Korean J Crop Sci 50(1) 39~44(2005)

Physiological and Biochemical Responses of Fifteen Rice Cultivars to UV-B Radiation

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ABSTRACT : This study was conducted to examine the physiological and biochemical responses against UV-B radiation in the seedling of 15 different rice cultivars, having the different physiological sensitivities. Out of 15 rice cultivars tested, moderate and susceptible groups showed significant decreases in biomass and RGR (relative growth rate). Contents of total chlorophyll were reduced remarkedly by irradiation of UV-B. In all rice cultivars tested, the content of chlorophyll a was strongly decreased, while the contents of chlorophyll b were slightly reduced without showing clear different among three groups and 15 cultivars. Carotenoid content was largely reduced by UV-B radiation, whereas polyamine content was moderately increased. The contents of MDA (malondialdehyde) that reflect the level of lipid peroxidation of cell membranes were clearly increased by UV-B stress, showing higher content in susceptible cultivars than moderate and torelant cultivars. The physiological important parameters highly related to visible injury were leaf color, chlorophyll, carotenoid, and lipid peroxidation, whereas biomass and polyamines were not closely correlated. Based on this results, it was concluded that changes of visible injury and the contents of chlorophyll and MDA could be adequately applied and utilized as physiological indicators to UV-B radiation.

Keywords**:** rice seedling, UV-B, RGR, chlorophyll, polyamine, lipid peroxidation

UV-B effects on the growth and the qualitative and quantitative yield of plants have been investigated in considerable researches (Caldwell *et al.*, 1995). An examination of more than 200 plant species reveals that roughly 20% are sensitive, 50% are moderately sensitive or tolerant and 30% are completely insensitive to UV-B radiation (Teramura, 1983). While the impact of enhanced UV-B radiation on plant physiology, morphology, and growth have been investigated extensively, little has been known about intraspecific differences in physiological responses against to the enhanced UV-B. Recently, intraspecific differences have been reported in flavonoid in soybean (Teramura & Murali, 1986; D'surney *et al.*, 1993) and *Arabidopsis thaliana* (Li *et al.*, 1993; Fiscus *et al.*, 1999), flavonoid and chlorophyll in rice (Teramura *et al*, 1991). Plant species and even genotypes within species could be different greatly in their responses to UV-B. Most researches for UV-B in the past two decades has been conducted in growth chambers and greenhouses where the unnatural spectral balance of radiation can lead to unrealistic conclusions, which may have substantially changed plant sensitivity to UV-B.

Rice is one of the world's most important staple food crops, and it would be required urgently to examine and determine how the growth and the yield of rice are affected by increasing the radiation of UV-B. Experiments in growth chambers have indicated significant variations among rice cultivars in terms of the effects of enhanced UV-B radiation on the production of aerial biomass On the other hand, few field studies have examined the effects of supplemental UV-B radiation on the growth and yield of rice.

In plant systems, the biologically ubiquitous polyamines, putrescine, spermidine and spermine are implicated in the control of growth and developmental processes (Bagni, 1989; Galston & Kaur-Sawhney, 1995; Kumar *et al.*, 1997) as well as the responses to a wide range of abiotic and biotic stresses, such as mineral nutrient deficiencies, osmotic stress, salinity, low external pH, temperature stress, hypoxia, atmospheric pollutants or infection by pathogens (Bouchereau *et al.*, 1999; Flores, 1991; Flores & Martin-Tanguy, 1991). The cationic nature of the polyamines at physiological pH, which enables them to interact with essential molecules such as nucleic acids, phospholipids and certain proteins, may account for many of their physiological functions in the cell. Among the different proposed mechanisms of polyamine action involved in plant response to adverse conditions, the maintenance of a cation-anion balance in the cell, a role as

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components of the intracellular buffering system and the protection of membrane integrity (Besford *et al.*, 1993; Flores, 1991; Reggiani *et al.*, 1989) are discussed. This study was conducted to determine and evaluate the intraspecific differences in physiological and biochemical responses of 15 rice cultivars to UV-B radiation in a growth chamber under the absence or presence of supplemental levels of UV-B radiation.

