Available online at www.sciencedirect.com
ScienceDirect
South African Journal of Botany 76 (2010) 493–498
SOUTH AFRICAN JOURNAL OF BOTANY
www.elsevier.com/locate/sajb

Intraspecific variation in sensitivity to ultraviolet-B radiation in endogenous hormones and photosynthetic characteristics of 10 wheat cultivars grown under field conditions

Yuan Li [a], Lilian He [b], Yanqun Zu [a,*]

[a] *Eco-environment Research Institute, College of Resources and Environment, Yunnan Agricultural University, Kunming 650201, PR China*
[b] *College of Agronomy and Biotechnology, Yunnan Agricultural University, Kunming 650201, PR China*

Received 3 February 2010; received in revised form 15 March 2010; accepted 18 March 2010

Abstract

Field studies were conducted to determine the potential of altering endogenous hormones and photosynthetic characteristics and intraspecific variation in sensitivity of 10 wheat (*Triticum aestivum*) cultivars (four tolerant, two middle sensitive and four sensitive) to enhanced ultraviolet-B (UV-B, 280–315 nm) radiation under field conditions. The supplemental UV-B radiation was 5.00 kJ m^{-2}, simulating a depletion of 20% stratospheric ozone. Responses were cultivar-specific. Out of the 10 tested wheat cultivars, six showed significant decrease in IAA content. UV-B radiation significantly increased ZR content in two wheat cultivars and significantly decreased in five cultivars. ABA content of three wheat cultivars was increased significantly, while that of five cultivars was decreased significantly. UV-B radiation significantly increased the stomatal conductance of three cultivars, and significantly decreased that of four cultivars. Intercellular CO_2 concentrations were significantly increased in five cultivars and significantly decreased in one cultivar (Mianyang 20). Transpiration rate of three cultivars significantly increased, while that of three cultivars significantly decreased. UV-B radiation significantly decreased the net photosynthetic rate of six cultivars. Intraspecific differences were found for the different measured parameters. For seven measured parameters, UV-B radiation had significant effects on five wheat cultivars, while no effect on the others. Significant correlations were observed between net photosynthetic rate and stomatal conductance, intercellular CO_2 concentrations and transpiration rate in eight cultivars. UV-B radiation might change stomatal conductance, intercellular CO_2 concentrations and transpiration rate, thus resulting in changes in net photosynthetic rate.

Keywords: Endogenous hormones; Field conditions; Intraspecific differences; Photosynthetic characteristics; *Triticum aestivum*; UV-B radiation

1. Introduction

Scientific assessment of ozone depletion provides clear evidence that stratospheric ozone for the period 1997–2001 was 3–6% less than pre-1980 average values. An increase in UV peak in response to decreasing ozone has been detected in New Zealand from summer 1978–1979 through to 1999–2000 (UNEP, 2002). Terrestrial plants are experiencing increased UV-B levels. During recent decades, numerous investigations concerning the influence of UV-B radiation on different plants species were conducted, and most were negatively affected (Kakani et al., 2003). Common observed UV-B effects on plants include physiological damage to the photosynthetic apparatus (Musil et al., 2003; Correia et al., 2005), IAA (Jansen et al., 2001), Gas, ZR, and ABA (Yang et al., 2004), ethylene (Predieri et al., 1993), damage to DNA (Hidema et al., 1999; Schmitz and Weissenbock, 2003), alteration in protein content and enzyme activity (Murakami et al., 2004), effects on membranes (An et al., 2000) and changed leaf chemistry (Takahama and Oniki, 2000). Morphological damage may also result and are evidenced by plant stunting, leaf discolouration or decreased vegetative biomass and grain yield (Li et al., 2000a; Kakani et al., 2003).

Abbreviations: ABA, abscisic acid; GA, gibberellic acid; IAA, indole-3-acetic acid; LAI, Leaf Area Index; MDA, malondialdehyde; PPF, photosynthetic photon fluence; RI, Response Index; SOD, superoxide dismutase; UV-B, ultraviolet-B; UV-B_{BE}, biologically effective UV-B; ZR, zeatin riboside.

* Corresponding author. Tel.: +86 871 5227942; fax: +86 871 5227550.
E-mail address: zuyanqun@yahoo.com.cn (Y. Zu).

0254-6299/$ - see front matter © 2010 SAAB. Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.sajb.2010.03.005

Sensitivity to UV-B radiation varies considerably within and between plant species. Intraspecific responses in maize (Correia et al., 1999), wheat (Li et al., 2000a,b; Zu et al., 2004), soybean (Teramura et al., 1990; D'Surney et al., 1993; Li et al., 2002), and rice (Dai et al., 1994; Kumagai et al., 2001) have been reported. Little is known about intraspecific differences in endogenous hormones and photosynthetic characteristics of plants to enhanced UV-B radiation. Due to our lack of understanding of the role of intraspecific response differences to UV-B radiation, further studies on its importance are needed.

