.15^{Cc}
	Average	103.14 ± 2.51^{Aa}	15.35 ± 1.53^{Aa}	126.66 ± 9.15^{Aa}	24.65 ± 2.41^{Aa}	86.33 ± 1.21^{Bb}	10.20 ± 0.41^{Cc}
Nanjing 44	2010	101.12 ± 3.14^{Aa}	16.07 ± 1.47^{Aa}	136.97 ± 10.21^{Aa}	26.04 ± 1.54^{Aa}	92.45 ± 1.21^{Aa}	11.97 ± 0.58^{Aa}
	2011	102.14 ± 4.35^{Aa}	15.67 ± 2.08^{Aa}	135.33 ± 14.97^{Aa}	25.88 ± 2.04^{Aa}	91.91 ± 0.94^{Aa}	12.93 ± 0.28^{Aa}
	2012	101.46 ± 1.64^{Aa}	16.47 ± 1.43^{Aa}	134.97 ± 6.47^{Aa}	25.21 ± 1.57^{Aa}	93.54 ± 1.57^{Aa}	13.21 ± 0.47^{Aa}
	Average	101.57 ± 1.04^{Aa}	16.07 ± 1.02^{Aa}	135.76 ± 2.14^{Aa}	25.98 ± 0.51^{Aa}	92.62 ± 0.85^{Aa}	12.70 ± 2.34^{Aa}
Nanjing 46	2010	102.14 ± 3.24^{Aa}	15.01 ± 1.32^{Aa}	128.14 ± 21.4^{Aa}	24.57 ± 1.27^{Aa}	88.51 ± 0.81^{Aab}	11.12 ± 2.98^{Bb}
	2011	105.67 ± 1.52^{Aa}	15.33 ± 1.58^{Aa}	125.00 ± 11.51^{Aa}	24.92 ± 0.92^{Aa}	89.53 ± 0.76^{Aab}	11.66 ± 5.54^{Bb}
	2012	103.51 ± 2.54^{Aa}	15.64 ± 0.67^{Aa}	127.89 ± 3.54^{Aa}	24.15 ± 0.56^{Aa}	87.21 ± 1.46^{Aab}	12.11 ± 3.02^{Bb}
	Average	103.77 ± 1.35^{Aa}	15.29 ± 0.38^{Aa}	127.01 ± 3.62^{Aa}	24.54 ± 0.31^{Aa}	89.19 ± 0.56^{Aab}	11.63 ± 1.36^{Bb}
Nanjing 5055	2010	99.81 ± 2.47^{Aa}	15.25 ± 1.91^{Aa}	131.14 ± 14.21^{Aa}	24.97 ± 1.47^{Aa}	90.51 ± 0.74^{Aab}	10.54 ± 2.41^{Bb}
	2011	103.33 ± 3.06^{Aa}	16.00 ± 1.73^{Aa}	130.30 ± 15.67^{Aa}	25.23 ± 2.71^{Aa}	90.16 ± 3.73^{Aab}	11.66 ± 5.65^{Bb}
	2012	101.24 ± 1.64^{Aa}	16.24 ± 1.37^{Aa}	131.24 ± 10.49^{Aa}	25.37 ± 1.57^{Aa}	89.47 ± 2.17^{Aab}	11.73 ± 1.32^{Bb}
	Average	101.46 ± 1.24^{Aa}	15.83 ± 1.21^{Aa}	130.89 ± 1.34^{Aa}	25.19 ± 0.24^{Aa}	90.05 ± 0.39^{Aab}	11.31 ± 1.34^{Bb}

Superscript letters in the same column indicate significant differences (capital letters: $P < 0.01$; lowercase letters: $P < 0.05$) among the different rice varieties. CK stands for a control variety with low yield in the present study.

DW of *japonica* rice varieties after flowering

Allocation of DW in a plant was the basis for grain yield of rice varieties. Thus, we investigated the changes in DW at the heading stages among the tested rice plants. The DW of panicles per plant of Nanjing 44 reached 9.57 g at 7 DAF, which was the heaviest of the four rice varieties. In contrast, the DW of Wuyunjing 7 only reached 5.67 g. That of Nanjing 44 reached 69.63 g at 42 DAF, while that of the control variety only reached 57.19 g (Table 3). The panicle weights of the other two rice varieties were intermediate between Nanjing 44 and Wuyunjing 7. The grain filling rate of Nanjing 44 in the early DAF was faster and lasted longer than that of the other three rice varieties, which would explain its overall high yield.

