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Full Length Article

Enhanced UV-B Radiation Inhibit Photosynthesis, Growth and Yield of two Rice Landraces at Yuanyang Terraces *In Situ*

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Abstract

Two rice landraces (*Oryza sativa* L.), Baijiaolaojing and Yuelianggu were cultivated in the situ terraced field with ambient and supplemental levels of ultraviolet-B (UV-B, 280–315 nm) radiation for three consecutive years at Yuanyang County Southwest China. The UV-B radiation at three levels of 2.5, 5.0 and 7.5 kJ m^{-2} was supplemented. The effects of enhanced UV-B radiation on the photosynthesis, growth and grain yield of the two rice landraces were considered. Results showed that UV-B radiation resulted in a notable decrease in the rice leaves' photosynthesis at tillering, jointing and heading stages decreased the tillers number and plant biomass altered the aboveground biomass proportion with a lower proportion of stalks and panicles and a higher proportion of leaves. Rice yield decreases were observed as a result of significant reductions in effective panicle numbers, seed setting rate and 1000 grain weight under the treatment of enhanced UV-B radiation. The photosynthesis suppression was the fundamental reason for the decreases in the above-ground biomass and yield of the two rice landraces at Yuanyang Terraces *in situ*.

Keywords: Ozone depletion; Landrace; Photosynthetic physiology; Biomass accumulation; Field condition

Introduction

Due to a depletion of stratospheric ozone, the radiation of ultraviolet-B (UV-B, 280–315 nm) reaching the earth surface have enhanced. The enhanced UV-B radiation usually injured the crops and the agricultural ecosystem due to its deleterious effects (Kakani *et al*., 2003; Ballare *et al.*, 2011; Wargent and Jordan, 2013). Rice (*Oryza sativa* L.) is a worldwide and important grain crop and UV-B radiation had a marked effect on rice growth, physiology and yield had received extensive attentions (Dai *et al*., 1994; Cinderby *et al*., 2009; Fedina *et al*., 2010; Wang *et al*., 2015; Chen *et al*., 2016).

Generally, the enhanced UV-B radiation led to a harmful consequence on the photosynthetic physiology of rice. The UV-B radiation decreased the contents of photosynthetic pigments (chlorophyll a, b and carotenes) in rice leaves (Wu *et al*., 2007; Yin *et al*., 2009; Lidon and Ramalho, 2011). Thus, enhanced UV-B radiation suppressed the photosynthetic performance of rice leaves (Yu *et al*., 2013; Wang *et al*., 2015). For example, an enhanced UV-B radiation treating for 1 and 7 days reduced the rice photosynthetic rate (Pn) by 20% and 14%, respectively (Lidon and Ramalho, 2011). Eight rice cultivars showed declines in photosynthetic rate by 16% to 60% under the enhanced UV-B radiation (Mohammed and Tarpley, 2011).

As a consequence of the depressing effects on photosynthetic physiology, the UV-B radiation commonly inhibited rice growth and declined the rice yield production. The growth of rice plant such as the height, tiller numbers, total leaves area and plant biomass were declined under high UV-B radiation treatment (Barnes *et al*., 1993; Hidema *et al*., 2005; Xu and Qiu, 2007; Sun *et al*., 2016). Tang *et al*. (2002) found that UV-B radiation decreased the rice shoot and root biomass by 45.3–59.8% and 54.9–59.0%, respectively. Rice yield components such as effective panicle per plant, total grain number per panicle, filled grain rate and 1000 grain weight also were declined by enhanced UV-B radiation (Xu and Qiu, 2007; Mohammed and Tarpley, 2010). Therefore, the rice grain yield decreased under enhanced UV-B radiation. Nine rice cultivars in southern USA declined by 31–79% (Mohammed and Tarpley, 2009). However, aforementioned results mostly obtained from breeding rice cultivars. The response from rice landraces to enhanced UV-B radiation received little attention.

