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Analysis of Antioxidant Characteristics and Related Gene Expression Profiles of Rice Drought-Tolerance Lines Derived from Embryo-Soaking with *Alternanthera philoxeroides* DNA Solution

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Research Article

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ABSTRACT

Drought is one of major abiotic stress limiting rice stable production. In the study, four rice cultivars, IAPAR9 (upland rice cultivar), H8 and H10 (drought-tolerance variant lines derived from 6527 embryo-soaked with *Alternanthera philoxeroides* DNA solution) and 6527 (ordinary rice cultivar), were used to study the antioxidant characteristics of drought-resistant varieties by superoxide dismutase (SOD) activity, peroxidase (POD) activity, malondialdehyde (MDA) content and their related gene expression profiles. The results showed that the SOD activity, POD activity and MDA content were increased significantly under drought stress, while decreased in the yield and its related traits such as seed setting ratio, 1000-grain weight and grain number per panicle. The SOD and POD activities in drought-tolerant rice (H8, H10 and IAPAR9) were significantly higher than those in drought-sensitive 6527. Less MDA content was produced in drought-tolerant rice (H8, H10 and IAPAR9) than sensitive 6527. The yield of H8 was significantly higher than that of other cultivars, and the seed setting ratio and 1000-grain weight from those with drought-tolerant were significantly higher than that of sensitive 6527. After drought stress, there were 11 genes related to antioxidant progress whose expression profiles changed significantly between H8 and 6527. These results suggested that drought tolerant cultivars maybe subdue harms from the peroxidation by inducing the express of related genes of antioxidant process, further increasing the SOD activity and POD activity. Thus, their enhancement of drought resistance could maintain the normal growth and development under drought stress and achieve maximum photosynthate storage.

INTRODUCTION

Rice is important food crop all over the world, and become main food for more than about 1/2 people. 95% of the world's rice is grown in less developed nations, primarily in Asia. The total planting area for rice in China is the second largest after India [1,2]. However, rice is a crop needing large water consumption, whereas serious water shortage existed in China. To solve the contradiction, important is the rice germplasm resources enhancement of drought resistance. Based on the good utilization of favorable genes within species in rice breeding, introduction of favorable genes from the wild sources or distant species becomes more and more important. *Alternanthera philoxeroides* is an extremely drought tolerant weed. Here, its whole DNA was used to introduction into rice cultivar 6527 with soaking-embryo method, a direct introduction technique of exogenous DNA with simple, operation easily and no limitation of plant species which provides quick and broader variation for breeders. Then, the variant line H8 and H10 with significant drought resistance were obtained by continually upland directional selection until F_{23} generations. Finally, they were valued by various drought resistance indexes [3].

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Drought stress is a serious limiting factor for rice production and yield stability. One channel of drought resistance is to improve the level of antioxidant metabolism in plant. It was found that drought stress reduces the dry matter production and final yield most due to the loss of balance between the production of reactive oxygen species (ROS) and the antioxidant system, which leads to accumulation of ROS and induction of oxidative damage to cell components [4,5]. So also plants have formed the basis of oxidant scavenging and ROS signaling systems and developed a variety of antioxidant enzymes, such as superxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), catalase (CAT) [6,7]. To date, some drought-tolerant genes identified in rice and physiological mechanisms for drought stress have also been understood [8-13]. However, little is known about how expression profiles changes for genes related to antioxidant characteristics between drought resistant varieties and sensitive ones. In the study, the SOD activity, POD activity, MDA content, together with the yield and its related traits were studied between drought-resistant rice (H_8, H_{10} and IAPAR9) and sensitive 6527. Besides, expression profiles of genes related to antioxidant metabolism were also researched between H8 and 6527 under drought stress. More information will be provided in the study about drought tolerance in rice.

MATERIALS AND METHODS

Experimental Site

The field experiment was conducted in 2012 at the Xiema experimental station (19°51′N, 106°37′E) of Southwest University, Beibei, Chongqing, China. The station is located 10 km south of Southwest University at an elevation of 350 m above sea level, and the area is classified as having a subtropical monsoon climate.