In the past three decades, most UV-B research has been conducted as short-term experiments in crop growth chambers and greenhouses, where the unnatural spectral radiation balance can lead to unrealistic conclusions. The plant response to UV-B radiation may be exaggerated relative to field conditions (Zu et al., 2004). On the other hand, most studies on UV-B radiation effects on crops were undertaken in the past on cell level, organ level and isolated plant level. However, the responses of plant crop to UV-B are more complicated than those of isolated plants (Teramura et al., 1990; D'Surney et al., 1993). Thus, community-level field experimentation is needed to evaluate realistic consequences of increased solar UV-B resulting from ozone reduction (Li et al., 2002).

Wheat is one of the major world food crops, the effects of enhanced UV-B radiation on growth, development, morphology, physiology, plant nutrients, leaf quality, total biomass, yield decomposition, and intraspecific differences to UV-B radiation have been reported (Li et al., 1998; Yue et al., 1998; Li et al., 2000a,b). Unfortunately, few studies have been conducted under field conditions. In our previous research, 10 wheat (*Triticum aestivum*) cultivars were chosen according to RI (Response Index, an integration of the effects of UV-B radiation on plant height, LAI, tiller number, shoot biomass and grain yield of wheat) from 20 wheat cultivars with different UV-B radiation backgrounds (latitude or elevation) (Li et al., 2000a). In this study, we grew 10 wheat cultivars in field conditions under ambient and supplemental levels of UV-B radiation with the objectives of: (1) determine if UV-B radiation affects endogenous hormones and photosynthetic characteristics of wheat under field conditions; and (2) evaluate intraspecific variations in responses of endogenous hormones and photosynthetic characteristics of 10 wheat cultivars to UV-B radiation in the field. We hypothesized that enhanced UV-B radiation would affect endogenous hormones and photosynthetic characteristics of wheat and would result in intraspecific variations in responses of endogenous hormones and photosynthetic characteristics to UV-B radiation under field conditions.

2. Materials and methods

2.1. Plant materials and growth conditions

The field experiment was conducted on an upland red soil at Yunnan Agricultural University, Kunming, China. No fertilization was necessary during the season. In our previous experiment, 10 wheat (*Triticum aestivum*) cultivars were chosen for this experiment according to RI (Response Index) from 20 wheat cultivars with different UV-B radiation background (latitude or elevation) (Li et al., 2000a). Ten cultivars included four tolerant cultivars (Liaochun 9, Mianyang 20, Mianyang 26 and Wenmai 3), two moderately sensitive cultivars (Wenmai 5 and Longchun 15), and four sensitive cultivars (Yunmai 39, Fengmai 24, Longchun 16 and Huining 18). Seeds of the 10 most common wheat cultivars in China were obtained from Yunnan Academy of Agricultural Sciences and Gansu Academy of Agricultural Sciences. Seeds were sown in rows spaced 0.2 m apart at a density of 80 seeds m^{-1} in 60 plots of 2×1 m each on 26 July 2002. Five border rows were sown round each plot in order to minimize microclimatic heterogeneity. The overall experimental design was a randomized complete block with two UV-B treatments and three replications. At the three-leaf stage, plants were thinned to 60 m^{-1} for uniformity in growth. This planting density is common sowing practice in 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. The wavelength of sunlamps was 280–315 nm and maximum radiation was 310 nm (Li et al., 2000a). 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 (absorbs all radiation <290 nm) for supplemental UV-B radiation or 0.13 mm polyester plastic films (absorbs all radiation <320 nm) as a control (Sullivan and Teramura, 1990). Cellulose diacetate filters were pre-solarized 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 Inc. Orlando, Florida, 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_{BE}. Six lamps were installed above each plot. The supplemental UV-B level was similar to that which would be experienced at Kunming (25°N, 1950 m altitude) with a 20% stratospheric ozone reduction during a clear day on the summer solstice (10.00 kJ m^{-2} UV-B_{BE}), according to the mathematical model of Madronich et al. (1995). Plants were irradiated for 7 h daily from three-leaf stage to ripening stage, centred around solar noon. Plants under polyester-filtered lamps received only ambient levels of UV-B radiation (10.00 kJ m^{-2} UV-B_{BE} 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 above the plants was adjusted weekly to maintain a distance of 0.40 m between the lamps and the top of the plants, and provided supplemental irradiances of 5.00 effective kJ m^{-2} UV-B_{BE}. Total daily photosynthetic photon flux (PPF between 400 and 700 nm) under lamp fixtures was 90% of that above the lamps.

