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Effects of Supplementary Ultraviolet-B Irradiance on Maize Yield and Qualities: A Field Experiment¶

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ABSTRACT

Stratospheric ozone depletion has caused an increase in the amount of ultraviolet-B (UV-B) radiation reaching the earth's surface. Numerous investigations have demonstrated that the effect of UV-B enhancements on plants includes reduction in grain yield, alteration in species competition, susceptibility to disease and changes in plant structure and pigmentation. Many experiments examining UV-B radiation effects on plants have been conducted in growth chambers or greenhouses. It has been questioned whether the effect of UV-B radiation on plants can be extrapolated to field responses from indoor studies because of the unnaturally high ratios of UV-B/ultraviolet-A radiation (320–400 nm) and UV-B/photosynthetically active radiation (PAR) in many indoor studies. Field studies on UV-B radiation effect on plants have been recommended to use the UV and PAR irradiance provided by natural light. This study reports the growth and yield responses of a maize crop exposed to enhanced UV-B radiation and the UV-B effects on maize seed qualities under field conditions. Enhanced UV-B radiation caused a significant reduction in the dry matter accumulation and the maize yield in turn was affected. With increased UV-B radiation the flavonoid accumulation in maize leaves increased and the contents of chlorophyll *a, b* and ($a + b$) of maize leaves were reduced. The levels of protein, sugar and starch of maize seed decreased with enhanced UV-B radiation, whereas the level of lysine increased with enhanced UV-B radiation.

INTRODUCTION

The loss of stratospheric ozone has prompted recent efforts in assessing the potential damage to agriculture and ecosystems due to enhanced solar ultraviolet-B (UV-B) radiation reaching the earth's surface (1–7). It is suggested that maximal ozone depletion and peak UV-B levels will occur during the next decade, with a return to pre-1980 levels of stratospheric ozone and UV-B by the middle of this century (8, S. Madronich, personal communication). However, many factors, including feedbacks from rising concentrations of greenhouse gases, could delay this process (9,10). Important changes in future crop production could be associated with plant growth and development under enhanced UV-B radiation if crop plants were sensitive to increased levels of UV-B radiation (11). Numerous investigations have demonstrated that the effect of UV-B enhancements on plants includes reduction in grain yield, alteration in species competition, susceptibility to disease and changes in plant structure and pigmentation (12,13). The enhanced UV-B radiation can cause deleterious effects to DNA, the photosynthetic system and other target molecules. Some effects on photosynthesis may also include alteration in light penetration into the leaf, changes in chlorophyll and stomatal density, and reduction in leaf area (14). The mechanism of UV-B protection includes the accumulation of UV-absorbing compounds in leaf tissue in response to UV-B radiation. The importance of the accumulation of flavonoids in the epidermis in terms of providing UV-B radiation protection has been considered (15,16). There have been many studies to examine UV-B effects on terrestrial plants using growth chambers or greenhouses (17,18). Commonly, the control treatment was one in which there was no exposure to UV-B and consequently, the environmental complex in these studies was artificial and the results obtained may not precisely simulate the field conditions (11). The studies of plants to enhanced UV-B radiation under field conditions are very important to an assessment of the responses of natural ecosystems to this stress factor (19,20). The present study reports the growth and yield responses of a maize crop exposed to enhanced UV-B radiation under field conditions. The UV-B effects on maize seed qualities were tested and discussed.

MATERIALS AND METHODS

The experimental field was established in the agrometeorological research station of Nanjing Institute of Meteorology, Nanjing, China (32.14°N, 118.42°E). A maize variety, Zhongnuo No. 1, the most commonly grown crop variety cultivar in Nanjing region, was evaluated under supplemental UV-B irradiance during the maize-growing season of 2002. Plants were

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Abbreviations: PAR, photosynthetically active radiation (400–700 nm); UV-B, ultraviolet-B radiation (280–320 nm).