Experimental Material and Design

Four rice cultivars were used in the experiment. H8 and H10 belong to drought-resistant rice derived from 6527 embryo-soaked with *Alternanthera philoxeroides* DNA solution, 6527 is a regular rice cultivar, sensitive to drought, IAPAR9 is an upland rice cultivar, resistant to drought [3].

The experiment was designed as split-plot. The main plots were control and drought stress treatments. The subplots were four rice cultivars with three replications. Plants for drought stress treatments were planted in field with a shed (3 m height) whose top was equipped with hard organic transparent material and whose bottom and sides was made with cement. Control Plants were planted in the same cement field without shed. Each plot includes 3 rows with row spacing of 26.4 cm, plant spacing of 12 cm, and density of 10 plants per row. Seeds was sown on March 20, 2012, and transplanted on April 21, 2012. In the drought stress treatment, water was cast away on 28 April 2012, and then 8000 mL of water was quantitatively irrigated with interval of 12 d into the every plot. Sufficient water was supplied in the control treatment until maturity.

Measurement of Antioxidant Indexes

Ten plants were selected randomly from each plot at 12 d after drought stress at the heading stage. The flag leaves with removed petiole were immediately placed in box with ice and then kept -20°C for analysis of antioxidant characteristics.

SOD crude extract was made according to the method of Bewley, with some modifications. 0.5 g of each samples was homogenized with a pestle in an ice-cold mortar, which contained 2 mL of buffer (50 mmol L^{-1} phosphate buffer, pH 7.8, 1% (v/v) PVP) [14]. The volume was corrected to 10 mL with phosphate buffer and then centrifuged at 10000 rpm for 15 min at 4°C. Measurement of the SOD activity was made using a testing kit from Nanjing Jiancheng Science and Technology Co., Ltd. (Nanjing, China). SOD activity was expressed as U mg^{-1} prot. Each sample was repeated to measure three times.

POD activity was assayed according to the method of Moerschbacher et al, with some modifications. 1 g of samples for each sample was homogenized with a pestle in an ice-cold mortar, which contained 10 mL of 20 mmol L^{-1} KH_2PO_4 [15]. The homogenate was centrifuged at 4000 rpm for 15 min at 4°C. 0.1 mL of supernatant was mixed with 2.9 mL of 50 mmol L^{-1} phosphate buffer (pH 5.5), 1 mL of 2% (v/v) H_2O_2, and 1 mL of 50 mmol L^{-1} guaiacol, and incubated in a water bath at 37°C. After 5 min, the absorbance at A470 was measured by a spectrophotometer (UV-5800PC, Shanghai, China). One unit of enzyme activity (U) was defined as a change of 0.01 in absorbance per min. POD activity was expressed as U g^{-1} FW. Each sample was repeated to measure three times.

MDA content was assayed according to the method of Heath and Packer, with some modifications. 1 g of each sample was homogenized with a pestle in an ice-cold mortar, which contained 2 mL of 10% (v/v) TCA, and then homogenized in 8 mL of 10% (v/v) TCA [16]. The homogenate was centrifuged at 4000 rpm for 10 min at 4°C. 2 mL of supernatant was mixed with 2 ml of 0.6% (v/v) TBA, and heated in a boiling water bath for 15 min. The cooling fluid was centrifuged at 4000 rpm for 10 min at 4°C. The absorbances at A450, A532, and A600 were measured by a spectrophotometer (UV-5800PC, Shanghai, China). Each sample was repeated to measure three times. MDA content was expressed as nmol g^{-1} FW.

RNA Extraction and Measurement of Gene Expression Profiles

Based on the results that H8 exhibited significant drought resistance than IAPAR9, and the drought resistance of H_{10} was nearly similar with IAPAR9 [3]. So, only H8 and its recipient 6527 were used as materials to analyze the expression profiles in the study. Three plants were selected randomly from each plot of H_8 and 6527 (drought stress and control) at 12 d after drought

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stress at the heading stage, in total 36 plants. Then the roots, culm, leaves and panicles were balance-mixed into 12 centrifuge tubes and labelled, and immediately frozen in liquid nitrogen for 30 min and kept -80°C for extract of RNA. RNA was extracted by using a TRIzol testing kit (TIANGEN, Beijing, China). The gene expression profiles were assayed by Shengzhen Huada Gene Research Institute (Shengzhen, China).