Table 3. Dry weights (DW) of the different parts of *japonica* rice plants from Nanjing, Jiangsu Province, China, in the days after flowering (DAF) in 2010-2012.

Variety	DAF (day)	Stem DW (g)	Panicle DW (g)	Leaf DW (g)	Total DW (g)
Wuyunjing 7 CK	0	54.93 ± 3.30^{Aa}	2.67 ± 0.29^{Gg}	9.25 ± 1.62^{Aa}	66.85 ± 4.49^{Ff}
Nanjing 44		56.06 ± 3.75^{Aa}	3.03 ± 0.60^{Gg}	10.43 ± 1.07^{Aa}	69.52 ± 4.39^{Ee}
Nanjing 46		53.48 ± 8.59^{Aa}	3.33 ± 0.13^{Gg}	8.13 ± 0.55^{Bb}	64.94 ± 8.35^{Ff}
Nanjing 5055		55.25 ± 0.89^{Aa}	3.01 ± 0.31^{Gg}	8.45 ± 0.21^{Aa}	66.71 ± 0.71^{Ff}
Wuyunjing 7 CK	7	54.21 ± 3.08^{Aa}	5.67 ± 0.09^{Gg}	6.96 ± 0.23^{Cc}	66.84 ± 3.17^{Ff}
Nanjing 44		54.83 ± 3.66^{Aa}	9.57 ± 1.24^{Ff}	7.69 ± 0.52^{Bb}	72.09 ± 5.35^{Ee}
Nanjing 46		56.63 ± 5.02^{Aa}	5.83 ± 2.56^{Gg}	8.12 ± 0.65^{Bb}	70.58 ± 4.65^{Ee}
Nanjing 5055		57.71 ± 1.55^{Aa}	7.67 ± 1.96^{Ff}	8.33 ± 0.17^{Bb}	73.71 ± 2.25^{Ee}
Wuyunjing 7 CK	14	52.77 ± 0.79^{Aa}	11.67 ± 0.81^{Ff}	6.67 ± 0.04^{Cc}	71.11 ± 1.43^{Ee}
Nanjing 44		54.19 ± 1.53^{Aa}	18.33 ± 3.27^{Ee}	7.25 ± 0.26^{Bb}	79.77 ± 3.71^{Dd}
Nanjing 46		55.67 ± 1.46^{Aa}	12.63 ± 1.11^{Ff}	6.87 ± 0.61^{Cc}	75.17 ± 3.11^{Ee}
Nanjing 5055		55.43 ± 4.18^{Aa}	16.52 ± 0.52^{Ff}	7.32 ± 0.89^{Bb}	79.27 ± 4.35^{Dd}
Wuyunjing 7 CK	21	51.67 ± 8.52^{Aa}	23.83 ± 1.48^{Ee}	5.73 ± 0.91^{Dd}	81.23 ± 8.29^{Dd}
Nanjing 44		52.37 ± 1.51^{Aa}	24.13 ± 4.35^{Ee}	6.38 ± 0.87^{Cc}	82.88 ± 4.61^{Dd}
Nanjing 46		49.83 ± 8.37^{Aa}	15.27 ± 2.17^{Ff}	6.28 ± 1.80^{Cc}	71.38 ± 5.19^{Ee}
Nanjing 5055		54.33 ± 4.97^{Aa}	29.67 ± 2.53^{Dd}	6.67 ± 0.72^{Cc}	90.67 ± 4.64^{Cc}
Wuyunjing 7 CK	28	43.73 ± 3.76^{Bb}	37.93 ± 15.76^{Dd}	4.23 ± 1.17^{Ee}	85.89 ± 12.43^{Cc}
Nanjing 44		44.61 ± 4.48^{Bb}	44.13 ± 8.12^{Cc}	5.63 ± 0.44^{Dd}	94.37 ± 12.23^{Cc}
Nanjing 46		47.33 ± 3.23^{Bb}	30.01 ± 4.63^{Dd}	3.34 ± 0.15^{Ee}	80.68 ± 4.25^{Dd}
Nanjing 5055		51.68 ± 4.56^{Aa}	33.33 ± 6.82^{Dd}	5.67 ± 0.27^{Dd}	90.68 ± 9.18^{Cc}
Wuyunjing 7 CK	35	44.33 ± 4.15^{Bb}	57.19 ± 2.08^{Bb}	2.47 ± 0.44	103.99 ± 6.62^{Bb}
Nanjing 44		43.43 ± 2.20^{Bb}	59.62 ± 1.19^{Bb}	3.32 ± 0.34^{Ee}	106.37 ± 3.63^{Bb}
Nanjing 46		46.11 ± 3.04^{Bb}	58.30 ± 1.15^{Bb}	2.93 ± 0.52^{Ee}	107.34 ± 4.28^{Bb}
Nanjing 5055		55.32 ± 4.07^{Aa}	45.67 ± 4.05^{Cc}	3.12 ± 0.22^{Ee}	104.11 ± 7.95^{Bb}
Wuyunjing 7 CK	42	44.55 ± 2.51^{Bb}	57.27 ± 2.60^{Bb}	2.51 ± 0.49^{Ee}	104.33 ± 1.25^{Bb}
Nanjing 44		43.27 ± 2.35^{Bb}	69.63 ± 2.05^{Aa}	3.18 ± 0.05^{Ee}	116.08 ± 4.14^{Aa}
Nanjing 46		46.43 ± 1.51^{Bb}	59.23 ± 1.17^{Bb}	2.93 ± 0.60^{Ee}	108.59 ± 3.71^{Bb}
Nanjing 5055		50.67 ± 2.03^{Aa}	62.33 ± 2.67^{Bb}	2.83 ± 0.49^{Ee}	115.83 ± 5.30^{Aa}