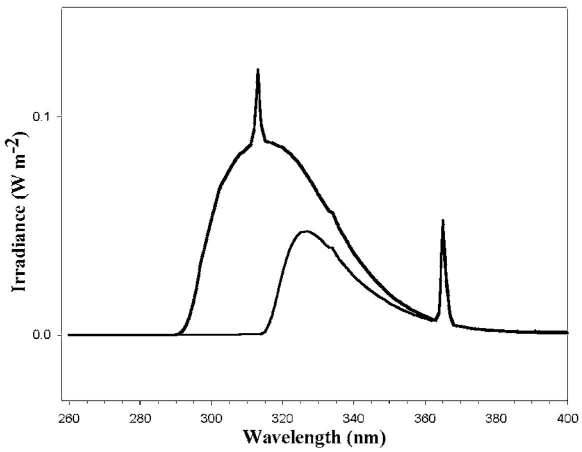

Figure 1. Spectral distribution of UV-313 lamps filtered with either cellulose diacetate (bold line) or polyester film (normal line). Measurements were made with an Optronics OL-754 spectroradiometer in the absence of sunlight.

seeded on Julian day 135, 2002 and were grown in the experimental field (silt loamy soil) with a density of 52 500 plants per hectare. The soil was cultivated with fertilizer applications of urea at 270 kg/ha (40%), acid phosphate at 225 kg/ha (16%) and potassium chloride at 325 kg/ha (50%).

Three UV-B irradiance treatments were applied in the experimental maize field through the whole growing season until the harvest (May 15–August 20). Each treatment plot was 3 × 4 m, and four replicates of the three treatments were performed. Six border-protective rows were around each plot to minimize marginal (border) effects. The treatments were two supplemental UV-B treatments, designated as T_1 and T_2, and a control treatment described as CK. The supplemental UV-B treatments T_1 and T_2 averaged 4.8% and 9.5%, respectively, more total (unweighted) UV-B irradiance than the natural UV-B irradiance received by the CK treatment according to the calculation with discrete ordinate multiple scattering code model (21) and measurement by UV-A, B TUVR UV sensor (EPPLEY instrument company, Newport, RI) (22). The UV-B irradiance delivered at the top of the plant canopy was checked every 3 days with a UVX digital radiometer (UVP Inc., San Gabriel, CA) and calibrated against an Optronic Laboratory (Orlando, FL) Model 754 Spectroradiometer, which was used to initially quantify lamp output. Artificial UV-B irradiance was supplied by fluorescent lamps (''Black-light,'' Shanghai, China) with a spectral output similar to that of Q-Panel UVB-313 lamps (Fig. 1) in the range of 280–400 nm and peak emission at about 313 nm (23). Lamps were filtered with either 0.13 mm polyester (spectrally equivalent to Mylar Type S) film (control or CK treatment), which absorbs nearly all radiation below 316 nm, or 0.13 mm Kodacel CTA (Eastman Kodak Company, Rochester, NY) for supplemental UV-B irradiance. The Kodacel films are cellulose triacetate materials with similar spectral properties to the more commonly used cellulose diacetate (24,25) in the ultraviolet-A (320–400 nm) region but with somewhat greater transmittance in the shortwave UV-B waveband (Fig. 1). The films were changed weekly to ensure uniformity of UV-B transmission. The lamps were oriented perpendicular to the plant rows and suspended above the plants. Lamps were fitted with 50 mm wide minireflectors and manually adjusted for time and height control. The photosynthetically active radiation (PAR, 400–700 nm) at the top of the maize canopy and ambient PAR were checked every 3 days with a quantum sensor (LiCor-6200, LiCor Biosciences, Lincoln, NE). Total daily PAR under the lamp fixtures was about 90% of that above the lamps (26). The lamps were suspended from wires stretched between steel poles at both ends of the planted rows. Supplemental irradiance was provided daily at a constant rate during the day for 8 h centered around solar noon controlled by a microprocessor (26). The UV-B irradiance was adjusted monthly to allow for seasonal changes in ambient UV-B. The different UV-B treatments were obtained by varying the distance between the lamps and the top of the plants. The height of the lamps above the plants was adjusted weekly to maintain constant lamp-to-plant distances as the plants grew. Biological sampling was performed every 5 days during the growing season in a 1 m^2 area of each tested plot for measuring the plant height, leaf length and width and the weight of fresh and dry plants (samples were carefully washed and then chamber-dried at 68°C for 68 h). The ear length, number of kernel per ear and the weight of 1000 grains were also measured after the harvesting. Flavonoid content was measured (27) by 725 UV–Visible Spectrophotometer at absorption wavelength 340 nm (absorptivity/g). The chloroplast content was measured at the absorption wavelengths of 645 and 663 nm separately and determined as chlorophyll $a = (12.7 \times \text{OD } 663 - 2.69 \times \text{OD } 645)/200$; chlorophyll $b = (22.9 \times \text{OD } 645 - 4.68 \times \text{OD } 663)/200$; chlorophyll $(a + b) = (20.2 \times \text{OD } 645 + 8.02 \times \text{OD } 663)/200$ (26), where OD represents the optical density. Total sugar and starch levels were measured by the anthrone colorimetry (28), the protein content was measured by Coomassie brilliant colorimetry and the lysine level was determined by ninhydrin method (29). All data are presented as means of 12–16 samples, and the corresponding standard deviation is indicated by ± in tables. For estimating significant differences of the means, a *t*-test with $\alpha = 0.05$ was performed. Significant differences are indicated by an asterisk in the tables.