Measurement of Yield and its Related Traits

Ten plants were sampled in the middle line from each plot at the maturity stage to measure the plant height, panicle number per plant, panicle length, 1000-grain weight, grain number per panicle, spikelet number per panicle, and seed setting ratio. Yield of plot were measured when all plants in each plot were harvested, and then were converted into yield per ha.

Statistical Analyses

Microsoft Excel 2003 was used for analyzing raw data. Analysis of variance was performed with DPS 12.5 software. Expression profiles of genes more than 2 times were analyzed, and 0 is represented null expression.

RESULTS AND DISCUSSION

Antioxidant Characteristics

Most plant physiology indexes changes after drought stress, and different varieties exhibit difference. As shown in variance analysis **(Table 1)**, the SOD activity, POD activity, and MDA content were all significantly influenced by both drought stress treatment and cultivars difference. The interaction between treatments and cultivars had a significant effect on the MDA content, but no on the SOD and POD activity.

Table 1. Variance Analysis of Antioxidant Characteristics (F Value).

Variation source	DF	SOD activity	POD activity	MDA content
Treatment	1	115.46^{**}	275.95^{**}	80.48^{*}
Cultivar	3	43.97^{**}	30.69^{**}	31.75^{**}
Treatment × Cultivar	3	3.23^{ns}	0.81^{ns}	4.54^{*}

* and ** indicate significant difference at P<0.05 and P<0.01, respectively. ns represent non-significant.

Compared with the control, the drought stress significantly increased the SOD activity, POD activity, and MDA content by 157.13 U mg^{-1} prot, 814.02 U g^{-1} FW, and 6.54 nmol g^{-1} FW, respectively **(Table 2).** Similar findings were also reported by Liu et al. [17]. Besides, significant differences in antioxidant characteristics were existed in drought-resistant cultivars and sensitive ones **(Table 2).** Compared with 6527(drought-sensitive), the SOD activity of H_8, IAPAR9 and H_{10} were significantly increased by 184.80, 80.26 and 75. 80 U mg^{-1} prot. The POD activity was accordingly increased by 1441.11, 1278.05, and 322.24 U g^{-1} FW, respectively. Especially, the SOD and POD of H8 were higher than that of H10 and IAPAR9. Moreover, the MDA content of H8, IAPAR9, H10 were decreased significantly by 10.69, 7.11, and 6.01 nmol g-1 FW as compared to 6527 **(Table 2).** Thus, we can conclude that drought-tolerant rice could resist the oxidative stress result from drought by increasing the SOD and POD activity, which was consistent with results of Lu et al. [18]. Finally, the rise ranges of SOD activity and POD activity in H8 were significantly higher than that of 6527, and its decreasing rage of MDA were significantly lower than that of 6527. While In H_{10}, only the change rage of MDA content existed significantly difference with that of 6527 **(Tables 2 and 3).** These results showed that H_8 was the most drought resistant than the other cultivars in antioxidant aspects.

Table 2. Effects of Treatment and Cultivar on Antioxidant Characteristics.

		SOD activity (U mg^{-1} prot)	POD activity (U g^{-1} FW)	MDA content (nmol g^{-1} FW)
Treatment	Drought	336.35 a	2949.58 a	27.42 a
	Control	179.22 b	2135.56 b	20.88 b
Cultivar	H8	357.37 a	3223.33 a	19.41 c
	IAPAR9	252.83 b	3060.27 a	22.99 b
	H10	248.37 b	2104.46 b	24.09 b
	6527	172.57 c	1782.22 b	30.10 a

Values followed by different letters are significantly different among cultivars at P<0.05.

Table 3. Change range of antioxidant characteristics in different cultivars by drought treatment.