Compared with the breeding rice, landraces have more complex genetic background, richer genetic diversity and heterogeneity (Pusadee *et al*., 2009). They are conserved and cultured from generation to generation by local farmers in a long time. During this process, they evolved with a synergistic interaction between the rice landrace and the local environment. Hence, the rice landrace gradually had a strong adaptability to the local environment (Pusadee *et al*., 2009). However, most of the studies focused on the

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adaptability of the rice landrace to environmental stresses such as diseases and pests, drought and cold (Shi *et al.*, 2010; Lenka *et al.*, 2011; Liu *et al.*, 2015). Relatively little was known about the rice landrace response to the enhanced UV-B radiation stress.

Yunnan Province is the genetic origin center of cultivated rice in Asian, which is located in the southwest of China (Zeng *et al.*, 2007). The Yuanyang Terraces in Yunnan Province, China was inscribed as a "World Natural and Cultural Heritage" by UNESCO in 2013 for its unique and harmonious rice farming tradition and culture (Hua and Zhou, 2015). The rice landraces were the key factor for the rice culture and production. At Yuanyang terraces, the rice landraces were high adaptive to the local environment and stresses like rice diseases, pests and low temperature (Cao *et al*., 2013). Thus, the rice landraces in Yuanyang terraces contributed to keep a stable yield production and were considered as sustainable and steady rice varieties (Jiao *et al*., 2012; Fullen, 2015). The scientists had paid attention to the genetic diversity (Tu *et al*., 2007), agronomic traits (He *et al*., 2011) and rice resource management (Jiao *et al*., 2012) of the rice landraces in Yuanyang terraces. Furthermore, due to the high altitude and high UV-B radiation at Yuanyang Terraces the rice landrace's adaptability to UV-B radiation began to attract researcher's attention (He *et al*., 2014; Li *et al*., 2014).

In this study, two rice landraces (Baijiaolaojing and Yuelianggu) were popularly planted for more than 300 years in Yuanyang terraces and selected for studying. Supplement UV-B radiation was provided by an artificial system at different levels in situ in the rice paddy fields. The growth and yield responses of the two rice landraces were investigated for three seasons from 2011 to 2013 under field condition. We hypothesized that responses of the two rice landraces to UV-B radiation could be reflected in the change of growth and yield components and there were the principal factors responsible for the changes of aboveground biomass and yield production. The aims of this study include: (1) the responses of rice leaves' photosynthesis, growth, aboveground biomass and grain yield to enhanced UV-B radiation; (2) the principal factors accounting for the changes in rice growth and yield.

Materials and Methods

Rice Field Conditions

Yuanyang Terraces is located at 102°27'–103°13' E and 22°49'–23°19' N in south of Yunnan Province, Southwest China. Its history is more than 1300 years. Yuanyang Terraces was built on gentle slopes of the mountains with natural plantations at the top. The scope of Yuanyang Terraces is beyond 3,000 steps and about 13,000 hm^2.

Two rice landraces, Baijiaolaojing and Yuelianggu, have been cultivating at Yuanyang Terraces for more than 300 years studied in this study. The two rice landraces can grow at Yuanyang Terraces at an altitude from 1400 to 1800 m. But the Baijiaolaojing is generally cultivated at an altitude of 1400~1600 m and the Yuelianggu at 1600~1800 m.

Two experimental fields were located at 1600 and 1800 m in Qingkou village, Xinjie town, Yuanyuang County and Yuanan Province. The latitude and longitude of the paddy field was 23°7′15.8″ N and 102°44′45.6″ E at 1600 m, 23°7′38.7″ N and 102°43′57.5″ E at 1800 m, respectively. The soil basic chemical properties were shown in Table 1.