RESULTS AND DISCUSSIONS

Effects of enhanced UV-B on maize yield

The measurement results showed that the enhanced UV-B irradiance caused a significant reduction in the dry matter accumulation in all four selected growing stages (Table 1). The effects of the supplemental UV-B irradiance on dry matter accumulation were different in different growth stages. The dry matter accumulation dropped most in the heading stage and was reduced to 59.6% under T_1 and 39.9% under T_2 compared with that in CK treatment. Supplemental UV-B irradiance also caused a decrease in dry matter weight in rice (30,31) and other crop plants (32). Because supplemental UV-B irradiance reduced the dry matter accumulation, the maize yield in turn was affected. The 1000-grain weight and grain number per ear were reduced with

Table 1. Maize dry matter weight and yield under different UV-B treatments

	Dry matter weight (g/plant) in different growing stages (% CK)						
UV-B treatments†	Jointing	Heading	Flowering	Maturing	Yield (kg/ha) (% CK)	1000-grain weight (g) (% CK)	Grain number per ear (% CK)
CK	20.93 ± 3.02 (100)	176.95 ± 20.35 (100)	372.27 ± 35.90 (100)	477.17 ± 53.28 (100)	6250.4 ± 589.2 (100)	205 ± 78.43 (100)	487.8 ± 68.2 (100)
T_1	18.47 ± 2.65 (88.2)	105.52 ± 9.8* (59.6)	270 ± 28.32* (72.5)	399 ± 52.6 (83.6)	5875.5 ± 685.2 (94.0)	200.81 ± 23.12 (98.0)	467.66 ± 52.5* (95.9)
T_2	16.64 ± 2.32 (79.5)	70.35 ± 8.23* (39.9)	210.2 ± 29.51* (56.5)	338.2 ± 37.51* (70.9)	5775.0 ± 634.2* (92.4)	199.31 ± 21.73* (97.1)	464.82 ± 58.1 (95.3)

†The supplemental UV-B treatments T_1 and T_2 averaged 4.8% and 9.5%, respectively, more total (unweighted) UV-B irradiance than the natural UV-B irradiance received by the CK treatment according to the calculation with discrete ordinate multiple scattering code model (21) and measurement by UV-A, B TUVR UV sensor (EPPLEY instrument company) (22).