Cultivar	Mean ± SD			Compared with 6527 (P value)			Compared with IAPAR9 (P value)		
	SOD activity (U mg^{-1} prot)	POD activity (U g^{-1} FW)	MDA content (nmol g^{-1}FW)	SOD activity	POD activity	MDA content	SOD activity	POD activity	MDA content
H_8	203.66 ± 42.37	1121.11 ± 113.67	3.55 ± 1.54	0.02	0.005	0.012	0.27	0.04	0.304
H_{10}	126.39 ± 8.67	681.09 ± 64.44	6.96 ± 1.65	0.23	0.29	0.066	0.06	0.04	0.265
6527	118.89 ± 13.00	600.00 ± 67.99	11.10 ± 1.62				0.04	0.01	0.049
IAPAR9	179.61 ± 46.38	853.88 ± 55.27	4.55 ± 2.04						

Research showed that drought stress can induce plants to produce large amounts of reactive oxygen species, which result in lipid peroxidation, undermine the stability of the cell membrane, and produce the MDA [19]. The SOD plays an important role in

the eliminating ROS, which could restore the super oxide anion to the peroxide hydrogen and oxygen, and is the first defense line for biological preventing ROS damage [19]. POD participate in a variety of physiological metabolism, which plays an important role in catalyze the synthesis of a variety of cell wall structure components, controlling cell growth and development and eliminate peroxide hydrogen, and is a key enzyme in the antioxidant enzymes protect system under stress [20]. Not only did our results confirm this conclusion, but also found that drought-resistant varieties had higher efficiency of scavenging active oxygen and stronger ability of removing hydrogen peroxide, and produced less MDA. Thus, drought-resistant rice could resist the oxidative stress resulting from drought by increasing the activity of SOD and POD, which is coherent with eliminating the damage of free oxygen ions and starting the antioxidant systems [17,18]. Of course, there are other ways to resist drought in drought resistant cultivars, such as increasing the osmotic pressure by osmotic regulation substances, i.e. proline, ions and soluble sugar [21,22]. They often need collaborative work.

Yield and Agronomic Traits

As shown in variance analysis **(Table 4)**, drought stress influenced yield, 1000-grain weight, grain number per panicles, and seed setting ratio significantly, but no on the plant height, panicle number per plant, panicle length, and spikelet number per panicles. There were significant effects on the yield and all agronomy traits among cultivars. Compared with the control, the drought stress decreased yield, plant height, panicle number per plant, panicle length, 1000-grain weight, grain number per panicle, spikelet number per panicle, and seed setting ratio by 58.97%, 14.20%, 33.47%, 6.04%, 10.66%, 40.23%, 10.39%, and 29.29%, respectively **(Table 5).** Similar findings were reported by cai et al. [23]. The yield of H8 were higher significantly than those of the other 3 cultivars. The panicle number per plant and grain number per panicle of H8 were significantly higher than those of IAPAR9 and 6527, no difference with that of H10. The 1000-grain weight and seed setting ratio of drought-tolerant cultivars (H_8, H_{10} and IAPAR9) were higher than those of sensitive 6527 **(Table 5).** The results showed that drought-tolerant rice cultivars had higher yield under drought stress, and simultaneously seed setting ratio and 1000-grain weight are responsible for their high yield, which was consistent with the reported papers [3,24]. Furthermore, The decreasing ranges of the yield, 1000-grain weight, grain number per panicle and seed setting rate in drought-tolerant rice cultivars (H_8, H_{10} and IAPAR9) were significantly lower than those of drought-sensitive rice 6527 **(Table 6)**, suggesting that drought stress influenced easily on grain filling progress, and the effects on drought-tolerant cultivars was smaller than on sensitive ones.

Table 4. Variance Analysis of Yield and Agronomic Traits (F Value).

Variation source	DF	Yield	Plant height	Panicle number per plant	Panicle length	1000-grain weight	grain number per panicles	Spikelet number per panicle	Seed Setting rate
Treatment	1	135.2**	9.22	13.51	3.99	62.27*	203.61**	8.58	221.72**
Cultivar	3	10.87**	9.31**	3.51*	19.85**	198.59**	4.92*	11.45**	69.12**
Treatment × Cultivar	3	3.94*	0.32	0.49	2.13ns	2.84ns	9.71**	0.06	67.6**

* and ** indicate significant difference at P<0.05 and P<0.01, respectively.

Table 5. Effects of treatment and cultivar on yield and agronomic traits.