Experimental Design

Rice seed of the two landraces were sown on the middle of March, 2011, 2012 and 2013. Rice seedlings were transplanted into paddy fields in the early May from 2011 to 2013. There were 12 plots (3.0 m×1.5 m) on each of the two experimental sites. Rice seedlings were planted in 15 rows with 11 plants in each row and one seedling per hill in each plot. The protection plot on each side of the experimental plot had 6 rows with 4 plants in each row. During the rice growth season, fertilizers and pesticides were not used according to the local rice management.

A system provided UV-B radiation by installing a 40 W UV-B tube (UV308 with light spectrum 280–315 nm, UV308, Beijing) above all the ninth plant in the row from the middle 11 rows in each plot. The UV-B tube covered a cellulose diacetate film which was to filter out radiations below 280 nm but to permit UV-B radiation to reach the plants. While the rice grew, a height adjustment on the tube was done to supplement UV-B radiation to a required intensity level at 297 nm wavelength measured at the canopy top using a ultraviolet radiation meter. The control plants were grown under natural condition and the treated plants perceived UV-B radiation at 2.5, 5.0 and 7.5 kJ m^{-2} amounting to depletion levels of stratospheric ozone at 10%, 20% and 30% in the Yuanyang Terraces, respectively, where the baseline value was 10.0 $kJ \cdot m^{-2}$ on solstice day. The rice plants were provided with UV-B radiation from 10:00 am to 17:00 pm for 7 h daily except on rainy days till to the harvest.

Measurements of Plant Growth and Yield

During the rice growth, ten rice plants were randomly selected to measure their height from each plot. And the number of tillers and panicles in an area of 1 m^2 was recorded for each plot (Kumagai *et al*., 2001).

After the harvest, 10 plants were selected in each plot to record the length of panicles and the number of spikelets. After a removal of unfilled grains the number of fully filled grains was counted. Seed setting rate was the filled grains number per panicle divided by the total spikelets number per panicle. For each plot, 20 filled grains were randomly selected to measure the seed length. The plant parts (stalks, leaves and panicles) were collected from a 1 m^2 area in the paddy field dried at 75ºC for 4 d and determined their dry biomass by an electronic balance. The 1000 seeds with three replicates were taken from each plot to measure the 1000 grain weight (Tang *et al*., 2002).

Measurements of Photosynthesis

The leaves' photosynthesis was recorded at tillering, jointing and heading stages by using a Portable Photosynthesis System (Li-6400) following a method of San-oh *et al.* (2006). The photosynthesis measurement was performed from 9:00 to 10:00 am. on a sunny and windless day. An upper fully-expanded mature leaf was selected and the light at an intensity of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was provided. The photosynthetic parameters were recorded including photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs) and intercellular CO_2 concentration (Ci). For each measurement, three data were collected for the second leaf from the top that was randomly sampled from three plants in each plot.

Calculation of Response Index

The Response Index (RI) for UV-B radiation was measured according to the formula of Li *et al.* (2000) as:

$$RI=\frac{PHt-PHc}{PHc}+\frac{TNt-TNc}{TNc}+\frac{TPt-TPc}{TPc}+\frac{BMt-BMc}{BMc}+\frac{PRt-PRc}{PRc}$$

Where PH- plant height at full mature stage; TN- number of total tiller per plant at tillering stage; TP- the number of effective panicles at heading stage; BM- total biomass of above-ground parts; PR-grain yield of rice.

Statistical Analysis

The differences between the treatments of ambient and supplemental UV-B radiation were tested by the least significant difference (LSD) method. The correlation analysis between photosynthetic parameter and aboveground biomass, yield components and grain yield were performed using the SPSS 22.0 software.

Results

Effect on Photosynthesis

UV-B radiation remarkably reduced the photosynthesis of the two rice landraces, resulted in a reduction on photosynthetic rate, transpiration rate and stomatal conductance of the two rice landraces at tillering, jointing and heading stages. Moreover, the adverse effect was exaggerated with the increase on UV-B radiation intensity reached a notable difference level at a high UV-B radiation of 5.0 and 7.5 kJ m^2 (Fig. 1).

