

Field Crops Research 67 (2000) 25-33



# Intraspecific responses in crop growth and yield of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions

Li Yuan<sup>a,b,\*</sup>, Zu Yanqun<sup>a</sup>, Chen Haiyan<sup>a</sup>, Chen Jianjun<sup>a</sup>, Yang Jilong<sup>a</sup>, Hu Zhide<sup>b</sup>

<sup>a</sup>Department of Environmental Science, Yunnan Agricultural University, Kunming 650201, PR China <sup>b</sup>Department of Chemistry, Lanzhou University, Lanzhou 730000, PR China

Received 30 June 1999; received in revised form 3 March 2000; accepted 8 March 2000

#### Abstract

Field studies were conducted for a season to determine the effect of enhanced ultraviolet-B (UV-B, 280–315 nm) radiation on crop growth, grain yield and the intraspecific variation in sensitivity of 20 wheat (*Triticum aestivum*) cultivars. The supplemental UV-B radiation was 5.00 kJ m<sup>-2</sup>, simulating a depletion of 20% stratospheric ozone. Out of 20 wheat cultivars tested, 10, 5 and 12 had significant change in plant height at 40 days after planting (DAP), 50 DAP and ripening stages, respectively. Sensitivity in plant height: ripening stage>40 DAP>50 DAP. Area per leaf (LA) of 5 cultivars and leaf area index (LAI) of 9 cultivars had significant difference between control and UV-B radiation. Sensitivity in LAI was more than that in LA. While 14 cultivars showed significant change in tiller number, 13 and 15 had significantly less shoot biomass and smaller grain yield, respectively. The result showed that 19 out of 20 wheat cultivars had a negative response index (RI), indicating inhibition by UV-B radiation on wheat growth, while only Dali 905, the most tolerant cultivar, showed positive response (RI 74.71). The response index of 7 tolerant cultivars was higher than -70; 5 out of 7 originated in South China (low latitude). Meanwhile, the response index of 9 tolerant cultivars was lower than -120, the most sensitive cultivars, i.e. Huining 18 (RI 231.91) and Longchun 16 (RI 224.23), originated in North China (high latitude). These UV-B tolerant cultivars identified and evaluated from our study might be useful donors for further breeding program. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Wheat; Stratospheric ozone depletion; UV-B radiation; Response index; Crop growth; Grain yield

#### 1. Introduction

The rapid decline in stratospheric ozone concentration has been confirmed by satellite measurements (Molina and Molina, 1992). The most pronounced thinning of the ozone layer has been measured over the Antarctic continent with up to 71% depletion

during the Antarctic spring (Kerr, 1993). Recent mathematical models predict a further increase in solar UV-B irradiation in future years (Madronich et al., 1995). UV-B effects on plants have been the subject of considerable research; approximately 350 papers have appeared (Caldwell et al., 1995). An examination of more than 200 plant species reveals that roughly 20% are sensitive, 50% are mildly sensitive or tolerant, and 30% are completely insensitive to UV-B radiation (Teramura, 1983). Whilst the impact of enhanced UV-B radiation on plant physiology,

<sup>\*</sup>Corresponding author. Present address: Department of Environmental Science, Yunnan Agricultural University, Kunming 650201, PR China.

morphology, growth and biomass has been investigated extensively, little is known about intraspecific responses of plants to enhanced UV-B radiation. Intraspecific responses in maize and wheat (Biggs and Kossuth, 1978), broad bean (Bennett, 1981), cucumber (Murali and Teramura, 1986), soybean (Teramura and Murali, 1986; Sullivan and Teramura, 1990), rice (Teramura et al., 1991; Barnes et al., 1993; Dai et al., 1994) have been reported. Plant species and even genotypes within species can differ greatly in their responses to UV-B radiation. Reasons for this are not clear (Caldwell and Flint, 1994). Due to our lack of understanding of the role of intraspecific responses to UV-B radiation, further studies on its importance should be undertaken

Most of the UV-B research in the past two decades have been conducted as short-term experiments in growth chambers and greenhouses, where an unnatural spectral balance of radiation may have substantially changed plant sensitivity to UV-B. It is important in experiments to maintain a realistic balance between various spectral regions, since both UV-A (315–400 nm) and visible (400–700 nm) radiation can have ameliorating effects on responses of plants to UV-B radiation (Caldwell et al., 1995). In growth chamber and greenhouse experiments, the visible and UV-A radiation are usually much less than in sunlight, thus, even if realistic levels of UV-B radiation are used in simulating ozone reduction, plant response may be exaggerated relative to field conditions. Unfortunately, only 15% of the reported studies have been conducted under field conditions. While laboratory and glasshouse studies provide information on mechanisms and processes of UV-B action, only field studies can provide realistic assessments of what will happen as the stratospheric ozone layer thins (Caldwell et al., 1995).