2.3. Endogenous hormone measurement

The endogenous hormone contents of the first three fully expanded leaves from the top to the base of the plants were determined in elongation stages of wheat. Two samples were taken from each plot. Samples were immediately frozen in liquid nitrogen and stored at−20 °C until analysis. Extraction and determination of endogenous hormones were performed, as described by Li et al. (2003). Briefly, leaves were ground with 3 ml pre-cooled 80% (v/v) aqueous methanol (containing 10 ml/l butylated hydroxytoluene to prevent oxidation) and extracted overnight at −20 ºC. The crude methanol extracts were centrifuged for 15 min at 16,000 g. One milliliter of the supernatant was purified by passing through C_{18} Sep-Pak Cartridge (Water Corp., Millford, Massachusetts, USA), the eluate was collected and 400 μl of which was dried under N_2. The residue was dissolved in 400 μl PBS (0.01 mol/l, pH 7.4) and submitted to ZR enzyme-linked immunosorbent assays (ELISA, obtained from Nanjing Agricultural University, PR China). A further 400 μl of filtrate was taken and dried under N_2. The residue was dissolved in 200 μl Na_2HPO_4 (pH 9.2), adjusted to pH 8.5 with HCl and partitioned three times with an equal volume of ethyl acetate. The remaining water phase was adjusted to pH 2.5 and extracted three times with an equal volume of ethyl acetate. The ethyl acetate phases were pooled and dried under N_2. The residue was re-dissolved in 200 μl 100% methanol for methylation with ethereal diazomethanol. The solution was dried under N_2 and 400 μl of BPS (0.01 mol/l, pH 7.4), and was then added to the residue for IAA and ABA ELISAs.

IAA and ZR was assayed using polyclonal antibody against IAA and ZR, respectively. ABA was assayed using monoclonal antibody against ABA. The cross-reactivity of IAA, ZR and ABA anti-bodies with hormone (IAA, ZR and ABA) analogues are <18, 10 and 3.5%, respectively. All data are means of six measurements per extract per leaf sample.

2.4. Photosynthetic characteristics measurement

Photosynthetic characteristics of the first three fully expanded leaves from the top to the base of the plants were measured in the elongation stage of wheat. Two measurements were undertaken in each plot. Stomatal conduction, intercellular CO_2 concentrations, transpiration rate and photosynthetic rate were determined with a CI-301 Photosynthesis System (CID, USA) at a photon flux density of 800 μmol m^{-2} S^{-1} from a light source coupled to the leaf chamber at 14:30 in clear sky conditions.

2.5. Statistical analysis

Statistical differences between means of control and UV-B radiation treatment of any measured parameter were analyzed using Student's *t*-test ($P<0.05$, $P<0.01$). Correlation analyses were utilized between measured parameters using SPSS 11.5 for Windows ($P<0.05$, $P<0.01$).

3. Results

3.1. Endogenous hormone contents

Under field conditions, UV-B radiation significantly decreased the IAA content of six cultivars (Mianyang 20, Mianyang 26, Yunmai 39, Fenmai 24, Longchun 16 and Huining 18) (Table 1). For the other four cultivars, no changes in IAA content were observed (Table 1).

The effect of UV-B on ZR content showed intraspecific differences (Table 1). Significant increases in the ZR content of Liaochun 9 and Mianyang 20, significant decreases in five cultivars (Longchun 15, Yunmai 39, Fengmai 24, Longchun 16 and Huining 18), and no effect on the other three cultivars were observed.

Table 1 shows that UV-B radiation had obvious effects on ABA content of most cultivars under field conditions. ABA content of Mianyang 20, Mianyang 26 and Longchun 15 were significantly increased, while that of Wenmai 5, Yunmai 39, Fenmai 24, Longchun 16 and Huining 18 were significantly decreased, and no effects were observed on Liaochun 9 and Wenmai 3.

3.2. Photosynthetic characteristics

UV-B radiation significantly increased stomatal conductance of Fenmai 24, Longchun 16 and Huining 18, significantly decreased that of Mianyang 20, Wenmai 3, Longchun 15 and

Table 1
Intraspecific variations in sensitivity to UV-B radiation based on endogenous hormone content of 10 wheat cultivars under field conditions.