Superscript letters in the same column indicate significant differences (capital letters: $P < 0.01$; lowercase letters: $P < 0.05$) among the different rice varieties. CK stands for a control variety with low yield in the present study.

Conversion characteristics of dry matter in different rice plant parts in DAF

When more of the DW of the source organs, such as leaf or stem, was transferred to the grain, the rice yield increased. This depends of the distribution of the grain. The percentage of dry matter distribution in different plant organs from the first DAF until 42 DAF were continuously measured (Figure 1). The results showed that the DW percentages of the stem and panicle, compared to the whole plant DW in Nanjing 44 were 76.06 and 13.28%, respectively, at 7 DAF. In contrast, those of Wuyunjing 7 were 81.10 and 8.48%, respectively. The percentages of the stem and panicle DW compared to the whole plant DW in Nanjing 44 were also larger than the two intermediate yield rice varieties. Furthermore, the percentage of panicle weight as compared to the whole plant in Nanjing 44 was the highest of all tested rice plants in this study. This indicates that the dry matter of Nanjing 44 is quickly transferred to the grain at the start of the grouting. At 42 DAF, the panicle weight percentage per total plant weight of Nanjing 44 was 59.97% and higher than those of Nanjing 46 and Nanjing 5055, while that of Wuyunjing 7 was 54.89%. Throughout the grain filling period, the dry matter of Nanjing 44 always had a high proportion to grain, even in the later-grain-filling stages. The conversion rate of the material in the stems, such as percentage of the exported matter in stem-sheath in Nanjing 44 was 20.81%. This was higher than that of Wuyunjing 7 (18.90%) (Table 4). Taken together, the results indicate that Nanjing 44 had the highest capability of exporting or transferring the dry matter from its stem to grains.

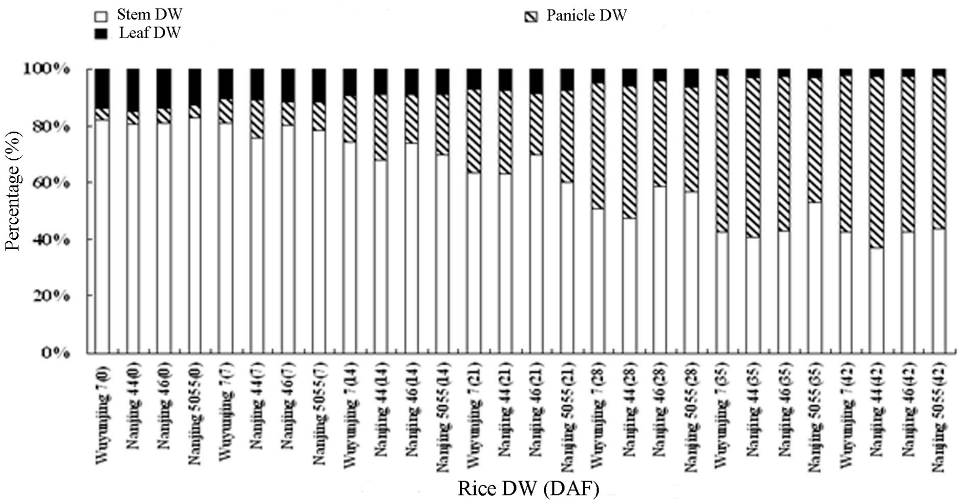

Figure 1. Percentage of dry matter of *japonica* rice in days after flowering (DAF) in Nanjing, Jiangsu Province, China, 2010-2012. DW = dry weight.