MATERIALS AND METHODS

Plant materials and growth condition

Fifteen rice cultivars showing the different physiological responses to UV-B radiation, which were divided into three different groups of tolerant, moderate, and susceptible, were grown in the environmental controlled growth chamber. Supplemental UV-B radiation was provided by UV-B fluorescent tubes (310 ± 10 nm) with filtering through 0.1 mm-thick cellulose diacetate film (Cadillac Plastic Co., Baltimore, MD, USA), which absorbs UV radiation below 290 nm. The irradiance in the UV-B region of the supplemental UV-B radiation at the plant canopy was 1 2 W m^{-2}. The UV-B irradiation was treated to plant canopy for 4 hrs during the photoperiod. To investigate physiological responses of rice plants, the fully expanded leaves were taken at 3 days after the treatment of UV-B radiation, frozen them immediately with liquid nitrogen and stored at -70°C.

Fresh weight and chlorophyll contents

Fresh weight of rice seedlings was measured at 3 days after the treatment of UV-B radiation, and RGR (relative growth rate) of rice seedlings was calculated. Chlorophyll and carotenoids were extracted by homogenizing 0 2 g fresh weight of shoot tissue in 10 ml 95% EtOH. After sealing, the extracted solution was boiled at 80°C and then immediately cooled on ice. Chlorophyll and carotenoid contents were analyzed spectrophotometrically with the supernatant at 470, 648, and 664 nm. Chlorophyll and carotenoid contents were determined and calculated with the following equation.

$$\text{Chl. a} = 13.36\times A664 - 5.19\times A648$$

$$\text{Chl. b} = 27.43\times A648 - 8.12\times A664$$

$$\text{Carotenoid} = (1{,}000\times A470 - 2.14\times \text{Chl.a} - 97.64\times \text{Chl.b}) / 209$$

Lipid peroxidation

Lipid peroxidation was measured as the amount of thiobarbituric acid reactive substances (TBARS) determined by the thiobarbituric acid (TBA) reaction as described by Heath & Packer (1968). A small segments (0.5 g) of control and treated leaf tissues were homogenized in 5 ml of 20% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 3,500 × g for 20 min. 1 ml of the aliquot of the supernatant was taken and 2.0 ml of 20% TCA containing 0.5% (w/v) TBA was added to the aliquot. The mixture was heated at 95°C for 30 min, and then quickly cooled on ice. The contents were centrifuged at 10,000 × g for 15 min, and the absorbance was measured at 532 nm. The value for non-specific absorption at 600 nm was subtracted. The concentration of TBARS was calculated using an extinction coefficient of 155 mM^{-1} cm^{-1}.

Polyamine analysis

Polyamines (putrescine, spermidine, spermine) were extracted, separated and detected by benzoylation and HPLC (Waters, USA) following slightly modification of the previous method (Redmond & Tseng, 1979). The samples were ground with mortar and pestle in liquid nitrogen, and extracted with 5% cold perchloric acid (PCA, 1:5, v/v). The homogenate was kept for 1 hr at 4 °C, and then centrifuged at 10,000 × g for 20 min. The supernatant was used for soluble polyamine determination. An aliquot of the supernatant (500 μl) was mixed with 1 ml of 2 N NaOH and 10 μl of benzoyl chloride. The mixture was incubated at room temperature for 20 min and the reaction was stopped by adding 2 ml of saturated NaCl. Benzoyl-polyamine was extracted into 2 ml of cold diethyl ether by vortexing for 10 - 20 sec. The diethyl ether phase was then evaporated to dryness, and the derivatized polyamines were redissolved in 64% MeOH(v/v). The benzoyl derivatives were separated on a 5 μm - 4.6 × 250 mm (C18) reverse phase column, using elution gradient from 40 to 60% acetonitrile in the mobile phase. Benzoyl-PAs were monitored by an UV detector (254 nm). The peaks were identified with reference to the retention times of PAs standard (Sigma, USA) prepared as described above.