Table 1: The soil chemical properties

Chemical property	Altitude 1600 m	Altitude 1800 m
pH	5.32	5.25
Organic matter (g kg^{-1})	26.8	28.4
Total nitrogen (g kg^{-1})	2.42	1.76
Total phosphorus (g kg^{-1})	0.75	0.72
Total potassium (g kg^{-1})	6.07	4.54
Alkaline-soluble nitrogen (mg kg^{-1})	67.5	69.4
Available phosphorus (mg kg^{-1})	20.7	22.9
Available potassium (mg kg^{-1})	150.1	175.9

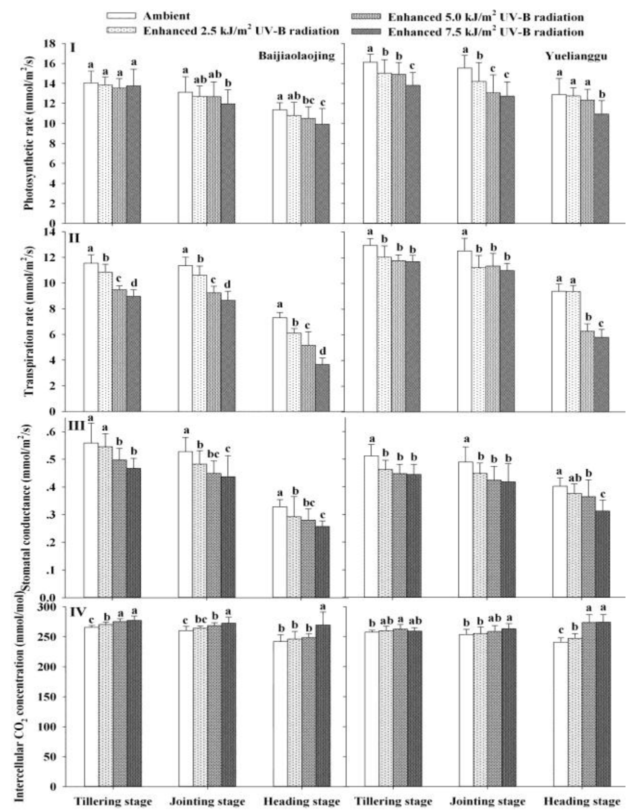

Fig. 1: Effects of enhanced UV-B radiation on photosynthetic physiology of rice leaves (same letters mean no significant difference, different letters mean significant difference, n=30)

Effect on Rice Biomass

From the seedling to full mature stage, UV-B radiation did not cause a discernible change in the two rice landraces' height based on the data of three consecutive seasons from year 2011 to 2013.

But the UV-B radiation caused the two rice landraces a less tillers number (Fig. 2). Under UV-B radiation at 7.5 kJ m^2 the rice tillers number declined significantly in both year 2011 and 2012 by 21.4-22.8%. In year 2013, the UV-B radiation also declined the rice tillers number but did not reach a significant level Due to the decline on the tillers number the above-ground biomass of the two rice landraces