Table 4. Transport of dry matter of different materials.

Variety	EPMSS (%)	TPMSS (%)	EPML (%)	TPML (%)
Wuyunjing 7 (CK)	18.90 ± 1.20^{b}	19.01 ± 1.20^{a}	72.86 ± 2.10^{a}	12.34 ± 1.10^{a}
Nanjing 44	22.81 ± 1.30^{a}	19.20 ± 1.10^{a}	69.54 ± 2.60^{a}	10.90 ± 1.20^{a}
Nanjing 46	13.18 ± 1.10^{c}	17.22 ± 1.00^{a}	67.91 ± 3.20^{a}	13.43 ± 1.40^{a}
Nanjing 5055	8.29 ± 1.10^{d}	8.08 ± 1.00^{b}	66.51 ± 2.30^{a}	9.47 ± 1.10^{a}

EPMSS: percentage of the export mater in stem-sheath; TPMSS: percentage of the transformation matter in stem-sheath; EPML: percentage of the export mater in leaf; TPML: percentage of the transformation matter in leaf. Superscript letters in the same column indicate significant differences (capital letters: $P < 0.01$; lowercase letters: $P < 0.05$) among the different rice varieties. CK stands for a control variety with low yield in the present study.

Diurnal variation of photosynthetic materials before and after flowering

More than 80% of the photosynthetic products in the leaves after flowering are converted to yield and the flag leaves are responsible for more than 50% of the overall photosynthesis of the plant (Li et al., 2011). Therefore, the P_n was measured at different times of day, before and after flowering (Figure 2), and so was the air temperature during those days (Figure 3). The minimum temperature was 10°C, the maximum temperature was 36°C, and the average temperature was 25.28°C (Figure 3). The P_n of the tested materials was usually highest at 9:00 am, with a decline at 13:00 pm, and a certain degree of recovery by 16:00 pm. It exhibited a typical diurnal variation observed in C_3 plant photosynthesis, which use C_3 photosynthesis depending on whether the primary photosynthesis product contains three carbons. We found that the P_n of Nanjing 44 was still the highest of the four tested varieties at 12 days before flowering. The P_n of Nanjing 44 at 9:00 am was as high as 25.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which was 10.00% higher than the control variety, Wuyunjing 7, on 12 DAF. The P_n of Nanjing 44 decreased less at noon during the DAF, as compared with the other three rice varieties, indicating that the photoinhibition of photosynthesis in the leaves of Nanjing 44 at noon was not as obvious. Thus, during the filling stage, the flag leaf of Nanjing 44 still maintained a high-photosynthetic function (Figure 2), which could provide more photosynthetic products to the leaves.

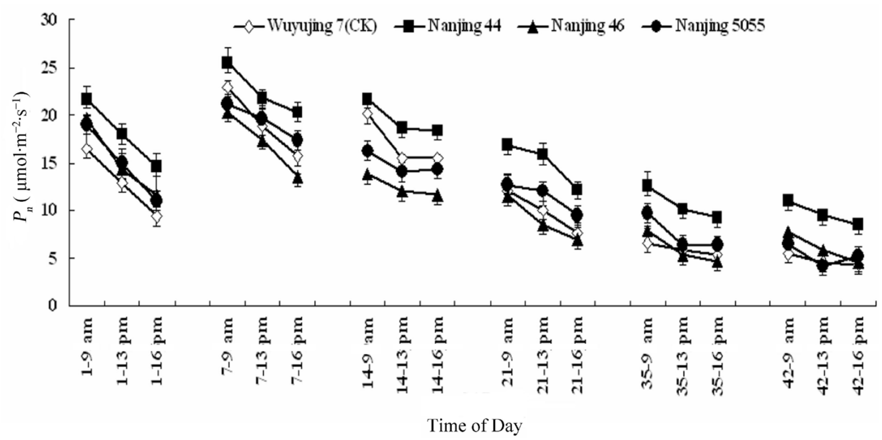

Figure 2. Diurnal variation of P_n in different varieties in Nanjing, Jiangsu Province, China, 2010-2012. Vertical bars represent SD, N = 5.