Vegetation communities function differently to plants in isolation and the behavior of the former can not be easily predicted from the latter. The history of research on elevated CO<sub>2</sub> shows the ecosystem-level effects can not be easily predicted from experiments with isolated plants (Korner, 1993). Community-level field experimentation is needed to evaluate realistic consequences of increased solar UV-B radiation resulting from ozone reduction.

Wheat is one of the major world food crops (Teramura, 1983), the effects of enhanced UV-B radiation

on photosynthetic characteristics, growth, development, leaf quality, morphology, tiller number, crop structure, plant nutrients, decomposition, competition interaction between wheat and wild oat, intraspecific responses, total biomass and yield have been studied (Biggs and Kossuth, 1978; Teramura, 1980; Gold and Caldwell, 1983; Barnes et al., 1988, 1990; Yue et al., 1998; Teramura et al., 1990; Li et al., 1998, 1999). Unfortunately, only few studies have been conducted under field conditions. In this study, we grew 20 wheat cultivars in the field under ambient and supplemental levels of UV-B radiation for a season with the objective to evaluate intraspecific responses in crop growth and yield. We hypothesized that enhanced UV-B radiation would affect crop growth and yield and result in intraspecific responses under field conditions.

### 2. Materials and methods

## 2.1. Plant materials and growth conditions

The field experiment was conducted at Yunnan Agricultural University, Kunming, China. No fertilization was necessary during the season. Seeds of 20 wheat (Triticum aestivum) cultivars, the most commonly grown wheat cultivars in China (19 cultivars) and Mexico (MY 94-9), were obtained from Lanzhou Agricultural Science Research Institute, Yunnan Academic of Agricultural Sciences, Gansu Academic of Agricultural Sciences and Henan Academic of Agricultural Sciences and sown in rows spaced 0.2 m apart at a density of 80 seeds m<sup>-1</sup> in 120 plots of  $2.0 \text{ m} \times$ 1.0 m each on 26 July 1998, an appropriate sowing date for wheat in Kunming. Five border rows were sown around each plot in order to minimize heterogeneity in microclimate. The overall experimental design was a randomized complete block with two UV-B treatments and 3 replications. At the three-leaf stage, plants were thinned to 60 m<sup>-1</sup> for uniformity in growth. This planting density is within commonly used sowing practices for the Kunming region.

## 2.2. UV-B radiation

Supplemental UV-B radiation was provided by filtered Gucun brand (Gucun Instrument Factory, Shanghai, China) 30 W sunlamps following the pro-

cedure outlined in Lydon et al. (1986). Lamps were suspended above and perpendicular to the planted rows (rows oriented in an east-west direction to minimize shading) and filtered with either 0.13 mm thick cellulose diacetate (transmission down to 290 nm) for supplemental UV-B radiation or 0.13 mm polyester plastic films (absorbs all radiation below 320 nm) as a control (Sullivan and Teramura, 1990). Cellulose diacetate filters were presolarized for 8 h and changed weekly to ensure uniformity of UV-B transmission. The spectral irradiance from the lamps was determined with an Optronics Model 742 (Optronics Laboratories, Orlando, FL, USA) spectroradiometer. The spectral irradiance was weighted with the generalized plant response action spectrum (Caldwell, 1971) and normalized at 300 nm to obtain UV-B<sub>RE</sub>. Six lamps were installed above each plot. Plants were irradiated for 7 h daily centered around solar noon, from the three-leaf to the ripening stage. Plants under polyester-filtered lamps received only ambient levels of UV-B radiation (10.00 kJ m<sup>-2</sup> UV-B<sub>BE</sub> during clear sky conditions on the summer solstice). Plants beneath the cellulose diacetate filters received ambient plus supplemental levels of UV-B. The lamp height was adjusted weekly to maintain a distance of 0.45 m from the top of the plants, and provided supplemental irradiances of 5.00 effective kJ m $^{-2}$  UV-B<sub>BE</sub>. This supplemental level was similar to that which would be experienced at Kunming (25°N, 1950 m) with a 20% stratospheric ozone reduction during a clear day at the summer solstice (10.00 kJ m<sup>-2</sup> UV-B<sub>BE</sub>) according to a mathematical model of Madronich et al. (1995). Total daily photosynthetic photon fluence (PPF between 400 and 700 nm) under lamp fixtures was 90% of that above the lamps.

## 2.3. Measurements and statistical analyses

Fifteen main shoots per plot were used to observe plant height, measured as the distance from the soil surface to shoot tip at 40 DAP (days after planting) and 55 DAP, and to spike tips at ripening stage.

