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Effect of Elevated UV-B Radiation on the Antioxidant System of Two Rice Landraces in Paddy Fields on Yuanyang Terrace

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Abstract

This study was performed to determine the effect of elevated UV-B radiation on physiological properties of rice plants under paddy field conditions. UV-B at different intensity levels (0, 2.5, 5.0 and 7.5 kJ/m^2) were applied to two local rice cultivars, Baijiaolaojing at 1600 m and Yuelianggu at 1800 m, growing in paddy fields on Yuanyang Terrace. Contents of H_2O_2 and malondialdehyde (MDA), superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) activity and total antioxidant capacity (T-AOC) in leaves were assayed. Results showed that after UV-B radiation treatments of Baijiaolaojing and Yuelianggu, plants at booting stage showed an increase of 52.3~79.3% and 86.0~195.4% in leaf H_2O_2 content, and 46.5~96.8% and 75.9~95.9% in leaf MDA content; At heading stage, plants had an increase of 35.2~66.0% and 77.2~121.3% in leaf H_2O_2 content, and 47.3~90.0% and 54.2~87.4% in leaf MDA content, respectively. UV-B radiation induced stronger enzymatic activity of leaf SOD, CAT and POD. The amount of SOD activity increased up to 86.0% or 73.5%; CAT activity up to 58.4% or 42.3% and POD up to 36.1% or 59.1% in Baijiaolaojing or Yuelianggu after the UV-B treatments. UV-B radiation led to higher leaf T-AOC, reaching the maximum of 45.3% and 32.2% in Baijiaolaojing and Yuelianggu, respectively. A highly significant correlation was found between leaf H_2O_2 and MDA contents and activity of SOD, CAT and POD and T-AOC in the two cultivars. These results indicated the accumulation of H_2O_2 and MDA would induce to the increased activity of antioxidant enzyme and the enzymatic activities would contribute to enhancing plants UV-B radiation tolerance.

Keywords: UV-B radiation; Yuanyang Terrace; Local rice cultivar; Oxidative injury; Antioxidant enzyme

Introduction

The stratospheric ozone layer in air protects the earth from the sun's harmful ultraviolet (UV) radiation. Reduced ozone layer results in more UV radiation (UV-B in the range of 280~320 nm wavelength) reaching the surface of the earth. The potential harmful impact of increased UV-B intensity on ecological and biological systems has attracted global attention (Caldwell *et al.*, 2007; Ballaré *et al*., 2011). Many studies have reported effects of strong UV-B radiation on the growth and physiological properties of crops, such as growth, plant morphology, photosynthesis, UV absorption substances, antioxidant systems, endogenous hormone regulation and yields (Hidema and Kumagai, 2006; Lizana *et al*., 2009; Surabhi *et al*., 2009; Kataria and Guruprasad, 2012).

Generation of reactive oxygen species (ROS) is one major process for UV-B radiation to cause damages to plants. ROS is harmful to plant cells affecting plant growth and development and physio-chemical reactions (Abd El-Baky *et al*., 2004; Triantaphylidès *et al*., 2008; Mahmood *et al*., 2012). UV-B radiation induced oxidative injury and the impact on the antioxidant system have been studied on modern hybrid rice cultivars including IR74 (Dai *et al*., 1997), Sasanishiki, Norin 1, Surjamkhi (Fedina *et al*., 2010) and Lemont and Dular (Wu *et al*., 2011). These experiments were mostly conducted under in-door conditions, and the hybrids were exposed to short-term UV-B irradiation treatments. How UV-B radiation affects local rice cultivars in the paddy field where plants are growing, and the resultant oxidative injury and antioxidant systems responses from local rice cultivars have not been thoroughly investigated. Local rice cultivars have a long cultivation history and they are well adapted to the local environment. These cultivars normally have conserved genetic traits and are highly tolerant of stress factors in the area. Understanding how the antioxidant systems were altered in landraces when plants are subjected to long-term UV-B exposure in paddy field is very important to accurately evaluate and understand the effect of UV-B radiation on those local cultivars.