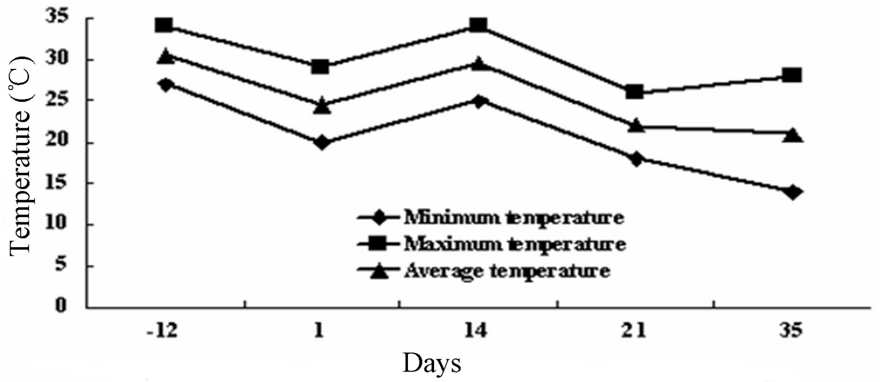

Figure 3. Daily maximum, minimum, and average air temperatures during the rice growing season in Nanjing, Jiangsu Province, China, 2010-2012. The temperature variation was measure 12 days before flowering (-12) and at 1, 14, 21, and 35 days after flowering.Vertical bars represent SD, N = 5.

Daily distribution of leaf light for the tested rice varieties

Figure 4 shows how the Chl contents changes post-flowering in the tested rice varieties. It was obvious that the Chl content began to decrease by 21 DAF. As compared with the Chl contents in the other three rice varieties, Nanjing 44 showed the lowest decrease in Chl contents in all DAF. By photooxidation identification, Nanjing 44 was identified as type 1, indicating that it is tolerant to photooxidation stress, and was of the same type as the control variety, Wuyunjing 7 (Table 5). Prior to the photooxidation treatments, the Chl content of Nanjing 44 was 25.30% higher than that of Wuyunjing 7. After the photooxidation treatment, Nanjing 44 was still 14.17% higher than Wuyunjing 7, in terms of Chl content. The leaf color grades of the intermediate rice varieties revealed that they were more sensitive to photooxidation than Nanjing 44. The Nanjing 44 photooxidation identification results are consistent with the observed lower decrease of Chl content at 42 DAF.

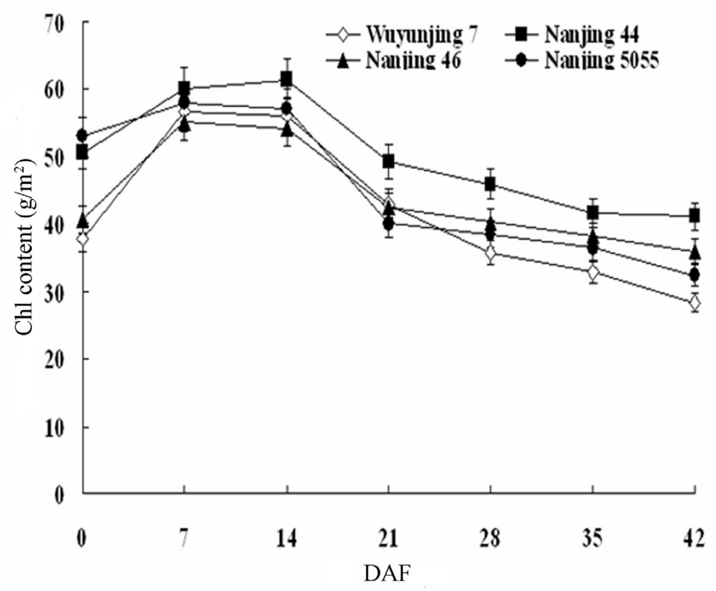

Figure 4. Changes in the chlorophyll (Chl) content at days after flowering (DAF) in the different rice varieties under field conditions in Nanjing, Jiangsu Province, China, 2010-2012. Vertical bars represent SD, N = 5.

Table 5. Effects of photooxidation treatment on chlorophyll (Chl) content in rice cultivars.