Cultivar	IAA (ng g^{-1})			ZR (ng g^{-1})			ABA (ng g^{-1})		
	Control	+UV-B	% change	Control	+UV-B	% change	Control	+UV-B	% change
Liaochun 9	42.42	38.17	−10.01	64.28	85.27	32.65**	110.10	117.91	7.18
Mianyang 20	68.57	44.15	−35.61**	80.83	98.84	22.28*	109.78	131.74	20.00**
Mianyang 26	64.34	48.07	−25.28*	84.26	92.68	9.99	186.12	248.77	33.66**
Wenmai 3	48.15	49.26	2.30	80.68	68.26	−15.39	107.33	123.24	14.82
Wenmai 5	47.36	50.02	5.61	70.76	80.45	13.69	190.71	164.15	−13.92*
Longchun 15	81.48	76.75	−5.80	82.53	64.43	−21.93*	134.11	167.50	24.90*
Yunmai 39	40.64	35.23	−13.31*	136.2	105.50	−22.54*	159.50	128.61	−19.37*
Fengmai 24	46.07	39.48	−14.11*	102.90	77.27	−24.90*	150.01	96.45	−35.7**
Longchun 16	48.66	39.45	−18.92*	102.63	63.62	−38.02**	241.21	120.02	−50.24**
Huining 18	36.89	32.87	−10.89*	107.89	85.15	−20.08*	247.21	162.75	−34.16**

**,*Significant difference between control and UV-B radiation at $P<0.01$ or $P<0.05$, respectively, by *t*-test. $n=6$. IAA: indole-3-acetic acid; ZR: zeatin riboside; and ABA: abscisic acid.

Yunmai 39, and had no effect on the three other cultivars (Table 2).

The effects of enhanced UV-B radiation on intercellular CO_2 concentrations are presented in Table 2. Intercellular CO_2 concentrations significantly increased in Longchun 15, Yunmai 39, Fengmai 24, Longchun16 and Huining 18, and significantly decreased in Mianyang 20, and were unchanged in the other four cultivars.

The effect of UV-B radiation on transpiration rate showed intraspecific differences (Table 2). Significant increases in transpiration rate of Fengmai 24, Longchun 16 and Huining 18, significant decreases in that of Mianyang 20, Wenmai 3 and Yunmai 39, and no effect on the other four cultivars were observed (Table 2).

Under field conditions, UV-B radiation significantly decreased the net photosynthetic rate of six (Mianyang 20, Longchthun 15, Yunmai 39, Fenmai 24, Longchun 16 and Huining 18) cultivars (Table 2). For the other four cultivars, no effect was observed (Table 2). Significant correlations were observed between net photosynthetic rate and stomatal conductance, intercellular CO_2 concentrations and transpiration rate in eight cultivars, except Liaochun 9 and Wenmai 5 (Table 3).

Table 3
Correlation coefficients (*r*) between net photosynthetic rate and stomatal conductance, intercellular CO_2 concentrations and transpiration rate of 10 wheat cultivars.

Cultivars	Stomatal conductance	Intercellular CO_2 concentrations	Transpiration rate
Liaochun 9	−0.046	−0.42	−0.025
Mianyang 20	0.85*	0.96**	0.92**
Mianyang 26	0.87*	0.65*	0.68*
Wenmai 3	0.93**	−0.85*	0.85*
Wenmai 5	0.38	−0.30	0.21
Longchun 15	0.86*	−0.89**	0.93**
Yunmai 39	−0.91**	−0.98**	−0.94**
Fengmai 24	−0.98**	−0.97**	−0.91**
Longchun 16	−0.93**	−0.80*	−0.96**
Huining 18	0.64*	−0.96**	0.83*

**,*Significant correlation of % change between two measured parameters at $P<0.01$ or $P<0.05$, respectively, calculated using SPSS 11.5 for Windows, $n=6$.

4. Discussion

To our knowledge, this is the first report to suggest the existence of intraspecific responses in endogenous hormones and photosynthetic characteristics of 10 wheat cultivars to enhanced ultraviolet-B radiation under field conditions.

4.1. UV-B and Endogenous hormones

Endogenous hormones play important roles in many plant processes, including growth, development, morphology, stress tolerance and adaptation to stress. Many studies report that enhanced UV-B radiation, as well as other environmental stresses, can induce hormonal changes in vegetative tissues (Yang et al., 2004).

Changes in contents of IAA and ABA of rice (Huang et al., 1998) and wheat (Yang et al., 2000) under UV-B radiation have been reported. In this study, IAA content was decreased by UV-B radiation in 50% of cultivars, thus affecting wheat growth, morphology and biomass (Li et al., 2000a). IAA is decomposed by UV-B radiation directly or by peroxidase stimulated by UV-B radiation (Borman, 1989; Jansen et al., 2001). On the other hand, UV-B radiation increased the activity of H_2O_2 enzymes, thus resulting in decreased IAA contents (Lin et al., 2002). Since IAA is vital for vegetative growth, decomposition of IAA may account for the morphological changes observed in plants when exposed to UV-B radiation (Ros and Tevini, 1995; Huang et al., 1997).