*Significant difference

Table 2. Flavonoid content (absorptivity/g) of maize leaves under different UV-B treatments

Growing stages	CK	T_1	T_1/CK (%)	T_2	T_2/CK (%)
Jointing	55.4 ± 7.83	56.7 ± 4.83*	102.3	62.1 ± 9.98	112.1
Heading	68.85 ± 11.64	79.3 ± 20.85	115.2	83.3* ± 11.25	121
Flowering	70.47 ± 11.53	89.2 ± 13.26*	126.6	103.7 ± 25.15*	147.2
Maturing	74.7 ± 10.81	102.6 ± 14.23*	137.3	123 ± 20.54*	164.7

*Significant difference

increased UV-B irradiance. The maize yield decreased 6% under T_1 treatment and 7.6% under T_2 treatment compared with that under the CK treatment.

Increased UV-B influence on the flavonoid and chloroplast levels of the maize

The flavonoids play many defensive roles in plants, and interception of UV-B by epidermal flavonoids is often proposed as an adaptive mechanism preventing UV-B from reaching the mesophyll and affecting photosynthesis (33). The flavonoid accumulation in maize leaves increased with increased UV-B irradiance (Table 2) in all tested growing stages. Compared with the CK treatment, the flavonoid accumulation was increased 2.3%, 15.2%, 26.6% and 37.3% under the T_1 treatment and 12.1%, 21%, 47.2% and 64.7% under T_2, respectively, with growing stages: jointing, heading, flowering and mature stages. The increasing rate of flavonoid accumulation was smaller in early growing stages and was increased significantly in late growing stages. Similar results were also observed by Stafford (34).

The contents of chlorophyll *a, b* and $(a + b)$ of maize leaves were reduced with increased UV-B irradiance (Table 3). The measurements of the chlorophyll contents under supplemental UV-B irradiance showed that the increased UV-B radiation treatments accelerated the chlorophyll decomposition. The decrease in chlorophyll content varied with different growing stages. Most of the chlorophyll content reduction occurred during the jointing period. In this period, the chlorophyll *a, b* and $(a + b)$ contents under T_1 were 69.52%, 65% and 68.77% of that under CK, and the chlorophyll *a, b* and $(a + b)$ contents under T_2 were 15.2%, 11.2% and 14.32% of that under CK. Chlorophyll *b* responded to supplemental UV-B radiation more sensitively than chlorophyll *a*.

Enhanced UV-B influence on maize quality and lysine level

To evaluate the impact of UV-B irradiance on maize seed quality, the levels of protein, sugar and starch were measured under different UV-B treatments. The results of the measurements are presented in Table 4. The levels of these three substances decide the maize seed nutrient value. Levels of all three substances decreased under both supplemental UV-B treatments compared with those in the CK treatment. The protein content decreased 26.34% under T_1 and 33.49% under T_2, whereas the sugar content went down 21.19% under T_1 and 35.39% under T_2. The starch is a main component of maize seed which is an important material for the production of food grade starch, high-content syrup, fuel and alcohol. The starch content decreased 2.42% under the T_1 treatment and 17.39% under the T_2 treatment. The lysine content in maize seed increased 8.16% under T_1 and 15.79% under T_2 compared with those in CK treatment. The higher level of lysine content in maize seed with supplemental UV-B irradiance improves the maize seed quality. The mechanism of increased lysine level associated with the supplemental UV-B irradiance needs to be studied further.