		Yield (kg hm^{-2})	Plant height (cm)	Panicle number per plant	Panicle length (cm)	1000-grain weight (g)	grain number per panicle	spikelet number per panicle	Seed setting rate (%)
Treatment	Control	5064.38a	109.48a	2.39 a	26.34a	24.77a	149.07a	194.57a	76.54a
	Drought	2077.87b	93.93 a	1.59 a	24.75a	22.13b	89.10 b	174.35a	54.12b
Cultivar	H_8	4688.83a	103.8 b	2.63 a	26.23b	21.08b	138.63a	191.80b	71.65a
	IAPAR9	3188.32b	114.87a	1.63 b	23.15c	31.17a	96.05 c	135.03c	71.04a
	H_{10}	3570.28b	98.83bc	1.93ab	27.96a	21.67b	132.69ab	184.03b	72.01a
	6527	2835.29b	89.32 c	1.76 b	24.83b	19.88c	108.97bc	226.98a	46.62b

Values followed by different letters are significantly different among cultivars at P<0.05.

Table 6. Change Rage of Yield and Agronomic Traits in Different Cultivars by Drought Treatment

Cultivar	Yield (kg hm^{-2})	Plant height (cm)	Panicle number per plant	Panicle length (cm)	1000-grain weight (g)	grain number per panicle	spikelet number per panicle	Seed setting rate (%)
H_8	2637.39	14.20	1.27	3.00	1.83	31.59	13.26	11.20
H_{10}	2409.65	14.07	0.80	1.16	1.33	33.36	26.49	7.96
6527	4462.59	21.37	0.58	2.53	3.75	144.24	19.59	59.38
IAPAR9	2432.80	18.27	0.60	2.12	3.67	30.71	21.54	11.16

Gene Expression Profiles

To further reveal the molecular mechanism of drought-tolerance in rice, the differences of expression profiles for antioxidant-related genes between 6527 and H8 were analyzed in **Table 7**. Eleven antioxidant-related genes were found existing difference between 6527 and H8 under drought stress. Among them, one gene with null expression in 6527 was up-regulated in H_8 after drought stress. The gene (LOC_Os05g11130.1) is located on the chromosome 5 with oxidoreductase activity and related to the precursor formation, whose expression profiles change was consistent with the increasing of activities of SOD and POD. It should be

the key gene in starting rice antioxidant system. Three genes were merely expressed in H8 under control and with null expression under drought stress and in 6527. LOC_Os07g02810.1 located on the chromosome 7 had oxidoreductase activity and related to the abiotic stimuli reaction. LOC_Os03g37290.1 located on the chromosome 3 bore peroxidase activity. LOC_Os12g42850.3 located on the chromosome 12 involved in the metabolic processes of hydrogen peroxide. Ding et al showed that induction of genes for oxidoreductases may improve drought tolerance of plants through the antioxidation system [25]. There were three genes exhibited no expression in H8, while One of them was up-regulated expression in 6527 after drought stress, and the other two were expressed in 6527 under the control, nor under drought stress. They were LOC_Os03g51920.1 located on the chromosome 3, with peptide transport function and related to the abiotic stimuli reaction or reactive oxygen metabolism, LOC_Os07g44430.1 located on the chromosome 7, with antioxidant activity and related to the peroxide metabolism, and LOC_Os07g48050.1 located on the chromosome 7 with antioxidant activity. Four genes with all expression in H8 and 6527 had different performance, which up-regulation in 6527 was down-regulated in H8 after drought stress. LOC_Os11g05380.1 was located on the chromosome 11 with the oxidoreductase activity, related to ferric ion binding and abiotic metabolic processes. LOC_Os07g05940.1 located on the chromosome 7 with the cation binding of carotenoid dioxygenase and related to stress response of abscisic acid metabolic process. LOC_Os05g50180.1 located on the chromosome 5 bore the ion binding and oxidoreductase activity. LOC_Os03g55800.1 located on the chromosome 3 with the oxidoreductase activity and ferric ion binding (Table 7). It is easy to find that some genes with up-regulation (down-regulation) expression were coherent with the increasing (decreasing) of SOD and POD, while others just the converse. These results indicated that the physiological activities of SOD and POD were regulated by many genes in the oxidation and peroxidation process. Expression of some genes were beneficial to drought resistance, while silence of other genes may be advantageous for drought resistance. Anyhow, these genes should be responsible for the high drought-resistance of H8. It will be important for understanding antioxidant mechanism by studying these genes deeply.