Synthesis of ABA was affected by stress conditions. UV-B radiation affected ABA contents were observed in this study. UV-B radiation may damage chlorophyll and cell membranes, decrease Mg-ATPase activity in membranes and pH in chloroplast, and result in increased ABA contents (Piere and Baschke, 1980). Accumulation in ABA may decrease stomatal conduction (Borman, 1989). Changes in ABA contents were negatively correlated with stomatal conduction in the cultivars ($r=-0.77$, $n=10$, $P<0.01$) with UV-B radiation in this experiment, thus resulting in changes in photosynthesis and growth (Borman, 1989).

Increased ZR under UV-B radiation may play a role in protecting plants from UV-B radiation. It is reported that ZR may improve SOD activity, eliminate peroxy free radicals, protect cell

Table 2
Intraspecific variation in sensitivity to UV-B radiation based on photosynthetic characteristics of 10 wheat cultivars under field conditions.

Cultivars	Stomatal conductance (mmol m^{-2} s^{-1})			Intercellular CO_2 concentrations (μl l^{-1})			Transpiration rate (mmol m^{-2} s^{-1})			Photosynthetic rate (μmol m^{-2} s^{-1})		
	Control	+UV-B	% change	Control	+UV-B	% change	Control	+UV-B	% change	Control	+UV-B	% change
Liaochun 9	320.37	363.87	13.58	316.11	315.97	−0.04	2.14	2.22	3.74	4.51	4.56	1.11
Mianyang 20	171.67	129.67	−24.47*	275.50	266.50	−3.27*	1.84	1.39	−24.46*	5.83	3.87	−33.62*
Mianyang 26	51.53	54.93	6.60	227.10	231.27	1.84	0.96	1.00	4.17	3.93	4.05	3.05
Wenmai 3	160.30	129.07	−19.48*	257.72	262.2	1.75	1.56	1.28	−17.95**	5.67	4.62	−18.52
Wenmai 5	157.30	163.37	3.86	290.33	286.07	−1.47	2.10	2.17	3.33	4.16	4.20	0.96
Longchun 15	171.07	141.17	−17.48*	265.40	276.80	4.28*	1.63	1.44	−11.66	4.71	3.41	−27.60*
Yunmai 39	170.01	140.37	−17.43*	277.53	289.57	4.34**	1.61	1.38	−14.29*	5.21	4.26	−18.23*
Fengmai 24	95.13	128.17	34.73**	272.10	284.10	4.41*	1.19	1.56	31.09**	5.41	4.04	−25.32**
Longchun 16	118.70	173.40	46.08**	254.51	285.85	12.32**	1.47	1.93	31.29**	4.34	2.21	−49.31**
Huining 18	147.31	185.11	25.66**	292.20	320.60	9.72**	2.07	2.35	13.53*	4.18	2.49	−40.43**

**,*Significant difference between control and UV-B radiation at $P<0.01$ or $P<0.05$, respectively, by *t*-test. $n=6$.

membrane and increase chlorophyll contents, while decreasing MDA contents. Such changes affect plant resistance and ageing (Yang et al., 2000). In our study, decreased chlorophyll contents and changes in SOD activity, ion leakage, and MDA contents of 10 wheat cultivars were observed with UV-B radiation (Li et al., 2000b), and these changes may be related to changes in ZR. The function of ZR was similar to ABA, but the key processes, the mechanisms of composition and regulation remain unclear under UV-B radiation conditions (Wang, 2000).

4.2. UV-B and photosynthetic characteristics

Changes in photosynthetic characteristics have often been used as an index to assess crop sensitivity to UV-B radiation. UV-B radiation decreased photosynthesis in rice (Teramura et al., l991), soybean (Mirecki and Teramura, 1984), maize (Correia et al., 2005) and legumes (Musil et al., 2003). Depression of photosynthesis by UV-B radiation mainly results from down-regulation of photosynthetic genes (Musil, 1996), dilation of thylakoid membranes, disintegration of the envelope around chloroplast, inhibition of photosynthetic enzymes (Teramura and Sullivan, 1994), reduction of electron transport rate, damage to photosystem II and decrease in Hill reaction (Teramura et al., 1991; Sullivan et al., 1994). Indirectly, UV-B radiation can also affect photosynthesis by altering stomatal control of CO_2 supply, CO_2-fixation of the Calvin cycle and photosynthetic pigment concentrations (Allen et al., 1998).