Variety	Chl *a*			Chl *b*			Total Chl content			Chl *a*/Chl *b*			Photooxidation color rating
	Before (B) (g/m²)	After (A) (g/m²)	A/B (%)	Before (B) (g/m²)	After (A) (g/m²)	A/B (%)	Before (B) (g/m²)	After (A) (g/m²)	A/B (%)	Before (B) (g/m²)	After (A) (g/m²)	A/B (%)	
Wuyunjing 7 (CK)	37.8 ± 0.6^{Bb}	32.1 ± 0.3^{Aa}	84.00 ± 1.00^{Aa}	14.8 ± 0.3^{Bb}	10.8 ± 0.01^{Aa}	73.00 ± 1.00^{Aa}	52.6 ± 0.9^{Bb}	42.9 ± 0.4^{Bb}	82.00 ± 2.00^{Aa}	25.6 ± 0.3^{As}	29.7 ± 0.03^{Aa}	116.0 ± 1.00^{Aa}	2
Nanjing 44	50.6 ± 0.5^{Aa}	37.4 ± 0.2^{Aa}	73.00 ± 1.00^{Bb}	20.2 ± 0.2^{Aa}	12.5 ± 0.02^{Aa}	62.00 ± 1.00^{Bb}	70.8 ± 0.7^{Aa}	49.9 ± 0.2^{Aa}	70.00 ± 1.00^{Bb}	25.0 ± 0.1^{Aaa}	30.0 ± 0.04^{Aa}	120.0 ± 2.00^{Aa}	1
Nanjing 46	40.7 ± 0.15^{Bb}	21.3 ± 0.3^{Bb}	52.00 ± 1.00^{Cc}	16.9 ± 0.2^{Bb}	8.8 ± 0.1^{Bb}	52.00 ± 2.00^{Cc}	57.6 ± 0.17^{Bb}	30.2 ± 0.4^{Cc}	52.00 ± 1.00^{Cc}	24.1 ± 0.6^{Aa}	24.3 ± 0.01^{Bb}	100.1 ± 3.00^{Bb}	3
Nanjing 5055	53.2 ± 0.2^{Aa}	17.5 ± 0.1^{Bb}	33.00 ± 1.00^{Dd}	21.4 ± 0.2^{Aa}	8.5 ± 0.2^{Bb}	39.00 ± 1.00^{Dd}	74.7 ± 0.3^{Aa}	26.0 ± 0.3^{Dd}	35.00 ± 1.00^{Dd}	24.8 ± 0.1^{Aa}	20.8 ± 0.04^{Cc}	84.00 ± 1.00^{Cc}	3

Observed color rating of photooxidation: 1: whole leaf green; 2: tip yellowish; 3: 1/3 yellowish; 4: 1/2 yellowish; 5: whole leaf yellowish. The values given are mean of three replications ± SE. Superscript letters in the same column indicate significant differences (capital letters: $P < 0.01$; lowercase letters: $P < 0.05$) among the different rice varieties. CK stands for a control variety with low yield in the present study.

Antioxidant enzyme activity and total non-enzymatic system antioxidant capacity

On 35 DAF, the MDA content of Nanjing 44 was 51.91% lower than that of the control (Figure 5A). As compared with the other rice varieties, the SOD, peroxidase (POD), and CAT activities in the Nanjing 44 flag leaf were also the highest. Compared to Wuyunjing 7, the SOD (Figure 5B), POD (Figure 5C), and CAT (Figure 5D) activities in Nanjing 44 were 7.03, 11.56 and 8.54% higher, respectively. Furthermore, the total antioxidant capacity of the non-enzymatic system in Nanjing 44 (Figure 5E) was 11.28% higher than that of the control variety. Likewise, the soluble protein of the flag leaves in Nanjing 44 was 5.1% higher than Wuyunjing 7 (Figure 5F). The values observed in the intermediate rice varieties were in between Nanjing 44 and Wuyunjing 7.