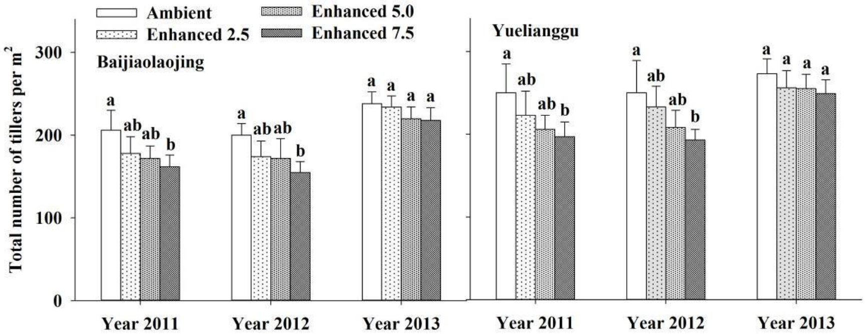

Fig. 2: Effects of enhanced UV-B radiation on the tillers number of rice

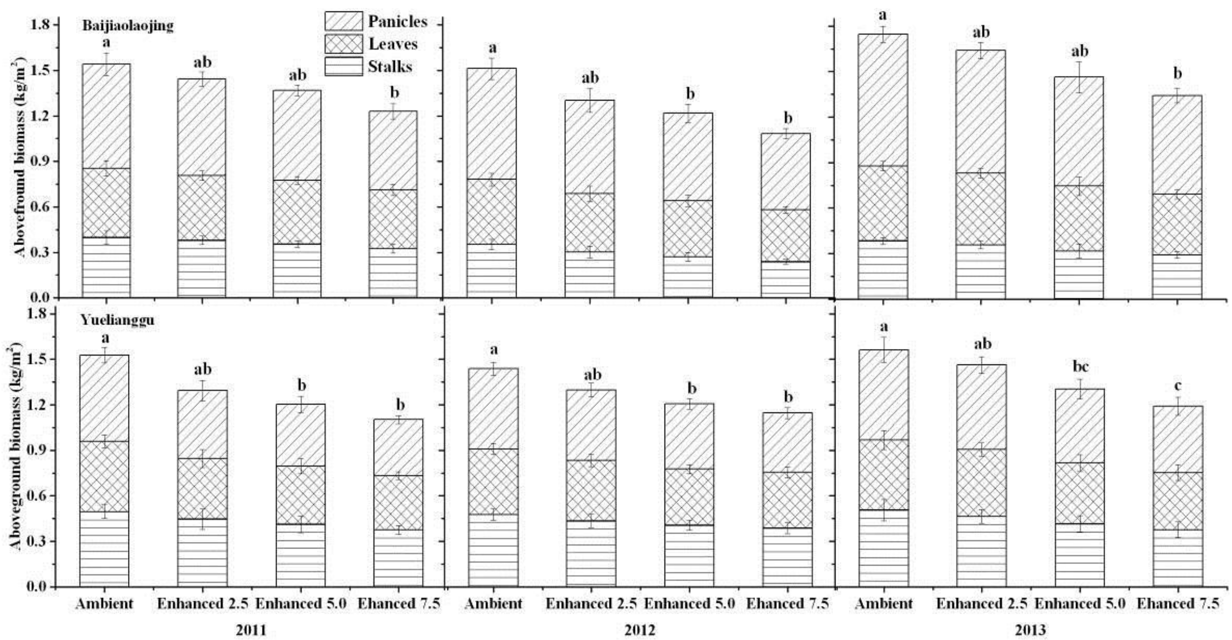

Fig. 3: Effects of enhanced UV-B radiation on the aboveground biomass of rice population

decreased under enhanced UV-B radiation (Fig. 3). Furthermore, the decrease in the above-ground biomass of rice stalks, leaves and panicles increased with increasing UV-B radiation intensity, which reached a significant level and was the greatest at 7.5 kJ m^{-2} UV-B radiation except the leaves biomass of Baijiaolaojing in year 2011 and Yuelainggu in year 2013. In many cases, 5.0 kJ m^{-2} UV-B radiation also caused a significant decrease in the rice biomass.

Meanwhile, UV-B radiation changed the biomass distribution between rice stalks, leaves and panicles. As UV-B radiation strength increased the biomass distribution of rice stalks and panicles decreased, while the proportion of rice leaves in total above-ground biomass increased.

Effect on Rice Yield

The effective panicles number of the two rice landraces declined with the increasing UV-B radiation strength (Fig. 4). For rice landrace Baijiaolaojing, there was an obvious decrease in the effective panicles number only under the highest UV-B radiation (7.5 kJ m^2) from year 2011 to 2013. For Yuelianggu, there was a significant decrease under the three UV-B radiation treatments during 2011, both high UV-B radiation treatments (5.0 and 7.5 kJ m^{-2}) during 2012 and the highest UV-B radiation (7.5 kJ m^2) in 2013.