In this study, stomatal conductance, intercellular CO_2 concentrations, transpiration rate and net photosynthetic rate were significantly changed by enhanced UV-B radiation. Thus, they might be used as response-indicators for assessing the sensitivity of wheat to UV-B radiation. UV-B radiation might change stomatal conductance, intercellular CO_2 concentrations and net transpiration rate, resulting in changes in net photosynthetic rate in eight wheat cultivars (Table 3). However, in some wheat cultivars, increases in intercellular CO_2 concentrations were observed with decreases in stomatal conductance (Table 2). This is a complex process and may be related to non-stomatal limitations. On the other hand, UV-B radiation significantly decreased the chlorophyll contents of 10 wheat cultivars (He et al., 2006), resulting in decreased net photosynthetic rate ($r=-0.77$, $n=10$, $P<0.01$).

4.3. Intraspecific differences to UV-B

Intraspecific responses in endogenous hormones and photosynthetic characteristics of wheat to enhanced UV-B radiation under field conditions are complex, as observed in most of the 10 wheat cultivars used in this experiment. Complex responses were also evident in the SOD activity, ion leakage, chlorophyll content and MDA content of the 10 cultivars (Li et al., 2000b). However, out of these cultivars, the ranking of every indicator was different (Tables 1 and 2).

The Response Index is an integration of the effect on plant height, LAI, tiller number, shoot biomass and grain yield of 20 wheat cultivars in the previous experiment, which could reflect the overall sensitivity of wheat cultivars to enhanced UV-B radiation (Li et al., 2000a). In the 10 wheat cultivars, correlation analysis showed that the Response Index (Li et al., 2000a) significantly correlated with ZR ($r=0.836$, $n=10$, $P<0.01$), ABA ($r=0.804$, $n=10$, $P<0.01$), net photosynthetic rate ($r=0.646$, $n=10$, $P<0.05$) and intercellular CO_2 concentrations ($r=-0.816$, $n=10$, $P<0.01$). There were no significant correlations with IAA ($r=-0.086$, $n=10$, $P>0.05$), stomatal conductance ($r=-0.519$, $n=10$, $P>0.05$) and transpiration rate ($r=-0.563$, $n=10$, $P>0.05$), respectively. UV-B radiation significantly affected ZR, ABA, photosynthetic rate and intercellular CO_2 concentrations, and changed physiological metabolism and wheat growth, resulting in differences in RI (Li et al., 2000a,b). UV-B radiation had significant effects on seven measured parameters in Yunmai 39, Fengmai 24, Longchun 16, Huining 18 and Mianyang 20, while no effect in the other five cultivars. This showed that the effect of UV-B radiation on seven measured parameters was related to the UV-B sensitivity of the cultivars. Tevini et al. (1990) demonstrated that in rye the dose-dependent increases in flavonoid production is sufficient to fully protect the photosynthetic machinery from UV-induced damage. Intraspecific variations in UV-B sensitivity in wheat may also be related to differences in the concentration of UV-B absorbing compounds in leaves (Murali and Teramura, 1986; Li et al., 2000b; He et al., 2006). In spinach and bean, however, such a relationship was not found (Kakani, et al., 2003). It is suggested that intraspecific differences in UV-B sensitivity may arise through a complex series of specific responses, rather than as a generalized response (Murali and Teramura, 1986).

In conclusion, endogenous hormones and photosynthetic characteristics can be used as indicators of the sensitivity of wheat cultivars to enhanced UV-B radiation under field conditions. In 10 wheat cultivars, the responses of each endogenous hormone and photosynthetic characteristic to UV-B radiation were different. Little is known about the tolerance mechanisms of wheat to enhanced UV-B radiation. To better understand these mechanisms, it is necessary to study a broad range of growth, physiological and genetic responses to UV-B radiation under field conditions.

Acknowledgements

This work was supported by the National Basic Research Programme of China (project 2006CB100203) and the National Natural Science Foundation of China (project 30160023). We wish to thank Professor Michael A. Fullen, The University of Wolverhampton, U.K., for his valuable improvements done on the English writing in this work.

References

Allen, D.J., Nogues, S., Baker, N.R., 1998. Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? Journal of Experiment Botany 49, 1775–1788.

An, L.Z., Feng, H.Y., Tang, X.D., Wang, X.L., 2000. Changes of microsomal membrane properties in spring wheat leaves (*Triticum aestivum* L.) exposed to enhanced ultraviolet-B radiation. Journal of Photochemistry and Photobiology B: Biology 57, 60–65.

Borman, J.F., 1989. Target sites of UV-B radiation in photosynthesis of higher plant. Journal of Photochemistry and Photobiology B: Biology 4, 145–158.