RESULTS AND DISCUSSION

Fresh weights and growth rates of rice seedling in three different groups of 15 cultivars, tolerant, moderate, and susceptible, were shown on Table 1. The irradiation of UV-B to the rice seedlings for a short time did remarkably influence in the reduction of fresh weight. The reduction rate of fresh weight of three different groups, tolerant, moderate, and susceptible, were 21.2%, 46.9% and 33.6% respectively. Among the three groups of fifteen cultivars which were selected and grouped based on the damage level on rice seedling leaves by the irradiation of UV-B, the effect of UV-B on fresh weight

Table 1. Changes of fresh weight (mg seedling^{-1}) and RGR (mg g^{-1} day^{-1}) with treatment of UV-B radiation in rice seedlings of fifteen cultivars having different UV-B sensitivity.

UV-B sensitivity	Cultivars		B.T.[1]		A.T.[2]		% decrease	T-test
			-UV-B	RGR	+UV-B	RGR		
Tolerant	Woonbongbyeo	306	422	0.11	380	0.07	36.0	ns
	Jinbongbyeo	297	369	0.07	356	0.06	18.1	ns
	Woonjangbyeo	247	378	0.14	358	0.12	15.1	ns
	Odaebyeo	230	381	0.17	366	0.15	10.3	ns
	Daeyabyeo	261	407	0.15	368	0.11	26.7	ns
	Mean	268 ± 16	391 ± 11	0.13	366 ± 5	0.11	21.2	
Moderate	Woondubyeo	376	519	0.11	420	0.04	69.2	**
	Seojinbyeo	346	448	0.09	434	0.08	13.1	ns
	Sobibyeo	381	547	0.12	426	0.04	73.2	ns
	Donganbyeo	430	547	0.08	469	0.03	66.7	ns
	Gancheokbyeo	361	509	0.11	491	0.10	12.2	ns
	Mean	379 ± 16	514 ± 20	0.10	448 ± 15	0.06	46.9	
Susceptible	Hwajoongbyeo	362	509	0.11	464	0.08	30.2	ns
	Yangjobyeo	347	583	0.17	518	0.13	27.5	*
	Daecheongbyeo	330	513	0.15	427	0.09	47.3	ns
	Chucheongbyeo	320	472	0.13	435	0.10	24.2	ns
	Anseongbyeo	334	491	0.13	430	0.08	38.9	**
	Mean	338 ± 8	514 ± 21	0.14	455 ± 19	0.10	33.6	

[1]B.T. : before treatment; [2]A.T. : after treatment

have appeared little different, although it was reduced the highest in UV-B moderate rice seedlings and reduced higher in UV-B susceptible than those in UV-B tolerant rice seedlings. The relative growth rates (RGR) of rice seedlings with the treatment of UV-B radiation were ranged from 0.03 to 0.15 (mg g^{-1} day^{-1}), while their rates without the treatment of UV-B radiation from 0.09 to 0.17 (mg g^{-1} day^{-1}). Considering the examined results of fresh weight, Odaebyeo, Jinbongbyeo, Woonjangbyeo, Seojinbyeo, and Gancheokbyeo were resistant cultivars to UV-B radiation. The contents of chlorophyll a and b and total chlorophyll in the leaves of rice seedling treated with the irradiation of UV-B were shown on Table 2. The contents of chlorophyll a were remarkedly reduced with the treatment of UV-B radiation. The reduction rates of tolerate, moderate, susceptible cultivars were about 29.1%, 37.2%, and 53.7%, respectively. The contents of chlorophyll b were not clearly different among three groups of cultivars. With these research results, it would be assumed that the irradiation of UV-B to the leaves of rice seedling could be remarkedly affected to the degradation of chlorophyll a rather than chlorophyll b. The results were similar in tendency to the previous researches that UV-B irradiation have decreased chlorophyll contents: in rice (Teramura *et al.*, 1991), and in soybean (Mirecki & Teramura, 1984), in wheat (Li *et al.*, 2000b). The correlation between percent change of chlorophyll a and percent change of chlorophyll b ($r = 0.125$, $p < 0.05$) was not significantly different (data not shown). Percent change of chlorophyll (a + b) was positively correlated with percent change of contents of chlorophyll a ($r = 0.947$, $p < 0.01$), while it was not correlated with chlorophyll b ($r = 0.403$, $p < 0.05$). Considering the examined results of chlorophyll a and b, Odaebyeo, Daeyabyeo, and Woonjangbyeo were resistant cultivars to UV-B radiation.