Yuanyang Terrace is well known for growing rice on terraced fields in Yunnan province. It has a mountain monsoon climate. Mountain tops are almost completely covered with natural vegetation. Irrigation water for the terrace comes from the mountain top, it flows along the gradients. More flat smooth slopes become the terrace having more than 3,000 steps and spanning across

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13,000 hm^2. Yuanyang Terrace has an over 1500 year's history (Hou, 2007). Terrace and natural ecological environment form a typical agro-forestry ecosystem. The rice landraces provide the bases for sustainable and stable rice production. But not much is known about how elevated UV-B radiation will affect sustainability of those local cultivars in this area.

Unfavorable environmental conditions lead to generation of ROS, which cause damage to cell membrane, protein and DNA (Gill and Tuteja, 2010). MDA has been used as a reliable biomarker for measuring oxidative injury level as the content is correlated to the level of superoxidation of membrane lipid (Del Rio *et al*., 2005; Wahid et al., 2007; Liang *et al*., 2012). Our hypothesis is that strong UV-B radiation may induce oxidative stress thus affecting antioxidant activity in leaves. The objectives were to estimate the oxidative injury in leaf tissues, the resultant changes in the leaf antioxidant capacity and to determine differential physiological properties in two rice cultivars.

Material and Methods

Experimental Details and Treatments

Experimental materials: Two rice landraces Baijiaolaojing and Yuelianggu were used. These cultivars have been used in the area for over 300 year, and crops are grown in terraced paddy fields at 1400~1800 m elevations (Gao *et al*., 2010). The Baijiaolaojing paddy field is at 1400~1600 m elevation and Yuelianggu is grown on the terrace at 1600~1800 m above sea level.

Experimental design: The terraced fields in Qingkou, Xinjie district, Yuanyuang County, Yuanan Province was selected as the experimental site. In 2011, Baijiaolaojing was planted on the 1600 m elevation terrace, the paddy field was located within the latitude and longitude of 23°7′15.8″ N, 102°44′45.6″ E. Soil total N, total P, and total K content was 2.42, 0.75 and 6.07 g/kg, respectively. Alkaline-soluble N content was 67.5 mg/kg, available P and available K each was 20.7 and 150.1 mg/kg. Yuelianggu was grown in the terraced paddy field at 1800 m elevation within the latitude and longitude of 23°7′38.7″ N, 102°43′57.5″ E. Soil total N, total P and total K each was 1.76, 0.72 and 4.54 g/kg, respectively. The alkaline-soluble N was 69.4 mg/kg, available P and available K each was 22.9 and 175.9 mg/kg. Seeds were sown on March 18, 2011, and on May 8 seedlings were transplanted into the experimental plots. On every cultivation sites there were 12 plots each being 3.0 m×1.5 m in size. In each plot, 15 rows with 11 single seedlings in each row were planted. Except for the UV-B treatments experimental plants were managed following local farmer's practice.

Treatments of UV-B radiation: UV light was provided by 40W UV-B light tubes (280~320 nm wavelength; UV308, Beijing). Light tubes were hanging at 20, 40 and 60 cm distances atop of the tillers, and the 297 nm wavelength radiation intensity at the canopy top was recorded using an UV-Intensity meter (Photo-Electric Instrument Factory, Beijing Normal University). UV-B radiation was applied for 7 hr from 10:00am to17:00pm except on rainy days. UV-B intensity was 2.5, 5.0 and 7.5 kJ/m^2, which equals to 10, 20 and 30% ozone decline in Yunayang terrace area where the UV-B radiation background level was 10.0 kJ/m^2 in summer.

Plant Sampling

Leaf samples were collected at tillering stage (July 15th), booting stage (August 6th), and heading stage (August 29th), from each cultivar and each of the four treatments. For each treatment 2 clusters were selected in each plot. Plants were wrapped in Kraft paper to prevent leaf damages. Whole plants including the roots were dug from the soil, and placed in plastic bucket before being transported to laboratory. The 2nd and 3rd leaves from the basal node were detached from plants; they were washed in distilled water and blotted dry with filter paper. The mid-sections of leaf blades, after removal of leaf vein tissues, were used for the analysis of physiological properties.