Plants in two subplots of  $0.5 \text{ m} \times 0.5 \text{ m}$  each were harvested from each plot to determine tiller number per subplot at 40 DAP, leaf area index (LAI) at 55 DAP, shoot biomass per subplot and grain yield per subplot at ripening stages. Total number of tillers produced were recorded. Total leaves and a subsample

of 15 leaves per subplot were collected at 55 DAP, and area per leaf (LA) of this subsample was measured with a Li-Cor 3100 (Li-Cor, Lincoln, NE, USA) area meter, then all leaves were oven dried at  $68^{\circ}$ C for 68 h and weighed. A regression relationship was developed between leaf weight and leaf area (r=0.6513, P<0.01). This linear regression was used to determine total LA per subplot, then LAI was determined. LAI is leaf area per unit ground area. Shoots and grain were oven dried at  $68^{\circ}$ C for 68 h and weighed.

The response index according to Dai et al. (1994) and Teramura and Murali (1986) was used to evaluate the overall response of wheat to enhanced UV-B radiation and was calculated as follows:

$$RI = \left(\frac{PHt - PHc}{PHc} + \frac{LAIt - LAIc}{LAIc} + \frac{TNt - TNc}{TNc} + \frac{SWt - SWc}{SWc} + \frac{GYt - GYc}{GYc}\right) \times 100\%$$

where, RI is the response index, PH the plant height, LAI the leaf area index, TN the tiller number, SW the shoot weight and GY the grain yield under t UV-B radiation and, c the control.

Statistical differences between means of control and UV-B radiation treatment of any measured parameter were determined by t-test at the P<0.05 or P<0.01 level.

### 3. Results

## 3.1. Plant height

UV-B radiation had obvious effect on plant height of the cultivars at 40 DAP, 55 DAP and ripening stage under field conditions (Table 1). At 40 DAP, UV-B radiation had a positive effect on 8 cultivars, and a negative effect on Longchun 8139 (*P*<0.01) and Longchun 15 (*P*<0.01). At 55 DAP, under UV-B radiation, plant height of Fan 19 (*P*<0.01), Yunmai 39 (*P*<0.01) and Bi 90-5 (*P*<0.05) increased significantly, while plant height of Longchun 8139 and MY 94-9 decreased significantly (*P*<0.01). At ripening stage, UV-B radiation increased height of 6 cultivars, and significantly decreased height of 6 cultivars. Table 1 reveals that 8, 3 and 6 cultivars of exhibited positive effects, while 2, 2 and 6 showed negative effects at 40 DAP, 55 DAP and ripening stage. Out of 20 cultivars,

Table 1
Intraspecific sensitivity to UV-B radiation based on plant height (cm) of 20 wheat cultivars under field conditions

Cultivar name	40 DAP			55 DAP			Ripening stage		
	Control	+UV-B	Change (%)	Control	+UV-B	Change (%)	Control	+UV-B	Change (%)
Bi 90-5	38.15	45.75	19.92**	42.90	51.80	20.75*	61.47	71.07	15.62**
Fengmai 24	44.30	48.45	9.37	72.10	72.50	0.55	63.03	69.74	10.65**
YV 97-31	36.60	38.15	4.23	60.80	61.20	0.66	52.67	60.20	14.30**
Fan 19	34.05	39.80	16.89**	40.30	45.40	12.66**	68.00	64.90	-4.52
Chuxiong 8807	44.00	39.80	-9.55	67.70	64.20	-5.17	66.07	65.90	-0.26
Mianyang 20	36.05	41.10	14.01**	47.20	50.70	7.42	73.27	66.44	$-9.32^{**}$
Dali 905	42.25	50.40	19.29**	65.30	69.50	6.43	57.17	62.09	8.61**
Qian 14	38.05	46.90	23.26**	51.00	53.90	5.69	81.91	71.05	-14.43
Wenmai 3	52.70	54.20	2.85	76.50	77.40	1.18	61.57	66.77	8.45
Yunmai 39	39.75	47.10	18.49**	43.90	49.70	13.21**	71.43	72.25	1.15
Mianyang 26	38.15	41.30	8.26	56.50	55.30	-2.12	59.20	66.93	13.06
Wenmai 5	44.85	47.80	6.58	77.80	74.80	-3.86	68.73	70.10	1.99
Liaochun 9	49.90	55.40	11.02**	97.70	101.60	3.99	79.35	91.85	15.75**
Lanzhou 80101	53.45	56.00	4.71	89.30	90.10	0.78	74.43	81.83	9.94**
Long 8425	55.95	61.20	9.38**	86.70	86.10	-0.69	78.77	71.67	$-9.01^{**}$
Longchun 8139	51.60	45.75	$-11.34^{**}$	89.30	79.80	$-10.64^{**}$	89.41	88.41	-1.12
Longchun 16	49.50	51.85	4.75	86.30	93.90	-2.78	78.10	72.57	$-7.08^{*}$
MY 94-4	47.20	45.50	-3.60	65.10	56.60	$-13.06^{**}$	92.00	80.73	$-12.25^{**}$
Longchun 15	58.10	45.15	$-22.29^{**}$	63.70	64.60	1.41	87.52	80.05	$-8.54^{**}$
Huining 18	47.80	45.80	-4.18	59.60	54.10	9.23	90.25	80.37	$-11.33^{**}$

<sup>\*</sup> Significant difference between control and UV-B radiation at P<0.05 according to t-test. Measurements were made on 15 main shoots per plot.