The determined data of carotenoid, polyamine, and MDA were presented in Table 3. Out of many kinds of antioxidants, changes of carotenoid and polyamine contents in rice seedling were measured before and after the treatment of UV-B radiation. MDA contents reflecting the level of lipid peroxidation were measured in leaf tissues. It was appeared that the irradiation of UV-B changed remarkably the contents of carotenoid or polyamines. The content of carotenoid was clearly decreased by irradiation of UV-B, whereas the content of polyamine was generally increased largely except for a few cultivars. The carotenoid contents of three groups, tolerant, moderate, and susceptible, were averagely reduced by the irradiation of UV-B to 31.2%, 55.3%, and 65.7%, respectively. It would be assumed that the damages of rice

Table 2. Changes of chlorophyll content with treatment of UV-B radiation in rice seedlings of fifteen cultivars having different UV-B sensitivity

UV-B sensitivity	Cultivars	Chlorophyll a				Chlorophyll b				Total chlorophyll			
		-UV-B	+UV-B	Δ%	T-test	-UV-B	+UV-B	Δ%	T-test	-UV-B	+UV-B	Δ%	T-test
		μg g^{-1}fw											
Tolerant	Woonbongbyeo	1,903	956	-49.8	**	662	625	-5.6	ns	2,565	1,581	-38.4	**
	Jinbongbyeo	1,678	988	-41.1	**	619	581	-6.1	ns	2,297	1,569	-31.7	**
	Woonjangbyeo	1,620	1,570	-3.1	ns	579	470	-18.8	*	2,199	2,040	-7.2	*
	Odaebyeo	1,559	1,153	-26.0	**	553	602	8.9	ns	2,112	1,755	-16.9	**
	Daeyabyeo	1,770	1,318	-25.6	**	571	607	6.3	ns	2,341	1,925	-17.8	**
	Mean	1,706 ± 67	1,197 ± 127	-29.1 ± 8.9		597 ± 22	577 ± 31	-3.1 ± 5.6		2,303 ± 86	1774 ± 104	-22.4 ± 6.2	
Moderate	Woondubyeo	1,555	932	-40.1	**	500	607	21.4	ns	2,055	1,539	-25.1	**
	Seojinbyeo	1,528	1,004	-34.3	**	518	600	15.8	**	2,046	1,603	-21.6	**
	Sobibyeo	1,591	941	-40.9	**	487	610	25.1	*	2,079	1,550	-25.4	ns
	Donganbyeo	1,459	896	-38.6	**	448	609	35.9	*	1,906	1,504	-21.1	**
	Gancheokbyeo	1,479	1,006	-32.0	**	469	546	16.3	*	1,948	1,552	-20.4	**
	Mean	1,522 ± 27	956 ± 24	-37.2 ± 1.9		484 ± 14	594 ± 14	22.9 ± 4.1		2,007 ± 38	1550 ± 18	-22.7 ± 1.2	
Susceptible	Hwajoongbyeo	2,107	886	-57.9	**	625	586	-6.2	ns	2,731	1,472	-46.1	**
	Yangjobyeo	1,467	668	-54.5	**	479	500	4.5	ns	1,945	1,168	-39.9	**
	Daecheongbyeo	1,743	790	-54.7	**	520	503	-3.3	ns	2,264	1,293	-42.9	**
	Chucheongbyeo	1,559	929	-40.4	**	469	495	5.6	ns	2,028	1,424	-29.8	**
	Anseongbyeo	2,252	881	-60.9	**	671	533	-20.6	*	2,923	1,413	-51.6	**
	Mean	1,825 ± 171	831 ± 52	-53.7 ± 3.9		553 ± 45	524 ± 19	-4.0 ± 5.3		2,378 ± 216	1354 ± 62	-42.1 ± 4.1	

Table 3. Carotenoid, polyamine contents and lipid peroxidation with treatment of UV-B radiation in rice seedlings of fifteen cultivars having different UV-B sensitivity.