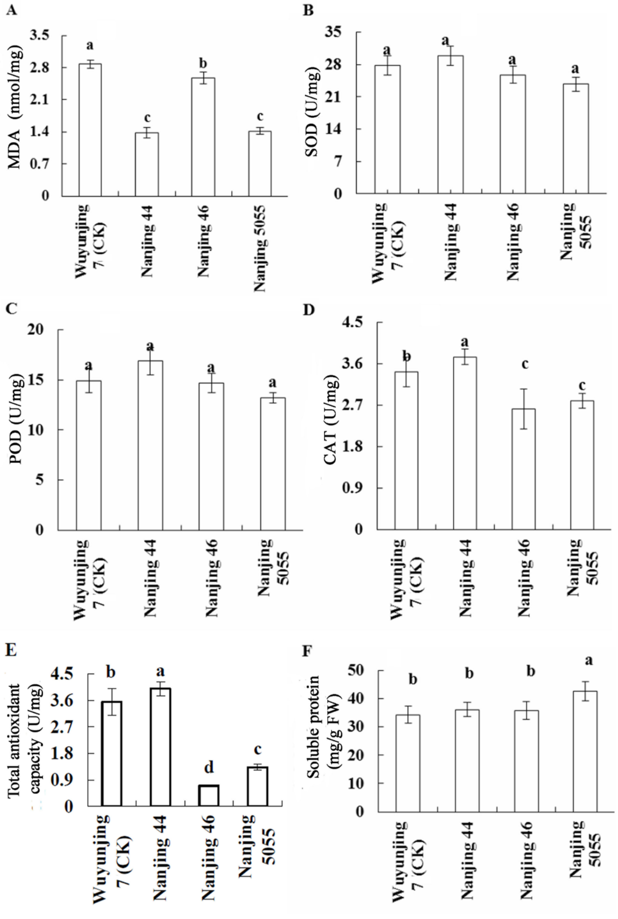

Figure 5. Antioxidant enzyme activities, total antioxidant capacity, and soluble protein of different rice varieties in Nanjing, Jiangsu Province, China, 2010-2012. Vertical bars represent SD, N = 5. **A.** MDA (malondialdehyde) content; **B.** SOD (superoxidase dismutase) activity; **C.** POD (peroxidase) activity; **D.** CAT (catalase) activity; **E.** total antioxidant capacity with non-enzymes; **F.** soluble protein content in flag leaves. CK = control variety. Letters above the bars indicate significant differences ($P < 0.05$).

Correlations between photosynthetic parameters and yield components

The correlation coefficient between panicles per plant and plant height was 0.70 ($P < 0.05$). The correlation coefficients between plant height and spikelet per plant or plant yield were 0.52 and 0.55, respectively ($P < 0.05$). The correlation coefficients between panicles per plant and the total spikelet per plant or yield per plant were 0.89 and 0.91, respectively ($P < 0.01$). The coefficient between grains per panicle and seed setting rate was 0.63 ($P < 0.05$), and those between grain weight per plant and panicles per plant or spikelet per plant were 0.55 and 0.78, respectively ($P < 0.05$). This indicates that the sink, including panicles per plant and spikelet per plant, were the main factors that determined the rice yield. The correlation coefficients between P_n at 13:00 pm on 21 DAF and the grains per panicle or spikes per plant were 0.61 and 0.59, respectively ($P < 0.05$). The correlation coefficients between P_n at 13:00 pm on 21 DAF and seed setting rate, 1000-grain weight or grain weight of plant were 0.74, 0.79, and 0.68, respectively ($P < 0.01$). The photosynthetic capability of flag leaves in rice varieties was the key trait determining the filling of grains, including the weight of the panicle and the flow rate of photosynthetic products for high yield, in the given plant type.

DISCUSSION

China's research on "super" rice varieties has incorporated the use of both morphological improvement and heterosis as technological routes. Morphological improvements involve shaping the ideal plant, which will produce an excellent plant type that can thrive under different environment conditions. Yang et al. (2000) have shown that the agronomic and physiological traits, as well as the yield of *japonica* rice, have been significantly improved. However, most results were from "super" hybrids (Cheng et al., 2007). In fact, many "super" hybrids often encounter adversity and exhibited lower seed setting rate, seriously affecting the performance of their yield potential (Yang et al., 2002), while high-yielding *japonica* can be adapted to a variety of conditions and has shown high seed setting rate (Jiao and Li, 2001; Zhang et al., 2009b; Yang and Zhang, 2010). It can be observed that increasing the intrinsic physiological functions of the rice, to improve the adaptability to adverse conditions, would be an important way to produce higher yields in rice.