10, 5 and 12 had significant difference (P<0.01 or P<0.05) at 40 DAP, 55 DAP and ripening stage, respectively. Sensitivity in plant height of 20 wheat cultivars to enhanced UV-B radiation varied with time as follows: ripening stage>40 DAP>55 DAP.

## 3.2. Leaf area and leaf area index

Under field conditions at 55 DAP, LA and LAI of 20 wheat cultivars were affected by UV-B radiation (Table 2). Out of 20 cultivars, Longchun 15 had a positive effect on LA (*P*<0.01), and another 4 cultivars, namely, Chuxiong 8807 (*P*<0.01), Fengmai 24 (*P*<0.05), YV 97-31 (*P*<0.05) and Fan 19 (*P*<0.05) had negative effects on LA. Out of 20 cultivars, UV-B radiation increased LAI of Dali 905 (*P*<0.01), and decreased LAI of 8 cultivars. Table 2 shows that LA of 5 cultivars and LAI of 9 cultivars had significant difference between control and UV-B radiation. Under UV-B radiation, Sensitivity in LAI was greater than for LA.

#### 3.3. Tiller number

Effects of enhanced UV-B radiation on tiller number at 40 DAP are shown in Table 3. Out of 20 cultivars, tiller numbers of Dali 905 (P<0.01), Mianyang 20 (P<0.05) and Wenmai 3 (P<0.05) were significantly increased by UV-B radiation, and those of 11 cultivars were significantly decreased. Table 3 shows that out of 20 cultivars, tiller number of 14 cultivars had significant differences, i.e. tiller number was sensitive to enhanced UV-B radiation.

## 3.4. Shoot biomass and grain yield

The effect of UV-B radiation on shoot biomass and grain yield of 20 wheat cultivars under field conditions is presented in Table 3. Out of 20 cultivars, shoot biomass of 13 cultivars and grain yield of 15 cultivars were significantly decreased. UV-B radiation had no positive effect on shoot biomass and grain yield. In

<sup>\*\*</sup> Significant difference between control and UV-B radiation at P<0.01 according to t-test. Measurements were made on 15 main shoots per plot.

Table 2
Intraspecific sensitivity to UV-B radiation based on area per leaf (cm<sup>2</sup>) and leaf area index (LAI) of 20 wheat cultivars under field conditions at 55 DAP

Cultivar name	LA			LAI			
	Control	+UV-B	Change (%)	Control	+UV-B	Change (%)	
Bi 90-5	27.11	23.61	-12.92	5.75	4.22	$-26.72^{*}$	
Fengmai 24	31.10	24.69	$-20.58^{*}$	5.75	3.40	$-40.98^{*}$	
YV 97-31	25.49	20.31	$-20.39^{*}$	5.63	4.76	-15.46	
Fan 19	27.71	22.64	$-18.14^{*}$	10.81	6.96	$-35.62^{*}$	
Chuxiong 8807	34.70	20.61	$-40.63^{**}$	11.19	5.04	$-55.02^{**}$	
Mianyang 20	32.31	29.11	-9.91	11.40	11.61	1.90	
Dali 905	26.90	27.80	3.35	4.00	4.76	18.89	
Qian 14	32.11	27.50	-14.33	8.15	7.05	-13.42	
Wenmai 3	23.59	23.80	0.85	3.79	4.17	9.97	
Yunmai 39	26.01	23.81	-8.46	7.51	4.70	$-37.54^{*}$	
Mianyang 26	25.01	23.80	-4.83	6.10	6.18	1.33	
Wenmai 5	25.90	24.21	-6.56	4.55	4.36	-4.16	
Liaochun 9	22.01	23.40	6.36	3.40	3.52	5.48	
Lanzhou 80101	26.71	27.81	4.12	4.45	4.35	-2.14	
Long 8425	23.51	24.20	2.98	3.40	4.08	2.18	
Longchun 8139	35.30	30.62	-13.31	8.28	5.92	$-28.45^{*}$	
Longchun 16	21.29	17.70	-16.90	3.24	2.04	$-37.06^{*}$	
MY 94-4	27.80	29.20	5.04	11.92	10.09	-15.34	
Longchun 15	29.80	41.59	39.60**	10.98	10.87	-1.03	
Huining 18	28.19	26.60	-5.67	11.01	6.80	$-36.65^{*}$	

<sup>\*</sup> Significant difference between control and UV-B radiation at P<0.05 according to t-test. Leaf area was measured on the last 15 leaves per plot. LAI was determined on 3 plots.

general, shoot biomass and grain yield were sensitive to enhanced UV-B radiation.

