A - 5.1.1 Mechanisms at a Whole Plant Level

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Abstract

Many studies have reported adverse effects of increased UV-B on crop growth and yield. Most of the studies, however, have been conducted in chambers or greenhouses, where plants are more sensitive to UV-B than in the field. In this study, we conducted enhanced UV-B irradiation to rice plants in a paddy field for 3 years 1993 - 1995. The UV-B enhancement was up to 1.7 times ambient UV-BBE (biologically-effective UV-B) or 6.76 kJ m^{-2} d^{-1} for seasonal mean daily integral UV-BBE. The UV-B irradiation caused a slight decrease in chlorophyll content, a slight increase in the UV-absorbing compounds, a substantial decrease in ascorbic acid, and an increase in dehydroascorbic acid, but no changes in glutathione content or anti-oxidative enzyme activities. The UV-B irradiation caused no significant changes in rice growth traits, e.g. plant height and biomass, but reduced the yield by up to 7 %, which can be translated into a 1 % yield loss by a 10 % UV-BBE increase. Rice yield loss will therefore be less than 2% with the projected UV-BBE increase by 15%, which is caused by the peak ozone depletion of ca. 7% for the summer-autumn season in the northern midlatitudes.

Key words: Ultraviolet radiation, Rice, Growth, Yield, Total ozone

1. Introduction

Many studies have reported that increased ultraviolet-B radiation (UV-B) with the wave length of 280-320 nm adversely affects growth and yield of crop plants [1, 2]. However, most of the studies have been conducted in greenhouses or chambers, where plants are reportedly more sensitive to UV-B than in the field. It may therefore be impossible to extrapolate the results of the chamber/ greenhouse experiments to the field in the real world [3, 4]. This is why the need for UV-B irradiation experiments in the field is often stressed.

2. Objectives

The objective of this study is to address the UV-B impacts due to the total ozone depletion on rice, which is clearly the most important food crop in Asia. If the UV-B increase were to affect the rice production adversely, the food supply in the region would be at risk under the pressure of the population increase in the future. Despite the importance of the species as the primary crop species, only 6 studies[5-10)] have addressed the UV-B impacts on rice, and, moreover, only 2[9, 10)] out of the 6 studies were conducted in the field with the rest in greenhouses or chambers.

In this study, we irradiated rice plants with UV-B in the field using the modulated lamp control system[10)], which automatically controls lamp UV-B irradiance in proportion to incident solar UV-B irradiance. The enhanced UV-B irradiation in this study should better simulate the UV-B increase in the future than the studies in chambers and greenhouses. We conducted the field UV-B irradiation for 3 years from 1993 through 1995 to address the UV-B impacts across the years of different weather regimes.

3. Methods

(1) UV-B irradiation in the field

We used the modulated lamp control system[10)] with some improvements in the hardware and software. The basic structure was, however, kept unchanged. Namely, the system has a PC, a controller/ data logger, 2 UV-B sensors (MS-210D, Eiko Seiki, Tokyo), 8 lamp frames each of which has 8 UV-B lamps (F40UVB, Philips Lighting, New Jersey, USA) (Fig. 1). The lamps in the UV-B enhancement plots (UV-B) were covered with cellulose diacetate film, which does not transmit ultraviolet radiation (UV) with shorter wavelength than 290 nm. Whereas the lamps in the control plots (Control) were covered with Mylar D or equivalent film, which does not transmit UV with shorter wavelength than 320 nm. The rice plants were thus irradiated with the lamp UV-A and B (UV-B) or lamp UV-A only in addition to the solar UV incident upon the field. The films were replaced weekly since they deteriorate with the use for the filtering. One of the UV-B sensors (S_1) was placed in the open to measure solar UV-B, and the other sensor (S_2) was placed at canopy top under the lamp frame in a UV-B plot to measure mixed lamp and solar UV-B. The sensor outputs from S_1 and S_2 were converted to the biologically-effective UV-B ($UV\text{-}B_{BE}$) weighted with the generalized plant action spectrum[11)] normalized to 300 nm. The conversion from the sensor outputs to UV-B BE was based on the calibration of the MS-210D sensors against a spectro-radiometer (MSR-7000, Opto Research, Tokyo), and accounted for the difference between the solar and the lamp UV-B in their spectral irradiance.