Assay of Antioxidant System

Total soluble proteins contents: Fresh leaf tissues (1.0 g) were homogenized with the aid of quartz sand in ice-cold saline water to extract total soluble proteins. After adding ice-cold saline water to a final volume of 10 mL, the mixture was centrifuged at 4000 rpm, 4°C for 10 min. Upon diluting the supernatant (1 mL) 4 times, 50 µL of the sample was used for protein assay following the Bradford method (Bradford, 1976). The absorbance of reaction mixture was measured at 595 nm. Bovine serum albumin (BSA) was used as standard. The total proteins were expressed as mg protein g^{-1} fresh weight.

H_2O_2 contents: Fresh leaf tissues (1.0 g) were homogenized in 3 ml prechilled acetone on ice to extract H_2O_2. After adding acetone to a final volume of 10 mL, the mixture was centrifuged at 10000×g, 4°C for 10 min. Supernatant (l mL) was then mixed with 3 mL of an extraction buffer (CCl_4: $CHCl_3$=3:l, v/v) and 5 mL of distilled water. After a thorough mixing followed by centrifugation at 4000×g, 4°C for 1 min, the upper aqueous phase solution (200 µL) was collected. H_2O_2 assay used the titanium sulfate spectrophotometric method (Patterson *et al*., 1984) and the value was expressed as $mmol \cdot g^{-1}$ protein.

MDA contents: Fresh leaf tissues (1.0 g) were homogenized in 5 mL of a prechilled 0.05 $mol \cdot L^{-1}$ phosphate buffer supplemented with 1% polyvinyl pyrrolidone for the extraction of MDA. After bringing the volume to 25 mL, 10 mL of the mixture was taken to centrifugation at 4000×g, 4°C for 10 min. MDA in the supernatant (200 µL) was assayed using the thiobarbituric acid method (Janero, 1990) and the value was expressed as $nmol \cdot mg^{-1}$ protein.

Antioxidant enzyme assay: Fresh leaves (1.0 g) were homogenized with a mortar pestle using liquid nitrogen in 10 mL of an extraction buffer (20 mM Tris-HCl in 1% polyvinylpyrrolidone, pH 7.4). After filtration through two layers of gauze to remove any debris, the homogenate was centrifuged at 10,000 g for 20 min. The supernatant was used for both the enzyme activity. SOD was determined on the basis of its ability to inhibit the photochemical reduction of nitro blue tetrazolium (Beauchamp and Fridovich, 1971). The reaction solution contained 50 mM phosphate buffer (pH7.8), 13 mM methionine, 75 μM nitro blue tetrazolium, 2 μM riboflavin, 100 nM EDTA and dd H_2O. The riboflavin was added last. The reaction mixture was read at 560 nm. One unit of SOD activity (U) was designated as the amount of enzyme that caused 50% inhibition of initial reaction rate. CAT was assayed by Aebi method (Aebi, 1984). Based on H_2O_2 hydrolysis, the decreasing absorbance was measured at 240 nm (A240). Reduction of 0.1 at A240 in 1 min was designated as one unit of enzyme activity. POD activity was measured by guaiacol spectrophotometry (Lagrimini, 1991). When exposed to H_2O_2, POD catalyzed the guaiacol to tetraguaiacol, which had optical density (OD) of 470 nm. The reaction solution contained 100 mM phosphate buffer (pH 6.0), 33 mM guaiacol and 0.3 mM H_2O_2. Specific activity of POD was calculated from the increase in OD470 for 30 s. Total SOD, CAT and POD activity was expressed as $U \cdot mg^{-1}$ protein.

T-AOC assay: 200 μL enzyme solution was used for the reaction, and the absorbance at 520 nm wavelength was used to calculate T-AOC following the instruction in an assay kit from Nanjing Jiancheng Bioengineering Institute (Yang *et al*., 2010) and the value was expressed as $U \cdot mg^{-1}$ protein.