## 3.5. Response index

The response index is an integration of the effect on plant height, LAI, tiller number, shoot biomass and grain yield, which could reflect the overall sensitivity of wheat cultivars to enhanced UV-B radiation. In this case, 19 out of 20 cultivars had negative response indices, indicating overall inhibition of UV-B radiation on wheat growth (Table 4). Huining 18 was most adversely affected (RI –231.91), while only Dali 905 showed positive response (RI 74.71). Across all cultivars tested in the present study, 9 cultivars had negative response indices lower than –120, the most sensitive cultivars were Huining 18, Longchun 16, Chuxiong 8807, Fengmai 24, Yunmai 39, MY 94-9, Fan 19, Longchun 15 and Longchun 8139. The seven

most tolerant cultivars were Dali 905, Liaochun 9, Mianyang 20, Mianyang 26, Wenmai 3, Bi 90-5, Lanzhou 80101, with response indices higher than -70.

#### 4. Discussion

This is the first report to identify intraspecific responses in crop growth and yield of wheat cultivars to enhanced UV-B radiation under field conditions. This study supports earlier findings of intraspecific responses in maize and wheat (Biggs and Kossuth, 1978), horsebean (Bennett, 1981), cucumber (Murali and Teramura, 1986), soybean (Teramura and Murali, 1986; Sullivan and Teramura, 1990), rice (Teramura et al., 1991; Barnes et al., 1993; Dai et al., 1994).

Reduction in plant height has often been used as an index to assess the degree of UV-B radiation sensi-

<sup>\*\*</sup> Significant difference between control and UV-B radiation at *P*<0.01 according to *t*-test. Leaf area was measured on the last 15 leaves per plot. LAI was determined on 3 plots.

Table 3
Intraspecific sensitivity to UV-B radiation based on tiller number, shoot biomass and grain yield of 20 wheat cultivars under field conditions

Cultivar name	Tiller number (per m <sup>-2</sup> )			Shoot biomass (g m <sup>-2</sup> )			Grain yield (g m <sup>-2</sup> )		
	Control	+UV-B	Change (%)	Control	+UV-B	Change (%)	Control	+UV-B	Change (%)
Bi 90-5	144	86	-40.28 <sup>*</sup>	450	460	2.22	112.5	115.0	2.28
Fengmai 24	154	59	$-61.69^{**}$	800	320	$-60.00^{**}$	278.3	87.2	$-68.67^{**}$
YV 97-31	108	127	17.59	780	450	$-42.31^{*}$	281.7	146.2	$-48.10^{**}$
Fan 19	378	243	$-35.71^*$	750	470	$-37.33^{*}$	127.6	54.2	$-57.51^{**}$
Chuxiong 8807	202	78	$-61.38^{**}$	1000	460	$-54.00^{**}$	378.5	172.5	-54.43**
Mianyang 20	250	327	30.80*	680	570	-16.18	171.6	134.2	-21.79
Dali 905	54	106	96.30**	740	620	-16.22	283.0	192.0	$-32.87^{*}$
Qian 14	210	215	2.38	760	510	$-32.89^{*}$	139.9	84.5	$-39.96^{*}$
Wenmai 3	105	138	31.43*	700	480	$-31.43^{*}$	229.5	124.2	$-45.88^{*}$
Yunmai 39	320	150	$-53.12^{**}$	580	330	$-43.10^{*}$	87.3	27.2	$-68.83^{**}$
Mianyang 26	256	288	12.50	590	540	-8.47	238.0	150.3	$-36.85^{*}$
Wenmai 5	90	100	11.11	870	640	-26.44	340.0	167.9	$-50.62^{**}$
Liaochun 9	63	60	-4.76	820	710	-13.14	302.5	255.5	-15.54
Lanzhou 80101	68	41	$-39.71^{*}$	1060	860	-18.87	400.5	3123	-22.02
Long 8425	63	60	-4.76	1040	630	$-39.42^{*}$	444.0	266.6	$-39.95^{*}$
Longchun 8139	198	108	$-45.45^{**}$	1500	1010	$-32.67^{*}$	497.5	403.5	-18.89
Longchun 16	121	24	$-80.17^{**}$	700	370	$-47.14^{**}$	242.5	114.5	$-52.78^{**}$
MY 94-4	371	241	$-35.04^*$	1460	690	$-52.74^{**}$	475.6	172.3	$-63.77^{**}$
Longchun 15	386	191	$-50.52^{**}$	1220	660	$-45.90^{**}$	265.8	129.1	$-51.43^{**}$
Huining 18	423	198	$-53.19^{**}$	1660	720	$-56.63^{**}$	154.5	40.0	$-74.11^{**}$