Caldwell, M.M., 1971. Solar UV-B irradiation and the growth and development of higher plants. In: Giese, A.C. (Ed.), Photophysiology, 6. Academic Press, New York, pp. 131–171.

Correia, C.M., Areal, E.L.V., Torres, M.S.P., 1999. Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. II. Physiological and biochemical aspects. Field Crops Research 62, 97–105.

Correia, C.M., Pereira, J.M.M., Coutinho, J.F., Bjorn, L.O., Torres-Pereira, J.M.G., 2005. Ultraviolet-B radiation and nitrogen affect the photosynthesis of maize: a Mediterranean field study. European Journal of Agronomy 22, 337–347.

Dai, Q.J., Peng, S.B., Chavez, A.Q., Vergara, B.S., 1994. Intraspecific responses of 188 rice cultivars to enhanced UV-B radiation. Environmental and Experimental Botany 34, 433–442.

D'Surney, S.J., Tschaplinski, T.J., Edwards, N.T., Shugart, L.R., 1993. Biological responses of two soybean cultivars exposed to enhanced UV-B radiation. Environmental and Experimental Botany 33, 347–356.

He, L.L., Zu, Y.Q., Li, Y., Wu, Y.S., 2006. Intraspecific differences in physiological responses of different wheat cultivars to enhanced UV-B radiation. Chinese Journal of Applied Ecology 17, 153–165.

Hidema, J., Kang, H.S., Kumagai, T., 1999. Changes in cyclobutyl pyrimidine dimer levels in rice (*Oryza sativa* L.) growing indoors and outdoors with or without supplemental UV-B radiation. Journal of Photochemistry and Photobiology B: Biology 52, 7–13.

Huang, S.B., Dai, Q.J., Peng, S.B., Chavez, A.Q., Miranda, M.A.L., Visperas, R.M., Vergara, B.S., 1997. Influence of supplemental ultraviolet-B on indoleacetic acid and calmodulin in the leaves of rice (*Oryza sativa* L.). Plant Growth Regulation 21, 59–64.

Huang, S.B., Dai, Q.J., Liu, X.Z., 1998. Influence of supplemental ultraviolet-B radiation on IAA and ABA content in the leaves of rice. Chinese Bulletin of Botany 15, 87–90.

Jansen, M.A., Den Noort, R.E., Tan, M.Y., Prinsen, E., Lagrimini, L.M., Thorneley, R.N., 2001. Phenol-oxidizing peroxidases contribute to the protection of plants from ultraviolet radiation stress. Plant Physiology 126, 1012–1023.

Kakani, V.G., Reddy, K.R., Zhao, D., Sailaja, K., 2003. Field crop responses to ultraviolet-B radiation: a review. Agricultural and Forest Meteorology 120, 191–218.

Kumagai, T., Hidema, J., Kang, H.S., Sato, T., 2001. Effects of supplemental UV-B radiation on the growth and yield of two cultivars of Japanese lowland rice (*Oryza sativa* L.) under the field in a cool rice-growing region of Japan. Agriculture, Ecosystems and Environment 83, 201–208.

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 Research 57, 253–263.

Li, Y., Zu, Y.Q., Chen, H.Y., Chen, J.J., Yang, J.L., Hu, Z.D., 2000a. Intraspecific responses in crop growth and yield of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. Field Crops Research 67, 25–33.

Li, Y., Zu, Y.Q., Chen, J.J., Chen, H.Y., Yang, J.L., Hu, Z.D., 2000b. Intraspecific differences in physiological responses of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. Environmental and Experimental Botany 44, 95–103.

Li, Y., Zu, Y.Q., Chen, J.J., Chen, H.Y., 2002. Intraspecific responses in crop growth and yield of 20 soybean cultivars to enhanced ultraviolet-B radiation under field conditions. Field Crops Research 78, 1–8.

Li, G.J., Wang, S.C., Xia, K., Zhou, X., 2003. Effect of yeast elicitor and salicylic acid on the fluctuation of phytohormone contents in Ti-transformed Salvia miltiorrhiza cell cultures. Plant Growth Regulation 39, 27–32.

Lin, W.X., Wu, X.C., Liang, K.J., Guo, Y.C., He, H.Q., Chen, F.Y., Liang, Y.Y., 2002. Effect of enhanced UV-B radiation on polyamine metabolism and endogenous hormone contents in rice (*Oryza sativa* L.). Chinese Journal of Applied Ecology 13, 807–813.

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.

Mirecki, R.M., Teramura, A.H., 1984. Effects of ultraviolet-B irradiance on soybean. V. The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. Plant Physiology 74, 475–480.