(2) 1993 experiment on UV-B impacts on 3 rice cultivars planted in pots.

Three rice cultivars (Koshihikari, IR45 and IR74) were planted in pots and irradiated with UV-B in the field. Among the 3 cvs, Koshihikari is the leading Japanese variety of Japonica type, and the others are Indica type varieties introduced from the International Rice Research Institute in the Philippines. The IR cultivars have been reported to be relatively sensitive to UV-B[6)]. After sowing, the plants were grown in a greenhouse for 29 days (Koshihikari) or

26 days (IR45 and IR74), and were transplanted in 14 l pots placed in the field. The UV-B irradiation was performed from 8 days after the transplanting through the harvest, which occurred 118 days (Koshihikari), 141 days (IR45) and 145 days (IR74) after the initiation of the UV-B irradiation.

Plant growth was monitored nondestructively for plant height and tiller number, and destructively for dry weight and leaf area. For chlorophyll and UV-absorbing compounds contents, leaves at canopy top were excised and extracted with 99.5% ethanol for 48h at 4℃ in darkness. The chlorophyll a and b contents were determined with the absorbances at 649 and 665 nm according to Knudson et al [12]. The UV-absorbing compounds, primarily flavonoids, were determined from the same ethanol extract as used for the chlorophyll analysis. The absorption spectra between 300 and 700 nm were measured with a scanning spectrophotometer (UV-1200, Shimadzu, Kyoto) and the peak absorbance at 340 nm was arbitrarily used for the analysis. The extract for the cv Koshihikari was further used to the determination of the antioxidants contents and antioxidative enzyme activities. The antioxidants included ascorbic acid (AsA), dehydroascorbic acid (DHA), reduced glutathione (GSH) and oxidized glutathione (GSSG), and the antioxidative enzymes included ascorbate peroxidase (AP), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR), superoxide dismutase (SOD) and guaiacol peroxidase (GP).

(3) 1994 experiment on UV-B impacts on 2 rice cultivars planted in the field.

Two cvs (Koshihikari and IR74) were used in 1994. Unlike the 1993 experiment, the rice plants were grown in a paddy instead of pots. After sowing, plants were grown in a greenhouse for 36 days, and transplanted in the paddy field. The UV-B irradiation began 10 days after the transplanting and lasted for 101 days (Koshihikari) or 123 days (IR74) through the harvest dates. Plant growth was monitored as in 1993, and chlorophyll content and UV-absorbing compounds concentration were determined also as in 1993.

(4) 1995 experiment on the effects of UV-B and shading on rice (cv. Koshihikari) planted in the field.

The 1995 experiment was a factorial of UV-B irradiation (UV-B and Control) and the shading (Shaded and Unshaded) with 2 replication. Cheesecloth shading covered the lamp frame and the rice canopy below it leaving a space for air ventilation at the very bottom of the canopy. The shading transmitted nominally 50% of incoming visible as well as UV radiation. The lamp UV-B was controlled to attain a constant proportion to the incident solar UV-B in an Unshaded UV-B plot. The same amount of lamp UV-B was added to the Shaded UV-B plots so as to maintain the same difference in UV-B_{BE} irradiance between the UV-B and Control plots for both Shaded and Unshaded plots. A third UV-B sensor of the same type as the other two was placed in a Shaded UV-B plot.

Rice plants (cv Koshihikari) were grown in the paddy field as in 1994, and were subjected to the UV-B irradiation and the shading. After sowing, plants were grown in a greenhouse for 21 days, and transplanted in the paddy field. The shading and the UV-B irradiation began 11 and 16 days, respectively, after the transplanting. The UV-B irradiation lasted for 91 days through harvest. Plant growth was monitored as in 1993, and chlorophyll content and UV-absorbing compounds concentration were determined also as in 1993.

4. Results

(1) UV-B_{BE} irradiances in the field experiments

Diurnal change of the UV-B irradiance is shown in Fig. 2 for a cloudy day (A) and a sunny day (B) during the 1993 experiment. The UV-B enhancement was maintained in proportion to the incident UV-B irradiance for most of the daytime except for the early morning and late afternoon, when the incident UV-B irradiance was very low. Under the very low solar UV-B irradiance, the supplemental lamp output required for the proportional irradiation was lower than the lower limit for stable control of the fluorescent lamp output, and hence the lamps were turned off on such occasions.