The three-year field study indicated that the enhanced UV-B radiation negatively influenced rice yield components, which included the seed number per panicle, seed setting rate and 1000-grain weight (Fig. 4). For instance, both high UV-B radiation treatments (5.0 and 7.5 kJ m^2) decreased the seed number per panicle of Baijiaolaojing during 2013. All the three UV-B radiation treatments significantly declined the seed setting rate of Baijiaolaojing in the three consecutive seasons and only the highest UV-B radiation (7.5 kJ m^2) significantly declined the seed setting rate of Yuelianggu in the three consecutive seasons as well as the UV-B radiation at 5.0 kJ m^2 in year 2011 and 2013. Similarly, there were significant declines in the 1000-grain weight of the two rice landraces induced by

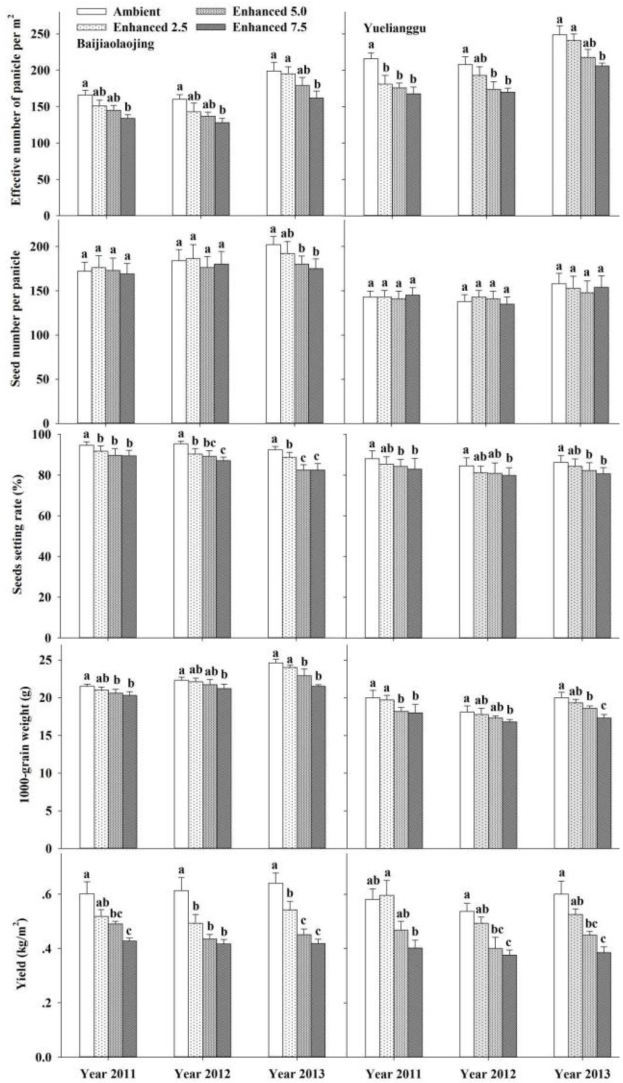

Fig. 4: Effects of enhanced UV-B radiation on the rice yield and its components

the highest UV-B radiation (7.5 kJ m^2) in the three consecutive seasons, and at 5.0 kJ m^2 in year 2011 and 2013. Moreover, the UV-B radiation lowered the panicle length and seed length of the two rice landraces yet such decrease did not reach the significant level.

Therefore, due to the decreases in the yield components all the three UV-B radiation caused significant declines in the rice yield in the three consecutive seasons for the two rice landraces and the decline degree expanded with the increasing intensity of UV-B radiation (Fig. 4).