CONCLUSIONS

This study reports the growth and yield responses of maize crop exposed to enhanced UV-B irradiance and the UV-B effects on maize seed qualities under field conditions, which will help to overall assess the influence of enhanced UV-B on agricultural crops due to stratospheric ozone depletion. The growing season of 2002 was typical in the tested region where the weather condition was normal. Enhanced UV-B irradiance caused a significant reduction in the dry matter accumulation and the maize yield in turn was affected. Analysis of yield structure indicates that the maize yield decrease with increased UV-B irradiance was evidently related to the decreased 1000-grain weight and grain number per ear. The relatively large reductions in yield parameters are important to document but somewhat surprising for a C4 plant because it has generally been assumed to be less sensitive to UV-B than C3 plants, such as cotton, soybean and wheat (35–37). Some of this sensitivity may be due in part to the use of cellulose

Table 3. Chlorophyll (chl) content (mg/g) of the maize leaves under different UV-B treatments

UV-B treatments	CK			T_1			T_2		
	Chl *a*	Chl *b*	Chl $(a + b)$	Chl *a*	Chl *b*	Chl $(a + b)$	Chl *a*	Chl *b*	Chl $(a + b)$
Growing stages									
Seedlings	1.94 ± 0.23	0.48 ± 0.12	2.42 ± 0.34	1.77* ± 0.67	0.37* ± 0.09	2.14* ± 0.6	0.94* ± 0.45	0.24* ± 0.09	1.48* ± 0.42
Jointing	2.69 ± 0.17	0.8 ± 0.18	3.49 ± 0.12	1.87 ± 0.58	0.52* ± 0.1	2.4 ± 0.66	0.41* ± 0.05	0.09* ± 0.01	0.57* ± 0.05
Heading	1.68 ± 0.69	0.72 ± 0.15	2.41 ± 0.81	1.51* ± 0.57	0.42* ± 0.09	1.93* ± 0.66	1.33* ± 0.34	0.43* ± 0.09	1.77* ± 0.43

*Significant difference

Table 4. Maize seed qualities test (percentage of content in seed) under different UV-B irradiance treatments

UV-B treatments	Protein (%)	Sugar (%)	Starch (%)	Lysine (%)
CK	8.39 ± 0.068	19.30 ± 0.099	69.36	0.380 ± 0.016
T_1	6.18 ± 0.023*	15.21 ± 0.208	67.68	0.411 ± 0.021*
T_2	5.58 ± 0.047*	12.47 ± 0.588*	57.30	0.440 ± 0.027*

*Significant difference

triacetate filters in this study because they do not entirely filter out the shortwave UV-B (*i.e.* <290 nm) contribution of the lamps. However, researchers have also noted significant reductions in growth, development and yield quality in species such as cotton (35) and soybean (38,39).

The experimental results showed that increased UV-B irradiance also caused the reduction of the contents of chlorophyll *a, b* and $(a + b)$ of maize leaves. The reduction of the chlorophyll content has a negative effect on plant photosynthetic efficiency. Enhanced UV-B irradiance increased the flavonoid accumulation in maize leaves, which can absorb markedly UV radiation of 280–315 nm and helps prevent UV-B from reaching the mesophyll and affecting photosynthesis (40). The contents of protein, sugar, starch and lysine in maize plant are critical to maize quality. The experimental results suggested that the levels of protein, sugar and starch of maize seed decreased with enhanced UV-B irradiance, whereas the level of lysine increased with enhanced UV-B irradiance. The supplemental UV-B irradiance contributed to degradation of maize quality in this experiment even though the higher level of lysine content in maize seed with supplemental UV-B irradiance improves the maize seed quality. The mechanism of increased lysine level associated with the supplemental UV-B irradiance needs to be studied further. Thus, the maize variety tested in this experiment appeared to be highly susceptible to damage from increased UV-B irradiance. This study only selected one maize variety, and it is of great interest to investigate the impact of increased UV-B irradiance on other varieties of maize plant using the same experiment so that the varieties could be compared under the same weather condition. Plant growth is a complex response that integrates the influences of many environmental factors, including UV-B radiation, on several physiological processes. It is also necessary to conduct future experiments with consideration to combine enhanced UV-B radiation with other stress factors on plants including increased CO_2, drought and high temperature.

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