UV-B sensitivity	Cultivars	Carotenoid (μg g^{-1}fw)				Polyamine (nmol g^{-1}fw)			MDA (nmol g^{-1}fw)			
		-UV-B	+UV-B	Δ%	T-test	-UV-B	+UV-B	Δ%	-UV-B	+UV-B	Δ%	T-test
Tolerant	Woonbongbyeo	682	280	-59.0	**	73	279	284.0	871	890	2.2	ns
	Jinbongbyeo	414	260	-37.3	**	112	99	-10.9	1,103	1,322	19.9	*
	Woonjangbyeo	414	409	-1.3	ns	91	142	56.7	813	1,264	55.6	**
	Odaebyeo	402	288	-28.3	**	66	136	106.2	1,135	1,174	3.4	ns
	Daeyabyeo	488	323	-33.8	**	111	124	11.1	1,322	2,083	57.6	**
	Mean	480 ± 59	312 ± 29	-31.9 ± 10.3		90 ± 11	156 ± 35	89.4 ± 58.9	1049 ± 104	1347 ± 222	27.7 ± 13.6	
Moderate	Woondubyeo	434	149	-65.7	**	99	141	12.0	980	1,890	92.8	**
	Seojinbyeo	388	201	-48.2	**	121	103	-14.7	987	1,567	58.8	**
	Sobibyeo	433	181	-58.2	**	123	166	42.9	1,142	1,541	35.0	**
	Donganbyeo	331	136	-59.1	**	129	144	34.4	1,077	2,128	97.6	**
	Gancheokbyeo	395	217	-45.0	**	97	121	25.1	697	2,735	292.6	**
	Mean	396 ± 21	177 ± 17	-55.3 ± 4.2		114 ± 7	135 ± 12	19.9 ± 11.3	976 ± 85	1972 ± 245	115.4 ± 51.2	
Susceptible	Hwajoongbyeo	567	123	-78.3	**	120	129	7.5	967	2,431	151.3	**
	Yangjobyeo	391	98	-75.1	**	99	140	41.2	929	3,966	327.1	**
	Daecheongbyeo	483	118	-75.5	**	149	100	-33.2	742	2,393	222.6	**
	Chucheongbyeo	418	278	-33.4	*	125	135	8.0	806	3,250	303.2	**
	Anseongbyeo	645	220	-66.0	**	87	127	46.1	813	3,773	364.3	**
	Mean	501 ± 53	167 ± 39	-65.7 ± 9.3		116 ± 12	126 ± 8	13.9 ± 16.0	851 ± 47	3163 ± 367	373.7 ± 42.9	

Table 4. Intraspecific differences of sensitivity to UV-B radiation based on changes of physiological and biochemical characteristics in seedlings of 15 rice cultivars

Rank	Visible injury	Fresh weight	SPAD 502 value	Chlorophyll a	Total chlorophyll	Carotenoid	Polyamines	MDA
1	Woonjangbyeo	Odae	Jinbong	Woonjang	Woonjang	Woonjang	Woonbong	Woonbong
2	Woonbongbyeo	Gancheok	Gancheok	Daeya	Odae	Odae	Odae	Odae
3	Daeyabyeo	Seojin	Woonbong	Odae	Daeya	Chucheong	Woonjang	Jinbong
4	Odabyeo	Woonjang	Woonjang	Gancheok	Gancheok	Daeya	Anseong	Sobi
5	Jinbongbyeo	Jinbong	Odae	Seojin	Dongan	Jinbong	Sobi	Woonjang
6	Sobibyeo	Chucheong	Daeya	Dongan	Seojin	Gancheok	Yangjo	Daeya
7	Donganbyeo	Daeya	Woondu	Woondu	Woondu	Seojin	Dongan	Seojin
8	Woondubyeo	Yangjo	Sobi	Chucheong	Sobi	Sobi	Gancheok	Woondu
9	Gancheokbyeo	Hwajoong	Hwajoong	Sobi	Chucheong	Woonbong	Woondu	Dongan
10	Seojinbyeo	Woonbong	Daecheong	Jinbong	Jinbong	Dongan	Daeya	Hwajoong
11	Anseongbyeo	Anseong	Yangjo	Woonbong	Woonbong	Woondu	Chucheong	Daecheong
12	Chucheongbyeo	Daecheong	Seojin	Yangjo	Yangjo	Anseong	Hwajoong	Gancheok
13	Yangjobyeo	Dongan	Dongan	Daecheong	Daecheong	Yangjo	Jinbong	Chucheong
14	Daecheongbyeo	Woondu	Anseong	Hwajoong	Hwajoong	Daecheong	Seojin	Yangjo
15	Hwajoongbyeo	Sobi	Chucheong	Anseong	Anseong	Hwajoong	Daecheong	Anseong