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CONCLUSION

Eleven antioxidant-related genes with significantly changes between H8 derived from Embryo-soaking with *Alternanthera philoxeroides* DNA and its recipient 6527 were found by gene expression profiling in the study. Together with the physiological analysis of antioxidant indexes for drought-resistant cultivars and sensitive ones, we concluded that drought-resistant cultivars maybe resist drought by inducing expression or silence of oxidant-related genes to improve the activity of SOD and POD for

Table 7. Differential Expression Profiling Of H8 and 6527 Under Drought Stress.

Gene identifier	Gene expression				Up regulation multiple		Down regulation multiple		Function	Process	Blast nr
	Control		Drought								
	6527	H_8	6527	H_8	6527	H_8	6527	H_8			
LOC_Os05g11130.1	0	0.57	0	1.42	—	2.49	—	—	Oxidoreductase	Generation of precursor	gi|48475241|gb|AAT44310.1|/0/ putative cytochrome P450 [*Oryza sativa* Japonica Group]
LOC_Os07g02810.1	0	1.14	0	0	—	—	—	—	Oxidoreductase activity	Response to abiotic stimulus	gi|115470345|ref| NP_001058771.1|/0/ Os07g0119400 [*Oryza sativa* Japonica Group]
LOC_Os03g37290.1	0	1.14	0	0	—	—	—	—	Oxidoreductase activity	—	gi|115453833|ref| NP_001050517.1|/0/ Os03g0570100 [*Oryza sativa* Japonica Group]
LOC_ Os12g42850.3	0	1.14	0	0	—	—	—	—	Peroxidase activity	Hydrogen peroxide metabolic process	gi|77556627|gb|ABA99423.1|/0/ amino acid permease family protein, putative, expressed [*Oryza sativa* Japonica Group]

LOC_0s03g51920.1	0.6	0	1.73	0	2.88	—	—	—	Peptidase activity	response to reactive oxygen species	gi|115455101|ref|NP_001051151.1|/0/0s03g0729000 [*Oryza sativa* Japonica Group]
LOC_0s07g44430.1	5.1	0	0	0	—	—	—	—	Antioxidant activity	Hydrogen peroxide metabolic process, response to stress	gi|115473617|ref|NP_001060407.1|/2.39095e-127/0s07g0638300 [*Oryza sativa* Japonica Group]
LOC_0s07g48050.1	47.1	0	0	0	—	—	—	—	Antioxidant activity	—	gi|8901180|gb|AAF65464.2|AF247700_1/2.83821e-152/peroxidase POC1 [*Oryza sativa* Indica Group]
LOC_0s11g05380.1	0.6	7.97	6.34	0.85	10.6	—	—	9.38	Oxidoreductase activity, iron ion binssding	Metabolic process	gi|115484209|ref|NP_001065766.1|/0/0s11g0151400 [*Oryza sativa* Japonica Group]
LOC_0s07g05940.1	1.2	9.96	6.34	0.85	5.28	—	—	11.7	Cation binding, carotenoid dioxygenase activity	Response to stimulus, abscisic acid metabolic process	gi|115470629|ref|NP_001058913.1|/0/0s07g0154100 [*Oryza sativa* Japonica Group]
LOC_0s05g50180.1	0.6	7.11	3.17	1.42	5.28	—	—	5.01	Metalion binding, oxidoreductase activity	—	gi|115465615|ref|NP_001056407.1|/9.69062e-79/0s05g0577500 [*Oryza sativa* Japonica Group]
LOC_0s03g55800.1	1.5	5.12	6.34	0.85	4.23	—	—	6.02	Oxidoreductase activity, iron ion binding, lyase activity	—	gi|115455571|ref|NP_001051386.1|/0/0s03g0767000 [*Oryza sativa* Japonica Group]

reducing the damage caused by peroxide, thereby making some important agronomic traits stable relatively to prevent decreasing yield under drought stress.

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