Murakami, T., Matsuba, S., Funatsuki, H., Kawaguchi, K., Saruyama, H., Tanida, M., Sato, Y., 2004. Over-expression of a small heat shock protein, sHSP17.7, confers both heat tolerance and UV-B resistance to rice plants. Molecular Breeding 13, 165–175.

Murali, N.S., Teramura, A.H., 1986. Intraspecific differences in *Cucumis sativus* sensitivity to ultraviolet-B radiation. Physiologia Plantarum 68, 673–677.

Musil, C.F., 1996. Accumulation effect of elevated ultraviolet-B radiation over multiple generations of the arid-environment annual *Dimorphotheca sinuate* DC. (Asteraceae). Plant Cell and Environment 19, 1017–1027.

Musil, C.F., Kgope, B.S., Chimphango, S.B.M., Dakora, F.D., 2003. Nitrate additions enhanced the photosynthetic sensitivity of a nodulated South African Mediterranean-climate legume (*Podalyria calyptrate*) to elevated UV-B. Environmental and Experimental Botany 50, 197–210.

Piere, M., Baschke, K., 1980. Correlation between loss of turgor and accumulation of abscisic acid in detached leaves. Planta 148, 174–182.

Predieri, S., Krizek, D.T., Wang, C.Y., Mirecki, R.M., Zimmerman, R.H., 1993. Influence of UV-B radiation on developmental changes, ethylene, CO_2 flux and polyamines in cv. *Doyenne* d'hiver pear shoots grown in vitro. Physiologia Plantarum 87, 109–117.

Ros, J., Tevini, M., 1995. Interaction of UV-radiation and IAA during growth of seedling and hypocotyls segments of sunflower. Journal of Plant Physiology 146, 295–302.

Schmitz, R., Weissenbock, G., 2003. Contribution of phenolic compounds to the UV-B screening capacity of developing barley primary leaves in relation to DNA damage and repair under elevated UV-B levels. Phytochemistry 64, 243–255.

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 Physiology 92, 141–146.

Sullivan, J.H., Teramura, A.H., Dillenburg, L.R., 1994. Growth and photosynthetic responses of field-grown sweetgum seedlings to UV-B radiation. American Journal of Botany 81, 826–832.

Takahama, U., Oniki, T., 2000. Flavonoids and some other phenolic substrates of peroxidase: physiological significance of the redox reaction. Plant Research 113, 301–309.

Teramura, A.H., Sullivan, J.H., 1994. Effects of UV-B radiation on the photosynthesis and growth of terrestrial plants. Photosynthesis Research 39, 463–473.

Teramura, A.H., Sullivan, J.H., Lydon, J., 1990. Effects of UV-B radiation on soybean yield and seed quality: a 6-year field study. Physiologia Plantarum 80, 5–11.

Teramura, A.H., Ziska, L.H., Sztein, A.E., 1991. Changes in growth and photosynthetic capacity of rice with increased UV-B radiation. Physiologia Plantarum 83, 373–380.

Tevini, M., Braun, J., Fieser, G., 1990. The protective function of the epidermal layer of rye seedlings against ultraviolet-B radiation. Photochemistry and Photobiology 53, 329–333.

UNEP, 2002. Executive Summary. Final of UNEP/WMO Scientific Assessment of Ozone Depletion: 2002. Prepared by the Scientific Assessment Panel of the Montreal Protocol on Substances that Deplete the Ozone Layer. UNEP, Nairobi (released 23 August 2002).

Wang, S.G., 2000. Roles of cytokinin on stress-resistance and delaying senescence in plants. Chinese Bulletin of Botany 17, 121–126.

Yang, J.H., Chen, T., Wang, X.L., 2000. Effect of enhanced UV-B radiation on endogenous ABA and free proline contents in wheat leaves. Acta Ecologica Sinica 20, 39–42.

Yang, H., Zhao, Z.G., Qiang, W.Y., An, L.Z., Xu, S.J., Wang, X.L., 2004. Effects of enhanced UV-B radiation on the hormonal contents of vegetative and reproductive tissues of two tomato cultivars and their relationships with reproductive characteristics. Plant Growth Regulation 43, 251–258.

Yue, M., Li, Y., Wang, X.L., 1998. Effects of enhanced ultraviolet-B radiation on plant nutrients, decomposition and leaf quality of spring wheat under field conditions. Environmental and Experimental Botany 40, 187–196.

Zu, Y.Q., Li, Y., Chen, J.J., Chen, H.Y., 2004. Intraspecific responses in grain quality of 10 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. Journal of Photochemistry and Photobiology B: Biology 74, 95–100.

Edited by R Van Heerden