Statistical Analysis

All data presented here are the mean value ± standard deviation (SD) calculated from thereplicates. Statistically significant differences among treatments (0, 2.5, 5.0 and 7.5 kJ/m^2 UV-B radiation) were determined by using the least significant difference (LSD) test. The correlation between leaf oxidative products (H_2O_2 and MDA content), antioxidant enzyme (SOD, POD and CAT) activity and total antioxidant capacity (T-AOC) were analyzed using a data processing system (DPS) statistical software package.

Results

H_2O_2 and MDA Content

In Baijiaolaojing, leaf H_2O_2 and MDA content showed a significant increase ($P<0.05$) in the treatment of 2.5 kJ/m^2 UV-B at booting stage, and in the treatments of the 2.5 and 5.0 kJ/m^2 UV-B at heading stage. A highly significant increase in H_2O_2 and MDA contents ($P<0.01$) occurred in the 5.0 and 7.5 kJ/m^2 treatments at booting stage and 7.5 kJ/m^2 UV-B treatment at heading stage. In Baijiaolaojing, upon UV-B radiation leaves contained 52.3~79.3% and 35.2~66.0% higher of H_2O_2, 46.5~96.8% and 47.3~90.0% higher of MDA content compared to the controls at booting and heading stages, respectively.

In Yuelianggu, leaf H_2O_2 content increased significantly ($P<0.05$) at booting stage in the 2.5 kJ/m^2 UV-B treatment. The 5.0 and 7.5 kJ/m^2 UV-B treatments at booting and heading stages showed highly significant effect in enhancing leaf H_2O_2 content ($P<0.01$). In the UV-B treatments, leaf MDA content increased highly significantly ($P<0.01$) at booting and heading stages. In Yuelianggu, UV-B radiation induced an increase of 86.0%~195.4% and 77.2~121.3% in leaf H_2O_2 content, and 75.9~95.9% and 54.2~87.4% in MDA content at booting and heading stages, respectively (Table 1).

SOD, CAT and POD Activity

At booting stage SOD activity showed a highly significant increase ($P<0.01$) after treatments with 5.0 and 7.5 kJ/m^2 UV-B in the two cultivars. At heading stage, only the 7.5 kJ/m^2 UV-B treatment resulted in a significant higher SOD activity ($P<0.05$). In Baijiaolaojing at booting stage leaf CAT activity increased significantly ($P<0.05$) in the 5.0 and 7.5 kJ/m^2 UV-B radiation treatments. In Yuelianggu, leaf CAT activity had a significant increase ($P<0.05$) in the 5.0 kJ/m^2 UV-B treatment at booting stage, and in the 2.5 kJ/m^2 UV-B treatment at heading stage. The 7.5 kJ/m^2 treatment at booting stage, and the 5.0 and 7.5 kJ/m^2 UV-B treatments at heading stage induced extremely strong CAT activity ($p<0.01$). In Baijiaolaojing, leaf POD activity showed a highly significant increase ($P<0.01$) at booting stage in all of the three UV-B radiation intensity treatments. At heading stage, only the 7.5 kJ/m^2 UV-B intensity had a significant effect ($P<0.05$). In Yuelianggu, leaf POD increased very significantly at booting stage in all the three UV-B treatments at booting stage, and only in the 5.0 and 7.5 kJ/m^2 UV-B treatments at heading stage ($P<0.01$). In both Baijiaolaojing and Yuelianggu, UV-B treatment stimulated strong antioxidant enzyme activity, which was shown as an increase of up to 86.0% or 73.5% in SOD, 58.4% and 42.3% in CAT, 36.1% and 59.1% in POD, from the untreated controls in the two respective cultivars (Table 2).

T-AOC

A highly significant increase in T-AOC ($P<0.01$) was found in the 5.0 and 7.5 kJ/m^2 UV-B reatments at booting stage, and in the 2.5 and 7.5 kJ/m^2 UV-B treatments at heading stage. At booting stage, the 5.0 kJ/m^2 UV-B treatment showed a significant effect ($P<0.05$), and it was the same for the 7.5 kJ/m^2 UV-B treatment at booting and heading stages ($P<0.05$). UV-B radiation induced up to 45.3% and 32.2% of increase in leaf T-AOC in Baijiaolaojing and Yuelianggu, respectively (Table 3).