seedling leaves by UV-B radiation have closely related to the reduction of carotenoid content. Unlike the content of carotenoid, the content of polyamines of three groups, tolerant, moderate, and susceptible, were increased by 89.4%, 19.9%, and 13.9%, respectively. The lipid peroxidation was distinctly induced by UV-B stress. The MDA contents in three rice cultivar groups, tolerant, moderate, and susceptible, were increased by 27.7%, 115.4%, and 373.7%, respectively. Particularly, the content was increased remarkedly in the susceptible rice cultivars. Based on three physiological and biochemical parameters, Woonjangbyeo, Woonbongbyeo and Odaebyeo could be classified as resistant cultivars to UV-B radiation. The biosynthesis of polyamines (putrescine, spermidine, and spermine) were immediately stimulated and increased by UV-B irradiation. UV-B affects to polyamine contents, especially putrescine, however, spermidine and spermine contents were slightly decreased and moderately increased, respectively (data not shown). Therefore, it was subjected that UV-B stress would induce putrescine biosynthesis rather than spermidine or spermine biosynthesis. This result was similar to the previous result in wheat (Li *et al.*, 2000b). Correlation analysis showed that polyamines contents were not correlated with change of leaf color, fresh weight, chlorophyll a + b, carotenoid contents, and MDA contents, respectively ($p < 0.05$).

Based on this research results, the ranking of 15 rice cultivars evaluated by the physiological indicators to UV-B radiation was slightly different from the three different groups (tolerant, moderate, and susceptible) of 15 rice cultivars evaluated and grouped by the degree of leaf damages to UV-B radiation in Table 4. However, UV-B tolerant rice cultivars showed higher tolerant level in physiological indicator parameters. The physiological characteristics related positively with visible injury were the leaf color, chlorophyll contents, carotenoid contents and MDA contents, whereas fresh weight and polyamine contents were not highly related. As evaluated collectively the UV-B sensitivity of rice cultivars on the basis of the physiological characteristics, we proved Woonjangbyeo, Woonbongbyeo and Odaebyeo to be better rice cultivars enduring environmental stresses, such as UV-B radiation. The main factors determining UV-B sensitivity would be chlorophyll a, total chlorophyll, carotenoid content, MDA level, and visible injury, whereas the leaf color and the content of polyamine would not be closely related. Consequently, this study demonstrated that visible injury, chlorophyll, carotenoid, MDA contents to UV-B radiation could be applied adequately as the physiological and biochemical indicators. In the previous study, rice cultivars originating from regions with high ambient UV-B are not necessarily more tolerant to enhanced UV-B radiation (Barnes *et al.*, 1993; Dai *et al.*, 1994). The UV-B tolerant cultivars identified in this study might be used as materials for breeding programs; however, the genetic basis for these differences must be further examined. In a soybean study, the effect of UV-B on total plant biomass may be dependent on the concentration of UV-B absorbing compounds (D'surney *et al.*, 1993). In spinach and bean, however, there was no relationship, suggesting that intraspecific differences in UV-B sensitivity may arise through a complexity of specific responses rather than a generalized responses (Teramura & Murali, 1986). Much is still unknown about the mechanism of UV-B tolerance in rice. To elucidate these mechanisms clearly, it will be necessary to study physiological and biochemical responses and genetic control to UV-B radiation.

ACKNOWLEDGEMENT

This study was conducted by sponsoring of research assistant fund of Chungbuk National University

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