<sup>\*</sup> Significant difference between control and UV-B radiation at *P*<0.05 according to *t*-test. Tiller number, shoot biomass and grain yield are expressed on a ground area basis. Measurements were made on 3 subplots per plot. Tiller number express the total tillers produced at tillering stage. Shoot biomass and grain were determined at ripening stage.

tivity (Biggs and Kossuth, 1978). Although UV-B radiation had no consistent effect on wheat height in a greenhouse experiment (Teramura, 1980), in this first study, UV-B radiation had clear effect on height of 20 wheat cultivars at 40 DAP, 55 DAP and ripening stage (Table 1). Sensitivity in height of 20 wheat cultivars to enhanced UV-B radiation was in the order: ripening stage>40 DAP>55 DAP; height at ripening stage was used in the response index. UV-B radiation significantly dwarfed spring wheat (Lanzhou 80101), primarily due to shorter internodes rather than node number (Li et al., 1998). This can be due to a photooxidative destruction of the phytohormone indole acetic acid followed by reduced cell wall extensibility as demonstrated in sunflower seedlings (Ros and Tevini, 1995). The levels of ethylene, which promotes radial growth and reduces elongation, are increased after irradiation with UV-B (Caldwell et al., 1995).

The mechanism of UV-B radiation increasing plant height remains unclear.

Table 2 shows that LA of 5 cultivars and LAI of 9 cultivars responded significantly to UV-B radiation. Under UV-B radiation, sensitivity in LAI was greater than for LA and so was used as a parameter for selection of UV-B tolerance. UV-B radiation may directly affect cell division and some intrinsic growth characteristics (Beggs et al., 1985). It may be associated with many of the changes observed following UV-B exposure, such as the changes in leaf area dynamics and tiller. LAI was contributed by area per leaf and leaf number per subplot. In this study, leaf number per subplot decreased with tiller number. This explains why LAI was more sensitive than LA under UV-B radiation.

Out of 20 cultivars, tiller number of 14 was significantly different under UV-B radiation (Table 3).

<sup>\*\*</sup> Significant difference between control and UV-B radiation at *P*<0.01 according to *t*-test. Tiller number, shoot biomass and grain yield are expressed on a ground area basis. Measurements were made on 3 subplots per plot. Tiller number express the total tillers produced at tillering stage. Shoot biomass and grain were determined at ripening stage.

Table 4
Response index (RI) of 20 wheat cultivars under enhanced UV-B radiation, together with their origin and habitat

$Rank^a$	Cultivar name	Origin	Habitat	RI	
1	Dali 905	South China	Upland, winter	74.71	
2	Liaochun 9	North China	Upland, spring	-12.48	
3	Mianyang 20	South China	Lowland, winter	-15.21	
4	Mianyang 26	South China	Lowland, winter	-18.43	
5	Wenmai 3	South China	High elevation, spring	-27.46	
6	Bi 90-5	South China	Lowland, winter	-49.10	
7	Lanzhou 80101	North China	Upland, spring	-68.52	
8	YV 97-31	South China	Upland, winter	-73.98	
9	Wenmai 5	South China	Lowland, winter	-81.20	
10	Long 8425	North China	low elevation, spring	-90.96	
11	Qian 14	South China	Lowland, winter	-98.32	
12	Longchun 8139	North China	Upland, spring	-126.58	
13	Longchun 15	North China	Lowland, spring	-157.42	
14	Fan 19	South China	Lowland, winter	-170.68	
15	MY 94-9	Mexico	High elevation, spring	-174.14	
16	Yunmai 39	South China	Lowland, spring	-201.44	
17	Fengmai 24	South China	Lowland, winter	-220.69	
18	Chuxiong 8807	South China	Upland, winter	-224.09	
19	Longchun 16	North China	Upland, high elevation, spring	-224.23	
20	Huining 18	North China	Upland, spring	-231.91	

<sup>&</sup>lt;sup>a</sup> Ranking 1-20 is in the order of increasing sensitivity to UV-B radiation.

Although UV-B radiation increased secondary tiller number of isolated wheat plants in the greenhouse (Teramura, 1980; Barnes et al., 1990), in another experiment of ours, under field conditions, it significantly decreased tiller number, while UV-B radiation exacerbated intraspecific competition and self-thinning of a spring wheat crop, increasing dead shoot number. In this way, head-bearing shoot number, LAI, total biomass and grain yield were decreased at ripening stage (Li et al., 1998). UV-B radiation also decreased tiller number in 14 of 16 rice cultivars (Teramura et al., 1991).

Shoot biomass is a good indictor of the effects of UV-B radiation on growth (Teramura, 1983). Decreases in shoot biomass in this study are similar to those found in greenhouse (Teramura, 1980, 1983; Barnes et al., 1990) and in field (Li et al., 1998). Other greenhouse experiments have reported either increase or no changes in biomass of wheat with enhanced UV-B radiation (Teramura, 1983).