Response Index

Response index (RI) comprehensively reflected the changes on rice growth, above-ground biomass and yield responding to UV-B radiation. All the RI of the two rice landraces was negative during the three growing seasons. Furthermore the absolute value of RI increased with the increasing UV-B radiation intensity (Table 2). The highest UV-B radiation

Table 2: Response index (%) of rice to enhanced UV-B radiation

Year	UV-B radiation (kJ m^{-2})	Baijiaolaojing	Yuelianggu
2011	2.5	-39.7	-48.1
	5.0	-60.7	-70.5
	7.5	-93.6	-94.8
2012	2.5	-51.9	-40.0
	5.0	-70.8	-78.9
	7.5	-102.4	-90.8
2013	2.5	-25.6	-27.2
	5.0	-55.8	-61.3
	7.5	-85.6	-87.5

(7.5 kJ m^2) had a strongest effect on the plant growth, above-ground biomass and grain yield of the two rice landraces.

Discussion

In previous studies, crop sensitivity to UV-B radiation can be measured by the growth changes responding to the UV-B radiation stress. There were greenhouse and field experiments of 23 crop species subjected to UV-B radiation and found that 54% of the species expressed the stress response as reduced biomass yield, 35% showed no significant changes and only 5% actually had some increases in biomass production (Kakani *et al*., 2003).

Generally, that UV-B radiation lowered crop biomass like the present study's results, which showed a decrease on the two rice landraces's biomass in Yuanyang Terraces under UV-B radiation. And that the biomass decrease mainly resulted from fewer tillers matched those previous studies (Kumagai *et al*., 2001; Xu and Qiu, 2007; Mohammed and Tarpley, 2010). In this three-year study, there were highly significant positive correlations between total tillers number and above ground-biomass of the two rice landraces at tillering stage and index was 0.92 and 0.91, respectively.

The reasons concerned changes in the tillers number may involve the contents of endogenous phytohormones and their ratio. The enhanced UV-B radiation reduced the content of IAA and $GA1_{/3}$ but increased ABA content in rice leaves (Liu and Zhong, 2009; Li *et al*., 2010). ABA triggers closure of the stomata and therefore has a negative effect on photosynthetic carbon assimilation. Consequently, a short-supply of carbohydrates may inhibit the initiation of secondary tillers eventually resulting in low biomass accumulation.

Additionally, the enhanced UV-B radiation induced oxidative injuries to leaves and then caused an accumulation of H_2O_2 (Fedina *et al*., 2010; He *et al*., 2014) cyclobutane pyrimidine dimer (CPD) (Hidema *et al*., 2001; Teranishi *et al*., 2012) and other harmful compounds (Kumagai *et al*., 1999). These harmful compounds were found to be

Table 3: Correlation coefficient between rice photosynthesis and aboveground biomass

Rice landrace	Rice stage	Photosynthetic rate	Transpiration rate	Stomatal conductance	Intercellular CO_2 concentration
Baijiaolaojing	Tillering stage	0.697	0.959**	0.964**	-0.962**
	Jointing stage	0.967**	0.959**	0.926*	-0.998**
	Heading stage	0.995**	0.999**	0.955**	-.0931*
Yuelianggu	Tillering stage	0.964**	0.971**	0.984**	-0.464
	Jointing stage	0.986**	0.932*	0.972**	-0.890*
	Heading stage	0.806	0.838	0.905*	-0.884*

Note: * means significant correlation, ** means very significant correlation, n=4

Table 4: Correlation coefficient between yield components and grain yield

Rice landrace	Effective number of panicle	Length of panicle	Seed number per panicle	1000-grain weight	Seeds setting rate
Baijiaolaojing	0.588*	0.855**	0.601*	0.582*	0.759**
Yuelianggu	0.688*	-0.233	0.290	0.843**	0.860**