Seasonal change of the daily integral UV-B irradiance is shown in Fig. 3 for the 1994 experiment. Despite the day-to-day fluctuation in the actual daily integral UV-B_{BE} (Fig. 3A), the ratio of the daily integral in the UV-B plot to that in the Control plot was maintained rather stable except for occasional dips (Fig. 3B). The dips occurred when the incident solar UV-B was very low throughout the day, and hence the lamps were kept off as noted above for most of the day. Seasonal mean daily integral UV-B_{BE} is listed in Table 1 for the 1993-1995 experiments. The daily integral of solar UV-B_{BE} (Ambient) was ca. 4 kJ m^{-2} for the 3 years with some variations among the cultivars, which had reached the maturity in different timings and hence the difference in the seasonal mean daily integral UV-B_{BE}. The mean daily integral in the UV-B plots was 70 % (1993), 60 % (1994) and 40 % (1995) above the Ambient UV-B_{BE}, and that in the Control plots was 25 % below the Ambient. The difference between the UV-B and Control plots was 95% (1993), 85% (1994), and 65% (1995) of the Ambient. In the shaded plots in the 1995 experiments, the difference between the UV-B and Control plots was equivalent to a 61% of the Ambient UV-B_{BE}. The differences between the Control and UV-B plots were comparable across the shading treatment.

(2) Impacts on rice growth and yield.

The UV-B irradiation had almost no effects on any of the growth traits in either experiment. The only statistical significance of the UV-B impact was found in the leaf area in Koshihikari and IR45 at harvest in the 1993 experiment. The chlorophyll content was slightly lower and the UV-absorbing compounds were slightly higher in the UV-B plots than the Control plots, but these changes were not significant statistically. The analysis of the antioxidants in the 1993 experiment showed a decrease of AsA, increase of DHA, and slight decrease of total ascorbic acid. Any of the antioxidative enzymes did not show changes due to the UV-B irradiation.

The effects of the UV-B irradiation on the rice yield are listed in Table 2. Statistically significant changes were found only in the 1994 and 1995 experiments, in which 9 % (1994) or 7% (1995) yield reduction was found. The shading in 1995 did not alter the yield response to UV-B.

5. Discussion

The yield reduction of 9% in 1994 and 7% in 1995 was caused by the increase of UV-B_{BE} by 85% (1994) and 65% (1995) of the ambient UV-B_{BE}. It could therefore be summarized that a 10% increase in UV-B_{BE} will cause a 1 % yield reduction. The increase in UV-B_{BE} can be related to ozone depletion with a model of radiative transfer 13) and the total ozone data at Tsukuba 14). The model has been coded 15) and published before 16). As shown in Fig. 3, the relationship between the total ozone depletion % (x) at Tsukuba in the rice growing season (May 1 - October 31) and the seasonal mean daily integral UV-B_{BE} (y) at the ground surface can be approximated by the equation:

$$y = 5.20 \exp(0.02\ x).$$

Since the effects of scattering by clouds and aerosols have not been accounted for, the equation would give a 'ceiling' for the surface UV-B irradiance. On a relative basis, however, the equation may give an appropriate estimate, if the attenuation by those factors is unchanged by the ozone depletion. Since the predicted ozone depletion is 6-7 % at its peak in the future during the summer-autumn season in the northern mid-latitudes 17), the UV-B_{BE} increase is projected from the above equation to be 15 % or less of the current level. The rice yield loss would therefore be 1.5% or less, which is far from devastating as opposed to the extrapolation from the results of chamber / greenhouse studies hitherto.

The discrepancy between the chamber studies and the field studies including this study can be ascribed for some differences between the two types of studies. At least a substantial portion of the discrepancy is simply the result of the difference in the UV-B dosage, which is in general higher in the chamber studies than in the field studies. This is because no UV-B is present in the control plots in chambers, whereas solar UV-B is present in the field control plots. Overestimation of the incident solar UV-B and the irradiation regime based on the overestimated solar UV-B should be another cause of the discrepancy between the chamber and field studies. Use of an inadequate model 18), and inadequate use of the simulation results would be both responsible for the overestimation of solar UV-B 19).