Very little is known about UV-B effects on grain yield of wheat (Teramura, 1983), with only a 8% decrease reported in a greenhouse study (Teramura et al., 1990). In another field study of ours, grain yield

of wheat was decreased significantly by UV-B radiation (Li et al., 1998). Grain yield is economically important and so was included as a parameter of the response index. Besides, comparisons between greenhouse and field observations revealed that UV-B sensitivity based on seed yield of soybean differs markedly, indicating that field validations are ultimately necessary for assessing the potential impacts of increased solar UV-B radiation (Teramura and Murali, 1986).

Response indices have been established as useful indicators of plant sensitivity to enhanced UV-B radiation (Dai et al., 1994). Comparability between studies is limited, however, because the various experiments have used different combinations of parameters. Also, in many cases parameters were measured on isolated plants, e.g. on cucumber and rice during short-term experiments in greenhouses (Murali and Teramura, 1986; Teramura et al., 1991; Barnes et al., 1993; Dai et al., 1994). Only in the soybean study of Teramura and Murali (1986) was grain yield included as a parameter. These studies have shown that plants respond differently to UV-B in each environment due to differences in genotype,

growing conditions, stage of growth, length of exposure to UV-B, and the ratio of incident PPF to UV-B (Teramura et al., 1991, 1985) and the fact that the responses of crops to UV-B are more complicated than those of isolated plants (Li et al., 1998). In this study, response indices were calculated from parameters measured on crops grown in the field and included grain yield as one of the parameters. Consequently, the results should provide realistic assessments of intraspecific responses among the 20 wheat cultivars to enhanced UV-B radiation.

Because ambient UV-B radiation level is great at lower latitude than that at higher latitude, it is generally assumed that crop cultivars originating near the equator are more tolerant to UV-B radiation. In this study, out of 7 tolerant cultivars, 5 cultivars originated from South China (low latitude). The most sensitive cultivars, i.e. Huining 18 (RI 231.91) and Longchun 16 (RI 224.23), originated in North China (high latitude). Similarily, rice cultivars originating from regions with high ambient UV-B are not necessarily the more tolerant to enhanced UV-B radiation (Barnes et al., 1993; Dai et al., 1994). These UV-B tolerant cultivars identified in our study might be used as possible donors for breeding program, however, the genetic basis for these differences must be further examined.

In conclusion, enhanced UV-B radiation had significant effect on plant height, LAI, tiller number, shoot biomass, and grain yield of wheat crops under field conditions. The response index presented here showed that wheat is potentially a UV-B sensitive species, although wheat has been previously shown to be UV-B resistant (Biggs and Kossuth, 1978). UV-B sensitivity might be associated with UV-B radiation influences and long-term accumulation (Li et al., 1998). Wheat is an economically important crop, its intraspecific response to UV-B radiation under field conditions is not clearly understood. Effects of UV-B radiation on plants are related to other environmental factors, including PPF, CO<sub>2</sub>, drought, phosphorus nutrition, temperature, ozone fumigation and heavy metal (Teramura et al., 1990; Caldwell et al., 1995), so, further field studies and an improved understanding of the relationship between UV-B radiation effectiveness and other environmental variables would greatly enhance our ability to more realistically assess

intraspecific responses of wheat to increased levels of UV-B radiation.

### Acknowledgements

This work was supported by the National Natural Science Foundation of China, the National Research Foundation for Post-Doctoral Research in China, Applied Base Research Foundation of Yunnan Province, China, and Research Foundation for academic leader in Yunnan Province, China. We wish to thank Elisabeth Kessler, the Editor-in-Chief of Ambio, for providing Ambio Vol. 24, Nos. 2 and 3, 1995.