Note: * means significant correlation, ** means very significant correlation, n=12

associated with low chlorophyll content, degradation of chlorophyll and chloroplast proteins (Lidon and Ramalho, 2011; Lidon *et al.*, 2012) changes of chlorophyll fluorescence parameters (Xu and Qiu, 2007) reducing activities of the photosynthetic key enzyme (Rubisco) and Ca^{2+}-ATPases (Yu *et al*., 2013). These UV-B radiation inducing changes in leaves were detrimental and eventually led to a low photosynthetic rate and total photosynthetic efficiency of rice plants (Lidon and Ramalho, 2011; Mohammed and Tarpley, 2011; 2013). In this study, the two rice landraces had lower photosynthesis after suffering the supplemental UV-B radiation. Correlation analysis found that the above-ground biomass had very significant or significant positive correlations with rice leaves' photosynthetic rate, transpiration rate and stomatal conductance in the year 2011 and very significant or significant negative correlations with intercellular CO_2 concentration (Table 3). This suggested a low photosynthesis induced by UV-B radiation could be the key factor for the suppression of rice growth.

The UV-B radiation also affected the biomass partition of rice above-ground plants. UV-B radiation caused the largest decline in panicle biomass and decreased the percentage of panicles in total biomass. In contrast, decline of the leaves biomass was relatively small and the percentage of leaves biomass was increased (Fig. 3). Such results were similar with some previous results by Li *et al.* (2000). One reason for the relatively higher percentage of leaves tissues in total biomass can be attributed to thicker leaves for reducing UV-B radiation strength entering leaves and protecting the biological tissues in the leaves. The thick leaves would contribute to shield the leaves from the UV-B radiation injuries (Santos *et al*., 2004). For the two rice landraces in Yunayang terraces, their leaves blades, upper and lower cuticle layers were thickened in plants under the enhanced UV-B radiation (Li *et al*., 2014).

For the two rice landraces in Yuanyang Terraces there were very significant or significant positive correlations between the grain yield with effective number of panicle, 1000-grain weight and seed setting rate (Table 4). These correlations indicated the main reason of the dropped yield of the two rice landraces would be a significantly reduction on the three yield components under enhanced UV-B radiation. Previous studies indicated that UV-B radiation dropped the rice yield by decreasing some yield components. For example, a significant decline in the panicles number per plant and the total panicles number in a population were found to account for a lower rice yield under enhanced UV-B radiation (Xu and Qiu, 2007; Mohammed and Tarpley, 2010). In addition, Mohammed and Tarpley (2011) found that low pollen germination rate generated by a strong UV-B radiation may be a causative reason for the smaller number of productive panicles and lower seed setting rate which would produce a low grain yield.

A certain sensitivity difference to UV-B radiation exists in rice varieties (Barnes *et al*., 1993). In a study by Mohammed and Tarpley (2010) found that eight cultivars did not experience the same degree of reduction in photosynthetic rate, leaves polyphenol content, pollen germination rate and grain yields and injuries to cell membrane system also varied among those cultivars. It was obvious that plant growth indices were very inconsistent in expressing changes responding to UV-B radiation and any single factor could not be used to fully determine the rice sensitivity to UV-B radiation.

To overcome this dilemma a response index should combine responses of the plant growth, physiology, biomass and yield to UV-B radiation. For instance, Dai *et al.* (1994) integrated changes in plant height, the tillers number, the total canopy area and dry matter weight to estimate the response index of rice under UV-B radiation. In the present study, indexes like plant height, the total tillers number, effective panicles, the above-ground biomass and grain yield were combined to calculate the response index of rice to UV-B radiation. That all the response indexes were negative indicating the two rice landraces were sensitive under UV-B radiation to a certain extent.

Conclusion

This study was helpful to expand our knowledge of the rice landrace's response to UV-B radiation. The supplemental UV-B radiation decreased the photosynthesis and biomass accumulation, affected the yield components and dropped the grain yield in the two rice landraces under field condition in a three consecutive seasons study. The suppression of photosynthesis may be the fundamental reason responsible for the decrease on the above-ground biomass and yield of the two rice landraces.

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