Spectral irradiance in chambers could be quite different from that in the field. Within the

UV-B range, the chamber experiments is richer in shorter wavelength than the field experiments 9), because the UV-B in chambers comes only from UV lamps which is richer in the shorter components than the solar UV-B. Should the real action spectrum have a greater weight than the Caldwell's Plant 300 11) in the shorter wavelength, the chamber studies would underestimate the UV-B dosage, and hence overestimate the UV-B impacts 20). Outside the UV-B range, UV-A and visible radiation are reported to protect and/ or to help recover from the UV-B damages 21). Without the protecting/ recovery mechanisms, the chamber studies would overestimate the UV-B impacts.

In summary, the cause of the discrepancy between the chamber/ greenhouse studies and the field studies needs further studies. However, the field studies are likely to give more realistic results than the chamber studies, and the results of this study suggested that the future ozone depletion of up to 7% will have only a minute impact, less than 1.5%, on rice yield.

6. References

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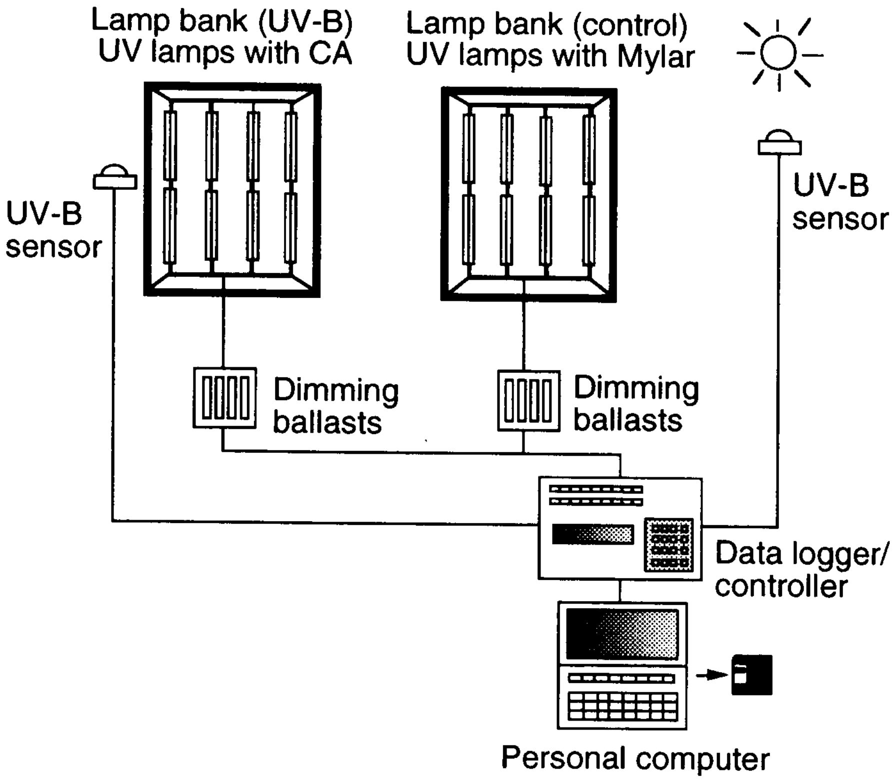

Fig. 1. Schematics of the modulating UV-B irradiation system in the field.