#### References

- Barnes, P.W., Jordan, P.W., Gold, W.G., Flint, S.D., Caldwell, M.M., 1988. Competition, morphology and canopy structure in wheat (*Triticum aestivum* L.) and wild oat (*Avena fatua* L.) exposed to enhanced ultraviolet-B radiation. Funct. Ecil. 2, 319–330.
- Barnes, P.W., Flint, S.D., Caldwell, M.M., 1990. Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. Am. J. Bot. 77, 1354–1360.
- Barnes, P.W., Maggard, S., Holman, S.R., Vergara, B., 1993. Intraspecific variation in sensitivity to UV-B radiation in rice. Crop Sci. 33, 1041–1046.
- Beggs, C.J., Schneider-Zeibert, R., Wellman, E., 1985. UV-B radiation and adaptive mechanisms in plants. In: Worrest, R.C. (Ed.), Stratospheric Ozone Reduction, Solar Ultraviolet Radiation and Plant Life. Springer, Berlin, pp. 235–250.
- Bennett, J.H., 1981. Photosynthesis and gas diffusion in leaves of selected crop plants exposed to ultraviolet-B radiation. J. Environ. Qual. 10, 271–275.
- Biggs, R.H., Kossuth, S.V., 1978. Impact of solar UV-B radiation on crop productivity. Final report of UV-B biological and climate effects research. Terrestrial FY 77, 11–77.
- Caldwell, M.M., 1971. Solar UV-B irradiation and the growth and development of higher plants. In: Giese, A.C. (Ed.), Photophysiology, Vol. 6. Academic Press, New York, pp. 131–171.
- Caldwell, M.M., Flint, S.D., 1994. Stratospheric ozone reduction, solar UV-B radiation and terrestrial ecosystem. Climate Change 27, 375–394.
- Caldwell, M.M., Teramura, A.H., Tevini, M., Bornman, J.F., Bjorn, L.O., Kulandaivelu, G., 1995. Effects of increased solar ultraviolet radiation on terrestrial plants. Ambio 24, 166–173.
- Dai, Q.J., Peng, S.B., Chavez, A.Q., Vergara, B.S., 1994. Intraspecific responses of 188 rice cultivars to enhanced UVB radiation. Environ. Exp. Bot. 34, 422–433.
- Gold, W.G., Caldwell, M.M., 1983. The effects of ultraviolet-B radiation on plant competition in terrestrial ecosystems. Physiol. Plant 58, 435–444.

- Kerr, R.A., 1993. The ozone hole reaches a new low. Science 262, 501.
   Korner, C., 1993. CO<sub>2</sub> fertilization: the great uncertainty in future vegetation development. In: Soloman, A.M., Shugart, H.H. (Eds.), Vegetation Dynamics and Global Change. Chapman & Hall, London, pp. 53–70.
- Li, Y., Yue, M., Wang, X.L., 1998. Effects of enhanced ultraviolet-B radiation on crop structure, growth and yield components of spring wheat under field conditions. Field Crops Res. 57, 253–263.
- Li, Y., Yue, M., Wang, X.L., Hu, Z.D., 1999. Competition and sensitivity of wheat and wild oat exposed to enhanced UV-B radiation at different densities under field conditions. Environ. Exp. Bot. 41, 47–55.
- Lydon, J., Teramure, A.H., Summers, E.G., 1986. Effects of ultraviolet-B radiation on growth and productivity of fieldgrown soybean. In: Worrest, R.C. (Ed.), Stratospheric Ozone Reduction, Solar Ultraviolet Radiation and Plant Life. Springer, Berlin, pp. 313–325.
- Madronich, S., Mckenzie, R.L., Caldwell, M.M., Bjorn, L.O., 1995. Changes in ultraviolet radiation reaching the earth's surface. Ambio 24, 143–153.
- Molina, M.J., Molina, L.T., 1992. Stratospheric ozone. ACS Symposium Series, Vol. 6. American Chemical Society, Washington, DC, pp. 24–35.
- Murali, N.S., Teramura, A.H., 1986. Intraspecific differences in Cucumis sativus sensitivity to ultraviolet-B radiation. Physiol Plant 68, 673–677.

- Ros, J., Tevini, M., 1995. Interaction of UV-radiation and IAA during growth of seedling and hypocotyl segments of sunflower. J. Plant Physiol. 146, 295–302.
- Sullivan, J.H., Teramura, A.H., 1990. Field study of the interaction between solar ultraviolet-B radiation and drought on photosynthesis and growth in soybean. Plant Physiol. 92, 141–146.
- Teramura, A.H., 1980. Effects of ultraviolet-B irradiances on soybean. I. Importance of photosynthetically active radiation in evaluating ultraviolet-B irradiance effects on soybean and wheat growth. Physiol. Plant 48, 333–339.
- Teramura, A.H., 1983. Effects of ultraviolet-B radiation on the growth and yield of crop plants. Physiol. Plant 58, 415–427.
- Teramura, A.H., Murali, N.S., 1986. Intraspecific differences in growth and yield of soybean exposed to ultraviolet-B radiation under greenhouse and field conditions. Environ. Exp. Bot. 26, 89–95.
- Teramura, A.H., Sullivan, J.H., Ziska, L.H., 1990. Interaction of elevated ultraviolet-B radiation and CO<sub>2</sub> on productivity and photosynthetic characteristics in wheat, rice and soybean. Plant Physiol. 94, 470–475.
- Teramura, A.H., Ziska, L.H., Sztein, A.E., 1991. Changes in growth and photosynthetic capacity of rice with increased UV-B radiation. Physiol. Plant 83, 373–380.
- Yue, M., Li, Y., Wang, X.L., 1998. Effects of enhanced ultraviolet-B radiation on plant nutrients and decomposition of spring wheat under field conditions. Environ. Exp. Bot. 40, 187–196.