Table 1: Leaf contents of H_2O_2 and MDA in rice *Baijiaolaojing* and *Yuelianggu*

Cultivar	UV-B Radiation (kJ/m^2)	H_2O_2 content ($mmol \cdot g^{-1}$ protein)		MDA content ($nmol \cdot mg^{-1}$ protein)	
		Booting stage	Heading stage	Booting stage	Heading stage
Baijiaolaojing	0	12.40±2.71b	36.31±0.81c	0.95±0.11c	2.23±0.30b
	2.5	18.90±3.01a	49.10±4.63b	1.39±0.13b	3.28±0.19a
	5.0	22.24±2.84a	47.71±8.11b	1.46±0.24b	3.37±0.88a
	7.5	21.53±3.04a	60.27±6.53a	1.87±0.21a	4.23±0.39a
Yuelianggu	0	5.68±1.57c	16.14±2.72c	0.76±0.24b	2.04±0.40b
	2.5	10.58±1.27b	28.60±5.17b	1.35±0.07a	3.15±0.48a
	5.0	16.79±2.81a	35.72±3.64a	1.50±0.14a	3.29±0.24a
	7.5	14.19±2.64ab	34.41±3.09ab	1.43±0.04a	3.82±0.31a

Table 2: Leaf SOD, CAT and POD enzyme activity ($U \cdot mg^{-1}$ protein) in *Baijiaolaojing* and *Yuelianggu*

Cultivar	UV-B Radiation (kJ/m^2)	SOD		CAT		POD	
		Booting stage	Heading stage	Booting stage	Heading stage	Booting stage	Heading stage
Baijiaolaojing	0	156.1±1.9c	281.2±53.8b	4.45±1.12b	12.54±1.95a	80.0±1.7b	225.7±14.4b
	2.5	240.2±15.7b	317.0±37.4ab	5.27±0.96ab	15.29±0.38a	105.4±0.6a	204.7±2.3b
	5.0	258.6±23.1ab	309.3±40.5ab	7.06±1.88a	15.86±1.31a	106.1±6.6a	223.1±7.4b
	7.5	290.2±42.3a	396.6±61.5a	6.85±0.45a	16.13±3.42a	109.0±6.8a	259.2±27.4a
Yuelianggu	0	136.6±11.3b	246.6±63.3b	2.20±0.19c	12.25±0.58c	77.0±3.4c	198.1±2.2b
	2.5	146.5±26.0b	293.0±38.9ab	2.43±0.14bc	13.48±0.43b	93.3±2.2b	225.9±28.6b
	5.0	236.9±3.6a	352.2±31.2ab	2.92±0.49ab	14.29±0.58 ab	103.6±2.9a	315.1±9.5a
	7.5	232.7±3.6a	367.7±83.5a	3.09±0.15a	14.99±0.54a	100.9±1.5a	293.1±5.1a

Table 3: Leaf T-AOC in Baijiaolaojing and *Yuelianggu* ($U \cdot mg^{-1}$ protein)

UV-B Radiation (kJ/m^2)	*Baijiaolaojing*		*Yuelianggu*	
	Booting stage	Heading stage	Booting stage	Heading stage
0	17.0±0.2 c	55.7±2.6 b	18.2±0.5 b	50.6±1.7 b
2.5	17.7±1.1 c	71.0±2.3 a	20.3±1.6 ab	58.3±6.3 ab
5.0	21.5±1.6 b	65.3±7.6 a	21.6±3.0 ab	56.3±7.5 ab
7.5	24.7±1.1 a	71.7±2.6 a	23.4±1.2 a	66.9±13.9 a

Mean ± standard deviation. Values sharing same letters differ non-significantly (P>0.05), n=3

Table 4: Correlation analysis of antioxidant parameters in *Baijiaolaojing* and *Yuelianggu*