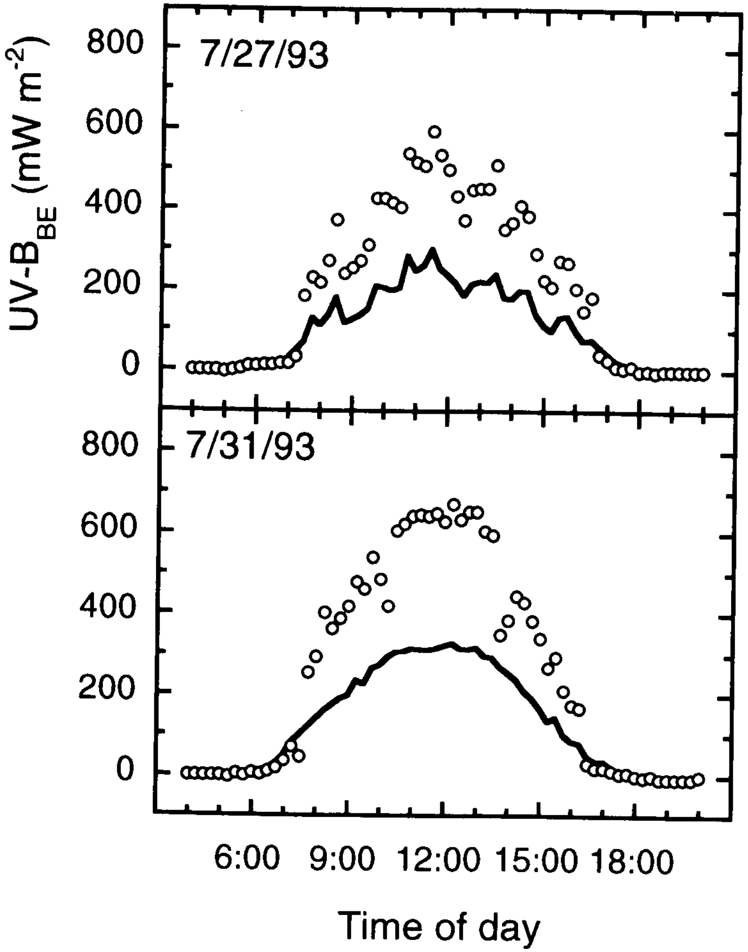

Fig. 2. Diurnal changes in the incident solar (Inc) and the enhanced (Enh) UV-B in 1993.

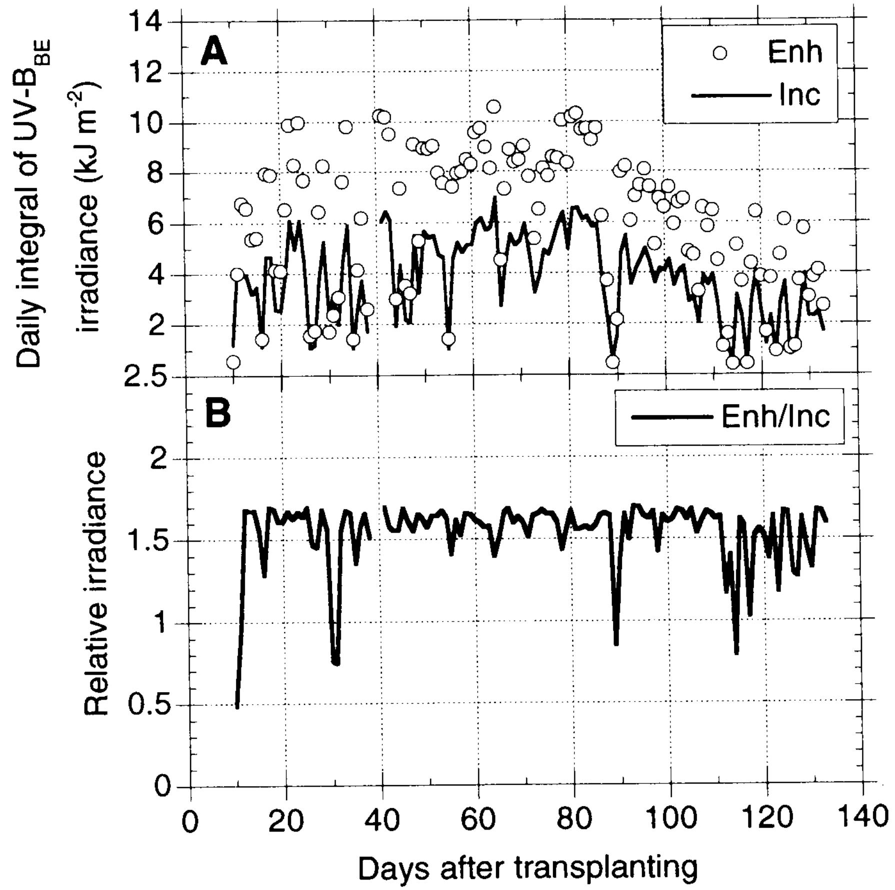

Fig. 3. Seasonal changes of UV-B irradiation in 1994.