In this paper, as a "super" *japonica* rice variety, Nanjing 44, from the Jiangsu Province of China, has enough panicles and longer, erect, thick narrow leaves, quite similar to the other three rice varieties tested. Furthermore, Nanjing 44 was found to have a strong photosynthetic physiological function at the single leaf level, which resulted in more photosynthetic products in the leaves and a faster transfer from stem to grain. In addition, the "super" rice variety Nanjing 44 had a more stable Chl content and was more tolerant to photooxidation. This allows it to thrive in bad environments at the later DAF (42 DAF). The higher activities of the antioxidative enzymes and the non-enzyme antioxidative capability in Nanjing 44 would also have aided the avoidance of the damaging photooxidative stress at the later DAF. The results were rather similar to those found in the hybrid rice variety, another "super" rice Liangyoupeiju (Zhang et al., 2010), and this response was also consistent with that induced by cold in *japonica* rice varieties (Bonnecarrère et al., 2011). The observed good plant type and the photosynthetic capacity of a single rice plant leaf can be used for screening, which would be a noteworthy breeding strategy.

In 1928, Mason and Maskell developed the concept of the source, sink and source-sink relationship. In recent decades, much research has focused on determining the source, sink and source-sink relationship (Venkateswarlu and Visperas, 1987; Yuan et al., 2005). In addition, identification of different types of species, including the source-limited type, sink-limited type, and those with optimized control of the source-sink relationship, has been performed (Lan et al., 2007). Murchie et al. (2002) also posed the question whether there were associations between grain-filling rate and photosynthesis in the flag leaves of field-grown rice. In field experiments, they found that rubisco accumulated to a level in excess of photosynthetic requirements, serving as a store of nitrogen for grain filling (Murchie et al., 2002). The photosynthesis efficiency in rice grain yield depends on the ability of material production (source), grain composition conditions (sink), and the operation and distribution of the photosynthetic assimilate (flow). The rate of operation and distribution of photosynthetic products is one of the key factors that affects the efficiency of grain growth and grain yield. During the rice grain formation stage, if the photosynthetic products quickly flow to the seed, it is conducive to the formation of high yield. Zhang et al. (1995) proposed that the best period for the accumulation of dry matter in super-yielding rice varieties was prior to the heading stage, and that the rate of energy accumulation in the rice was also higher at that period (Lin et al., 2006). A study of the rice leaf age model found that, although the stem and sheath of the low-yielding varieties had higher output, the yield was still not high because of a lower dry matter accumulation from leaf (stem) to grain during the heading to maturity stages (Yang et al., 2013). Hence, it seems that the grain increase is also related to the transfer of dry matter from stem to grain. Therefore, views on the accumulation of starch dependency and the heading of high-yield rice varieties were put forward. These views emphasized the importance of the leaf system, stem reserves, and production at the later growth stages of rice, especially the flowering stage (Ling et al., 1993). Murchie et al. (2002) reported that a rapid grain-filling phase occurred approximately 10 days after flowering in most varieties. But the results found in the present study suggest that the photosynthetic apparatus in the high-yielding Nanjing 44 remained stable until 21 DAF, which is also important to satisfy the longer grain-filling time.

In this paper, we found that the high yield capability of the “super” rice Nanjing 44, was related to three obvious advantages in the photosynthetic function of the leaves during the late developmental stage. First, the highest photosynthetic characteristics of jointing and booting not only form a strong source (leaf) and a large sink (spike), but also allow filling of the grains as soon as possible. Second, the stable P_n of the flag leaf during the heading stage and throughout the whole day, especially under the high light intensity and air temperatures at noon, indicated that the external environmental conditions had less influence on the storage and conversion of photosynthetic products to grain. Furthermore, the higher antioxidant capabilities at the late filling stages (42 DAF) also protected the photosynthetic apparatus of the flag leaves, which allowed a longer filling period. For example, the endogenous reactive oxygen scavenging enzymes, such as SOD and POD, had higher induced activity levels in the flag leaves. Third, the conversion efficiency of photosynthetic products from stem to grain in Nanjing 44 was relatively high, thereby ensuring that the accumulation of photosynthetic products was transformed smoothly to the grain of the “super” rice variety during the 42 DAF.

“Super” rice research is an important topic in the world, and, as Yuan (2001) proposed, “super” rice production targets should vary with age, the eco-regions, and planting season. The standards should also change according to these variables (Peng et al., 2009). Based on good plant types and good photosynthetic physical advantages, the high and “super” high yield rice varieties are achieved by increasing the source, accelerating the flow, the expansion of the sink (leaf), and other steps. The problems with the yields of some current varieties have been found to be due to environmental stresses in different regions, and research on rice with broad adaptability and increased tolerance to stress will be necessary.

Conflicts of interest

The authors declare no conflict of interest.

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