Cultivar	Antioxidant parameters	H_2O_2	MDA	SOD	CAT	POD
Baijiaolaojing	MDA	0.987**				
	SOD	0.889**	0.912**			
	CAT	0.976**	0.948**	0.820*		
	POD	0.951**	0.912**	0.816*	0.962**	
	T-AOC	0.939**	0.937**	0.791*	0.991**	0.962**
Yuelianggu	MDA	0.972**				
	SOD	0.966**	0.940**			
	CAT	0.873**	0.929**	0.865**		
	POD	0.947**	0.955**	0.923**	0.960**	
	T-AOC	0.884**	0.952**	0.879**	0.992**	0.951**

*and **means significant and highly significant correlation, respectively

Discussion

Plants subjected to UV-B radiation accumulate H_2O_2 in leaves, and intracellular MDA and other harmful products are also induced (Wang *et al*., 2010; Li *et al*., 2012). In this study, UV-B radiation led to an increase in the contents of H_2O_2 and MDA in leaves, which indicates that UV-B radiation caused great injury to those tissues. Previous reports showed that UV-B radiation results in fast regeneration of oxidative oxygen, over-production of H_2O_2, extensive oxidation of membrane lipids, and higher MDA content in leaves of rice plants (Dai *et al*., 1997; Fedina *et al*., 2010; Mohammed and Tarpley, 2010).

In this study on Baijiaolaojing and Yuelianggu, leaf contents of H_2O_2 and MDA had a positive correlation ($p<0.01$) with the activity of SOD, CAT and POD and T-AOC (Table 4). These results indicate that UV-B irradiation activated over-production of oxidative products, which in turn induced stronger antioxidant enzyme activity and higher total antioxidant capacity to remove those harmful products. Plants use antioxidant enzymes to directly or indirectly remove ROS in cells thus ensuring normal

metabolic reactions, which is major mechanism to ameliorate the toxic effect of ROS (Mittler, 2002; Limón-Pacheco and Gonsebatt, 2009; Gill and Tuteja, 2010).

SOD, CAT and POD are major antioxidant enzymes of endogenous antioxidant systems in plants. Those enzymes are mainly responsible for the removal of free radicals with a rather long lifetime such as $O^{2\cdot}$ and H_2O_2, to reduce the degree of injury due to lipid oxidation of cell membrane (Mittler, 2002). In Baijiaolaojing and Yuelianggu, leaf SOD, CAT and POD enzyme activities were enhanced upon UV-B radiation, which indicates that plants had built a larger capacity to remove ROS, which could be a tolerance mechanism to UV-B stress.

Dai reported that upon UV-B radiation treatment of rice 'IR74' for 14 d, leaf CAT and POD enzymatic activities were greatly increased; but the two enzymes declined after 28 d (Dai *et al*., 1997). The amount of leaf SOD, CAT and POD activity increased in Sasanishiki, Norin 1 and Surjamkhi, (Fedina *et al*., 2010), but only SOD activity was enhanced in Lemont and Dular by UV-B treatment (Wu *et al*., 2011). Those studies were mostly performed under indoor conditions and the physiological responses of antioxidant system to UV-B radiation cannot represent field conditions. There are always some discrepancies between results from in-door and field experiments, long- and short-term treatments, and studies at individual and at population levels. Therefore, results obtained from those in-door experiments cannot be simply used to interpret the responses of the antioxidant systems to UV-B radiation among rice landraces growing in field condition.

Under field conditions, physiological responses of plants to elevated UV-B radiation are affected by microclimate and other factors. Additionally, the two local rice cultivars have been cultivated over 300 years in the Yuanyang Terrace. They have stable genetic traits to produce reliable yield (Yan and Li, 2008). Those local cultivars have developed adaptations to local ecological conditions. A stable paddy field ecological system has been formed; therefore, these cultivars may express a response mechanism to UV-B radiation that is different from hybrid rice. Therefore, it is necessary to strengthen researches on those landraces on their responses to UV-B radiation under field conditions. Such information is essential for an accurate assessment of the impact of enhanced UV-B radiation on rice ecological systems.

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