A: Daily integral UV-B$_{BE}$irradiance, B: Ratio of the enhanced to incident UV-B$_{BE}$.

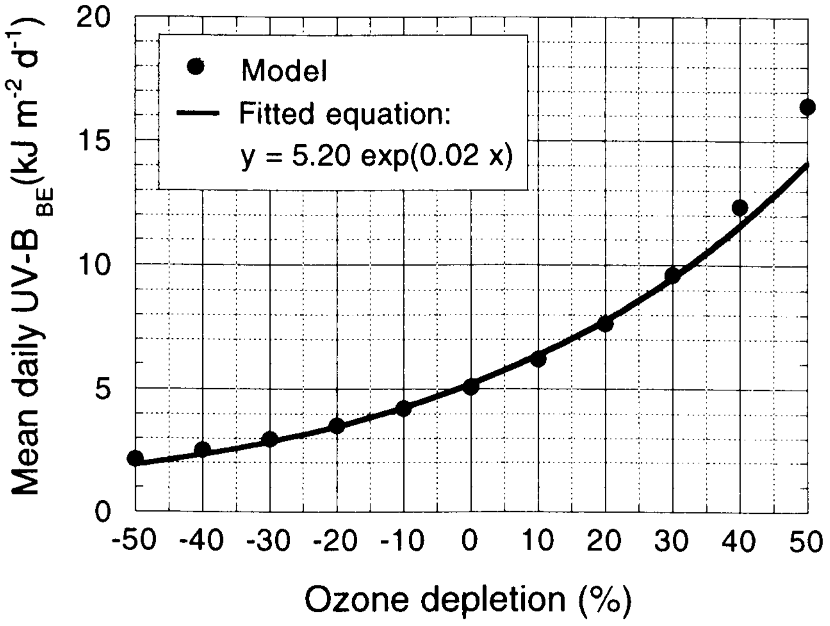

Fig. 4. Effect of ozone depletion on biologically effective UV-B radiation (Caldwell's PLANT-300).

Baseline (0% depletion): Tsukuba, May 1 - Oct.31, 1992.
Model: Bjorn and Murphy (1985) with no cloud, no aerosol.

Table 1. Mean daily integral UV-B irradiances for the 1993-1995 experiments.

		Daily integral UV-B (UV-B$_{BE}$[a], kJ m^{-2})			Relative value		
Year	Cultivar	Ambient	Control	Enhanced UV-B	Ambient	Control	Enhanced UV-B
1993	Koshihikari	3.98	2.99	6.76	100	75	170
	IR74	3.70	2.78	6.30	100	75	170
	IR45	3.73	2.80	6.36	100	75	170
1994	Koshihikari	4.21	3.17	6.70	100	75	159
	IR74	3.83	2.88	6.06	100	75	158
1995	Koshihikari (Unshaded)	3.90	2.90	5.47	100	74	140
	Koshihikari (Shaded)	3.90	1.67	4.07	100	43	104

[a] Biologically-effective UV-B irradiance weighted with Caldwell's generalized plant response normalized to 300 nm.

Table 2. Effect of UV-B irradiation on rice yield.[a]

		Number of seeds[b]		Total seed weight (g) [b]		Sorted grain weight (g) [b]	
Year	Cultivar	Control	Enhanced UV-B	Control	Enhanced UV-B	Control	Enhanced UV-B
1993	Koshihikari	2849	2795	53.7	52.7	-	-
	IR74	3038	3073	14.6	14.2	-	-
	IR45	3394	3080+	25.8	25.7	-	-
1994	Koshihikari	26588	27701	702	718	514	538
	IR74	28581	25888*	967	929*	623	566*
1995	Koshihikari (Unshaded)	28246	26628*	743	692**	551	509+
	Koshihikari (Shaded)	17548	16422*	433	404**	264	249+

[a] Statisticaly significant differences between the control and the enhanced UV-B treatments are indicated with + ($p \leq 0.1$), * ($p \leq 0.05$) and ** ($p \leq 0.01$).

[b] Values are per pot (1/2,000a) basis for 1993, and per m^2 basis for 1994 and1995.